The Seven Sins of Evolutionary Psychology

nly recently have psychologists seriously considered how the various abilities of the human mind were created during the long course of neural evolution. This approach, called evolutionary psychology, has captivated many investigators (see WRIGHT 1994; BETZIG 1997: BUSS 1999; COSMIDES/TOOBY 2000). and it has encouraged the conceptualization of a variety of special-purpose evolutionary solutions genetically (e.g., ingrained adaptive functions or 'modules') that may exist within the human brain. The aim of this essay is to analyze the extent to which such approaches are providing unsubstantiated explanations of human behavior rather than clarifying realities of human and animal brain/minds. Many investigators, including ourselves, feel that evolutionary psychology has recently gone too far in its epistemological agenda, as it attempts to uncover

Abstract

Modern evolutionary psychology is demonstrating, once again, that an uncritical enthusiasm for the gene's-eye point of view can easily lead to conceptual excesses that go far beyond the available evidence. Seven major flaws in the evolutionary psychology agenda are outlined. With its enthusiasm for human inclusive-fitness issues, this variant of sociobiology has expressed little interest in what we already know about the brains and behaviors of non-human animals--facts that should be of foundational importance for thinking about many human abilities. To create a lasting understanding of 'human nature', we must incorporate the lessons from the past half-century of research on subcortical emotional and motivational systems that all mammals share. Seven examples of how a study of these systems can highlight some of the core problems of evolutionary psychology are outlined. From this perspective, the developmental interactions among ancient specialpurpose circuits and more recent general-purpose brain mechanisms can generate many of the 'modularized' human abilities that evolutionary psychology has entertained. By simply accepting the remarkable degree of neocortical plasticity within the human brain, especially during development, genetically-dictated, sociobiological 'modules' begin to resemble products of dubious human ambition rather than of sound scientific reasoning.

Key words

Sociobiology, evolutionary psychology, brain, modularity, emotional systems, epigenetic landscapes, inclusive fitness, human nature.

the brain 'mechanisms' that constitute 'human nature'. In our estimation, such issues cannot be resolved without a full confrontation with the relevant cross-species, neuro–psycho–behavioral evidence.

Although we now realize that the 20th Century image of the whole brain as simply a massive generalpurpose learning machine was fundamentally incorrect, investigators have yet to demonstrate the existare many special-purpose, genetically-dedicated circuits for various emotions and motivations in subcortical regions shared by all mammals.

The interactions between those specific brain operating systems and life experiences can, presumably, mediate the formation of an enormous diversity of 'modularized' software functions in higher neocortical regions of the brain. If this view is largely

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ence of any sociobiologimechanisms cal that evolved in the massive human neocortex within the Pleistocene Environment of Evolutionary Adaptation (EEA). There is yet no well-established empirical reason for viewing any of those association areas of the neocortex as genetically pre-ordained 'modules' that generate specific types of psychological strategies. Although we have gained a new taste for natural mental kinds (e.g., intrinsic emotional categories) within the human brain (Brown 1991: Betzig 1997), we must remember to be especially cautious in ascribing discrete special-purpose functions to brain association areas that appear at birth to be largely general-purpose 'computational' devices. Many of the apparent special-purpose functions in the higher regions of adult brains may only emerge as a result of specific types of life experiences. In contrast, there correct, we must proceed in a more epistemologically disciplined way than has become common practice in modern evolutionary psychology. Although we applaud the willingness of evolutionary psychologists to open up the Pandora's box of innate faculties within psychology once more, we fear that the parochial tendencies of many current views may promote needless controversies reminiscent of those that characterized the 'sociobiology wars' of the past quarter century. Although an appreciation of the power of inclusive-fitness can be incredibly productive in addressing many issues in population genetics and behavioral ecology, it cannot serve as a precise tool to dissect the nature of brain/mind mechanisms. How, then, might we generate credible perspectives that diminish the likelihood of arousing incendiary political passions, such as those that characterized the 'sociobiology wars'?

