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REVIEW ARTICLE

Psychopathology or Adaptation? Genetic and Evolutionary Perspectives on Individual Differences and Psychopathology

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Abstract A greater understanding of psychopathology will be found in the integration of genetic and evolutionary perspectives on adaptation and function. Evolutionary theory proposes that adaptive traits are reproduced more successfully than maladaptive ones. However, some traits, while contributing to fitness in the ancestral environment, may contribute to fitness no longer. This is known as mismatch theory. Evolutionarily informed research into various "pathologies" has yielded interesting results, some based on this theory. This paper serves to distinguish between genetic and evolutionary perspectives on psychopathology as well as to examine some recent research on the selective forces that may be implicated in psychopathy, anorexic behavior, and ADHD. We suggest that research into psychopathy in general would benefit from an evolutionary perspective and an examination of the assumptions behind past research.

Of all the facts of life, the most important is evolution. If psychology is to take its legitimate place among the family of life sciences, it must eventually integrate its basic theories and facts with those of evolution. If we are to understand abnormal behavior, we must do so in the context of a psychology so conceived and so formulated.

Rosenthal [1]

Introduction

This powerful statement, used by David Rosenthal to introduce one of the classic books on psychopathology and genetics, emphasizes the importance of the theory of evolution for understanding both normal and abnormal behavior. But after the introductory chapter, there is very little about evolution in his book. Important concepts such as fitness, stabilizing selection, preadaptation, or speciation appear neither in the glossary nor the index. The concept of adaptation, which Rosenthal [1] defines as "the adjustment of an organism or population to an environment", which is essential to understanding the role of natural selection in the shaping of anatomy, physiology, and behavior, is given only cursory treatment.

Genetic Theory and Abnormal Behavior is exactly what its title suggests it is – a book on genetics and human psychopathology. As such, it is an excellent book, but why did Rosenthal introduce it with a statement about Darwin's theory of evolution by natural selection if evolutionary theory was not to play an important part in it? He apparently assumed that since the science of genetics is concerned with the transmission of hereditary information from generation to generation, and that since the theory of evolution depends on the transmission of hereditary information from generation to generation, that therefore, the genetic and evolutionary perspectives on psychopathology are synonymous. Many psychologists, anthropologists, sociologists, and biologists seem to share this view. It is a view that is incorrect. Moreover, it is a view that has retarded the development of bio-cultural explanations of human psychopathology.

When evolutionary theory is applied to current human behavior, we are concerned, not with the processes of natural selection, but with adaptations, the products of natural selection. In this article, we will take a brief look at the genetic perspective, followed by a review of the evolutionary approach and some current evolutionarily informed research on psychopathology. Our focus is on how evolutionary theory can be used to understand how the products of evolution function in the current environment. Readers desiring additional reading on evolution by natural selection should consult extensive reviews, such as Williams [2], or Buss [3].

The Genetic Perspective

The science of genetics is concerned with how hereditary information encoded in DNA is transmitted from generation to generation, and how that information is involved in the development of the anatomy, physiology, and behavior of individuals. The search for the genetic components of a pathology usually begins with the search for a single locus or chromosome effects. The objective is: (1) to discover the mode of inheritance (dominant, recessive, sex-linked, etc.), (2) to describe the details of the metabolic pathway, (3) to explain its disruptive effect on physiological and anatomical development, and finally, (4) to show how the abnormalities of development affect behavior. Using precisely controlled breeding experiments on non-human animals, geneticists have done a magnificent job of elucidating the principles of the hereditary transmission of information. Progress has been much slower with humans because experimental crosses cannot be performed, environmental control cannot be imposed, the generation interval is relatively long, and the number of offspring per family is small [4]. When Mendel's laws don't work, geneticists may postulate gene-environment interactions or the actions of genes at multiple loci.

The Evolutionary Perspective

Evolutionary theory is concerned with the evolution of species-typical traits, traits that are shared by all members of a species. It thus seems that evolutionary theory may have little practical value in explaining how or why different types of behavior occur. But an explication of the concept of adaptation reveals how the theory of evolution by natural selection can provide some powerful concepts for understanding the role of the environment in producing individual differences in general, and in normal and abnormal behavior in particular.

