On the Universality of Human Nature and the Uniqueness of the Individual: The Role of Genetics and Adaptation

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ABSTRACT The concept of a universal human nature, based on a species-typical collection of complex psychological adaptations, is defended as valid, despite the existence of substantial genetic variation that makes each human genetically and biochemically unique These apparently contradictory facts can be reconciled by considering that (*a*) complex adaptations necessarily require many genes to regulate their development, and (*b*) sexual recombination makes it improbable that all the necessary genes for a complex adaptation would be together at once in the same individual, if genes coding for complex adaptations varied substantially between individuals Selection, interacting with sexual recombination, tends to impose relative uniformity at the functional level in complex adaptive designs, suggesting that most heritable psychological differences are not themselves likely to be complex psychological adaptations Instead, they are mostly evolutionary by-products, such as concomitants of parasite-driven selection for biochemical individuality An evolutionary approach to psychological variation reconceptualizes traits as either the out-

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put of species-typical, adaptively designed developmental and psychological mechanisms, or as the result of genetic noise creating perturbations in these mechanisms

Personality psychology has two distinct traditions the search for a universal human nature, and the search for an explanation of individual differences in psychological traits (Buss, 1984) These two traditions have developed in parallel, but cohabit in the same field uneasily because the conceptual relations between them are cloudy and often seem contradictory Paradoxically, theories of human nature make claims about a universal human psychology, whereas personality research into individual differences depends on the existence of stable, interesting differences between individuals, and correspondingly tends to ignore, deny, or minimize universals Of course, one half of the reconciliation between the two is a straightforward commonplace of psychological thinking A human nature composed of uniform psychological mechanisms may produce individual differences as a result of different individual experiences It is the existence of genetic differences between individuals that poses problems It renders the study of the causation of individual differences difficult, and, more importantly, it calls into question the very idea of a universal human nature Indeed, some behavior geneticists are forceful about challenging the value of characterizing a shared human nature, given their estimation of the magnitude of genetic differences For this reason, they tend to focus on variation rather than on universality "The questions that most often confront scientists studying human behavior are those dealing with differences among people And genetics, the study of variation of organisms, is uniquely qualified to aid us in analyzing these individual differences" (Plomin, DeFries, & McClearn, 1980, p 11)

The tension between the two traditions in personality psychology has had its direct analog in evolutionary biology (Buss, 1984) Theories of and claims about species-typical behavioral adaptations appear to conflict with the discovery, through molecular genetic techniques, of vast reservoirs of genetic variability (Hubby & Lewontin, 1966, reviewed in Ayala, 1976, and Nevo, 1978, Lewontin & Hubby, 1966) Systematists find species to be clearly and recognizably characterizable by species-specific, species-typical physical and behavioral traits, and yet on genetic grounds, each individual is a unique combination of genes (with their associated traits), and varies in tens of thousands of ways from its conspecifics Is the concept of the psychic unity of humankind,

of a single, universal human nature, insupportable in the light of what is known about human and nonhuman genetics? Can the uniqueness of the individual be reconciled with the claim of a universal human nature?

We believe that evolutionary biology provides the conceptual framework that allows this reconciliation Both the psychological universals that constitute human nature and the genetic differences that contribute to individual variation are the product of the evolutionary process, and personality psychology must therefore be made consistent with the principles of evolutionary biology This means that every personality phenomenon is, from an evolutionary perspective, analyzable as either (*a*) an adaptation, (*b*) an incidental by-product of an adaptation, (*c*) the product of noise in the system, or (*d*) some combination of these Standards for recognizing these three varieties of evolutionary outcome will allow one to discover new, adaptively patterned personality traits and to place previous findings in evolutionary perspective In this article, we attempt to sketch out some of these standards In the process, we will argue that (*a*) some personality differences may be the expression of different, environmentally triggered adaptive strategies, (*b*) different adaptive personality strategies cannot, in principle, be coded for by suites of genes that differ from person to person, and (*c*) most *heritable* personality differences are *not* the expression of different adaptive strategies They are either mutationally driven genetic noise, or else an incidental by-product of an adaptation that has nothing to do with personality per se—pathogen-driven selection for biochemical diversity (Tooby & Cosmides, 1988)

Evolutionary Foundations

An evolutionary perspective on nature and nurture

The environment as the product of evolution An evolutionary perspective is not a form of "genetic determinism," if by that one means the idea that genes determine everything, immune from environmental influence Anyone with a biological education acknowledges that the phenotype is the result of the interaction between genes and environment, and all aspects of the phenotype are equally codetermined by this interaction Developmental programs (i e , the regulatory processes that control development) are directed by the genes, but they require and depend upon an entire range of properties of the environment being reliably and stably present in order to successfully produce

a healthy individual If either the genes or the environment are sufficiently changed, the result will change Thus, as with all interactions, the product cannot be analyzed into separate genetically determined, as opposed to environmentally determined, components

However, because of the nature of the evolutionary process that creates this interaction, "genes" and "environment" exist in a highly structured relationship that is very different from popular conceptions of separate but parallel genetic and environmental "influences " Many social scientists have labored under the false impression that only certain things are under the "control" of the genes, that evolutionary approaches are relevant only to those traits under such "control," and that the greater the environmental influence or control, the less evolutionary analyses apply In place of evolutionary analyses of those things purportedly under genetic control, they conduct atheoretical or nonevolutionary explorations of those traits under (what they believe to be) "environmental" control This kind of erroneous thinking is associated with the idea that genes are "biological," whereas "the environment" is nonbiological, the "social environment" is thought to be the opposite of "biological determination " But a close examination of how natural selection actually drives evolutionary processes leads to a very different view of how "genes" and the "environment" are related Evolution acts *through* genes, but it acts on the *relationship* between the genes and the environment The "environment" is as much a part of the process of evolutionary inheritance as are the "genes," and equally as "biological" and evolved No organism reacts to every aspect of the environment Instead, the developmental programs rely on and interact with only certain defined subsets of properties of the environment, while others are ignored For example, different diets transform a female ant into a worker or a queen, but there is no diet that will transform her into a dog, and guitar music or religious exhortation does not affect her growth Over evolutionary time, genetic variation in developmental programs (with selective retention of advantageous variants) explores the properties of the environment, discovering those that are useful sources of information in the task of regulating development and behavior, and rendering those features of the environment that are unreliable or disruptive irrelevant to development Across generations, this process of exploration of alternative gene-environment relations operates by varying developmental programs with respect to (*a*) what kinds of inputs from the environment they accept or are sensitive to, and (*b*) how they

shape phenotypic outcomes in response to these inputs "The environment" of an animal—in the sense of which features of the world it depends on or uses as inputs—is just as much the creation of the evolutionary process as the genes are Thus, the evolutionary process can be said to store information necessary for development in both the environment and the genes, in that it shapes the relationship of the two so that both are necessary participants in the ontogenetic construction of adaptations Both are "biologically determined," if such a phrase has any meaning

Environmentalism depends on nativism "The environment," per se, is powerless to act on the psyche of an animal, except in ways specified by the developmental programs and psychological mechanisms that already happen to exist in that animal at a given time These procedures take environmental information as input and generate behavior or psychological change as output The actual relationship between environment and behavior is created solely and entirely by the nature and design of the information-processing mechanisms that happen to exist in the animal, and in principle, information-processing mechanisms could be "designed" to create a causal relationship between any imaginable environmental input and any imaginable behavioral output The smell of excrement may be repulsive to us, but it is attractive to dung flies Aside from a few gross effects, such as gravity, the relationship between the environment and the behavior of the organism is not a matter of physical necessity, but is decided by the structure of the organism's psychological mechanisms

The information-processing procedures that exist in an organism at a given time are either (*a*) genetically specified, that is, innate, or (*b*) the product of other, prior procedures In the event they are the product of other, prior procedures, such prior procedures must themselves be either innate or the product of still other, even more antecedent procedures After ruling out infinite regression as a tenable theory of the origins of psychological structure, one must necessarily conclude that the psyche of an organism at any point in time is the product of its innate procedures, plus the changes—including any constructed procedures and their effects—created by those innate procedures operating on a sequence of environmental inputs Therefore, innate procedures must exist, are the necessary foundation of any full model of the psychology of any organism, and are always *necessarily entailed* by any envi-

ronmentalist claim Environmentalist theories depend on prior nativist theories, and therefore environmentalism and nativism are not opposed, but are instead interdependent doctrines

Thus, valid environmentalism inescapably posits innately regulated psychological mechanisms Any environmentalist claim about the influence of a given part of the environment entails a claim about an innately specified relationship between the environment and the hypothesized psychological output Consider, for example, the claim that girls learn gender-appropriate behavior by watching their parents This entails the claims that (*a*) girls have innate mechanisms specialized for learning gender-appropriate behavior (otherwise, why wouldn't a girl be just as likely to imitate her father?), (*b*) these mechanisms compute the frequency with which each parent performs various behaviors, and, for each behavior, compare the mother's tally to the father's, and (*c*) these mechanisms cause girls to imitate behaviors that their mothers perform more frequently than their fathers, and to avoid the behaviors that their fathers perform more frequently than their mothers Rather than escaping claims of innateness, this "socialization hypothesis" tacitly posits some rather sophisticated and specialized innate machinery linking informational input to behavioral output

Every coherent psychological theory has at its foundation innate mechanisms or procedures, either explicitly recognized or tacitly entailed To say such procedures are innate means that they are specified in the organism's genetic endowment, that is, in how genetically based programs regulate the mechanisms governing development This genetically specified, innate foundation of the psyche is the product of the evolutionary process, and is the means through which the evolutionary process organizes the psychology of the animal over generations Evolutionary biology is relevant to psychology because it studies the evolutionary processes responsible for shaping the innate foundations of psychological mechanisms, just as it does for physiological mechanisms

Manifest variability and innate universals What is human nature? Genetics had enormous difficulty making progress as a science until geneticists drew the distinction between genotype and phenotype, that is, between the inherited basis of a trait and its observable expression This distinction allowed them to move beyond the bewildering complexity of surface characteristics to an underlying level of clear principles that explained the surface variability We believe a similar

distinction will be equally useful for an evolutionarily informed personality psychology We will refer to this as the distinction between an individual's innate psychology and his or her manifest psychology and behavior If one believes in a universal human nature, as we do, one observes variable manifest psychologies, traits, or behaviors between individuals and across cultures, and views them as the product of a common, underlying evolved innate psychology, operating under different circumstances (see, e g , Daly, Wilson, & Weghorst, 1982) The mapping between the innate and the manifest operates according to principles of expression that are specified in innate psychological mechanisms or in innate developmental programs that shape psychological characteristics, these expressions can differ between individuals when different environmental inputs are operated on by the same procedures to produce different manifest outputs (Cosmides & Tooby, 1987, Tooby & Cosmides, 1989) This set of universal innate psychological mechanisms and developmental programs constitutes human nature Individual differences that arise from exposing the same human nature to different environmental inputs relate the study of individual differences to human nature in a straightforward way Those researchers who are interested in applying an evolutionary perspective to individual differences can investigate the adaptive design of these universal mechanisms by seeing whether different manifest outputs are adaptively tuned to their corresponding environmental input Does the algorithm which relates input to output show evidence of complex adaptive design?

