Review article

Evolutionary biology: a basic science for psychiatry?

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Evolutionary biology has much to offer psychiatry. It distinguishes between ultimate and proximate explanations of behavior and addresses the functional significance of behavior. Subtheories, frequently voiced misconceptions, specific applications, testable hypotheses and limitations of evolutionary theory are reviewed. An evolutionary perspective is likely to improve understanding of psychopathology, refocus some clinical research, influence treatment and help integrate seemingly unrelated findings and theoretical explanations.

Key words: evolutionary biology; psychiatric theory; psychiatric research

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Introduction

Recent advances in evolutionary biology have implications for psychiatric theory, research and clinical practice. Evolutionary theory introduces a broad and much needed deductive framework; it facilitates the functional analysis of behavior; it identifies important differences between ultimate causes and proximate mechanisms; it promotes a reassessment of current views about etiology and pathogenesis; and it alters treatment strategies and options. Evolutionists acknowledge that much human behavior is a product of personal and cultural experience, but argue that mind and culture themselves are products of evolution and are better understood when analyzed within the evolutionary framework.

Our assessment of the contributions that an evolutionary point of view can make to psychiatry begins with an analysis of its theoretical contributions followed by a discussion of common misconceptions. Possible applications to psychiatry are then evaluated. Finally, the limitations of the theory are reviewed.

Only selected parts of evolutionary theory are discussed. More comprehensive discussion of the theory can be found in Williams (1), Wilson (2) and Alexander (3).

Overview of the evolutionary approach to psychiatry

Behavior

Consider behaviors such as acquiring a mate, sexual intercourse, having offspring, parent-offspring bonding, stranger anxiety, infant and juvenile play, sibling rivalry, competition over resources, preferential investment of resources in kin, reciprocal exchanges among nonkin, competition for social status, recognition and rejection of cheaters, deception of others and self-deception. Natural selection has shaped predispositions (strong biases) to engage in such behaviors. Predispositions range from strong (such as withdrawal from a painful stimulus) to weak (such as preference for particular styles of music).

The strengths of predispositions vary across individuals. Experience and learning, which is also an evolved capacity, modify predispositions. Environmental options and constraints interact with evolved and prioritized behavior strategies to affect the probability of immediate and long-term behavior. Psychological mechanisms (such as cognitive and psy-

chodynamic ones) filter, modify, organize and focus information that influences behavior. Behaviors to which most persons are not predisposed (such as playing the piano) can be mastered, but usually after considerable effort. Nonetheless, the general behavior profiles and patterns of human behavior are set by the species' genome and, within limits, unfold in predictable ways.

The above and other behaviors are of special interest to psychiatry for several reasons: 1) mental disorders are associated with detectable abnormalities in the expression of such behaviors, such as reduced frequency of reciprocation (4–6); 2) an adequate understanding of some mental disorders (such as phobias, depression and somatoform disorders) requires an appreciation of the functional significance of such behaviors and of the evolved mechanisms that regulate them (7, 8); and 3) treatment strategies may change (for example greater emphasis on functional outcomes and increased attention to environmental variables) with increasing appreciation of the evolutionary perspective.

Natural selection favors brain mechanisms that result in behaviors conferring a reproductive advantage. Generally, such behaviors are neither atypical nor pathological. With few exceptions, however, mental disorders are atypical, pathological and maladaptive. Evolutionary theory provides a framework for analyzing adaptive behavior, the mechanisms that regulate it and the circumstances interfering with its normal expression (9). Psychopathology can be illuminated by insights into its normal adaptive precursors. Most phobias, for example, are exaggerated normal fears (10, 11); minor adaptive rituals such as perfectionism are precursors for obsessive-compulsive disorder (10); normal mood swings can be viewed as precursors for manic-depressive illness (12); and normal sadness and social withdrawal may be precursors to clinical depression (13–15).

Subtheories

Since the early 1960s, a number of testable subtheories have been developed to explain specific behaviors. Examples include: inclusive fitness or kin selection, reciprocal altruism, parent-offspring conflict, and cognitive/feeling mechanisms.

