PART I

Conceptual Issues

Chapter 1

EVOLUTION AS A FOUNDATION FOR PSYCHOLOGICAL THEORIES

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Charles Darwin's (1859) *Origin of Species* was published a few years before the emergence of psychology as a scientific discipline. One would expect that the theory of evolution would have had a major impact on shaping psychology. Clearly, there was some impact, but the history of evolutionary thinking in psychology is very complex, even convoluted, and a definitive history has not been written. Until recently, the major impact of evolution on psychology was through the genetic/heredity route, although there were also some influences on behavioral theories in psychology developed during the past century.

One reason for the complexity of the story of evolution in psychology is the complexity of the story of evolution in biology. Evolution by natural selection had no proximal explanatory mechanism for about 50 years, until the concept of the gene was well established. The mix of genes and natural selection was supposed to provide a "grand synthesis" for biology. However, to a considerable extent, the study of genetics has remained a discipline separate from other facets of evolutionary biology, especially behavioral biology. That same separation is manifest in psychology. To a considerable extent, behavioral genetics is a discipline apart from the more recent development of evolutionary psychology.

This chapter chronicles and remains faithful to the complexity of the main areas of contact between evolution and psychology. The first section provides a brief history of some of the connections between evolution and psychology since Darwin. Before tackling evolution and modern psychology, it is useful to examine evolutionary biology briefly, the task of the second major section. We will see that the reigning paradigm for a quarter-century did try to trace a direct sequence from controlling gene all the way to complex social behavior. There were many theoretical arguments in evolutionary biology. Two issues are surveyed to give the flavor of the controversies: the unit of selection and the evolution of sex. As we will see, evolutionary biology is in a continuing state of conceptual flux.

Against this background, current work in evolution and psychology is described under the two broad categories in which such work is done: behavioral genetics and evolutionary psychology. Behavioral genetics will not make sense to most people without a minimal understanding of basic genetics. Thus, a tutorial section, "Molecular Genetics and Evolution," precedes the section on behavioral genetics.

EVOLUTION AND PSYCHOLOGY: A BRIEF HISTORY

One line of thinking views evolution as permeating psychology from its beginning. Another view is that the major impact of evolutionary thinking is quite recent, occurring perhaps only 25 years or so ago.

In favor of the first view, Kimble and Wertheimer (1998) named Darwin as one of the top 20 psychologists of all time. Masterson (1998) referred to Darwin as the "father of evolutionary psychology," noting a chapter on instinct in *Origins.* Further, Darwin's *Expressions of Emotions in Man and Animals* (1872) clearly is of psychological interest, as is *The Descent of Man, and Selection in Relation to Sex* (1871/1981). An interesting volume on evolutionary thought in the United States, edited by Persons (1950), included an extensive chapter by E. G. Boring (1950). As Boring noted, Galton's (1869) volume on the inheritance of genius stimulated an interest in individual differences and, indirectly, psychological testing. Although Germany had the most influence on the creation of experimental psychology in the United States, people such as William James and John Dewey were tremendously influenced by Darwin. In fact, Boring claimed that evolution permeated the development of functional psychology and pragmatism. Evolution also influenced the development of comparative psychology. The notion of evolution of mind became common currency, a theme strongly echoed in somewhat modern form by Kantor (1935).

Other interesting sources on the relations between psychology and evolution include Gruber (1998), Alexander (1992), and Glickman (1992). A fascinating article by Dewsbury (2002) described the "Chicago Five," eminent psychologists trained under Karl Lashley at the University of Chicago from 1929 to1935: Norman Maier, Theodore Schneirla, Frank Beach, Donald Hebb, and Krechevsky (later David Krech). Dewsbury discussed nine guiding principles loosely held by the Chicago Five. Almost all of the principles have an evolutionary halo. The two most explicit are numbers 4 and 8:

> 4. Understanding the evolution of mind and behavior in general and its emergent characteristics in particular, is important to psychology.
>
> 8. Behavioral development is an epigenetic process resulting from the continuous, dynamic interaction of genes, environment, and organisms. (pp. 25, 28)

The notion of epigenesis is a contentious issue in some areas of evolutionary biology (see Markos, 2002, for a history of the concept of epigenesis). The current strong emphasis on molecular biology tends to deify "the gene." Biologists who work with whole organisms, especially developmental biologists, are more likely to lean toward an epigenetic approach.

The second view of evolution in psychology is that the influence of evolutionary thinking had little impact until E. O. Wilson's (1975) *Sociobiology.* This controversial volume soon stimulated a huge literature (e.g., see Crawford, 1989; Crawford & Anderson, 1989; Crawford, Smith, & Krebs, 1987).

Despite the richness of literature noted above for the first view, my own impressionistic view is that after the onset of Watson's behaviorism early in the twentieth century, psychology had a long dry spell of environmentalism, with the charge led primarily by several decades of learning theory. To test such impressions, I consulted the PsychINFO database for citation counts of several terms. The term "evolutionary theory" appeared in the database 638 times (as of February 5, 2003). From the beginning in 1887 through 1980, evolutionary theory appeared only 77 times. The pace picked up from 1981 to 1990 (132 times). From 1991 to February 2003, the term appeared 428 times. Clearly, the interest in evolutionary theory has grown strongly in psychological literature, particularly over the past dozen years.

Other terms give a fuller picture. Psychologists were very interested in genetics; this term appeared 15,860 times. "Evolution" appeared 18,614 times, but the number doesn't mean much because evolution is also used generically for change of any kind. Psychologists were relatively interested in sociobiology; the term appeared 735 times, more than for evolutionary theory. It seems clear that evolution is of rapidly growing interest in many areas of psychology and will increasingly affect psychological theorizing. In fact, it already has; the term "evolutionary psychology" appears to have been coined only in the 1980s (e.g., Tooby, 1988).