Such a research program, however, would be obstructed if it were true that human nature is not everywhere the same if different individuals had qualitatively different innate psychological mechanisms and developmental programs, which reflected qualitatively significant genetic differences between humans It is certainly a well-established fact that humans and other similar species manifest enormous genetic diversity (Ayala, 1976, Nevo, 1978, Plomin, 1986, Plomin, DeFries, & Loehlin, 1977, Plomin et al , 1980, Scarr & Kidd, 1983) How can this genetic diversity be reconciled with a universal human nature? This question is central to personality psychology, and is the issue primarily addressed in this article We will argue that despite the existence of genetic differences, the hypothesis of different human natures is incorrect By considering evolutionary constraints on how adaptations must be implemented, and by considering recent developments in evolutionary genetics, we conclude that the relationship of genetically caused individual differences to universal psychological mechanisms is circum-

scribed Characteristics in which individuals differ because of genetic differences are an unrepresentative subset of human phenotypic characteristics, and are generally limited to quantitative variation in the components of complex, highly articulated, species-typical psychological mechanisms Such genetically caused differences are almost entirely constrained variation within an encompassing, universal, adaptively organized superstructure human nature

Evolution produces adaptive organization and a residue of nonadaptive disorder Reconceptualizing psychology from an evolutionary perspective requires the careful use of concepts developed in evolutionary biology, of which the most important is adaptation Evolutionary biology explains the characteristics of living processes primarily through relating their organization to adaptive requirements If evolution has anything to contribute to personality psychology, it will be through investigating which personality phenomena are adaptations and which are not To address this issue, one needs clear standards for recognizing adaptations An adaptation is a characteristic of the phenotype developmentally manufactured according to instructions contained in its genetic specification or basis, whose genetic basis became established and organized in the population because the characteristic systematically interacted with stable features of the environment in a way that promoted the reproduction of the individual bearing the characteristic, or the reproduction of the relatives of that individual (Dawkins, 1982, Hamilton, 1964, Williams, 1966) Adaptations are mechanisms or systems of properties "designed" by natural selection to solve the specific biological problems posed by the physical, ecological, and social environments encountered by the ancestors of a species during the course of its evolution The evolutionary biologist's definition of adaptive function is subtly but profoundly different from either common-sense notions of function or many psychologists' notions of function The promotion of the reproduction of the individual and/or his or her relatives is a very different standard of functional operation from such intuitively reasonable standards as happiness, social harmony, success, welfare, well-being, adjustment, long life, health, goal realization, and self-actualization, although in many circumstances and at many levels of explanation they may correspond Nevertheless, in seeking an explanation for the organization of our innate (i e , evolved, genetically specified) psychological mechanisms and developmental programs, it is the biological definition of function and adaptation that tracks the forces that have shaped us

To properly account for psychological phenomena in evolutionary terms, one must recognize that evolution produces both adaptations and nonadaptive aspects of the phenotype, and distinguish between them carefully (Williams, 1966) Although natural selection is the single major organizing process in evolution, promoting adaptive coordination between organism and environment, evolutionary outcomes are shaped, however weakly, by many other processes, many of which disrupt such coordination (e g , mutation, recombination, genetic hitchhiking, antagonistic pleiotropy, engineering constraints, antagonistic coevolution)

The outcomes from evolution break down into three basic categories (*a*) adaptations (often, though not always, complex and polygenically specified), (*b*) concomitants of adaptation, and (*c*) random effects Adaptations are the result of coordination brought about by selection as a feedback process, they are recognizable by "evidence of special design"—that is, by a highly nonrandom coordination between properties of the phenotype and the environment, which mesh to promote fitness (genetic propagation) Concomitants of adaptation are those properties of the phenotype which do not contribute to adaptation per se, but which are tied to properties that are, and so are incorporated into the organism's design, they are incidental by-products of adaptation Bone happens to be white, but was selected not for its color but for its rigidity Such concomitant aspects will tend to be selectively neutral, in comparison to the functional advantages conferred by the adaptive aspect of the concomitant system Similarly, there are an infinite number of personality traits one can define and measure, but evolutionarily analyzable order will tend to be found only in those causally related to adaptive function Finally, entropic effects of many types act to introduce disorder into the "design" of organisms They are recognizable by the lack of coordination between phenotype and environment that they produce, and by their variability Examples of such entropic processes include mutation, environmental change, and rare circumstances

In analyzing personality phenomena from an evolutionary perspective, adaptations will tend to be recognizable because of the functional coordination of psychological characteristics or behavior Complex organization which systematically leads to adaptive outcomes constitutes evidence of "special design" (Dawkins, 1986, Symons, 1987, Williams, 1966) Moreover, complex architecture or articulation of parts per se suggests (though does not prove) that the properties were organized by natural selection, since random entropic effects are unlikely to construct complex systems of covariation by chance Uniformity with-

out adaptive patterning or apparent functional significance (e g , all bones are white, all blood is red) suggests the characteristics in question are incidental concomitants of adaptation Finally, unstructured variation will tend to be the result of entropic processes, and will often be adaptively neutral Entropic processes will also cause maladaptation, either through disruption of developmental organization or through a mismatch between the organism and the environment

By applying these standards one can determine whether a personality trait is the product of an adaptation, a concomitant of adaptation, or noise

Constraints on organic design

Many psychological adaptations will be complex Few would deny that humans successfully perform a wide array of tasks, including many that are functionally similar to what other animals do finding mates, having offspring, helping relatives, seeing objects, identifying food, and so on Described in terms of their goals, such activities can seem transparently simple Introspectively, we experience many of them (e g , seeing objects) as effortless But when one tries to discover sets of procedures that will actually implement such goals, their real complexity, intricacy, and difficulty become oppressively clear (see, e g , Marr, 1982, on vision) The history of artificial intelligence has largely been the history of discovering how complex information-processing procedures must be if they are to perform even very simple tasks (e g , moving around half a dozen blocks in a small area) Work in cognitive science and artificial intelligence has shown that mechanisms capable of solving even supposedly simple real-world cognitive tasks must contain very complex "innate" prespecified procedures or information, matched narrowly to the structural features of the domains within which they are designed to operate (Boden, 1977, Marr, 1982, Minsky, 1986, on the "frame problem," see Brown, 1987, Fodor, 1983)

Expectations derived from evolutionary biology reinforce the conclusion that many psychological mechanisms will be complex and function-specific Our ancestors had to be able to solve a large number of different adaptive problems, and any attempt to specify procedurally how to solve such problems demonstrates that many of them, at least, are both intricate and dependent for their solution upon mechanisms that differ in structure from one another For example, successful cooperation requires the coordinated operation of a surprising number

of information-processing procedures that are function-specific (Cosmides, 1985, 1989, Cosmides & Tooby, 1989), other adaptive problems (e g , avoiding poisonous foods, dealing with threats) are solved by other mechanisms

At the heart of Darwin's theory of the origin of adaptations is the following precept The more important the adaptive problem, the more intensely selection should have specialized and improved the performance of the mechanism for solving it Consequently natural selection tends to produce functionally distinct adaptive specializations—a heart to pump blood, a liver to detoxify poisons, and so on This insight led Chomsky (1980) to argue that the innate information-processing mechanisms of the human mind should include a number of functionally distinct cognitive adaptive specializations Just as the human body is composed of many complex, functionally distinct physiological organs, he argued, one can expect the human mind to be composed of many complex, functionally distinct "mental organs " Indeed, we have argued elsewhere that a psyche that contained nothing but general-purpose information-processing procedures could not, in principle, generate adaptive behavior, and therefore is an evolutionary impossibility (Cosmides & Tooby, 1987)

Thus, the lessons for psychology from artificial intelligence and evolutionary biology are twofold First, most or all innate psychological mechanisms will be highly complex in their procedures and design Second, this complexity will usually be structured in function-specific ways Our ancestors would not have been able to solve the large array of adaptive information-processing problems necessary for survival and reproduction without a large array of complex, function-specific information-processing mechanisms (Barkow, 1989, Cosmides & Tooby, 1987, Rozin, 1976, Symons, 1987, Tooby & DeVore, 1987)

Complex adaptations are monomorphic within an integrated functional design Viewed from a biological perspective, organisms are complexly designed systems In fact, there is no nonliving system, natural or artificial, that rivals the complexity of organic design (Dawkins, 1986) Moreover, biological complexity is not a random collection of unconnected properties, but rather an intricate and articulated set of interdependently organized parts that function together in an adaptive mesh to promote fitness

It is this interdependence among subcomponents that requires a monomorphism of integrated functional design In any specific system

of interdependent parts, each part must present a uniform, regular, and predictable set of properties to the system, so that the other parts can interact with it in a predictable and organized fashion Any automobile engine can be brought to a halt by significantly altering the design properties of almost any of its parts Of course, the function of the system can be used to divide the properties of its parts into two sets those properties whose variation does affect the functional operation of the system, and those whose variation does not (e g , the color of the radiator hose) We will term the first functional variation, and the second, superficial variation

The structure of functional interdependence shapes what kinds of variation the system can tolerate Incremental functional variation is easy to tolerate If a part or subassembly varies in a way that improves or degrades performance somewhat without disrupting the operation of the rest of the system, such variation can be introduced, tolerated, and evaluated through its effect on comparative performance On the other hand, a radical change in the design of a part will bring the rest of the system to a halt unless compensatory design changes are simultaneously made in the other parts, in order to preserve their functional integration For this reason, when a human engineer makes a major change in the design of a computer or car, the "variation" introduced into the design is usually coordinated variation A change in one part is linked in tandem to a suite of associated compensatory changes, simultaneously introduced in other parts

Variation, then, can be classified as (*a*) *superficial variation,* within design tolerance limits, not changing the functional operation of the system significantly, (*b*) *limited functional variation* deriving from incremental changes in a single part or a small number of parts, which either improves or degrades the functional performance of the system, (*c*) *disruptive variation,* where the changes introduced violate the functional integrity of the system, causing it to fail, or (*d*) *radical but coordinated functional variation,* where entire sets of parts vary simultaneously between discrete alternatives, so that each set is functionally integrated Such variation corresponds to discretely different designs different models of a car, or different species, or different morphs (e g , male and female) within a species