Inclusive fitness. Preferential investment in kin is prominent in humans, as it is in other species. The tendency is to invest more in close than in distant kin, and for parents to invest more in offspring than vice versa. Hamilton (16) postulated that certain kin-related behavior is selected because it favors individuals who share genes. A behavior costly to the self may nevertheless evolve if it increases the survival and reproduction of kin who share the genes responsible for that predisposition. Kin-selection theory explains how altruistic behavior among kin facilitates the replication of genes shared by kin. The theory predicts, for example: that parents will invest more in their offspring than vice versa; that such investment is greater with higher parental assessment of the offspring's reproductive potential; and that stepchildren are more likely to be abused that biological offspring. These predictions are well supported by evidence (17–19).

Reciprocal altruism. Although kin selection explains investment in kin, unrelated individuals also help each other (20). Such reciprocity exchanges are not confined to humans. Vampire bats, for example, share their blood meals after returning to their roost at dawn (21). Such exchanges even occur between species (22); alarm calls by one species alert members of other species, and cleaner fish remove parasites from inside the mouths and gills of larger fish who protect cleaners from predation (23).

Reciprocal altruism theory predicts: 1) A will help B (nonkin) if, in A's view, the probability of reciprocation by B times the probable benefit of this reciprocation equals or exceeds the initial cost to A (reciprocal behavior is distinguished for mutualism, where both parties gain simultaneously); 2) failure to reciprocate evokes moralistic aggression; 3) nonreciprocation will rise at the end of a period of association (24); and 4) nonreciprocators will have fewer allies. These predictions are also supported by available evidence (25, 26).

Evolutionary theory also explains why such emotions as pride, happiness, guilt and moralistic anger and such behaviors as guilt induction, intimidation and social ostracism have evolved. They facilitate reciprocal relationships (20, 25, 27, 28). Much of development and learning deals with refining reciprocal behaviors, such as how to successfully manage reciprocity exchanges without being exploited or rejected – battles among children often focus on who owes what to whom (29). Deviations from expected patterns of early kin and non-kin social relationships may contribute to disordered reciprocity relationships later in life (30).

Parent-offspring conflict and sibling rivilary. Although cooperation between parents, offspring and siblings is promoted by the genes they share in common, conflicts can be explained by the fact that many of their genes are not shared (31). Parental fitness (the number of parental genes replicated among offspring) is enhanced by the reduction of investment in maturing offspring in order to sooner reproduce again. Existing offspring try to counter this reduction and maximize their own fitness by delaying the birth of new siblings and by extracting as much from par-

ents as they can. The tendency in many species for offspring to object to weaning supports this view. The conflict has a natural end-point when existing offspring's inclusive fitness is increased more by having a sibling with many shared genes than by continuing to try to extract more resources from parents (31).

Sibling rivalry has a parallel explanation and may arise in the same way. Siblings aid each other because they share genes, but simultaneously compete for parental resources.

Other conflicts. Similar evolutionary-based explanations account for male-female differences and aspects of marital relationships. Males, for example, are more promiscuous, take more physical risks, and engage in more antisocial behavior (2, 32, 33). Spousal relationships combine reciprocity, kin selection and the management of conflict between kin. Spouses' mutual dependence for their reproductive success leads to common interests and reduces conflict (34), while conflict results from pressures on the partner to provide more care for offspring (31), to raise offspring in specific ways, to help nongenetic relatives or to reciprocate help more completely.

Cognitive/feeling mechanisms. Specific mental capacities appear to have evolved to serve specific functions, such as the ability to spot cheaters (35–38). Similar points apply to assessing the value of different types of reciprocation, the reproductive potential of offspring and the adaptive value of different behaviors.

The cognitive, physiological and behavioral predispositions that characterize fear offer selective advantages in dangerous situations (10). Behavior that is phylogenetically predisposed is not necessarily inevitable, however. Indeed, it can, on occasion, be changed dramatically (10). For example, the fear of blood injury is strongly familial, develops in childhood and is characterized by a vasovagal response and syncope. Yet it can be permanently eliminated with a few hours of systematic exposure therapy. The same applies to strongly predisposed fears of snakes or other animals. (Similarly, even innate defensive responses in molluscs, mantids and birds can be eliminated by habituation analogous to exposure therapy.) The capacity for change is a built-in, selected trait that adjusts the behavioral preferences characteristic of the species.

A better understanding of such evolved mechanisms is likely to deepen our insights into psychopathology. For instance, stranger anxiety, separation anxiety and phobias of heights, animals, storms and leaving one's home range appear to be prepotent stimuli to which pre-prepared fear is readily connected (10). Over-responsiveness and/or rigidity of such mechanisms may help to explain some anxiety disorders. In other disorders, deficits in mechanisms for reciprocity negotiation seem probable. Such deficits may be a product of proximate mechanisms leading to social isolation and associated chronic depression.