Biological adaptations that enabled our relatively recent ancestors to deal with their environment must now help us deal with an environment that may differ in many ways from the Pleistocene environment where *Homo Sapiens*' adaptations were shaped. In most cases, these adaptations are adequate. If they were not, our species would be extinct. In some cases, however, their operation may result in behaviors that are maladaptive or even pathological when viewed in the present context. In other words, there may be mismatch between adaptations and their environments.

It must be emphasized that it is not necessary to assume that a behavior is currently adaptive in order to use the theory of evolution by natural selection to help understand it. However, if the theory of evolution is to be used in developing explanations of human behavior, then it must be assumed that adaptations that evolved in prehistoric times can still affect our behavior in some way [5].

Adaptation and natural selection are the central ideas of evolutionary theory. An adaptation is any anatomical structure, physiological process, or behavior pattern that contributed to an ancestral individual's ability to survive and reproduce in competition with other members of its species [6]. The teeth of lions, the hooves of horses, the hands of humans, the cub killing behavior of male lions [7], and love in humans [3] provide examples of adaptations that evolved through natural selection.

Behavioral Adaptation

The mating behavior of male scorpionflies (Figure 1) provides a very instructive example of a behavioral adaptation. Males have three strategies for acquiring a mate [8]. A male may find a dead insect, present it to a female and copulate with her while she eats it. If he

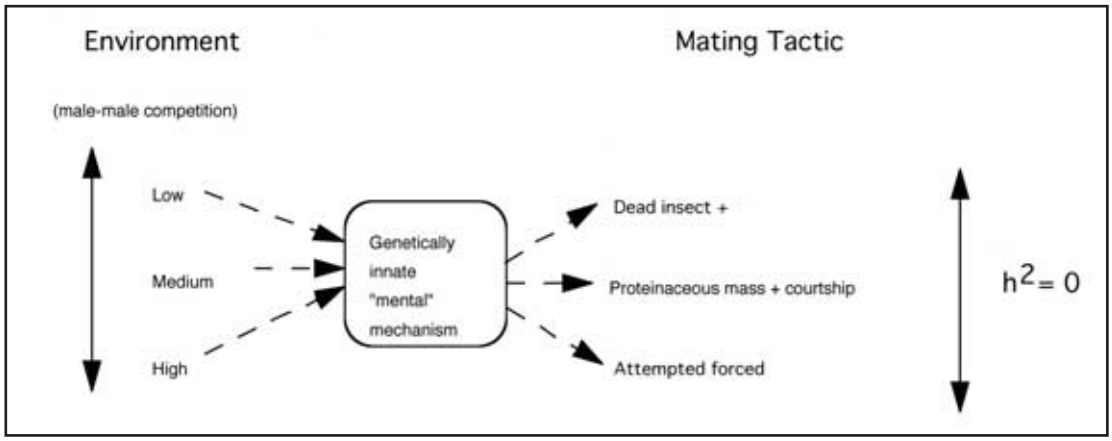

Figure 1: Mating tactics in scorpionflies (*Panorpa sp.*). The level of male-male competition determines the reproductive tactic used. Heritability of the tactics is zero because all males have alleles for all tactics. From "The Theory of Evolution: Of What Value to Psychology?" by C.B. Crawford, 1989. Copyright © 1989 by the American Psychological Association. Adapted with permission.

cannot obtain a dead insect, he may produce a proteinacious mass and feed it to the female and copulate with her as she eats it. Males who cannot obtain an insect or produce the proteinacious mass attempt to copulate forcibly with females. Males also possess an organ that assists them in forcible copulation, helping to restrain an unwilling female. It is not necessary when females are willing.

Thornhill [8] has shown that the strategy employed depends on a male's success in male-male competition. Even dominant males become vigorous forcible copulators if their resources are restricted. The alternate mating tactics of the male scorpionflies are an example of concurrently contingent behavioral programs [9]. Species-typical genetic information, in conjunction with information from the current environment, determines which tactic from a limited repertoire of tactics is produced. In other words, the expression of mating tactics in scorpionflies is contingent on environmental conditions.