Neo-Darwinism is an account of how functional integration in biological systems can arise through selective retention of a superior functional variant—superior in the sense that the variation modifies the functioning of the system in ways that promote the variant's own propa-

gation Because the generation of variation through mutation is believed to be a random process, elementary probability indicates that coordinated functional variation ([*d*], as defined above) will come into existence by chance mutation very rarely or never, and therefore such "hopeful monsters" will play only a minor role in evolution Despite some recent modest challenges to this view (Gould & Eldredge, 1972), both theory and evidence indicate that evolution by natural selection generally proceeds by using the second type of variation—incremental functional variation of limited magnitude, which does not require coordinated, compensatory changes in the rest of the system (Dawkins, 1986) Such evolution takes place within the context of an existing integrated monomorphic design, so that variation within a design either is superficial rather than functional, or consists of incremental random steps away from existing designs of each subcomponent (Although typological thinking has been properly replaced by populational thinking [Mayr, 1982], the nature of complex adaptations constrains how variation operates within sexually reproducing species [1])

Human physiology is monomorphic within an integrated functional design This line of analysis is confirmed by commonplace biological observation The architecture of human physiology, which is better understood and easier to observe than psychological functioning, nicely illustrates these constraints on organic design

As any biological anthropologist can attest, the "architecture" or physiological design of humans is both distinctively species-specific and species-typical When one examines the organs, with their complex design and interlocking architecture, one finds (within a sex, and to a large extent between sexes) monomorphism of design Virtually everyone has two lungs, one neck, a stomach, a pancreas, a tongue, two irises, 10 fingers, blood, hemoglobin, insulin, and so on And, although there is a great deal of superficial variation—no two stomachs are exactly the same size or shape, for example (Cosmides, 1974, Williams, 1958, 1967)—each organ system has the same basic design The locations and connections between organs are topologically the same, and the internal tissue structures and physiological processes have a uniformity

1 Such a view reconciles the populational thinking necessary for understanding how evolutionary change proceeds (Mayr, 1982) with an understanding of how complex adaptations (i e , adaptations with interdependent parts) can emerge, operate and evolve within populations over time (Fisher 1930/1958)

of structure and functional regulation One has to descend to specific enzymatic pathways before design differences—as opposed to quantitative variation—start showing up Individual proteins may indeed differ due to genetic differences between individuals, but genetically specified, coordinated functional variation in biochemical pathways between individuals of the same sex and age is very rare

There are no substantive reasons to suspect that the kinds of evolutionary forces that shaped our innate psychological mechanisms are fundamentally different from those that shaped our innate physiology Indeed, Chomsky's arguments on the necessity for innate, modular, complex design in human linguistic cognition are well-known, and have been aptly termed "the new organology" (Chomsky, 1980, Marshall, 1980, see also Marr, 1982) Of course there can be individual variation in cognitive programs, just as there is individual variation in the size and shape of stomachs This can be true of any structure or process in a sexually recombining species, and such genetic variation constitutes the basis for inherited psychological differences But even relatively simple cognitive programs or "mental organs" must contain a large number of interdependent processing steps, limiting the nature of the variation that can exist without violating the functional integrity of psychological adaptation Thus, personality variation is not likely to consist of an alternative, wholly different, coordinated design that differs "from the ground up " On the basis of population genetics considerations described below, we find implausible the notion that different humans have fundamentally different and competing cognitive programs, resting on wholly different genetic bases

The paradox of design monomorphism in a world of genetic polymorphism Obviously, there is a natural tension between complex functional interdependence in a system and the existence of a large amount of variability in its components For living systems, design is controlled by the genetic programs that regulate development If the design of organisms is truly monomorphic, the genes underlying the design should also be monomorphic Why, then, does there appear to be substantial genetic polymorphism[2] within populations?

This mystery is deepened by the fact that almost all complex or-

2 Genetic polymorphism refers to the existence within a population, of two or more alternative alleles (genes) for a given trait (or more exactly, at a given locus) It may also be used to refer to genetic variation in the aggregate, without reference to a specific trait

ganisms reproduce sexually, that is, when reproduction occurs, genes from two parents are randomly recombined to form genetically differentiated, genetically unique offspring Sexual reproduction, through recombining genes, introduces potentially disruptive variation into a functional design that in the parental generation was functionally integrated enough to reproduce For this and other reasons, the function of sexual recombination has been obscure, and it has been the subject of intense interest in the evolutionary community (Bell, 1982, Maynard Smith, 1978, Williams, 1975) The alternative, asexual reproduction (i e , cloning), seems much saner from an evolutionary and from an engineering point of view In asexual reproduction, each offspring has exactly the same genetic programs as its parent, keeping the integrated design of the parent wholly intact Moreover, asexual reproduction offers efficient evolutionary progress as well Functional variants can be effectively incorporated through mutation and selection (for discussion of these issues see Bell, 1982, Maynard Smith, 1978, Williams, 1975) Traditional claims that sex has been favored because it accelerated evolutionary progress have not withstood recent critical scrutiny (Maynard Smith, 1978, Williams, 1975)

The role of genetic polymorphism and the adaptive significance of sexual reproduction are linked questions (Tooby, 1982) Indeed, they are two sides of the same coin If all individuals were alike genetically, recombining their genes would be pointless, just as exchanging identical parts on a mass production line does not change the functional end product Why swap identical parts? The more genetic polymorphism there is, the more sexual recombination produces genetically differentiated offspring Both interact to produce unique and genetically differentiated individuals, a system that potentially disrupts functionally integrated monomorphic design

This is all the more puzzling because sex is clearly an adaptation The high cost and coordinated complexity of the physiological and psychological systems that are necessary if sexual reproduction is to occur are evidence of special design, the hallmark of adaptation (Williams, 1966, 1975)

Sexual reproduction and genetic variation Evolved defenses against pathogens?

Recent developments in evolutionary biology may hold the answer to the linked questions of the adaptive significance of sex and the role of genetic polymorphism These developments may have significant

implications for the study of human nature and individual differences as well Over the last decade, a growing number of researchers (Bell & Maynard Smith, 1987, Hamilton, 1980, Hamilton & Zuk, 1982, Jaenike, 1978, Rice, 1983, Tooby, 1982) have argued that the selection pressures created by parasites acting on the genetic systems of host populations have the properties required to explain why almost all higher organisms reproduce sexually Indeed, there is a great deal of ecological and experimental evidence supporting the theory that pathogens selected for the evolution of sex (Hamilton & Zuk, 1982, Kelley, Antonovics, & Schmitt, 1988, Rice, 1983, Tooby, 1982, and others) As Tooby (1982) and Rice (1983) have pointed out, this hypothesis also answers the interlocking question Why have so many different alleles at so many different loci in a population? The argument is summarized briefly below (see Tooby, 1982, for details, evidence, and supporting references)

Large, complex, long-lived organisms constitute ecological environments for immense numbers of short-lived, rapidly evolving parasites —disease-causing microorganisms For this reason, parasites and hosts are locked in an antagonistic coevolutionary race The hosts are selected to evolve defenses against these parasites, and the pathogens are selected to evolve around those defenses In this evolutionary race, the pathogens have one crucial advantage They have a shorter generation time than host species, often by a factor of millions, and, other things being equal, can evolve around host defenses faster than host species can evolve new defenses or countermeasures During an individual host's lifetime, a particular pathogen species may have nearly one million generations in which to adapt to the host's particular physiology, proteins, and biochemistry Once a pathogen species has "cracked" that host's defenses, by evolving around them, it has simultaneously cracked the defenses of all genetically identical individuals For an asexually reproducing individual, this means all of its offspring and kin According to this theory, there are almost no long-lived asexual animal lineages because they fall prey to rapidly evolving diseases

On the other hand, sexual reproduction is the act of reproducing individuals with a unique new genotype a never-before-encountered set of genes By mixing genes with those of another individual through sexual recombination, an organism can protect its offspring from the pathogens that have adapted to its biochemistry and physiology during its lifetime Instead of being perfectly adapted to an individual's offspring, they will have to "start from scratch" with each new offspring

Sexual reproducers foil the decisive evolutionary advantage pathogens have with their rapid generation times by genetically differentiating between parent and offspring, and among siblings, so that each new individual constitutes a unique habitat that must be independently adapted to Long-lived organisms can survive in a world of rapidly evolving parasitic antagonists because they reproduce sexually

Among other things, genes code for the proteins which participate in every physiological process These proteins form the microenvironment of the pathogen (Damian, 1964, 1979) As mentioned earlier, if all individuals were alike genetically, then recombining their genes through sexual reproduction would be pointless, as exchanging identical parts does not change the end product Alternative alleles at a locus code for alternative proteins Thus, the more alternative alleles exist at more loci—i e , the more genetic polymorphism there is—the more sexual recombination produces genetically differentiated offspring, thereby complexifying the series of habitats faced by pathogens Most pathogens will be adapted to proteins and protein combinations that are common in a population, making individuals with rare alleles less susceptible to parasitism, thereby promoting their fitness If parasitism is a major selection pressure, then such frequency-dependent selection will be extremely widespread across loci, with incremental advantages accruing to each additional polymorphic locus that varies the host phenotype for a pathogen This process will build up in populations immense reservoirs of genetic diversity coding for biochemical diversity (Clarke, 1979, Tooby, 1982)

In other words, the existence of multiple alternative alleles at a large proportion of loci is a prediction of the pathogenic theory of the evolution of sex Indeed, there is considerable evidence that selection has driven the accumulation of allozymic diversity in populations It is far greater than can be accounted for by random processes acting on selectively neutral alleles (Brues, 1954, 1963, Lewontin, 1974, Nevo, 1978, Tooby, 1982) In short, pathogens supply an intense selection pressure for sexual over asexual reproducers, and are an intense and general source of frequency-dependent selection for protein polymorphism

Monomorphic design out of polymorphic materials

The pathogen theory suggests that the evolution of multicellular organisms has depended on simultaneously satisfying two conflicting, almost mutually exclusive, demands (*a*) that a species' complex adaptations

be monomorphic in their design properties, and (*b*) that those properties that parasites target and depend upon be polymorphic What makes the satisfaction of these conflicting demands possible is that parasites decompose the properties of the host's phenotype differently from the way that the demand for "functional design" does To make this clear, imagine three tract houses, all identical in layout, but made of different materials wood, brick, and stone The termites that eat the wood cannot migrate next door to eat the brick or stone The ants that dig through the brick mortar cannot digest wood or stone, and so on For the human occupants, the layouts are identical, but for the insects, the materials the houses are built from make them different Protein polymorphism appears to function similarly within the context of physiological design The organ system and within-organ functional design are relatively uniform, with each component presenting a regular and predictable set of functional properties to the system But to find "design diversity" or qualitative diversity as opposed to quantitative diversity (e g , size, rate), one must descend to the level of protein structure This is because the biochemical microenvironment that a pathogen inhabits is a function of protein structure To reproduce, pathogens use the enzymes, substrates, and biochemical pathways they are exposed to, rather than, necessarily, the ultimate functional product of such pathways