An important aspect of evolved cognitive/feeling mechanisms is the distinction between symptoms and disorders. Some mental signs and symptoms, such as anxiety, sadness, irritability and withdrawal may be normal and adaptive when not severe. Like other aversive states, such as pain and nausea, they may point to circumstances liable to decrease individual fitness, but not necessarily be manifestations of disorders (7, 39). Interfering with their expression thus may be disadvantageous for the patient, just as blocking coughing or vomiting reflexes can be dangerous for patients with pulmonary or gastrointestinal infection. (Such behaviors are distinguishable from signs and symptoms that are more direct consequences of mental disorders, such as hiding from others because of persecutory delusions.)

The evolutionary arguments discussed thus far are reasonable, intuitively acceptable and supported by research findings in some respects. Several points relevant to psychiatry emerge. First, many behaviors are strongly predisposed, such as sibling rivalry, moralistic aggression and familial rejection of nonmaturing relatives. Second, some features of psychopathology reflect the prepotent and preparedness of responses. Third, features of disorders may reflect the normal operation of an adaptive response. Depression following the loss of a loved one or a decline in social status is not only expected from an evolutionary perspective (13), but also may be temporarily adaptive in evoking social support from kin and friends (40). Similarly, jealousy, anger, deception, self-deception and anxiety may be temporarily adaptive. Fourth, evolutionary interpretations are compatible with proximate mechanism explanations, such as postulated physiological changes associated with depressive disorders, inheritance of disorder vulnerability (pedigree studies) or compromised learning following aversive early experiences. Evolutionary theory offers existing psychiatric theories a context in which interrelationships between different findings and explanations emerge, and ultimate evolutionary and proximate mechanism explanations are clarified.

Misconceptions about evolutionary theory

Evolutionary theory applies mainly to other animals

This view appears to assume that evolutionary biology consists primarily of reconstructing a species' phylogeny. Evolutionists argue instead that even if humans had no close phylogenetic relatives, evolu-

tionary theory (or a similar theory) would be necessary to help explain human behavior. Mechanisms of adaptation operate primarily at the individual level and shape behavior accordingly (functional analysis). Viewing humans in an evolutionary context leads to predictions that fit many otherwise hard to explain facts (such as prepotency for many behaviors, step-parent abuse, sibling rivalry and parent-offspring conflict). Moreover, the theory leads to unexpected connections that are unlikely to be made without its guidance. Examples include: the possible adaptiveness of some antisocial behavior (such as cheating as an adaptive strategy) (41); abandonment of kin who are poor reproductive bets; child abuse by step-parents; male and female sexual jealousy and possessiveness (42); and agoraphobia as an extraterritorial fear associated with past threats when venturing outside the home range (10, 43, 44).

Any species-characteristic behavior has a distribution limited in width by natural selection. Individuals vary in capacities to empathize, reciprocate, develop new goal-achievement strategies, compete and maintain physiological and/or psychological homeostasis (45). Human variations in these behaviors may have led to successful adaptation in many different environments. Seeming facets of disorders, both symptoms and personality, may thus be consequences of a range of variation rather than manifestations of psychopathology. In evolutionary terms a trait can be regarded as biologically normal if it enhances adaptive capacities. Severe psychopathology nearly always reduces fitness (46). Compared to normal people, those with mental disorders help kin less and are less helped by kin; they more often fail to reciprocate help from nonkin and have fewer friends; and they have reduced resource access and control (McGuire, submitted).

Evolutionary theory provides psychiatry with some explanatory tools regarding individual differences: 1) a framework that specifies the range of adaptive species-characteristic behavior patterns against which the behavior of individuals can be compared; 2) a general theory and subtheories to interpret the adaptive significance of behavior; and 3) a framework to explain cross-person differences in attributes (trait distribution).

Evolutionary biology ignores individual learning

The human capacity to learn is vastly greater than that of other species. The view that evolutionary biology ignores individual learning seems to arise from the incorrect assumption that if something has been learned then it has no evolutionary roots. However, the capacity to learn has been selected, like every other trait (47). Each species, including *Homo sapiens*, learns certain things more easily than others. Evolutionists do no ask, "Is it learned or innate?", but rather, "How easily can this particular response be learned?". A child's readily learning to speak, for example, reflects built-in design features based on adaptive cognitive, sensory, and behavioral algorithms. Playing the piano, however, is difficult to learn – it has not been selected for.