Adaptations as Sets of Decision Rules

From a scientific view, an adaptation can be described in terms of a set of decision rules that enabled an ancestral individual to deal with contingencies in its environment. These decision rules are assumed to be instantiated in the neural hardware [10] and can be conceptualized as managing the activities of the organism. But if the rules that are instantiated in the neural hardware were shaped by natural selection, then they can only be changed by natural selection. Since natural selection can only change the frequencies of alleles that code for proteins, we can not consider these rules as completely independent of the physiology in which they are instantiated.

Although most psychologists are willing to admit that physical features and processes may have been shaped by natural selection, they are often reluctant to admit that mental processes are the result of ancestral selection pressures. Although cognitive science and the computer model currently provide the paradigm that most psychologists employ in their work, the assumption of the tabula rasa, the general problem solver, remains dominant. However, this view is untenable if we assume that human beings evolved by natural selection [11, 12]. These authors argue that the theory of evolution requires that the human mind is a highly structured and organized organ that evolved to deal with Pleistocene environmental conditions. From an evolutionary perspective, the mind is a collection of specific mechanisms that each contribute to solving the problems facing it, in the same way that a collection of specific mechanisms is necessary to the digestive functioning of the stomach.

Possible Outcomes when Natural Selection Meets Genetic Variation

There are four possible outcomes from the interaction of natural selection with genetic variation. Imagine that there is an ancestral adaptation X in which there is genetic variation. Natural selection acts upon it. The two possible affects of selection are that a) variability in X is exhausted or b) variability in X is not exhausted. As a result, there are four possible remaining genetic influences on the development of X. If variability in X has been exhausted, development could be freed from genetic influences or genetic influences on development could remain. If variability in X is not exhausted, genetic variation remains and could affect X's functioning or genetic variation remains but it not related to X's functioning.

In general, natural selection acts to eliminate genetic variance. But if variability is exhausted, how likely is it that development is completely freed of genetic influences? This is the tabula rasa, or blank slate, view, and in many ways it is quite unsatisfactory. Imagine a tabula rasa creature living in a variable environment. There are many problems that it will face and solutions to these problems must be learned in order to survive and reproduce. Organisms whose brains make them somewhat prepared to learn something may survive better than those not prepared to learn these things. For example, eating rotten meat can lead to disease and death. It would be adaptive to learn very quickly

that meat with a certain smell or appearance should be avoided. Individuals who were predisposed to avoid certain smells or those that could easily learn to avoid them would have had a better chance of surviving.

It seems more likely that when variability is exhausted, genetic influences on behavior remain. Under such conditions, there would be zero heritability for a trait. This could also be referred to as the pure innate view, the trait will always be expressed. Examples might be that humans all have two eyes, or that scorpionsflies all have the same set of mating strategies, but express them variably depending on the environment they find themselves in. But in fact, empirical evidence suggests that some genetic variation almost always exists [4]. Which raises the question of why such variation exists if natural selections acts, in general, to eliminate it. Many have suggested that the answer is parasites. Or rather parasite protection [13].

Genetic Variation and Evolution

The science of genetics is concerned with how gene differences are involved in the production of phenotype differences. Without these heritable differences in fitness related traits, natural selection cannot shape or change adaptations. Thus, for an adaptation to come into existence, there must have been genetic variation with respect to that adaptation in the ancestral population in which it evolved. However, genetic variation need not remain once the adaptation has been formed. Tooby and Cosmides [10] have argued that genetic variation may, in fact, disrupt the functioning of an adaptation, and therefore, that genetic variation associated with an adaptation should be the exception rather than the rule. They argue that most genetic variation is not related to the adaptiveness of the organ that manifests it, but that it is the result of selection to vary the structure of the organ at the protein level to help the organism to avoid the attacks of parasites.

Consider the following problem. Suppose it was found that identical twins raised in markedly different environments differ as adults on a particular trait, such as extroversion-introversion. Can this finding be interpreted as meaning that genes are not acting on the development of the trait?