There are many ways that evolutionary concepts may affect psychological theorizing. In fact, there will undoubtedly be much fragmentation in conceptual approaches over the next several years. Why? Because the various disciplines that form evolutionary biology are in fractious disagreement, ranging from the role of the gene to the place of the ecological habitat in evolution. Before focusing on psychology, it will be useful to make a modest excursion into biology.

EVOLUTIONARY BIOLOGY: A BRIEF EXCURSION

The Reigning Paradigm

As is famously known, Darwin had no mechanism to explain how natural selection led to species formation and change over time. He was unaware of Mendel's experiments, and it was well into the twentieth century before genetics was joined with natural selection. During the 1930s, several volumes were published connecting genetics to Darwinian evolution, culminating in Dobzhansky's (1937) *Genetics and The Origin of Species,* the defining volume of what was named the neo-Darwinian synthesis (Fisher, 1991). During the 1950s, molecular biology developed strongly, beginning with the discovery of the double helix form of the genome (Watson & Crick, 1953). Molecular biology gradually became a dominant intellectual force in the study of evolution. For biologists who viewed everything about an organism as under genetic control, evolution could be simply defined as relative change in gene frequency within a population over time. The processes for genetic change include gene mutation, genetic drift, migration of organisms across populations, and natural selection (construed as differential reproduction). Natural selection is by far the most important process for evolutionary change, according to most evolutionary biologists. Differential reproduction goes hand in hand with better adaptations in the environment in which selection occurs.

During the 1960s, a spate of theorizing about behavior and evolution (especially social behavior) occurred, stimulated by Hamilton's (1964a, 1964b) pair of articles on the genetical evolution of social behavior. His concept of inclusive fitness allowed limited altruism toward genetic relatives, in addition to one's own children. These relatives also carry some portion of one's genes. So, genes may be propagated both by direct descendants and indirectly by other genetic relatives.

Following Hamilton's papers, a flood of writing on social behavior occurred. Some of the more important work included the parental investment model (Trivers, 1972), evolution of reciprocal altruism (Trivers, 1971), parent-offspring conflict (e.g., Alexander, 1974), evolution of deception strategies (Alexander, 1974; Trivers, 1971), and the evolution of sexuality (Symons, 1979). This sequence of thought that traces a linear trend from the controlling gene to social behavior might be called the "hard-line" approach to the evolution of social behavior. Loosely construed, this approach is the "standard model" for behavioral evolution. This hard-line approach is, by and large, the set of assumptions for what became evolutionary psychology.

There have always been dissents from and questions about the standard model of organismic evolution. Two illustrations (from many possible ones) are discussed briefly: the unit of selection and the issue of why sexual reproduction evolved.

What Is the Unit of Selection?

The unit of selection is a time-honored debate in biology, a debate that is far from closure. For most of the era since Darwin, biologists considered the group, or perhaps the species, as the unit for which evolution selected. One main reason for this assumption was the existence of sexual reproduction. In a sense, sex is costly to the individual because only 50% of the genes are passed on. So sex must be for the benefit of the species, or group, because it speeds up the evolutionary process, presumably leading to ever better adaptations. An extreme version of group selection views a set of behaviors as benefiting the group (altruism) without any benefit to the individual (e.g., see Wynne-Edwards, 1962). After a few years, group selection theory was severely criticized. Although most biologists would allow for some kinds of group or kin selection, they were not viewed as important forces in evolution (e.g., Ridley, 1996).

In a very influential book, Williams (1966) argued for the individual organism as the basic unit of selection, with the gene as the underlying basis for that selection. The "unit" organism is basically selfish, although altruistic behavior is recognized. Much ink has been spilled over how evolution produces altruism out of the selfish organism. Dawkins (1976) skirted this issue by claiming the "selfish gene" as the basic unit of selection. Dawkins received much criticism for his view (see Stove, 1992, for a particularly pungent critique). It soon became clear, however, that Dawkins was using "gene" as an abstract concept to designate the unit that replicates. Dawkins (1982) made clear that any part of a chromosome, large or small, could serve as a replicator. The concept of replicator in turn spawned its own literature (e.g., see Richards, 2002). A good review is given by Godfrey-Smith (2000).

Waller (1999) proposed a more extreme version of Dawkins's idea. Waller argued that the gene is not the unit of selection. Rather, the part of the genome concerned with reproduction is the basic unit of selection. It is assumed that these sexual reproduction genes (SRGs) are carried by the most successful members of a breeding group. Variation in genetic diversity provides SRGs the best prospects for future replication. The individual organism counts for nothing in this approach:

> Proportionate transfers of parental genetic material have no relevance whatsoever. The fundamental effect of sexual reproduction is the perpetuation of SRGs. Individuals are puppets, not puppeteers. (p. 9)

One might suppose that SRGs are well-defined molecular units on a chromosome. Kimura (1983) developed a neutral theory of molecular evolution that argued that at the molecular level changes are random and more or less cancel out. Positive Darwinian selection must operate at a higher level, presumably at the organismic level. Neutral theory generated an explosion of literature. Current thinking appears to be that there can be non-neutral molecular evolution, but its nature is far from clear (e.g., Golding, 1994).

Among biologists, one can note a trend toward broader thinking, even as molecular biology continues to make great strides. Harold (2001), a cell biologist, tried to mediate between the extremes of molecularism and holism inherent in evolutionary and ecological biology. That mediating link is the cell. In a pithy chapter title, Harold (p. 99) made the important point that "it takes a cell to make a cell," suggesting that the minimal unit that makes sense as life is the cell.