Culture is an alternative to evolutionary explanations

It is a mistake to see biology and culture (a set of behavioral rules) as sharp opposites (48–50). Culture is not an alternative explanation to evolutionary theory. Rather, the ability to absorb culture is an evolved trait. Behavioral predispositions shape culture and are shaped through it, leading, for example, to stable patterns of sexuality, pair-bonding, child-rearing, nonkin reciprocation and social status relationships. The forms of these behaviors vary across societies, but all societies have stable patterns and values associated with strongly predisposed behavior. Amplification of biological predispositions is illustrated by avoidance of inbreeding (incest taboos), which is observed across cultures and among all studied primates (51). Similarly, deviant behavior (such as excessive risk-taking, impulsive behavior and non-reciprocation) that jeopardizes others' health and resource control evoke rejection of the deviant (25).

Evolutionary ideas are not relevant to treatment

Advances in basic knowledge are more likely to lead to better formulations of treatment-relevant problems than to immediate changes in treatment procedures. Optimal treatment and prevention presupposes detailed knowledge about etiology and pathogenesis. Pediatric hospital procedures improved following Bowlby's evolutionary-based studies of attachment behavior. Appreciating the high probability of child abuse among stepchildren is likely to increase the recognition of the need for vigorous preventive measures. Therapists who understand the principles of reciprocal altruism and the possible functions of self-deception and repression (52, 53) are more likely to enhance the rehabilitation of social skills. And attention to person-environment interactions is likely to optimize the selection of therapeutic recommendations: for example, teaching patients to select social environments that are responsive to their needs.

Evolutionary hypothesis can not be tested

Evolutionary hypotheses are eminently testable. For example, Daly et al. (42) provide extensive support for the prediction that, in most societies, sexual jeal-

ousy should be more extreme in males than in females. Essock-Vitale & McGuire (18) confirm that, within kin networks, resources flow from older to younger persons. Buss (54, 55) has shown that the frequency of divorce increases in infertile marriages. There is mounting evidence for the prepotency and preparedness of fear (10). Scenarios of past evolutionary events cannot be proven, but the number of possible scenarios can be limited, because given scenarios predict certain outcomes, some of which can be tested. For example, the hypothesis that domain-specific cognitive and feeling mechanisms mediate reciprocal exchange implies that basic exchange rules will be comparable across cultures, and that precursors will be present in our close phylogenetic relatives (35).

Natural selection should eliminate genes for mental disorders

If most mental disorders are maladaptive, then why do they persist? Evolutionists have advanced several explanations for the persistence of mental disorders. First, atypical or deviant traits tend only to reduce, not eliminate, the number of offspring. Thus, once a disorder appears in a population, it may remain for a considerable time. Reduced reproductive success is seen in obsessive-compulsive disorder, for example, but success is only marginally lower than among normals (10). Second, many disorders (such as late-onset depression, Huntington's disease and Alzheimer's disease) mostly appear after peak reproduction periods, so that inclusive fitness is less affected.

A third possibility is heterosis, in which even if it is maladaptive to have the entire set of genes that is needed to produce a given disorder, having some of them (short of the number necessary for the full disorder) may be advantageous in certain environments. Possessing all the genes for sickle cell anemia (homozygous state) leads to an early death, but carrying only some of them (heterozygous state) enhances resistance to malaria. Manic-depressive psychosis and obsessive-compulsive disorder are maladaptive, but cyclothymic and meticulous personalities may provide an adaptive advantage in certain environments. (A variation of this idea has been suggested for the persistence of senescence (44, 56): the very genes that lead to senility in old age may be those that confer some benefit in youth.)

Fourth, recessive traits may be hard for natural selection to eliminate if they only partially compromise adaptation, and many forms of mental illness are so infrequent that selection may be slow. Finally, some behaviors that are disorders in one culture might not be disorders in other cultures. Dyslexia, some forms of antisocial behavior and certain unstable personality variants are examples.