In other words, the resolution of this conflict is to produce variation which is significant from the point of view of the pathogen's life cycle, but superficial from the point of view of the ultimate functional design of an organ system Selection can create protein variation that thwarts pathogenic function, while not disrupting the functioning of the organism too radically

Pathogens mix human genetic diversity, making individuals different, but ethnic groups similar

People find it easy to believe that there are profoundly different types of humans (e g , Block, 1971, Block & Ozer, 1982, Jung, 1921) Indeed, people in many cultures have historically harbored the belief that there were important "blood differences" between themselves and whatever other ethnic groups they knew of, and that these others constituted different types of human beings Are ethnic groups differentiated in a fundamental way because of significant and substantial genetic differences, so that each ethnic group has a set of genes shared by members of the group, but not shared by others? In terms of ethnic differences,

one could imagine (as many folk beliefs have it) that neighbors from the same group are very similar "hereditarily," "of one blood," but that members from different groups or different races are very different Even according to standard biological reasoning, such a result would be easy to account for People do, after all, mate locally, and given genetic drift and selection to local circumstances, one could easily imagine local gene pools that are internally homogeneous, but very different from each other (Gould, 1985)

The measures provided by modern molecular genetics have shown that there is no basis for such a belief Leaving aside the genetic monomorphism at the sequence level (in excess of 99 99%), and at the protein level (60% to 75%), the examination of the distribution of genetic variation that exists among humans leads to a surprising result Members of any one human group do not all share fixed combinations of genes that members of other groups lack, or even share single genes that members of other groups entirely lack Human groups do not differ substantially in the types of genes found, but instead only in the relative proportions of those alleles Eighty-five percent of human genetic variation is within-group variation, 8% is between tribes or nations within a "race," and only 7% is between "races" (for discussion and references, see Gould, 1985, Lewontin, 1982, Lewontin, Rose, & Kamin, 1984, Nei, 1987) What this means is that the average genetic difference between one Peruvian farmer and his neighbor, or one Bornean horticulturist and her best friend, or one Swiss villager and his neighbor, is 12 times greater than the difference between the "average genotype" of the Swiss population and the "average genotype" of the Peruvian population (i e , the within-group variance is 12 times greater than the between-group variance) Indeed, as Lewontin, Rose, and Kamin put it (1984, p 127), "The remarkable feature of human evolution and history has been the very small degree of divergence between geographical populations as compared with the genetic variation among individuals " This result, contrary to what ideas of local selection or genetic drift might lead one to believe, is consistent with the pathogenic theory People catch diseases from their neighbors, so it is important to be genetically different from them, such selection attracts and recruits genetic variants from outside the local group, promoting local within-group diversity and reducing intergroup diversity (Tooby, 1982) There is no structured genetic substrate separating human groups discretely into different kinds Although there is a sea of genetic diversity (measured at the protein level), it is a well-mixed sea

On the nonheritability of inherited human nature Panspecific versus idiotypic nativism

The tale of the Tower of Babel cautions that common enterprises may be defeated if the languages used by those attempting to cooperate are too different Certainly, cooperation between ethology, behavioral ecology, comparative psychology, behavior genetics, cognitive science, and social and personality psychology has been seriously damaged by the use of the same terms to mean different things Although researchers are generally (although not always) careful and precise in their usage within their own discipline, when terms and results get exported to neighboring fields meanings frequently become inadvertently shifted, leading to persistent misunderstandings For example, the terms "genetic" and "heritable" have come to mean very different things to geneticists and psychologists This has caused many researchers to erroneously believe that in order to show that a trait is an evolved adaptation, one must demonstrate that it has a high heritability These problems reflect a larger confusion within the social sciences that has resulted from the failure to distinguish consistently between what we will call *idiotypic nativism*—the study of which genetic differences cause which individual differences—and *panspecific nativism*—the study of the innate developmental and psychological mechanisms that all humans share

In any species, there are features of the genetic system that vary between individuals, and there are features that are species-typical and shared by all normal members of the species Because differences are easier to investigate, control for, and experimentally manipulate, the bulk of experimental genetics (and behavior genetics) is about within-species genetic differences This methodologically derived emphasis on investigating genetic differences has had its effect on the conceptual orientation of many geneticists For example, Plomin, DeFries, and McClearn (1980) state that "the scientifically useful question is For a particular behavior, what causes differences among individuals? Research in behavioral genetics is directed toward understanding differences in behavior" (p 6) In behavior genetics texts, phrases such as "genetic effects," "genetic influences on behavior," the "genetic hypothesis about behavior," "the role of heredity," "the influence of genetic factors," and "the action of the genes" are used to refer to how genetic differences between individuals affect behavioral differences between individuals—idiotypic nativism The fact that genetics methods, of necessity, have focused primarily on differences has led

to the widespread misimpression among many psychologists that evolutionary, "biological," or nativist approaches all attempt to explain phenomena solely or primarily through reference to genetic differences

However, the single most important fact to realize about these studies of differences is that they bypass entirely the question of what all humans have in common how the genetic inheritance that all humans share produces (in conjunction with existing human environments) the human nature we all share, including our complex psychological adaptations Because the elaborate functional design of individuals is largely monomorphic, our adaptations do not vary in their architecture from individual to individual (except quantitatively) Thus, they are not "genetic" in the carefully delimited sense in which behavior geneticists use the term—that is, caused by genetic differences between individuals They are, however, genetic, hereditary, or inherited in the sense that nongeneticists use these terms Their structured design has its characteristic form because of the information in our DNA, which we all share by virtue of the fact that we are human and not members of another species This is all that evolutionists mean by "genetic" when they are making claims about evolved adaptations in human psychology For this reason, scientists tend to study complex adaptations using assumptions and concepts drawn from a panspecific nativist orientation

Confusion also arises from the diversity of ways psychologists interpret the significance of the heritable differences uncovered by behavior geneticists For selection to produce evolutionary change, traits responsible for differences in fitness must be heritable For this reason, population geneticists, in modeling selection, are interested in heritable differences (Fisher, 1930/1958) Because of this, the assertion is often made that evolutionary claims about traits cannot be valid unless the trait in question can be shown to be heritable, that is, to vary between individuals because of genetic differences among individuals (Lewontin, Rose, & Kamin, 1984) However, this belief results from a confusion between the input to the evolutionary process and its output Nonadaptively organized, randomly generated, heritable variation is the raw material selection uses to produce evolutionary change, but the output of the evolutionary process is not variation, rather it is monomorphic adaptive design at the genetic level Although heritable variation is necessary for selection to act, natural selection is a process that *eliminates* variation (Fisher, 1930/1958) (Despite widespread belief to the contrary, even stabilizing selection eventually eliminates genetic variation, Felsenstein, 1979) Barring balanced polymorphism, the longer selec-

tion acts, the more heritable variation is used up The better variant becomes more common, until it is fixed in the gene pool and thus becomes a universal part of the species' genetic endowment At that point in the process, the trait has a *zero* heritability But no sensible person would claim that when it became universal it ceased to have a genetic basis

For example, there is virtually no variation in leg number We all have two legs at birth Therefore, the trait "having two legs" has a zero heritability in the human population (Loehlin & Nichols, 1976) Yet no one would deny that leg number is specified in the genome Leg number, the presence of a prefrontal cortex, hemoglobin, the capacity for language, an immune system—all these things have zero heritability, are adaptations, have a genetic basis, and are the product of the evolutionary process Their lack of heritability supports, rather than undermines, the presumption that they are innately specified adaptations

In fact, not only is heritability not required to establish adaptation, heritable variation in a trait generally signals a *lack* of adaptive significance The longer selection has operated on a trait and the more intensely it has operated, the less heritable variation is left Consequently, those traits that have high heritabilities will generally be those traits that are not adaptations (Crawford & Anderson, in press), although they may interact in interesting ways with adaptations Therefore, behavior geneticists tend to be studying phenomena that are not themselves adaptations (however interesting they may be for other reasons), but the raw material out of which future adaptations may someday be made Those interested in studying complex psychological adaptations should be most interested in design features that are inherited, but not heritable

To fully appreciate this point, one must keep in mind the distinction between studying heritable variation in a design and studying the design against which variation is measured This distinction is important because mutation and pathogen-driven diversifying selection inject heritable differences into nearly every aspect of our species-typical design Let us assume, for example, that all humans have a complex psychological mechanism regulating aggression (which we believe to be true), but that pathogen pressure has created heritable variation in that mechanism's threshold of activation As a result, some people would have a "shorter fuse" than others, and this difference would be heritable Nevertheless, this would not mean that the complex "aggression" mechanism is not an adaptation It is (by hypothesis) universal, and therefore has zero heritability It would mean, however, that the

variations in the exact level at which the threshold of activation is set are probably not adaptations Similarly, stomachs vary in size, shape, and acidity, yet stomachs are still adaptations Those features of the system that can be described in terms of uniform design are likely to be adaptations, whereas the heritable variations in the system are not The task is to extract a description of the mechanism from the noisy variation in such a way that uniformity of design appears and heritability localizes in nonessential parts of the design Comparing the relative heritability of various candidate design features can help one accomplish this Moreover, although the genetic differences studied by behavior geneticists are mostly not adaptations, they are a rich set of natural experiments in the perturbation of our complex adaptations, the "fracture lines" that genetic differences cause in human behavior are a rich source of information about the design of these adaptations and the genetic, neurophysiological, and developmental mechanisms that underlie them

The one exception to the rule that selection uses up heritable variation is the case of balanced polymorphism For example, if alternative variants become more fit the rarer they are, the evolutionary result is often a stable balance of heritable alternatives in the population A typical instance is variation in appearance in prey species When predators form a search image of the most common color pattern of their prey, prey with rare color patterns are less frequently eaten, and this selection pressure creates stable diversity in prey color, similarly, as discussed above, the fact that parasites adapt to the most common proteins of their hosts selects for biochemical diversity between hosts Such frequency-dependent selection leads to a situation where heritable differences subserving adaptive functions may stably persist in the population indefinitely As Maynard Smith (1982) and others have shown using game theoretic techniques, this kind of reasoning may also apply at the phenotypic level to many kinds of social strategies (e g , cooperators and defectors in an iterated prisoner's dilemma, or "hawks" and "doves" in a series of aggressive encounters) As will be argued below, however, these phenotypic alternatives are unlikely to be specified through suites of genetic differences, because sexual recombination breaks apart the functional coordination of the component parts Therefore, although alternative social strategies may well exist, they are probably not an explanation for much of the heritable variation in psychological traits

Implications for Personality Psychology

Clearly, environmental and genetic variation makes humans behave differently from one another, and one can arbitrarily lump or divide humans into as few or as many kinds and categories as one pleases, depending on one's purpose In applying an evolutionary perspective to personality psychology, however, there are several obvious questions of interest (*a*) Because differences must be located within the encompassing framework of universal human psychological architecture, the initial question is, what is the adaptive organization of our universally shared psychological mechanisms (i e , what is human nature)? (*b*) Which individual differences covary, and which do not? (*c*) Do those individual differences that covary divide humans into different personality types, and if so, are these "types" adaptively organized behavioral strategies, with clear-cut evolutionary functions? (*d*) Do those individual differences that do not covary—that are randomly distributed with respect to one another—have any adaptive function? (*e*) Is there an evolutionary explanation for why some individual differences are cross-situationally stable, while others are situationally evoked? Answering these questions constitutes an entire research program, but certain tentative conclusions can be drawn about the probable relationship of individual differences, behavioral strategies, and personality types

Morphs, personality types, and strategies Are there discrete kinds of humans?