Even a hard-line biologist such as Maynard Smith (1998) has softened his original position. He argued that we need to consider both developmental genetics and the holistic tradition of self-organization with the complex behavior patterns that can emerge from dynamical systems. We must "pay attention to dynamical processes as well as to genetic control" (p. 2). Still more extreme, Avital and Jablonka (2000) argued that selection at the level of genes is not sufficient to account for behavior. Evolutionary explanations must take into account the transmission of learning across generations. Thus, the authors argue for a behavioral inheritance system as an addendum to Darwinism evolution.

The question of the unit of selection has not yet been answered. D. S. Wilson (2001) titled his review of L. Keller's (1999) edited volume on levels of selection "Evolutionary Biology: Struggling to Escape Exclusively Individual Selection." Many other volumes have been written on the issue of selection during the past two decades, with no resolution in sight. The concept of the gene has become equally nebulous. In an edited volume, Beurton, Falk, and Rheinberger (2000) presented many varied conceptions of the gene, so many, in fact, that Griffiths (2002) titled his review of the volume "Lost: One Gene Concept. Reward to Finder." We must conclude that currently there is no consensus on what the unit of selection might be, and there is confusion about the nature of "the gene." This lack of closure should be kept in mind when we examine possible contributions of evolution to psychological theory.

Evolution of Sex

When Williams (1966) and others settled on the individual as the unit of selection, sexual reproduction immediately became a problem. Why? In the backhanded language of biologists, sex is "expensive," relative to asexual reproduction (e.g., Lewis, 1987). First, as noted previously, a sexual individual can pass on only 50% of its genetic material to its offspring. Second, the mixing of two gametes may easily lead to bad outcomes. Third, finding a suitable mate, reproducing, and caring for the young is very effortful. If genes are truly selfish, one would expect asexual reproduction to be more common.

A large literature was soon generated attempting to account for why sexual reproduction evolved. Williams (1975) presented several possible models; Maynard Smith (1978) also described a diverse set of models. No single model fully satisfied theorists (e.g., see Ghiselin, 1988), and by the 1990s, 20 different theories had been proposed to account for the evolution of sex (Fehr, 2001).

Three concepts are crucial in conceptualizing sex: genetic recombination, reproduction of offspring (or replication), and gender (Stearns, 1987). Recombination is not an automatic part of reproduction. "The production of offspring can occur sexually or asexually, with or without recombination" (Stearns, 1987, p. 16). For species with differing genders, gender "is the principal consequence of a history of sexual selection" (p. 17).

Sexual reproduction is viewed as an important adaptation by biologists. But exactly what its adaptive significance is no one can yet say. "No one has yet given a convincing, single-generation, micro-evolutionary and experimental demonstration of the advantages of sex, which must nevertheless exist" (Stearns, 1987, pp. 26–27). Space precludes discussion of the many advantages theorized for sex. However, for each advantage, a disadvantage can be proposed. Some excellent readings are included in edited volumes by Abramson and Pinkerton (1995), Michod and Levin (1988), and Stearns (1987). One interesting theory of sex evolution, the parasite hypothesis, is explored in fascinating detail by the science writer Matt Ridley (e.g., 1993a, 1993b).

Despite the fact that biologists cannot yet explain why sex is an evolved adaptation, many writers nevertheless focus on reproduction as the overwhelming fact of life. For example, "Reproduction is the sole goal for which human beings are designed; everything else is a means to that end" (Ridley, 1993b, p. 4). Although not usually so boldly stated, this assumption is one major cornerstone of the new discipline of evolutionary psychology (e.g., Buss, 1999; Kenrick & Trost, 1989; Kirkpatrick, 1998).

We should tread carefully in accepting this assumption as fact. We should remember the "costs" of sexual reproduction. Taking the classic view of genes as relatively discrete units, the major cost of mating is that only half of our remaining genes will be passed on in each succeeding generation. Assuming mating as a random process over generations, in only 25 human generations (about 500 years) only 0.5^{25} of our genes would remain in our descendants, a very small fraction indeed! The notion of "genetic immortality" through one's genes is a cultural myth (e.g., Hendrick, 2002). On the other hand, if we were bacteria, undergoing cell division every 20 minutes, we would soon have (assuming no mutations) 2^{25} copies of ourselves, or about 33 million genetic replicas. If we lust for genetic immortality, asexual reproduction is clearly the way to go. The notion of selfish genes and related ideas of replicators need serious rethinking. There is nothing wrong with some anthropomorphism: It can stimulate new ideas. But when we project such thinking to the molecular level, we are easily led astray, especially when such thinking is projected back to the everyday level of human life.

As these two excursions on units of selection and the evolution of sexuality make clear, evolutionary biology is in a state of continuous theoretical ferment and change. That is good for biology; disciplines must grow and change or become moribund. Such continuous change, however, can become a problem for a borrowing discipline such as psychology. To not fixate at a certain level of conceptual development in biology, psychologists must stay abreast of the ongoing changes in biological knowledge. To do so is extremely difficult, and the process may transform psychology into something other than what it is now. Whether such transformation is good or bad is ultimately a question of values.

EVOLUTIONARY IDEAS AND MODERN PSYCHOLOGY

I noted previously that genetics appeared in the PsychINFO database over 15,000 times. Clearly, psychology has historically had a keen interest in genetics, inheritance, and the like over the past century. Most of this interest has little to do with evolution per se; rather, the interest stems from possible heritability of behavioral patterns such as criminality, retardation, and mental illness.

The section that follows provides an overview of genetics and evolution; the second section deals with behavioral genetics; and the third section gives an overview of evolutionary psychology.