To provide an answer, consider the behavior of identical triplet male scorpionflies reared in three different environments. The first triplet is raised in an environment with many dominant males. Since he loses in male-male competition, he attempts to copulate forcibly with females. The second triplet is raised in an environment with moderate male-male competition. Although he is not successful enough to obtain a dead insect to use as a nuptial gift, he can obtain enough resources to generate the proteinacious mass to attract a willing female. The third triplet is reared in an environment populated by subordinate males. He obtains a dead insect and uses it in his courtship. If the heritability of male courtship behavior were computed, it would be zero because the scorpionflies are genetically identical triplets, and therefore all variation between their behaviors is environmental in origin. However, the behavior employed within each environment is determined genetically.

Although gene differences do not produce the differences in behavior, the genes that all scorpionflies possess, in conjunction with varying environmental conditions, determine the behavior that is expressed. The primary focus of the evolutionary perspective is on the genetic architecture that all members of a species possess that guides the development of the adaptations enabling them to interact successfully with their environment.

From an evolutionary perspective, the critical question is not whether the observed behavioral differences are associated with genetic differences, but whether they are correlated with reproductive success in the environment in which they are observed, or if the environment of the species has changed, the environment in which they evolved. An understanding of evolutionary ecology is leading us to a new kind of environmentalism: all individuals in a given species may have genes for a number of strategies, and the one used depends on the environmental conditions encountered [14]. Such a perspective focuses attention on traits: (1) that have zero or low heritability, (2) that were closely related to reproductive function in an ancestral environment, and (3) for which sensitivity to environmental conditions would have been adaptive in an ancestral population.

There are two reasons for the interest in traits with low or zero heritability. First, such traits are likely to have been important in the ancestral environment. If a trait was important in mediating survival, growth, and/or reproduction, it is likely that natural selection would have acted strongly on it, and thereby eliminated most of its additive genetic variance [15]. Second, by focusing on traits with minimal genetic variation, it is possible to get a clearer picture of how variations in these traits are involved in facilitating the organism's interactions with varying environmental conditions. Just as geneticists are interested in reducing the effects of environmental variation so that they can more clearly discern the rules governing the transmission of genetic information, those involved in the study of adaptation are interested in reducing the genetic differences between individuals so that they can more easily perceive how a putative adaptation enables its possessor to deal with varying environmental conditions. For example, Baker and Bellis [16] are unraveling the exquisite way that the human female manages sperm in response to a variety of contingencies.

The focus on traits closely related to reproductive function is because the costs of ancestral reproduction would have been very high, and naturally, natural selection is likely to have shaped adaptations for adjusting it to varying conditions in the environment. The focus on traits that were sensitive to variations in ancestral circumstances is because such traits are also likely to be sensitive to present environmental circumstances. They are therefore traits that can help us to understand how we deal with current environmental contingencies.

Finally, evolutionary psychologists are interested in innate behavioral mechanisms that produce differences in behavior as a function of differing environmental circumstances. Although genetic variation is essential for the evolution of adaptations, it is not essential to the functioning of the adaptation once the adaptation has been produced [10].

Psychopathology as Disease or Adaptation?

One can think of two views of psychopathology. According to one, psychopathology is due to non-adaptive errors, breakdowns, or malfunctions. According to the other, psychopathology may represent the activation of (previously) adaptive strategies. An evolutionary approach points out that, based on natural selection, traits are selected, not on the basis of arbitrary definitions of happiness, well-being, or social conformity, but by their effects on reproduction rates in subsequent generations. Evolutionary explanations and theories have been advanced for many "pathologies" including: mood disorders [17, 18], psychopathy [19, 20], and rape [21]. Nesse and Williams [22] note that diseases and disorders can be perpetuated by genes that have been retained by natural selection either because their effects were beneficial in ancestral environments (fondness for sweets and diabetes) or because the same genes that influence the disease have benefits in some other sphere (sickle-cell anemia and protection against malaria).

The decision rules discussed previously can be seen as the means by which goals are achieved. They are context dependent and entrained to the presence or absence of certain signals. Their flexibility and signal dependence helps individuals to avoid pursuing goals that cannot be obtained or would decrease fitness is pursued regardless of cost [23]. Not only are many sets of decision rules designed to be flexible, but this flexibility is subject to developmental influences. For example, adverse rearing experiences can significantly affect maturation and functioning [24, 25]. As children mature in certain environments, some behavioral strategies will become elaborated while others will be less developed into the individual's personality [26]. A child whose parents are unresponsive to distress may learn that others are unreliable and focus on self-reliance, while a boy who grows up in an environment surrounded by individuals with low life-expectancy may become a risk-prone individual, discounting his future.