Although integrated adaptive design requires functional monomorphism, such monomorphism is necessary only within discrete kinds, or "morphs " All automobile engines of a given brand and model are monomorphic in design, but different models can and do have entire suites of design differences They display *coordinated* functional variation

Different species certainly correspond to different designs or "models," and these different phenotypic designs are the product of systematic design differences in the species' genetic endowments Sometimes, however, evolution produces discrete alternative "models" *within* a species different "morphs " Morphs are alternative designs that differ from one another in substantial, discrete, and adaptively coordinated ways Different morphs are the incarnation of different adaptive strategies For example, males and females constitute different morphs of the same species The two sexes are distinguished by entire suites of co-

ordinated differences, and this distinguishing variation is discrete An individual has the necessary physiological traits either of a female or of a male, but not a mixture of the two (except in pathological individuals)

The biological world contains numerous examples of multiple morphs within a species Within many social insect species, for example, females are divided into different "castes"—"soldiers," "workers," and "queens"—whose morphology and behavior differ from each other in such substantial, discrete, and coordinated ways that they sometimes look and act like completely different species (Oster & Wilson, 1978, Wilson, 1971) All animal species contain different juvenile and adult morphs, which, depending on the species, may be nearly identical or as startlingly different as caterpillar and butterfly, tadpole and frog

One need not think of morphs as differing only in gross physical morphology Two individuals of a species whose behavioral strategies differ in substantial, discrete, and coordinated ways—i e , two individuals who differ in "personality"—might also be considered different morphs For example, recent game theoretical and ecological work has shown that alternative adaptive behavioral strategies, such as "hawks" and "doves" (individuals who escalate violent conflicts and individuals who retreat from them), can stably coexist within a species (Maynard Smith, 1982, Maynard Smith & Price, 1973) Using the theory of evolutionarily stable strategies (ESS), one can determine whether such alternative "personality types" can coexist in a population, or whether one personality will be selected for over another, until it becomes a universal, species-typical trait (see Maynard Smith, 1982, for a comprehensive treatment of ESS theory)

If there are discrete personality "morphs" in humans, they are obviously far more modest than the striking physiological difference between workers and queens in the social insects, or between males and females in most species It is not the *amount* of variation between individuals that determines whether they constitute different morphs, but the *organization* of this variation To sustain the claim that different personality types constitute discrete morphs, the traits must show, through the complex coordination of their parts, evidence of adaptive design

Are there discrete human personality morphs? This question is central to personality psychology and needs to be addressed at two levels, the phenotypic and the genetic

At the phenotypic level, human males and human females clearly qualify as different morphs, and the study of sex differences is the study

of their coordinated design differences Also, if one samples within-sex human design at sufficiently separated points during development, from zygote to embryo to puberty to senescence, age can provide another example of coordinated design change in humans Aside from these two dimensions, however, which manifest themselves in humans in dramatic physiological ways, there is no evidence for discrete, physiologically differentiated human morphs As discussed above, despite persistent folk beliefs, there is overwhelming genetic evidence that different ethnic groups are not discretely differentiated, and do not constitute "types " If any genuine kinds of human type exist in addition to age-sex categories, they are clearly far more modest than adult-child or male-female differences Since other physiologically recognizable "types" have not been found among humans, if there are any additional discrete types still to be discovered, they will be psychologically, rather than morphologically, differentiated types

Have personality psychologists, by finding organized systems of personality variation, found alternative adaptive strategies in humans? A related question is, are the heritable components of personality differences likely to be adaptations? Although the first question is difficult to answer with confidence at this time, below we develop standards of evidence for addressing it The answer to the second question, we will argue, will usually be "no," although some kinds of selection pressures may account for some such variation

The possibility that the various personality variables currently under investigation constitute alternative adaptive strategies is difficult to assess in the abstract Nevertheless, evolutionary principles provide standards of evidence that personality psychologists can use in exploring this question The first criterion is whether the personality trait under discussion represents a single quantitative variable, or whether an entire range of variables covaries in an organized, coordinated fashion If it is a single quantitative trait involving heritable variation, it is less likely to be an adaptive strategy, since most strategies require finely sculptured performances beyond the power of a single gene or an additive quantitative genetic system to specify The second criterion is, do the variables covary in a way that makes adaptive sense? If they do, this adds plausibility For example, does "large and strong" covary with "aggressive," and "small and weak" covary with "restrained"? Evidence of *special design* is the primary criterion for imputing adaptation It is not sufficient to show that a trait sometimes provides a benefit, one must show that its parts function together in a way that suggests that

they were specially designed to solve that adaptive problem efficiently (Williams, 1966)

Finding that two alternative strategies are heritable—that they are coded for by genes that differ from person to person—is *not* a criterion of adaptation From the point of view of natural selection it does not matter whether an alternative strategy is activated in an individual by a gene, an environmental cue, or a cognitive assessment of the situation All that matters is that the innate mechanism is designed such that the right alternative is activated under the right circumstances In the next section we argue that environmental cues or situational assessments are usually the best way to accomplish this, and therefore most alternative adaptive strategies will *not* show up as heritably determined Because alternative strategies can also be switched on or off by a single gene difference—a genetic "switch"—one cannot rule out the possibility that some alternative strategies may show adaptively patterned heritable variation We argue, however, that alternative, coordinated adaptive strategies cannot, in principle, be coded for by *suites* of genes that differ from person to person Our argument is based on a consideration of the structure of coordinated variation at the genetic level (And, of course, mutation pressure and selection for biochemical individuality are expected to inject some measure of nonadaptively patterned heritable variation into all systems)

One genetic architecture Multiple phenotypic designs Different species, of course, constitute different integrated designs at the phenotypic level This difference across species between integrated designs is caused by systematic coordinated genetic differences between species Different species are different designs because of different suites of genes The genetic and the phenotypic levels reflect each other Contrary to intuition, however, the coordinated variation between different morphs within a species does not reflect coordinated variation at the genetic level between morphs Different morphs do not owe their different designs to alternative underlying suites of genes present in some individuals and absent in others This is true even though, in an engineering sense, it would be an effective way to specify different designs The obvious way to create, for example, a female, would be to have all the genetic information necessary to specify the development of a female linked into a single unrecombining genetic unit, and have it transmitted only to females Nevertheless, this is not how genetic systems actually operate Alternative morphs within a species must be genetically "engineered"

in another manner, without recourse to alternative heritable genetic bases

This surprising fact derives from the evolutionary genetics of sexual recombination Sexual recombination efficiently and systematically tears apart linked genetic associations, and does so throughout the genome, so that genes do not form functionally organized superunits, for all practical purposes genes are eventually atomized, and they are thrown together in random, effectively unlinked permutations by the process of sexual reproduction Species are species by virtue of the fact that the individuals that compose them interbreed The result of this interbreeding is that genes circulate in continuously changing combinations over generations This means that genes that are in one kind of individual appear in subsequent generations in other kinds of individuals All of the genes in women have been, in previous generations, in both men and women All of the genes in men (with the exception of the Y chromosome, a genetic "switch", see below) have been in women and men All of the genes in infants have been in adults In social insects, all of the genes in workers have been in queens The differences between men and women, fetuses and adults, workers and queens, and so on, are not primarily genetic (in the sense that they have different genes) With the exception of genetic switches such as the Y chromosome, they have the same genes Different functional subsets of genes are activated and inactivated in different morphs, but are present in all individuals

Complex adaptations, such as organs, require a great deal of genetic specification—far more than could be provided for by any single gene Single genes are insufficient to specify all of the different regulatory steps necessary to build such complex systems Instead, complex adaptations are constructed by developmental programs, which in turn are regulated by genetic programs These genetic programs comprise hundreds or thousands of genes, operating within a fixed developmental background created by the rest of the genome (Gilbert, 1985) For example, human females have an enormously intricate system of interlocking tissues which allow reproduction The uterus, fallopian tubes, hormonal receptors in the preoptic area of the hypothalamus, a system of milk secretion, and so on, require the coordinated action of thousands of separate genes (Gilbert, 1985) Even organisms as simple as bacteria depend on coordinate gene expression in gene sets numbering more than 50 (Youngman et al , 1985) If all of the genes that acted to specify female organ systems existed only in females, and all of the genes that

acted to specify male organ systems existed only in males, what kind of offspring would they produce when they mated? Sexual reproduction randomly selects half of the genes from each parent and combines them to produce genetically different offspring Consequently, sexual reproduction would take some of the genes responsible for male organ systems and mix them with some of the genes responsible for female organ systems, to produce a series of children that were pathological because they were randomly intermediate individuals, each would have some of the traits necessary to be male, some necessary to be female, but without all of the necessary features to be either successfully Genes recombine in an uncoordinated way,[3] and complex design requires coordination among its functional parts

If there is a complex series of interdependent adaptations required to produce a sex, a behavioral strategy, or a personality type, there is only one way to insure the necessary coordination All of the parts of the genetic programs necessary to build the integrated design must be present when needed in every individual of a given type The only way that the 50 genes, or 100 genes, or 1,000 genes that may be required to assemble all of the features defining a given type can rely on each other's mutual presence is if they are all present in every individual If they are present in everyone, then they can be activated as alternative developmental programs

For this reason, different coordinated designs, psychological or physiological, cannot be the direct product of suites of genetic differences Different genetic programs (corresponding to subsets of genes) are activated in one morph or another, but are present in all individuals In short, the conclusion from evolutionary genetics is that different species have different designs because of different genes, but that within a species, different designs emerge from the same genes (excepting genetic "switches")

3 Though linkage may sometimes occur to a limited extent, as a general rule chromosomes and crossing over break linked genes apart, especially in long-lived organisms such as humans The developmental programs that specify complex adaptations require hundreds of genes, and there is no evidence that the linkage of, say, 100 functional genes into a single supergene has ever occurred in humans Processes such as inbreeding, selection, assortative mating, chance, and functionally interacting mutations occurring close together on the same chromosome all might bring together a very small number of functionally interacting genes into temporary linkage, but linkage between 20, 50, 100, or 1,000 functionally interacting genes is simply not observed—and not expected