Molecular Genetics and Evolution

According to E. F. Keller (2000), the terms "genetics" and "gene" were coined in 1906 and 1909, respectively. At first, the gene was only a hypothetical entity, but by the

1930s it had become a material, fixed entity in the minds of most biologists. People, including scientists, tend to attribute powerful, even magical properties to unseen entities, relative to mundane, everyday visible reality. So it was with the gene. In time, the gene became the sole basis for heredity, and even the unfolding of life itself, from the fertilized egg to mature organism. The discovery of the double helix of DNA in 1953 finally gave material proof of the gene's reality, and the gene became the foundation concept for biology. However, the very success of molecular biology during the second half of the twentieth century gradually undermined the solid materiality of the discrete gene. The gene became a lot more complicated with respect to its structure, and in its relation to evolution.

Classic work in evolution distinguished between the concept of a genotype (the underlying genetic structure specified by gene pairs across chromosomal loci) and phenotype (the phenomenal manifestation of genotype and environmental influences in the actual organism). According to Schuster (2003):

> The success and efficiency of Darwinian evolution is based on a dichotomy of genotype and phenotype: The former is the object under variation; whereas, the latter constitutes the target of selection. (p. 163)

Further, "Genotype-phenotype relations are highly complex and hence variation and selection are uncorrelated" (p. 163). This presumed lack of correlation has allowed molecular biologists to focus primarily on genetic structure and function, and evolutionary psychologists to focus primarily on presumed mechanisms of behavioral evolution.

However, as hinted above, the discrete gene has morphed into a more complicated system. First, not all genes code, but genes that do code (i.e., DNA) mostly code for amino acids; amino acids in turn create proteins, some of which serve as enzymes that provide feedback and repair of DNA sequences that keep the process going in a complex, circular fashion. Ultimately, the entire cell is involved in the maintenance of genetic structure and function. Perhaps Harold (2001) was correct; perhaps the cell must be taken as the primary conceptual unit for the study of molecular evolutionary processes, a proposition with which E. F. Keller (2000) agreed.

Darwin was mostly interested in biological change. Perhaps even more remarkable than change is the stability of a phenotype over long periods. What accounts for such stability, and how much instability is needed for evolutionary processes to work? Instability (or mutability) itself appears to be genetically regulated. Stability and mutability are both equally at the mercy of enzymatic processes. This delicate balance itself is under cellular regulation, and that balance can change in response to changes in the cellular environment (Radman, 1999).

This kind of thinking is far removed from the idea of the gene as a stable molecule, subject only to occasional mutations. This cellular complexity better fits the pattern of nonlinear dynamical systems (Crutchfield & Schuster, 2003), a conceptual approach increasingly evident in biology. Further, given the idea of neutral evolution noted previously (Kimura, 1983), it is clear that most genetic change does not result in any direct phenotype change (i.e., the two are relatively independent). Genotypes vary constantly, usually in small ways, yet the phenotype remains true to type over long periods.

An interesting demonstration of genotype/phenotype independence was reported by Papadopoulos et al. (1999) across 10,000 generations of the bacterium *E. coli:*

> As has often been suggested, but not previously shown by experiment, the rates of phenotypic and genomic change were discordant, both across replicate populations and over time within a population. (p. 3807)

Genomic change was ongoing and relatively continuous, whereas phenotypic attributes (e.g., cell size) evolved much more slowly and in a discontinuous fashion. Another comparable experiment (Elena, Cooper, & Lenski, 1996), using 3,000 generations of *E. coli,* found that evolution of increased cell size followed an abrupt step function during the first 1,500 generations, after which size remained stable for the next 1,500 generations. Apparently, many small genetic changes accumulate over generations until such change hits a critical point, resulting in a sudden, nonlinear shift in some feature of the phenotype. On a large scale, this kind of species change might account for the (then) controversial concept of punctuated equilibria in species evolution proposed by Gould and Eldredge (1977). A later summary review (Gould & Eldredge, 1993) indicated that punctuated equilibrium is now widely accepted.

E. F. Keller (2000) suggested that, given the dynamic conjunction of stability and mutagenesis, living beings may have evolved second-order mechanisms to ensure their continued evolvability. If so, mutagenesis itself would have been positively selected (Radman, 1999; Radman, Matic, & Taddei, 1999). Evolvability is a dramatic concept (an excellent brief overview is provided by West-Eberhard, 1998). In fact, Keller declared evolvability as "molecular biology's challenge to neo-Darwinism" (p. 36). Other theorists agree (e.g., Gerhart & Kirschner, 1997; Kirschner & Gerhart, 1998; Shapiro, 1999). One interesting consequence of evolvability is that the concept "strongly implies the operation of selection on levels higher than the gene, and higher even than the individual organism" (Keller, 2000, p. 38). Natural selection may not be about reproduction per se, but about reproduction only insofar as it contributes to species evolvability. This notion is, of course, very contentious for the current received view of evolution.

Ironically, the term "evolvability" may have been first coined by Dawkins (1989), the scholar who had previously argued for the selfish gene as the basic unit of selection. Dawkins's shift in conception occurred because of an interest he developed in computer programs that can evolve into new programs. This field of study became known as "artificial life," a field invented by Langton (e.g., 1997).

Artificial life concerns the question of how closely evolution can be simulated, and with what degree of realism. In one sense, this is pretend biology, but it has led to fields of important new scholarship. For example, Franklin (1995) wrote a large book on "artificial minds." Kauffman (1993) inquired as to the origins of order in the natural world. He explored the concept of self-organization and how that concept might bear on selection processes in evolution. These areas (and others) point toward the ultimate question of whether there can be a universal biology of pure organization, independent of the material world (Moreno, Etxeberria, & Umerez, 1994). However, there are real-world implications of such thinking. The concept of genetic algorithms (Holland, 1995) was developed to help understand complex adaptive systems. One branch, genetic programming, has led to computer programs sophisticated enough to discover patentable inventions (Koza, Keane, & Streeter, 2003). These fascinating areas cannot be pursued further here for lack of space.