Existing theories in other disciplines explain findings at least as well as evolutionary theory

Evolutionists accept this view for certain features of current theories. Evolutionary theory does not replace other psychiatric theories. Rather, it 1) offers an additional perspective, 2) helps explain heretofore overlooked and understudied features of disorders and 3) provides an integrating framework. By adding ultimate causation to the current focus on proximate factors (such as genes, physiology, learning and psychodynamics), the theory identifies biases and constraints of behavior and physiological systems. Proximate psychiatric theories explain many of the mechanisms of disorders, such as the biochemical explanations of depression, reduced serotonin turnover among chronic abusive criminals (57) and petty criminality as the substrates on which evolution acts (58–60). Evolution can help to explain why these mechanisms exist at all.

The degree to which psychiatry is likely to incorporate an evolutionary perspective will depend on specific applications that inform our understanding and improve treatment. We now turn to the subject of applications.

Applications

Criteria for distinguishing normal from abnormal behavior

The current criteria for defining mental disorders include: 1) association with a somatic lesion (anatomical to molecular); 2) statistical deviances from normality (such as excessive self-centeredness, learning disabilities and bipolar illness); and 3) subjective distress. Some authors have suggested "biological disadvantage" as a more appropriate criterion for identifying mental disorders (61, 62). This view accords with an evolutionary approach. A disorder must impose some form of fitness disadvantage. Statistical deviance does not directly equate with disorders – mental retardation is a disorder but genius is not. Moreover, it is difficult to know whether a condition is pathological without considering the environment in which it occurs. Depression may be adaptive in a supportive social environment, just as schizoid personality may be adaptive in isolated areas. Insofar as our present-day environment differs from past environments in which current traits were adaptive, past adaptive behaviors may become maladaptive (such as the prepotency of animal fears being more fitting for our ancestors). Subjective suffering has a high probability of association with maladaptive situations, whether caused by external circumstances or by brain disorders. Feelings of pleasure and pain probably evolved to tell us whether prevailing circumstances are adaptive (27). Yet, even emotional suffering may be useful, just as pain, nau-

sea and fatigue are useful, although all indicate the presence of some danger.

The preceding points imply that both the features of disorders and the disorders themselves should be evaluated in the context of evolution. Further, features of disorders may be adaptive or result as a consequence of ultimate causation. These possibilities result in alternative etiological explanations of disorders, raise questions about classification and imply different approaches to treatment.

Pathogenesis

Evolutionary theory focuses attention on distinctions between etiology (cause) from pathogenesis (mechanism). Showing that depression is associated with alterations in norepinephrine or serotonin neurotransmission (mechanism) does not reveal its cause (etiology). Biochemical alteration may be a common end product reflecting an environmental or genetic etiology, or both. Serotonin neurotransmission is altered by changes in social status, and testosterone and cortisol levels rise in response to a variety of social events (25, 63). Such changes, in turn, alter the probability of behavior (such as responsiveness to others and vigilance), how information is processed and response to drugs (64). Certain social interactions are as essential for physiological and psychological homeostasis among adults as they are among infants. Persons vulnerable to mental disorders tend to have reduced capacities to manage their social environments to produce homeostasis and a greater probability of developing a disorder (45). Such evolutionary-oriented studies focus on behavior-physiology interactions and provide data for the empirical foundation of a more comprehensive model of mental disorders (65).

Evolved psychological mechanisms

As mentioned, natural selection is likely to have favored the development of cognitive/feeling mechanisms preadapted to particular situations. Examples include: respond immediately to perceived external danger; avoid or retaliate against those who inflict pain; assess others' ability to reciprocate helping; detect cheaters; and be vigilant towards actual and potential competitors. The characterization of such mechanisms is likely to be a major focus of research during the next decade. This research should lead to a description of mental disorders in terms such as underactive and overactive mechanisms (for example, over-reading or under-reading environmental dangers) as well as in the specification of such responses to behavior, physiological states and functional consequences: for example, chronic anxiety results from an overactive response to danger and/or from the failure of mechanisms that inform one that a danger has passed. Conversely, we may come to recognize new disorders characterized by defects in capacities for anxiety, normal sadness and jealousy. A clear implication is that appropriate treatment depends on both the mechanism involved and how it is awry (66).