What design? Genetic "switches" versus environmental cues If the genetic programs that regulate the development of alternative designs are universal, what determines which design an individual has? There are several methods of determination, of which the simplest are genetic "switches" and environmental cues Which is used depends on the specific system under discussion In humans, for example, sex determination is controlled by a genetic switch the presence or absence of a single gene, the H-Y antigen on the Y chromosome (for a review of sex-determining mechanisms, see Bull, 1983) It is important to realize that although this design difference, male or female, is triggered by a single gene, this gene does not contain the information necessary for building the alternative designs, it acts only as a switch, in a binary fashion, activating one of two extensive functionally integrated genetic subsystems, both of which are simultaneously present in all humans As an alternative system, in many vertebrates such as silverside fish and alligators, sex is determined via an environmental cue, usually temperature during incubation (Bull, 1983), rather than a genetic switch This cue acts as the switch that shunts development onto the male or female path, activating male or female genetic programs

In general, environmental cues or assessments are a better way of determining what morph to become A genetic switch determines an individual's future at conception, so that individual has one set of adaptations and not another regardless of how suited they might be to the local situation A far more effective system, in general, is to determine what to be as a response to what environment one finds oneself in, for example, be aggressive in those environments where one is victimized for passiveness and peaceful in those environments where one is penalized for aggressive behavior An individual can better tailor its morphology and behavior to its local environment by relying on environmental cues, or by assessing the relationship between itself and its environment For this reason, genetic personality determination, as an adaptation, is expected to be rare, although it cannot be ruled out

Determination of adaptive strategy by genetic switches seems to be favored only when the decision of what type to be must be made early in development, irreversibly, in order to develop physiological specializations during embryological differentiation In mammals, for example, sex determination takes place early, without environmental cuing, because physiological differentiation must take place early in development, prior to any reliable sampling of the environment The cost of using genetic switches is that the individual is subsequently

committed to pursuing that strategy, even if it finds itself in situations where that strategy is radically inappropriate It is possible that strategies that require extensive periods of learning might also require early and irreversible commitment, in a way that parallels commitment to embryological specialization Given the payoffs of making one's behavior appropriate to one's situation, however, one expects that alternative psychological specializations are chosen, whenever possible, through cues or assessments of one's situation This should prove true regardless of the amount of irreversible commitment required in pursuing a behavioral strategy The major requirement for the evolution of such a system is the existence of reliable cues that at present indicate (if strategies can be rapidly adopted or discarded) or reliably predict (if strategies must be prepared for) the kind of situation the individual faces Lacking reliable cues, genetic switches whose frequency in the population has been adjusted by recent selection remain the only alternative

Categories of genetic differences and their relationship to individual differences

The relationship between genetic differences and phenotypic differences turns out to be a surprising one Adaptively coordinated individual differences will not generally be coded for by extensive systems of genetic differences, but instead will be universal human potentialities, activated (perhaps irreversibly) by situational assessments, by environmental cues, or by the minimal genetic input of a genetic switch

On the other hand, uncoordinated phenotypic variation commonly will be created by randomly distributed genetic differences between individuals (By uncoordinated variation, we mean individual differences that do not covary in an adaptively coordinated way with the presence or absence of other individual differences) This variation breaks down into three components (*a*) differences that are adaptive (the smallest category), (*b*) differences that are maladaptive, and (*c*) differences that are effectively neutral (the largest category)

Adaptive differences Uncoordinated phenotypic variation can be adaptive when the phenotypic feature making it adaptive is simple enough to be specified by a single gene for example, lactose metabolization (selected for in milk-drinking cultures, McCracken, 1971), and the sickle cell gene (inhibiting malaria, Livingstone, 1958, Neel, 1949) Some adaptive variation is due to favorable mutations, which are in

the process of spreading through the population These are rare, yet do appear with regularity These generally consist of single-step additions to the genetic programs that underlie physiological and psychological mechanisms Given estimated rates of evolution, however, only a small fraction of existing genetic variation consists of favorable genes displacing unfavorable genes Additionally, frequency-dependent selection can give rise to stably maintained uncoordinated variation, where all of the alternative alleles are fit (Lewontin, 1974) Hamilton (1987) has argued that the diversity of niches in human social life may select for genetic diversity in psychological traits, a process that invokes frequency-dependent selection Finally, local ecological, cultural, and social circumstances, if they persist long enough, may select for genes that are locally adaptive but not generally adaptive (e g , the genes for lactose metabolism and malaria inhibition cited above) It is unlikely that local optima for metabolic rate, or mean arousal, or threshold for anger are everywhere exactly the same, and so selectively driven quantitative deviations between populations are a possibility (although such processes are very slow, require conditions that are stable for long periods, and depend upon relative genetic isolation) Given the wealth of genetic polymorphism, which injects minor amplifications, inhibitions, and modifications throughout our psychological and physiological mechanisms, it would be surprising if there were not at least some local adaptations and frequency-dependent adaptations As we have argued, however, the major constraint on the emergence of genetic differences as adaptations arises from recombination Adaptations require that all their parts be present, and so cannot be coded for by a series of genes at different loci that are present in some individuals in the population and not in others The destructive power of recombination is proportional to the number of different loci involved An adaptation wholly coded for by a single gene can survive this filter without any problem, single genes that quantitatively modulate mechanisms or processes can as well, and, in addition, may collectively add up into systems of quantitative genetic variation As a result, arguments that genetic differences are adaptations depend on the proposed adaptation being coded for on a single gene (or at most a few genes), or being a quantitative modifier of an existing process Complex adaptations resting on genetic diversity cannot survive the destructive filter of recombination, and so cannot be a significant factor explaining human genetic diversity

Maladaptive differences Much uncoordinated phenotypic variation is maladaptive minor modifications that degrade the performance of an

integrated functional design (e g , flat feet, malocclusion, astigmatism, dyslexia), or modifications so major that the integrity of the entire system is disrupted (e g , phenylketonuria, Penrose, 1952) These deleterious alleles, which appear through mutation pressure and are on their way to being eliminated, are present in every individual (Cavalli-Sforza & Bodmer, 1971, Nei, 1987)

Neutral differences Finally, a huge reservoir of genetic variability exists that creates psychological differences that are expected to be neutral, on balance, neither consistently adaptive nor consistently maladaptive This will be either because the genetic differences have no selectively important phenotypic consequences (Kimura, 1983), or because pathogens select for allelic diversity (Clarke, 1976, 1979, Rice, 1983, Tooby, 1982), which carries along as an incidental concomitant psychological variation Pathogens select for protein diversity, introducing the maximum tolerable quantitative variation and noise into the human system The less a psychological or physiological characteristic is under intense natural selection, the more variation can be tolerated as a way of defeating pathogens Where design constraints are relaxed, variation will differentially accumulate Consequently, one expects to find that heritable diversity is inversely proportional to adaptive importance

Therefore, each human of a given sex and age should be, in *overall potential functional architecture*, nearly the same as every other individual of the same sex and age, with variation generally confined to generally nonadaptive random fluctuations around this monomorphic design, or in those parts of the functional architecture that have been developmentally activated Below the level of functional architecture, however, there is a sea of uncoordinated protein variation Given the intricate design complexity of the nervous system (as well as of other organ systems), this protein variation gives rise to a wealth of quantitative variation in nearly every manifest feature of the psyche Tastes, reflexes, perceptual abilities, talents, deficits, thresholds of activation, motor skills, verbal skills, activity level, abilities to remember different kinds of things, and so on—all vary from individual to individual in a quantitative way (see, e g , Kalmus, 1967, McKusick, 1971) The nearest comparison might be to imagine what would happen if everyone were initially identical, but had 10,000 microscopic lesions, as well as a few larger lesions, placed randomly in each brain The microscopic lesions correspond to the sea of genetic diversity that causes subtle individual differences, the larger lesions correspond to the disruptive mutations or combinations that regularly crop up, that push the system

outside of the envelope of quantitative variation and into occasional violations of adaptive design

The differential activation of mental organs creates adaptively coordinated personality traits

The differential activation of mental organs can give rise to personality traits that are *adaptively coordinated* To see how this can happen, we will consider a concrete example a mental organ that evolved to solve the adaptive problems posed by sexual infidelity We will treat such a mental organ as hypothetical, although we believe work done by Symons (1979), Daly and Wilson and colleagues (Daly & Wilson, 1988, Daly et al , 1982), and Buss (1988) have provided strong evidence that such a mental organ exists

Males and females tend to suffer fitness costs (though in somewhat different ways) if their sexual partners engage in relations outside the established (or hoped for) relationship It would therefore be reasonable to expect the human mind to contain a mental organ designed to increase fitness by producing behaviors that encourage fidelity, penalize "cheating," and interfere with sexual competitors Suppose then, that the human mind contains a mental organ specialized for seeking out and processing information about potential infidelity When activated, this mental organ produces the coordinated set of thought patterns, behavior patterns, physiological responses, and phenomenal feelings that we would recognize as "sexual jealousy"

Evolutionary analyses tell us that this mental organ should differ somewhat between males and females, because their reproductive strategies differ (Daly et al , 1982, Symons, 1979) Whether one has the male or female form of this mental organ is determined by the same genetic switch that determines one's sex the H-Y antigen

If one constructs a personality scale that probes adaptively relevant questions about sexual jealousy, one would therefore expect to find two discrete, functionally coordinated adaptive personality types one for males and one for females These two "personality morphs" should share many common features, because the adaptive problems they evolved to solve are similar But because infidelity poses somewhat different problems for males and females, there will also be qualitative differences between the cognitive programs that compose each morph These qualitative differences should lead to quantitative differences on many of the dimensions assessed in the personality scale For example,

catching a partner either kissing or giving expensive gifts to a sexual competitor should make both men and women very jealous, but the kissing may bother men more and the gifts may bother women more Jealous men might be more likely than jealous women to compete for their lover's attention by making it known that they have received a job promotion, whereas women might be more likely than men to compete by enhancing their physical attractiveness (Buss, 1988) Nevertheless, the fact that one finds quantitative differences on any single dimension does not mean that the differences between men and women will be merely quantitative The various dimensions should cluster into distinctive configurations that show the coordinated adaptive patterning predicted by evolutionary theory Thus, when comparing the male and female morphs of the mental organ governing sexual jealousy, one expects to find differences in kind, and not just of degree

All normal men will have the male morph of this mental organ, and all normal women will have the female morph The probability that any given individual will lack this mental organ entirely is very low—comparable to the probability that one might lack any other organ, such as a pancreas or a spleen Thus, this mental organ will exist latently in every individual This does not mean, however, that every individual will have experienced sexual jealousy An individual whose mental organ has never been activated will have never experienced sexual jealousy

The mental organ contains specialized situation-recognition procedures, which seek out and evaluate evidence suggesting infidelity Situational cues indicating that an infidelity is likely to take place will set these detectors off, strongly activating the mental organ When it is activated, the person will experience an episode of sexual jealousy

Insofar as they are transitory, however, these situationally evoked episodes of sexual jealousy fall outside the realm of trait psychology They are "states," not "traits " Can a universal, situationally activated mental organ lead to stable, within-sex, individual differences?