Ideas such as evolvability led E. F. Keller (2000) to conclude that "by now, we have abandoned the hope of finding in the molecular structure of particulate genes an adequate explanation for the stability of biological organization across generations" (p. 40). She might have also added that the current neo-Darwinism synthesis will therefore undergo dramatic revision as well.

Keller's statement implies that the concept of gene as a distinct, material unit of heredity is no longer viable. As new ideas of hereditary units develop, they will undoubtedly strongly affect the area we turn to next: behavioral genetics.

Behavioral Genetics

"Behavioral genetics aims to identify genetic and environmental influences underlying individual differences in behavior" (Segal & MacDonald, 1998, p. 165). This succinct definition captures the essence of behavioral genetics as traditionally conceived. Perhaps this area is best known for the calculation of heritability coefficients (Fuller, 1987), but more recent developments include linking a heritable behavior to a relevant genetic locus on a chromosome and more intensive study of the environment, particularly genotype-environment interactions.

Disciplinary Considerations

Behavioral genetics is interdisciplinary. However, it appears to be increasingly dominated by psychology. The recent massive volume *Behavioral Genetics in the Postgenomic Era,* published by the American Psychological Association (Plomin, DeFries, Craig, & McGuffin, 2003) suggests that the discipline of psychology is firmly stamping its imprint on behavioral genetics. Psychiatry is also getting involved, as witnessed by the recent volume *Molecular Genetics and the Human Personality,* published by the American Psychiatric Association (Benjamin, Ebstein, & Belmaker, 2002).

This disciplinary emphasis by psychology is reflected in newsletters of the American Psychological Association. For example, a recent article in *Monitor on Psychology* (Azar, 2002b) touted the search for genes to explain our personalities. The same issue announced the formation of a Working Group on Genetics Research Issues, created by the Board of Scientific Affairs of the APA (Azar, 2002a). This eminent group of six scientists provided a brief initial report (Hewitt et al., 2003) with the promise to post a final report and recommendations on the APA Web site. More broadly, over 120 professional societies created the National Coalition for Health Professional Education in Genetics to define the core competencies needed by health professionals in dealing with the genetics of health and disease (see Patenaude, Guttmacher, & Collins, 2002, for an overview). These core competencies include many skills and knowledge that most psychologists do not currently have. The Working Group of the APA was very clear that genetics must be incorporated into the graduate training curriculum if psychologists are to be competitive in areas of genetics as diverse as clinical services, research, ethical expertise, and public policy work (Patenaude et al., 2002). In truth, the postgenomic era will create many new services and niches for professional practice in numerous disciplines. The need to compete to get "our share" of the business is very real. The slight sense of urgency to get psychologists trained, at least minimally, in genetics is also real and probably warranted.

Finding Genetics in Behavior

In one sense, behavioral genetics rests on a very thin thread. Roughly 99.9% of human DNA sequence is identical across all humans, leaving only 0.1% of the genes to vary (Plomin et al., 2003). But from that tiny percentage derives all the wondrous individual differences that constantly absorb human attention. A powerful discipline has emerged from this focus on individual differences. Most areas of psychology focus on the "universals," or a search for normative laws of behavior that hold generally. In such a general focus, individual differences are a nuisance, or "error variance."

Behavioral genetics treats variation as the norm. This perspective on individual differences views attributes as normally distributed and continuous. Thus, rarity (e.g., mental retardation or genius) is simply the extremes of a normal distribution. This approach is quantitative, relying on dimensional analyses rather than categorization. Traditionally, this quantitative approach attempted to partition behavioral variation into genetic and environmental components. Heritability can be a tricky concept. Technically, for a given attribute, heritability is the ratio of genotypic variation to phenotypic variation within a population. The complementary concept is environmentality, the ratio of environmental variation to phenotypic variation (Sternberg & Grigorenko, 1999). Thus, heritability is the proportion of individual difference in a population that is inherited. As a statistical concept it says nothing about an individual. The concept is also relative to the phenotypic variation in the population. If phenotypic variation increases, the heritability ratio decreases; if phenotypic variation decreases, the heritability ratio increases. Seven myths about heritability and education are engagingly discussed by Sternberg and Grigorenko. The eminent geneticist Richard Lewontin (e.g., 1987) has also taken some interesting swipes at the misinterpretations of heritability. There are many ways of estimating heritability and related concepts (e.g., see Carey, 2003, for an excellent, but somewhat advanced introduction).

According to Plomin et al. (2003), there are two worlds of genetics: the quantitative approach of behavioral genetics and traditional molecular genetics. According to these authors, molecular genetics (similar to most areas of psychology) took a species-universal perspective in a search for universal genetic laws. Thus, the two approaches drifted apart early in the twentieth century. These two approaches to genetics are beginning to come together, as exemplified in the Plomin et al. volume: "The future of behavioral genetic research lies in identifying specific genes responsible for heritability" (p. 11). Further, "For behavioral genetics, the most important next step is the identification of the DNA sequences that make us different from each other" (p. 12). This future approach might be called "molecular genomics." This general approach to finding out how genes work is gaining the label of "functional genomics." Applied to the behavioral level, Plomin et al. dub it "behavioral genomics" (p. 13).