Psychopathology and Developmental Instability

Gangestad, Yeo and colleagues [27] have explored the idea of a link between developmental instability and schizophrenia. They define developmental instability as the imprecise expression of a genetic plan for development due to the introduction of developmental noise and suggest that it contributes to individual variations in handedness, functional hemispheric asymmetries for cognitive tasks, and cortical asymmetries. Lalumiere and colleagues [20] have also used developmental instability in focusing on psychopaths.

Psychopaths are deceitful, selfish, manipulative, irresponsible, impulsive and aggressive individuals who have no concern for the welfare of others and experience little remorse or guilt as a result of their antisocial behavior [28]. Compared to other criminals, the crimes psychopaths commit are more goal-oriented and violent. Their behavior has an early onset in life and while they tend to exhibit less cerebral lateralization than nonpsychopaths, there is no evidence of lesions or brain damage [29]. This appears to be a trait in which genetic variation remains and affects development under certain conditions.

There are two views on the development of psychopthy. The first, psychopathy as psychopathology, sees it as a serious personality disorder, a brain-based pathology, or a virulent strain of conduct disorder, [30, 31]. According to this view, the development of psychopathic individuals has been disturbed so that they are unable to experience moral sentiments such as empathy or remorse, cannot appreciate the consequences of their actions and therefore cannot behave in prosocial ways.

The second view is one particularly informed by evolutionary psychology. It is psychopathy as special design [20]. This view is that psychopaths are different by design, not as a result of a deficit. Instead, the behavioral, emotional, cognitive and neuropsychological characteristics of psychopaths are seen as a set of organized, functional and specialized features that formed a viable reproductive social strategy during human evolutionary history. Harpending and Sobus [32] used game theory research to demonstrate that a cheater (nonreciprocator) could achieve reproductive success when: cheaters are difficult to detect, highly mobile, verbally skilled, and skilled at persuading females to mate. Quinsey, Harris, Rice and Cormier [33] have suggested that "psychopathy can be considered to be a life-history strategy consisting of short-term mating tactics, an aggressive and risky approach to achieving social dominance, and frequent use of nonreciprocating and duplicitous tactics in social exchange." These ideas suggest that the defining features of psychopaths are not pathological outcomes of impaired development but instead features of an adaptation designed to thrive in an interpersonal environment dominated by social cooperators.

Lalumiere *et al*. [20] used the concept of developmental instability to examine whether adult psychopathy is the result of pathological or non-pathological development. They looked for signs of developmental perturbations in non-psychopathic and psychopathic offenders and measured fluctuating asymmetry (random deviations from bilateral symmetry) or FA in psychopathic and non-psychopathic offenders as well as non-offenders. The psychopathic offenders showed less evidence of developmental instability than non-psychopathic offenders. Interestingly, the psychopathic offenders had higher FA than non-offenders except for offenders who met the highest psychopath criterion. Those psychopaths had the lowest FA measures of all.

Anorexic Behavior and Reproductive Suppression

Understanding the ultimate causation of a psychological phenomenon can enrich proximate hypotheses, suggesting whole new areas of related inquiry. For example, Polivy & Herman [34] present a model of the proximate causation of several eating disorders, which involves cognitive cues overriding the normal physiological cues of satiety and hunger. This is hypothesized to occur in response to strong societal pressure to be thin. It is an elegant model but leaves unanswered the following questions: 1) What is it about industrialization that encourages a thin standard of beauty? 2) Why do some girls progress to levels of emaciation far thinner than the accepted standard of beauty? 3) Why do we not see "pathologies" associated with other aspects of attractiveness (pathological drives for shiny thick hair, etc.) and 4) What environmental variables are likely to drive the passion for a thin form?