Enduring individual differences are the focus of trait psychology Many psychological mechanisms, however, are only temporarily activated to deal with passing situations Most psychological phenomena will be of this kind The psyche is there to produce behavior that is responsive to the environment, and so sensitivity to environmental change is a ubiquitous feature of psychological adaptation The idea that there could be individual differences that remain stable, despite changes in one's situation, superficially conflicts with the idea that adaptive behavior should be governed by the demands of the situation one is in But

universal mental organs can give rise to enduring individual differences when conditions that differentially activate or modulate them endure, or when the activation of a mental organ is irrevocable This process can give rise to adaptively coordinated differences between individuals of the same sex For example

1 *Enduring situations may stably activate a mental organ, creating adaptively patterned stable individual differences* To address adaptive problems functionally, in most cases mental organs should remain activated as long as the activating situation endures, and some situations may endure for months, years, or a lifetime For example, the sexual jealousy mental organ of a woman who knows her husband is having an affair should remain activated at least as long as the affair lasts Stable individual differences are expected between those women whose mates are faithful (or believed to be so) and those whose mates are not

2 *An enduring individual-environment relationship may calibrate a mental organ's threshold of activation* Individual circumstances that are stable may, instead of activating mental organs, recalibrate them Thus, adaptively patterned stable individual differences may be found in the relationship between individual circumstances and thresholds of activation People carry with them, from situation to situation, the knowledge that they have a large family to call on for help (or not), that they are more or less attractive than average, that they can defend themselves against most violent threats if made, and so on What it is adaptive to do and to be depends on one's prior traits, one's personal situation, what environment one is in, and what environment or situation one is likely to experience in the future It is therefore reasonable to expect that a mental organ will be designed to assess those enduring individual-environment relationships that are adaptively relevant, and calibrate the threshold and strength of activation of its various processes accordingly

Imagine, for example, a man whose attractiveness on the "marriage market" is lower than his wife's This enduring personal situation may lower his sexual jealousy mental organ's threshold of activation, so that his mental organ will be activated with less confirmatory data than others require Consequently, he will become jealous more easily, and therefore more often, than other men His jealousy may even appear situationally inappropriate or "irrational," in the sense that his wife is faithful, devoted, and attempts to reassure him Nevertheless, hundreds of thousands of parallel ancestral situations will select for a mental organ that is responsive to the *average outcome* of such situations, and his mental organ may handle different cues separately Emotional re-

assurance from his wife may not suppress the effects of the separately processed conclusion that she is more desirable as a mate than he is If, over thousands of generations, reassurances from one's spouse did not reliably predict his or her long-term fidelity, but an inequality in desirability was reliably associated with an increased risk of infidelity, then natural selection would have designed a mechanism that responds to inequality in desirability, and not to reassurances Although in any individual case, a lowered threshold may lead to disastrously maladaptive consequences (e g , Othello), the fit between the cue and the direction of calibration indicates adaptive patterning Being jealous under these circumstances may be "realistic," in the sense of having led to adaptive outcomes *on average* in ancestral environments

Such differences in thresholds or strength of activation should show up as adaptively coordinated relationships among personality variables, between personality variables and socioeconomic status (SES), or even between personality variables and physical characteristics For example, a man's self-esteem may be, in part, a function of his desirability in the marriage market And, according to evolutionary theory, his desirability in the marriage market should rise and fall with his ability to provide economically for a woman Thus, a formerly secure husband who has lost his job might suffer a loss in self-esteem, which would recalibrate the threshold and strength of activation of his "sexual jealousy" mental organ by the process described above This might then dispose him to become more violent toward his wife Such a process would create a structured relationship between personality variables and SES A high score on a personality scale that assesses sexual jealousy will be correlated with a low score on one that assesses self-esteem, and both will be correlated with low SES Similarly, his desirability on the marriage market may also be a function of his physical attractiveness If so, then the calibration process will create a relationship between a personality variable and a physical variable A low sexual jealousy score will be correlated with high physical attractiveness (In the section on "Reactive Heritability," we will show how this process can lead to the apparent heritability of mental organs)

A full inventory of what enduring conditions are evolutionarily relevant to a given adaptive problem may provide a principled way of analyzing person-situation interactions As psychologists are well aware, enduring conditions for an individual (relative attractiveness, participation in a solid romantic relationship, and so on) will be "brought" by that individual to an experimental situation, and will play a crucial

role in how mental organs relevant to those conditions are activated in an experimental situation Models of the differential activation of mental organs by enduring conditions may prove to be useful tools in understanding person-situation interactions, and may be a good way to conceptualize "dispositions "

3 *Early environmental cues may calibrate mental organs irrevocably* Local variation in ecological, cultural, and demographic conditions in the Pleistocene may have meant that individuals faced discriminably different social worlds in their small hunter-gatherer bands Although most members of modern industrial nation states face similar encompassing social worlds, prestate societies varied (and vary) widely For example, an infant born into a Yanomamo village can expect to be involved in violent conflict and small-scale warfare for most of his or her life, and will marry polygynously when grown But an infant born into a !Kung San band can look forward to a relatively peaceful life and a monogamous marriage

Evolved psychological mechanisms will monitor cues that have proven reliable over evolutionary time in predicting the nature of the social and physical environment, and early environmental cues may provide a best estimate of the kind of social world the child will be maturing into Such cues may be used to calibrate the strength or threshold of activation of mental organs For example, the social behavior of family members is one's first sample of the social world, and as such, supplies valuable cues Violent treatment in childhood increases the likelihood that a person has been born into a social environment where violence is an important avenue of social instrumentality Therefore, the threshold or strength of activation of one's mental organs must be adjusted so that one is prepared to act in and cope with such a world The observation that abused children are disproportionately aggressive as adults may be accounted for by a mechanism of this kind (Garbarino, 1986, Lewis, Pincus, & Glaser, 1979, Loeber, Weissman, & Reid, 1983, McCord, 1979, 1983, Tarter, Hegedus, Winsten, & Alterman, 1984)

Instead of calibrating mental organs, early cues may be used to differentially activate alternative, mutually exclusive, coordinated adaptive strategies For example, Draper and Harpending (1982, 1987) have argued that the presence or absence of a father in the life of a young girl is an evolutionarily reliable cue to the type of sexual relations—polygynous or monogamous—common in the society she has been born into From studies of African societies, they argue that this cue

shunts the girl's socioemotional development into a coordinated adaptive strategy that is appropriate to her society An absent father indicates a polygynous society, and activates a coordinated adaptive strategy of early sexuality, promiscuity, high fertility, and low levels of parental investment per child, a present father indicates a monogamous society, and activates an adaptive strategy of later and more selective sexuality, lower fertility, and high levels of parental investment per child

Early environmental cues may affect development in an irrevocable manner, leading to stable, life-long individual differences in personality Irrevocable changes are to be expected for those domains where extensive training or developmental specializations are required, or when the cue signals a condition that, during the Pleistocene, would have remained invariant throughout an individual's lifetime Alternatively, early cues can shunt development along a path that is self-perpetuating, either through the reactions it evokes in others, or through the types of environments it causes the individual to choose (see discussions of active genotype-environment relations described by Plomin et al , 1977, and Scarr and McCartney, 1983) Either way, they can cause lasting, adaptively coordinated individual differences

4 *Are different personality types frequency-dependent adaptive strategies?* The Snowshoe hare changes color with the seasons, from gray-brown in summer to pure white in winter, allowing it to evade predation by blending with its background environment An individual Snowshoe hare is better off making this seasonal color change, no matter how many of its conspecifics make the same change In other words, the fitness of being one color versus the other is *frequency-independent* In some cases, however, the fitness of two alternative morphs is *frequency-dependent* The rarer the morph is in the population, the more fit it is Imagine, for example, a species of moth that can be either brown or green, with brown being the more common color Imagine further that the birds that prey on this species of moth form a search image of the most common moth color This means that the rarer, green-colored moths will be less frequently detected and eaten Consequently, the green moths will become more frequent in the population, while the brown ones, which are being picked off and eaten, are becoming less frequent This process will continue until the previously rare color becomes more common, and the predator's search image flips to green moths, reversing the selection pressure The result Brown and green moths will coexist in a stable equilibrium

The possibility of frequency-dependent selection leading to stable

equilibria between morphs raises the following question for personality psychologists Do different personality types or "positions" on dimensional traits constitute different, adaptively patterned behavioral morphs that are being maintained at equilibrium levels by natural selection in the human population?

To demonstrate that this is the case, one must first show that the traits in question constitute alternative adaptive strategies that they meet the two criteria set forth earlier (see "*Are there discrete human personality morphs?*") One must then determine whether their fitness is frequency-independent or frequency-dependent This means that a third criterion must be met One must show that the traits fit into a stable frequency-dependent analysis, that is, that the adaptive payoff of a strategy decreases with its increasing frequency in a population This requires game theoretic modeling of population dynamics (Maynard Smith, 1982) To pick an economic analogy, rather than one involving personality traits, situations involving a division of labor provide many opportunities for increasing advantage to rarer careers If everyone else in the social system is a farmer, then becoming a baker may be more profitable than becoming a farmer

Let us say that Extraversion and Introversion (Eysenck, 1973) have been shown to be alternative adaptive strategies To show that their distribution in the population is frequency-dependent, one would have to show that the fitness of these two strategies is frequency-dependent Do the advantages of being an extravert (if any) depend on how many other extraverts are around? Given that human social relations are complex and subtle, and often involve coalitional cooperation, one might find an argument to justify such a claim One could imagine that impulsive individuals might need a certain number of prudent people around to save them from their folly, while prudent individuals might need the enthusiasm of the impulsive to push them into risky but rewarding endeavors We would caution, however, that meeting this third criterion requires more than such vague speculation One would need to show that extraverts and introverts do, in fact, affect each other in these ways, that this would lead to a stable equilibrium between extraverts and introverts under a realistic set of social-ecological conditions, and that this stable equilibrium matches the proportion of extraverts and introverts actually found in the population At our present state of knowledge, these are difficult requirements to meet If all three criteria are met, then one has established a prima facie case for the existence of a system of frequency-dependent adaptive strategies To date, however, we

know of no personality traits that have been shown to meet all three standards of evidence