Applications of Behavioral Genetics

Several substantive areas are represented in the Plomin et al. (2003) volume. Cognitive abilities and disabilities receive much attention (eight chapters). Psychopharmacology is also prominent (three chapters). Personality (three chapters) and psychopathology (four chapters) share about one-third of the volume. The section on psychopathology includes chapters on hyperactivity disorder, schizophrenia, affective disorders, and dementias. Additional pathologies are discussed in a review article (Plomin & McGuffin, 2003).

It appears that research and publications on the genetics of abilities and personality are about equal in volume. As noted previously, the "other" APA volume is devoted to a broad array of personality topics and genetics. Other recent examples include heritability of subjective well-being and dominance in chimpanzees (Weiss, King, & Enns, 2002) and a 42-page query as to what we can learn about personality from animal research (Gosling, 2001).

Millon (1990) noted the resurgence in personology beginning in the 1980s. Thus, it makes sense that evolution (genetic and behavioral) would be linked to the study of personality. In fact, Millon was a pioneer in this interface with the 1990 publication of his classic *Toward a New Personology: An Evolutionary Model.* This volume was followed by numerous chapters applying his model of evolution to various facets of personality. Some examples include "normality" (Millon, 1991), normal and abnormal personality (Millon & Davis, 1994), personality disorders (Millon & Davis, 1996), and attributes of personality (Millon, 2002).

Millon's (2002) theory "seeks to generate the principles, mechanisms, and typologies of personality through formal processes of deduction" (p. 5). His general approach is an analogue to Darwin's attempt to explain the origin of species, but specialized to derivation of the origins of "the structure and style of personalities that have previously been generated on the basis of clinical observation alone" (p. 5). Millon's deductive base begins with four foundational concepts: existence, adaptation, replication, and abstraction. Three of these concepts entail universal polarities: existence (pleasure and pain), adaptation (passivity and activity), and replication (self and other), The fourth, abstraction, applies primarily to the human level.

From this deductive foundation, a massive attempt has been made to classify personality disorders and their modes of therapy (Millon & Davis, 1996). Millon's general approach should be compared to evolutionary theorizing by Buss (e.g., 1991) on personality as an evolved set of mental mechanisms. Millon's systematic application of evolutionary principles to psychotherapy might also be contrasted with approaches described in an eclectic edited volume by Gilbert and Bailey (2000), *Genes on the Couch*.

Millon's evolutionary theory has been used as a vast organizing device to collate disparate areas in personality, psychopathology, and psychotherapy. That is one powerful function of a good theory. As noted in a previous quote, this organization was based on previously generated clinical observations. To date, that is a weakness of the theory. Many theories can be fitted to a given field of data. It is the ability to foresee and predict new findings that makes a great theory. Thus, the next big push for the theory should be, in my opinion, the generation of strong novel predictions that can be confirmed.

It should be noted that this vast effort to link evolution to personality is only one of Ted Millon's many contributions to personology.

All Is Not Quite Well in Paradise

The hope of the new behavioral genomics is that we will soon be able to map ever increasing polygenic complexity onto complex behavioral attributes, especially that complex omnibus called "personality." It is a grand vision. However, even Plomin et al. (2003) noted in passing "the slower-than-expected progress to date in finding genes associated with behavior" (p. 13). Given that the human genome has been fully sequenced, why would progress be slow? There are several reasons.

First, consider the concept of evolvability discussed earlier. Kirschner and Gerhart (1998) analyzed evolvability at the molecular, cellular, and developmental levels. Several processes are discussed that may aid in second-order evolvability. Linkage, as one example, refers to the dependence of one process on another. When linkage is weak, dependence is weak. According to Kirschner and Gerhart, "Weak is a characteristic of information transfer (regulatory) pathways, e.g., signal transduction, neural relays, or transcriptional control circuits" (p. 8421). Weak linkage means that variation and selection can occur downline, far removed from direct gene control. To the extent that neural processes are weakly linked, one can immediately intuit the tremendous difficulty of mapping genes onto complex behavior.

An example of this complexity is given by Ezzell (2003). Cloned animals do not yield identical animals. Cloned pigs showed much behavioral variability, about the same as did normal pigs. In a herd of cloned cattle, the usual social hierarchy still developed. The genes are identical, but behavior is widely variable. Mapping genes onto behavior is impossible in this case. Such difficulties are reinforced by the growing literature on developmental plasticity (West-Eberhard, 2003), developmental instability (Polak, 2003), and cellular evolution and embryology (Gerhart & Kirschner, 1997).

Other problems come from the environmental direction. The environment includes not only the external physical world, but also the complexities of the body as it develops and changes over time. Some examples include "developmental-behavioral initiation of evolutionary change" (Gottlieb, 2002), evidence showing that environmental influences routinely affect gene activation (Gottlieb, 1998), biocultural orchestration of developmental plasticity (Li, 2003), the interactivity of genes and environment in the developmental process (Turkheimer, 1998, 2000), and the coming recognition that the genome is "fluid" (Ho, 1997).

The concept of shared and nonshared environments was developed to help account for the many differences between children in the same family (Plomin & Daniels, 1987). In strong critiques, Turkheimer (2000; Turkheimer & Waldron, 2000) found that objectively defined nonshared environmental variables do not account for much variability. Why? According to Turkheimer (2000, p. 163), the answer is "because of the unsystematic effects of all environmental events, compounded by the equally unsystematic processes that expose us to environmental events in the first place." Space does not permit more detailed exploration of this fascinating topic. Only time will tell whether behavioral genetics can truly become behavioral genomics.