Functional capacities and disorder classification

Functional deficits are considered in Axis V in DSM-III-R, but they are accorded far less importance in the day-to-day practice than are Axes I and II. The concept of function and functional deficits is not the province of evolutionary theory. However, evolutionary theory provides a conceptual framework in which to organize and interpret functions and, in an evolutionary-derived classification, an assessment of functional capacities would be a pivotal taxonomic category. Persons with high anxiety, moderate depression, self-deception, mild bipolar illness and, in some instances, schizophrenia, often function above average. The same is true for some people who have socially unattractive traits, such as extreme self-centeredness and extreme needs to dominate and control others. For some disorders, decreased functional capacity is the primary finding, as is the case with antisocial personality and malingering.

Assessment of functioning may also help explain within-disorder variance among current classification categories. Generalized anxiety disorder with minimal functional consequences may be classified separately from generalized anxiety disorder with major functional consequences. A focus on functional capacities would also alter treatment strategies and choices. A number of drugs that effectively reduce symptom intensity also reduce functional capacities (such as decreased motivation and ability to concentrate).

Integrating current theories

Advocates of one school of psychiatry frequently disregard findings developed by other schools. Biological psychiatrists are seldom interested in the findings of psychoanalysts or social psychiatrists, and some behaviorists ignore physiological aspects of mental disorders. Can such parochialism be changed?

Evolutionary theory can encompass the major conceptual frameworks of psychiatry, help integrate relevant findings, appraise new ones and introduce additional possible explanations. Biological psychiatry focuses on genetic-physiological predispositions and proximate mechanisms contributing to disorders, social psychiatry on environmental contributions, behavioral psychiatry on atypical behavior and

psychoanalysis on thoughts and feelings. Each of these focuses may best explain certain abnormal features, although in differing degrees within and across disorders. The addition of ultimate causation (such as predispositions to behave in certain species-characteristic ways), functional assessment, the possible adaptive function of certain features of disorders, trait distribution and the physiological consequences of person-environment interactions enriches the database of psychiatry and allows us to address what is intuitively obvious, the concept of multiple bases for disorders.

Evolutionary theory also offers psychiatry a deductive framework and a set of testable hypotheses. For example: multiple family placements of young children during critical periods of development is predicted to lead to both suboptimal refinement or learning of basic social skills and to the expression of certain predisposed traits that otherwise might not be expressed; diminution of within-disorder adaptive traits because of drug treatment would be predicted to result in noncompliance with treatment recommendations; and relinquishment of behavior that is offensive to others will occur only if alternative behaviors are associated with desired benefits.

Limitations of evolutionary theory

A number of questions and unresolved issues remain. The limits of evolutionary explanations have not been fully explored, particularly where 2 or more tendencies conflict (such as reciprocate by helping another *vs* invest in kin). For some behaviors, evolutionary explanations may prove to be the most parsimonious: for example, excessive risk-taking, antisocial behavior and depression following loss. Nevertheless, proximate events (such as the critical physiological details of a drug overdose) associated with many disorders are best judged from existing theories.

Second, there may be limits to the degree to which evolutionary theory can be applied to individuals. The current form of the theory derives largely from population genetics and behavioral ecology, which focus on the behavior of groups, not of individuals. Potential difficulties due to this history are illustrated by considering trait distribution: on the one hand, the concept informs our understanding of trait variance; on the other, there are limits to what can be inferred from a distribution curve to an individual. Similar limitations apply to all major etiological and pathogenic theories of psychiatry.

Third, the weights assigned to and the timing of many experiences are not significantly informed by the theory. Although there is general agreement throughout psychiatry and among evolutionary biologists on the critical importance of certain developmental experiences in the shaping of individuals, the importance of specific events and the time-frames in which they optimally occur remains largely an empirical issue. Extreme upbringing conditions (such as the total social deprivation of infants) have clear developmental effects, as do instances of the absence of essential neurochemicals for normal development (such as Tay-Sacks disease) or chromosomal aberrations (such as Down's syndrome). However, much of our knowledge is based on atypical situations that do not themselves directly inform our understanding of the complex process of development, its timing, and the impact of conditions generally accepted as being within the normal range.

Conclusion

A strong case can be made for evolutionary biology deepening our perspective by clarifying the concepts and explanatory power of ultimate to proximate explanations and by offering psychiatry an integrating paradigm. The theory puts humans back into an ecological context and raises questions about the normal operation of adaptive mechanisms, particularly those elicited by unusual circumstances. Perhaps surprisingly, its understanding and recognition of variation results in a particularly humanistic orientation to people's problems.

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