Nonadaptive stable individual differences

Although the functional architecture of a mental organ may be uniform from person to person, quantitative features in that architecture will tend to vary as a result of mutation or pathogen-driven selection for biochemical diversity Nonadaptive, random fluctuations in the monomorphic design of a mental organ can give rise to heritable individual differences in nearly every manifest feature of human psychology Obviously, this quantitative variation can lead to stable individual differences in simple, single-variable attributes, such as phoneme articulation, intensity of a specific reflex, or the ability to taste a chemical It can also lead to stable individual differences in the adaptively patterned output of a complex psychological program

Latent psychological programs are activated through exposure to cues that have proven evolutionarily reliable The co-occurrence of other people expressing fear in the presence of snakes indicates the possibility of a venomous bite, and provides cues for the activation of a snake phobia (Seligman, 1971, Seligman & Hager, 1972) Researchers studying identical twins have found evidence for such heritable variation in fears and phobias (Rose & Ditto, 1983) But random variation in quantitative features of that program can give rise to individual differences in the required strength, number, or lack of ambiguity of the diagnostic cues that must be present before the latent program is activated Such differences would affect the program's threshold of activation Similarly, there can be random quantitative variation in how strongly a program is activated, or in how long its activation endures This variation can also lead to certain kinds of psychopathology, such as those due to the activation of mechanisms under inappropriate circumstances or in inappropriate intensities For example, the sexual jealousy mental organ is so easily and strongly activated in some individuals that they display morbid, obsessive jealousy (Shepard, 1961)

Variation in quantitative factors can create the spurious appearance that some people have a mechanism that others lack Exposed to identical conditions, one person may develop a snake phobia while another does not, simply because there is quantitative variation between individuals in the threshold of activation of the human universal snake phobia mechanism Described in terms of manifest expression, some

individuals will have the trait "afraid of snakes," while others will not, described in terms of innate mental organs, however, all individuals will have the snake phobia mechanism, which through differential experience or heritable differences in threshold will be activated in some individuals and not others

Under what circumstances should we expect to find these kinds of random, nonadaptive individual differences? Variation tends to occur wherever uniformity is not imposed by selection, and selection acts to impose its organizing influence in proportion to how significantly a feature impacts fitness People display more diversity in their preferences for hat color or in their beliefs about gods and spirits than in their desire to continue breathing, their attraction to sex, or their desire to avoid pain (Sperber, 1984) Consequently, the more irrelevant a dimension of human psychology is to Pleistocene adaptation, the more likely that dimension is to accumulate and manifest individual differences For this reason, many categories of individual differences may show no adaptive patterning whatsoever

Reactive heritability Adaptive responses to one's genetic endowment

It is plausible to suppose that larger, stronger, defter, less fearful individuals will prevail more often in fights It seems equally plausible to suppose that size, strength, motor coordination, and physical courage vary across individuals, presumably as a result of genetic differences, environmental differences, and their interaction If, as seems likely, the human mind contains mechanisms that regulate behavior according to the rule "Be aggressive when aggression is likely to be a successful method for attaining goals," then larger, stronger, more coordinated individuals will resort to aggression or aggressive intimidation more often than individuals who are smaller, weaker, and less coordinated Such a psychological mechanism may be absolutely invariant, showing no variation in its structure attributable to genetic differences, and yet its individual output, the trait "aggressiveness," may show considerable heritability, because the variables that the psychological mechanism assesses include individual traits that show heritable differences

Evolutionary biology leads to the expectation that adaptively designed psychological mechanisms will generally be monomorphic in structure The expression of such uniform mechanisms will show heritable differences, however, whenever there are heritable differences in the variables that these psychological mechanisms assess A reaction to

a heritable difference gives "reactive heritability" to the performance of a mechanism that itself has zero heritability. Such variation is an adaptive response to differential input (in this case genetically influenced input), rather than noise in the system. Selection operates through the achievement of adaptive goal states, and any feature of the world—either of the environment, or of one's own individual characteristics—that influences the achievement of the relevant goal state may be assessed by an adaptively designed system. Assessment processes could explain the relationship between temperament and body type, if it exists (Hendry & Gillies, 1978; Sheldon, 1940, 1942). For example, it is reasonable to expect that "muscular physique" is a factor that would be assessed by a mechanism that embodies the strategy "Be aggressive when aggression is likely to be a successful means of attaining your goal," which may explain why juvenile delinquents are disproportionately mesomorphic (Glueck & Glueck, 1956, 60% are mesomorphic, whereas fewer than 5% are ectomorphic). Because psychological mechanisms assess individual traits in regulating behavior, tracking heritable variation in psychological traits back to its "source" may prove difficult. "Aggressiveness" (i.e., differences in the tendency to activate the psychological mechanisms governing aggression) may be heritable because there are heritable differences in the psychological mechanisms, or in some variable the mechanisms assess.

One fruitful source of personality research is attempting to identify important variables that psychological mechanisms can be expected to adaptively assess. Functional analyses derived from evolutionary framings of adaptation allow a straightforward identification of many such variables: sexual attractiveness, health, age, gender, whether one is in an established spousal relationship, whether one has children, whether one lives in an environment that threatens one with violence, control over socially desired resources or "wealth," aggressive formidability, amount of familial or social support, social status, and so on. Honing in on personality characteristics and personal situations which, for practical reasons, must be functionally accommodated, gives a rationale in personality psychology for treating some traits and variables as causally prior to others. Some variables may be assessed for only limited purposes, but others may be important and may be assessed by a multitude of different psychological mechanisms. Where this is the case, coordination among personality traits will emerge as the result of their all being partially determined in response to assessment of the same input variable. Being male, large, and muscular may have a large number of

systematic consequences on one's personality Physical action may be more attractive, in small group situations, people may be more attentive, women may treat such men differentially, other males of the same age and approximate status may be more threatened, or more interested in recruiting such men as coalition members, and so on

CONCLUSION

Human psychological characteristics appear in three forms (*a*) universal functional design, (*b*) unstructured variation, and (*c*) organized systems of covariation The mapping of universal functional architecture is clearly worth doing, and depends upon the evolutionary definition of adaptive problems (Buss, 1984, Cosmides & Tooby, 1987, Daly & Wilson, 1988, Symons, 1987) Below this level of functional uniformity exist psychological phenomena that show unstructured variation, much of it genetic in origin Such phenomena are worth studying for many reasons, including (*a*) as interesting phenomena that may be important for ordinary human purposes (e g , understanding drug action, intervention to prevent illness, psychopathology), (*b*) as natural experiments that assist in discovering the design or "natural joints" of mental organs and developmental mechanisms, and (*c*) as a selective environment that must be adapted to Such genetic differences may help to pinpoint, by the phenotypic differences they create, the outlines of functional mechanisms, in much the same way as the study of neurological lesions is informative

Structured systems of coordinated individual differences are a major focus of personality psychology (Cattell, 1957) In fact, one of the major findings of personality psychology is that there appear to be a restricted number of independent personality dimensions or superfactors (at least five) that constitute significant systems of covariation among personality traits (e g , McCrae & Costa, 1987) Covariation, if genuine, must be explained, and an evolutionary orientation suggests that there are three alternative ways such systems can be accounted for

1 *Condition-responsive adaptive strategies* Systems of covariation among personality traits may constitute adaptive responses by uniform, innate, psychological mechanisms to given individual characteristics and circumstances, processed as "input conditions " Assessments of the same input variables by multiple mechanisms will coordinate adaptive outputs To the extent such assessed input variables are shaped by heritable differences, such covarying systems of personality traits

may display "reactive heritability" This seems to be the most plausible explanation for adaptively covarying systems of personality traits An evolutionarily logical relationship among the traits (e g , strong with aggressive) is the hallmark of condition-responsive adaptive strategies

2 *Frequency-dependent adaptive strategies* Covariant systems may constitute alternative frequency-dependent behavioral strategies, a construct in personality psychology that would correspond to evolutionarily stable polymorphic strategies in evolutionary biology If a frequency-dependent strategy requires systematic modifications in many different mechanisms at once to implement or facilitate the strategy, such a result could show up on personality measures (e g , hawk, dove) Because of the requirement for functional organization among the psychological mechanisms, heritability should play only a small role in the creation of such systems, for example as a system of simple genetic switches, or as an initial biasing factor that makes the choice of one developmental path more likely than another A better design would be to use a system of environmental cues, designed to detect local rarity or "undersubscription" of the strategy (and one's own ability to pursue the strategy successfully) Adaptive coordination among the component traits should be apparent in such situations

3 *Nonadaptive developmental amplification* Covariation may be the result of the impact of the same neurophysiological peculiarity on different mental organs Psychological mechanisms are implemented neurologically, and different mechanisms may share neurophysiological resources or respond to the same trigger Anything that influences some aspect of a widely distributed neurophysiological process may create covariation among the output of different psychological mechanisms For example, endorphins participate in many kinds of psychological processes A mutation in receptor or endorphin structure may have very widespread effects Moreover, these systems of covariation may even appear to have an adaptive logic, because evolution has often shaped neurological mechanisms so that those that are usually functionally activated together are potentiated by the same chemical signal (e g , norepinephrine, serotonin, testosterone, Ellison, 1979) Modifications in the production of such chemical signals may lead to systems of covariation in which the components are related to each other in adaptively nonarbitrary ways that appear coordinated (e g , higher testosterone may be related to increase in muscle mass, faster metabolic rate, lower threshold of violence, greater suspiciousness, heightened competitiveness, etc) What will be lacking is an adaptive logic in a relationship between the environment and the individual differences

Heritable variation is expected to play a prominent role in such systems of personality variation It seems likely that much of what personality psychologists recognize as temporally and cross-situationally stable individual differences will be of this kind

Obviously, all three processes may interact to produce a patterned outcome

Few personality measures have been generated because the investigator was interested in discovering evolved adaptations So throughout, we have generated standards of evidence for assessing whether or not personality traits that have already been discovered are adaptively patterned Nevertheless, implicit in the evolutionary perspective we have been advocating is an alternative approach to personality psychology

An evolutionary approach would focus on the adaptive coordination of traits from the beginning First, one would identify what adaptive problems the human mind must be able to solve Then one would generate measures that reveal what kind of mechanisms we have for solving them, and whether these mechanisms assess other traits in determining what strategy to use Thus, the search for adaptive coordination would guide the process from beginning to end Buss's work on human mate preferences is a good example of this new approach to personality (Buss, 1987, 1989) He first asked what evolutionary theory predicted about sex differences in mate preferences and then constructed measures that could assess whether these sex differences truly exist He has found consistent differences in the strategies that men and women use in attracting members of the opposite sex (Buss, 1988), and if he finds individual differences within a sex in strategy adopted, he will be able to ask if these correlate with other individual differences in an adaptively patterned way It should be pointed out that this approach not only allows one to discover stable individual differences, it also provides a window into the structure of universal human nature

By proceeding in this way, adaptive problem by adaptive problem, one should be able to construct measures that will eventually reveal the organized structure of the human personality

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