The reproductive suppression hypothesis (RSH) answers these questions. Industrialization is particularly problematic for the reproductive prospects of adolescent girls because it is associated with early menarche and a long period before marriage during which girls may receive attention from large numbers of young men without much adult supervision. Thus, sexual activity is difficult to avoid though pregnancy is very costly. Therefore, most girls experience a desire for thinness related unconsciously to the need to slow down their rate of sexual maturation. As well, individual girls in industrialized societies may experience menarche even earlier than their peers, or lack the social skills appropriate for their age, so that they experience the reproductive stresses even more strongly [35]. As for "pathologies" associated with other aspects of beauty, we do not see them because only fatness is directly linked to fertility.

Finally, the RSH [36, 37] enables us to make predictions about two types of environmental variables associated with the desire for thinness. First, environmental stressors that would have made reproductive suppression adaptive in an ancestral population are likely to be associated with the desire for thinness, such as high female competition or unwanted male attention. Second, any current environmental variable, such as a rich diet, that lengthens the period between sexual maturity and social, intellectual, and emotional maturity brings girls into situations in which they are likely to become pregnant without the adequate resources to raise a child. Unconscious perception of such a situation is also hypothesized to activate the reproductive suppression mechanisms and, hence, a desire for thinness. The mechanism itself has no genetic variation, but there is variation in susceptibility, due perhaps to a combination of genetic variation and environmental influences.

ADHD as a Disorder of Adaptation

Some mental disorders can be viewed as an adaptive response to early pathogenic environments (trauma or neglect) while others reflect the optimization of brain function to some (often early) environments at the cost of poorer response to the demands of other environments [38]. As a result, symptomatic descriptions, as in the DSM-IV, ignore the importance of adaptation in general and, in particular, disregard the shaping of human brains and behaviour by experience [39].

ADHD (attention-deficit/hyperactivity disorder) is characterized by three general symptoms: inattention, hyperactivity, and impulsivity. ADHD may reflect the effects of maternal smoke exposure in utero, brain injury, child abuse, or a combination of environmental experiences coupled with predisposing genes. But an evolutionary model of ADHD may be better able to explain discrepant findings in the literature, provide testable hypotheses, and clarify the relationship between health and disease.

What adaptive problems might these traits have been designed to solve in an ancestral environment?

Ancestral environments would have varied in several characteristics relevant to ADHD, including safe versus not safe, resource-rich versus impoverished, and time-optional versus time-critical [38]. At one extreme environment, human survival would have depended on being, hypervigilant, rapid-scanning, quick to pounce or flee, and motorically hyperactive (foraging, etc.), a response-ready individual. This type of individual would have been advantaged under the harsh conditions of the frozen steppe or humid jungle. However, not all environments would be that harsh, and as societies have become more industrialized and organized, the advantage has moved towards those who display problem-solving and analytic strategies, restraint of impulsivity, and the controlled deployment of energies, a problem-solving individual. Genetic variation in the trait remains in the population and affects the development of this behavior.

This has serious implications for our school system which provides an environment that favors the problem-solving child. Alterations in the environment may reduce the adaptive strain on a child's nervous system whose set point may be at the other extreme from the environment they find themselves in. Further study, including cross-species comparisons of the traits, is needed on the individual components of ADHD (attention, motor activity, and impulsivity) and how they may be beneficial in some settings while non-adaptive in others.

Conclusions

In many ways, it is difficult, and yet important, to integrate genetic and evolutionary perspectives. The genetic perspective focuses on a constant environment, examining genetic variation, as opposed to evolutionary psychology holding genes constant, looking at the impact of the environment. But both views are crucial to a complete understanding of psychopathology. One can see anorexic behavior as a single life history, all women possess the reproductive suppression mechanism but it is only activated in some women who encounter exaggerated ancestral cues and who may also have some type of personal susceptibility. ADHD and

psychopathy are examples of multiple life history strategies in which two genetic strains exist. In the case of ADHD this genetic variation has likely been maintained by different environments, though it is likely that the ADHD strain will decrease over time in our more "problem solving" modern world. On the other hand, the psychopathy life history may actually be increasing. In general, it is only a successful strategy when there are very few in the population, but in our highly mobile big city world, they have advantages they never would have had in small face-to-face populations. We hope that an evolutionary perspective will continue to shed more light on the ultimate causes of various psychopathologies and assist in their management.

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