Evolutionary Psychology

"Behavioral genetics and evolutionary psychology remind us of ships passing in the night" (Segal & MacDonald, 1998, p. 159). Scarr (1995) called attention to the fact that evolutionary psychology focuses on the *typical* in the search for general evolutionary laws of behavior, in contrast to behavioral genetics' focus on variation and individual differences. Fuller (1987) noted that behavioral genetics and sociobiology have almost nothing to do with each other. All three of these papers called for an integration of the two areas. However, the fact that behavioral genetics and evolutionary psychology appear to be two very different conceptual paradigms will make true integration exceedingly difficult.

What Is Evolutionary Psychology?

This question is not easy to answer. In a volume entitled *Sense and Nonsense,* Laland and Brown (2002) titled an early section "A Guide for the Bewildered" (p. 8) and noted, "In truth, there are many ways of using evolutionary theory to study human behaviour and there is much disagreement within the field as to the best way to do it" (p. 9). If anything, the history of the field is even more complicated. One line of descent traces back to animal ethology in the 1950s (a photo of ducklings following Konrad Lorenz must be in every introductory psychology text). An early contributor to ethology (Tinbergen, 1963) described four kinds of scientific questions one can pose: (1) proximate causes of behavior, (2) the unfolding development of an individual, (3) the function of a behavior and its evolutionary advantage, and (4) the evolutionary history of a trait, including comparisons across species. The early ethologists focused on proximate mechanisms, a question quite different from asking about the evolutionary function of a behavior.

Different approaches to answering the four questions emerged over the past 50 years, leading to somewhat different research disciplines with much disagreement among them. Animal sociobiology developed around the work of biologists such as Hamilton, Trivers, Symons, and Maynard Smith, discussed earlier. It remained for E. O. Wilson (1975) to synthesize this work and coin the term "sociobiology." Applied to animals, this research tradition was not controversial. In review, some key concepts of animal sociobiology are the gene (the unit of selection), kin selection and inclusive fitness, reciprocal altruism, and parent-offspring conflict, among others. This research tradition is still pursued by evolutionary biologists and is sometimes referred to as behavioral ecology (Laland & Brown, 2002).

E. O. Wilson's (1975) inclusion of a chapter on humans made his book very famous, and controversial. Human sociobiology has had a contentious history, but space precludes recounting that history. For our purposes, human sociobiology diverged into two streams: human behavioral ecology and evolutionary psychology (other emerging areas include memetics and gene-culture coevolution, but they are not discussed in this chapter). Behavioral ecologists and evolutionary psychologists often strongly disagree with each other. To an untutored eye, these fights often appear to be over how best to split hairs! Home disciplines matter: Behavioral ecology is the preserve of biological anthropologists primarily, whereas evolutionary psychology stems primarily from academic psychology.

Human behavioral ecology is interested in the adaptive nature of human behavior under its current conditions insofar as that behavior maximizes reproductive success (for an excellent overview, see the volume by Cronk, Chagnon, & Irons, 2000). This approach is broad in its nature because environmental effects on behavior lead to different behavioral strategies that, in the large, create different cultures. In a sense, behavioral ecology is most interested in human behavioral differences (providing an analogue to behavioral genetics) and how such differences are adaptive responses to the different environments in which people live. The assumption is that people optimize their behavioral strategies, and much labor is invested in mathematical models of optimization.

The most general criticism of behavioral ecology is that it studies the current function of behavior, rather than any true evolutionary processes. One illustration of the subtle nature of the criticism will suffice. Ecology studies the adaptiveness of behavior. But is that the same as an adaptation? Evolutionary psychologists would say no. According to Laland and Brown (2002):

> An *adaptation* is a character favoured by natural selection for its effectiveness in a particular role; that is, it has an evolutionary history of selection. To be labeled as *adaptive,* a character has to function currently to increase reproductive success. (p. 132)

Behavioral ecology views humans as evolved for *adaptability* for many different environments. Specific adaptations are less important; further, it is often difficult to say whether or not a given trait is an evolved adaptation.

Evolutionary psychologists take a different approach and have harshly criticized behavioral ecology. They do strongly believe in adaptations as the root concept of Darwinian evolution (e.g., Symons, 1990). As Symons noted, Darwinism is a type of historical explanation, and what it explains is the "origin and maintenance of *adaptations*" (p. 435). Tooby and Cosmides (1990) also strongly subscribe to this view in an article entitled "The Past Explains the Present" (p. 375). Evolutionary psychologists also believe that behavior itself cannot be selected directly; rather, evolution selects underlying psychological mechanisms (e.g., Cosmides & Tooby, 1987; Symons, 1987). The notion of psychological mechanism is perhaps the key concept of evolutionary psychology. Such mechanisms serve as *the* intervening variable between evolution and output behaviors. This approach implies a modular approach to mind, rather than mind as a general-purpose information processor. This approach also assumes that the mental mechanisms provide a proximate level of explanation and thereby "[gives] rich insight into the present and past selective pressures" (Cosmides & Tooby, 1987, p. 283).

A further key notion is that our current form evolved and was fixed during the Pleistocene era. "Our species spent over 99% of its evolutionary history as hunter-gatherers in Pleistocene environments" (Cosmides & Tooby, 1987, p. 280). One implication is that in the current era we are out of step with our "environment of evolutionary adaptedness." Explanation using this approach involves a complex set of six steps (Tooby & Cosmides, 1989). Suffice it to say here that these six steps require strong inference as to the adaptive problems that had to be solved in the Pleistocene era and perhaps a uniformity of the adaptive problems across all human groups in all habitats.

Evolutionary psychology perhaps arrived at full credibility through the publication of a respected book, *The Adapted Mind* (Barkow, Cosmides, & Tooby, 1992). Since then, theoretical contributions have exploded. For example, Buss (1995) proposed evolutionary psychology as a new paradigm for the psychological sciences. A substantial handbook (Crawford & Krebs, 1998), an interesting volume by Hardcastle (1999), and several annual review articles (e.g., Caporael, 2001; Jones, 1999; Siegert & Ward, 2002) were published. An introductory psychology text follows an evolutionary approach (Gaulin & McBurney, 2001), although a review (Denniston, Waring, & Buskist, 2003) suggests that this approach may not yet be quite ready for prime time. A surprising number of upper-level texts have been written (e.g., Badcock, 2000; Buss, 1999; Cartwright, 2000; Palmer & Palmer, 2002). The volumes are reasonably consistent with each other. For example, Buss (1999) has good chapters on the history and definition of the field, three chapters on sexual strategies, and chapters on parenting, kinship, cooperation, aggression, gender conflict, and status/dominance. Many specialty volumes have been edited. Examples include volumes on cognition (Heyes & Huber, 2000), intelligence (Sternberg & Kaufman, 2002), and mind (Cummins & Allen, 1998). The literature is so vast that one is almost forced to conclude that evolutionary psychology has emerged as a new discipline.

Critiques of Evolutionary Psychology

In a manner similar to human sociobiology, evolutionary psychology arouses passions and argumentation. The intramural fights between behavioral ecology and evolutionary psychology have been noted. There are also criticisms from other quarters, mostly over conceptual issues, but some empirical findings have been disputed as well. One volume (Rose & Rose, 2000) was subtitled "Arguments against Evolutionary Psychology." Other writers are equally pessimistic about the possibilities for evolutionary psychology. One chapter began: "If it were the purpose of this chapter to say what is actually known about the evolution of human cognition, we could stop at the end of this sentence" (Lewontin, 1990, p. 229; also see Lewontin, 1998). In support of Lewontin's (1998) critique of adaptation, Lloyd (1999), an eminent philosopher of biology, is severely critical of Cosmides and Tooby: "Cosmides and Tooby's interpretations arise from misguided and simplistic understandings of evolutionary biology" (p. 211). Panksepp and Panksepp (2000) discussed "the seven sins of evolutionary psychology" (p. 108). Recent evolutionary interpretations of rape are chastised by de Waal (2002). The concept of "environment of evolutionary adaptedness" has been severely criticized (Foley, 1995). The concept does appear to involve an infinite regress: Today we are adapted to the Pleistocene era; Pleistocene inhabitants were adapted to a previous era, and so on. The concept needs a more rigorous logical analysis.

The concept of a "psychological mechanism" also needs closer scrutiny. In a careful analysis of the general concept of mechanism, Machamer, Darden, and Craver (2000) gave a clear definition: "Mechanisms are entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions" (p. 3). The notion of a psychological mechanism must always contain a metaphorical element because the material entity component of the mechanism is missing. For example, "mental modules" is clearly metaphorical; no physical modules are clipped somewhere in the brain. As I noted in a critique (Hendrick, 1995) of the use of mental mechanism by Buss (1995), there is at best a very loose analogy between a mind mechanism and a clearly defined mechanistic function of a bodily organ. Lacking that material substrate to hang the mental mechanism on, such mechanisms cannot pass the test posed by Machamer et al. (2000) that a mechanism must be "productive of regular changes from start or set-up to finish" (p. 3). Clearly, the mental mechanisms of evolutionary psychology are metaphors. In fairness, however, psychology deals heavily in metaphors; the material substrate for most of our major concepts cannot be defined.

CONCLUSIONS

To what extent is the theory of evolution a foundation for psychological science? As we have seen, there are many versions of evolutionary theory, and there are an even larger number of psychological sciences. So the question has no simple answer. My own conjectures are something as follows. First, behavioral genetics and evolutionary psychology will remain far apart for the foreseeable future. Second, behavioral genetics will outstrip evolutionary psychology in growth and appeal for the next decade or so. Why? Primarily because of the growth of employment opportunities for psychologists in a variety of genetics-related areas. This prediction holds, however, *only* if psychology doctoral programs strongly incorporate training in genetics into doctoral training.

I am pessimistic that behavioral genetics will ever progress to the point of complex behavioral predictions from complicated polygenic configurations of genes. If the concept of evolvability proves valid, genetic predictions will have to become cellular systems' predictions. So far as we can see now, predictive equations will be highly nonlinear. But perhaps detailed predictability is not needed. If behavioral genetics progresses to allow a much stronger handle than we have now on mental illness, retardation, and similar deficits, perhaps that will be progress enough.

Third, I do not believe that evolutionary psychology will survive in its current form. E. F. Keller's (2000) quip about molecular biology's challenge to the neo-Darwinian synthesis suggests that another synthesis is in the offing. If so, that change will necessarily impact evolutionary psychology. In fact, the discipline is under assault from many directions. The leading theorists have made a strong set of Popperian conjectures, and they are being subjected to an equally strong set of refutations.

Thus, change is inevitable, but the exact directions are difficult to predict. One promising new approach meshes dynamical systems theory with evolutionary psychology (Kenrick, 2001; Kenrick, Li, & Butner, 2003; Kenrick et al., 2002). Other promising approaches will undoubtedly emerge. It is unlikely that the discipline will become extinct! Individuals such as Cosmides, Buss, Kenrick, and Tooby have theorized boldly and courageously. They were a powerful stimulus to the growth of the discipline. They have also been punished for their boldness. But it does not matter if they were wrong on specific points. Out of the matrix of strong conjectures and refutations a stronger and more rounded theory will emerge. Indeed, perhaps in a couple of generations, Scarr's (1995) appeal for the joining of genetics with evolutionary psychology may occur. At that point, evolution will become the foundation for psychology. Indeed, if this joining occurs, psychology will *become* evolutionary psychology.

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