Biologists have long accepted evolutionary perspectives as historical scenarios for the emergence of all bodily organ systems. However, biologists have also come to recognize that evolutionary viewpoints are not especially useful for most of their ongoing experimental investigations. Evolutionary scenarios provide only marginal insights for guiding the experimental analyses of how biological systems actually function. Scientific demonstration of the functional mechanisms within the brain still need to be achieved through traditional experimental approaches. This poses a great dilemma for modern evolutionary psychological perspectives, for it is much easier to postulate adaptive 'modules' in the brain/mind than to demonstrate their neuropsychological nature. Such considerations lead to one overarching conclusion: Real neural functions across a variety of species should provide definitive constraints on speculation about what evolution did or did not create within human and animal brain/ minds.

A new breed of evolutionary psychologists appears to disagree with such a marginal utility view of evolutionary scenarios. For the past dozen years they have been asserting, often with a tone of revolutionary fervor, that our ability to peer into the hazy crystal ball of 'recent' human ancestry will help us fathom the intrinsic nature—the evolutionary epistemology—of the human brain/mind. We, as well as many other scholars who have long accepted evolutionary principles as being ontologically correct, are forced to question this new and potentially virulent strain of dubious neo-DARWINIAN thinking. Without a strong linkage to neuroscientific research, evolutionary psychology has no credible way of determin-

ing whether its hypotheses reflect biological realities or only heuristics that permit provocative statistical predictions.

These considerations become especially pertinent when we consider that some evolutionary psychologists now explicitly claim their approaches can shed light on how the brain controls mind and behavior (e.g., see TOOBY/COSMIDES 2000). To us, this seems highly unlikely. Accordingly, we offer the following analysis to help direct psycho-evolutionary thinking in a more balanced and productive direction, where the available empirical riches from the Affective, Behavioral and Cognitive Neurosciences can be used effectively to construct a genuine image of how the human brain/mind is actually organized. In the first half of the paper, we take a conceptual approach, using the 'TOOBY & COSMIDES tradition' as the most prominent example of current thinking in the field. In the second half, we proceed to real brain issues that can be dissected empirically. We will not attempt to summarize specific sociobiological findings in this paper, and we shall assume that readers are reasonably familiar with the types of views that have been espoused by evolutionary psychologists during the past decade. At the outset, we regret that space constraints do not allow us to discuss all of the available evolutionary views in the detail needed for a comprehensive analysis.

The Creative Excesses of Evolutionary Psychology

To begin, we will briefly consider the general historical threads that have led to the present revolution in evolutionary thinking and then discuss several distinct ways to conceptualize the adaptive functions of the brain/mind. What is currently hailed as mainstream evolutionary psychology (i.e., symbolized most commonly by the cognitively-based tradition initiated by BARKOW/TOOBY/COSMIDES 1992) is making radical theoretical claims concerning the human mind, some of which are contrary to what is already known about the mammalian brain. We believe the evidential disparity between their adaptive theory of 'human nature' and current neuroscience understanding is largely due to the separate and remarkably non-interactive paths taken by psychological and biological approaches to the brain/ mind during the 20th century.

Once upon a time many philosophers and psychologists believed that the mind was a *tabula rasa* upon which raw experiences were transformed into knowledge through the power of associative learn-

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ing. That era should have dimmed forever once DAR-WIN (1872) opened the door to a deeper understanding of human and animal minds. Evolution surely has constructed a variety of robust and perhaps fundamentally similar intrinsic potentials in the ancestral, neuro-mental apparatus of all mammals. However, since behavioral and bodily change are the only things we can directly measure in other animals, the search to uncover the nature of the intrinsic neuropsychological processes of the brain was delayed. Before the Neuroscience Revolution became fully recognized, modern evolutionary theory, especially with the robust concept of inclusive-fitness, provided psychologists with a substantive way to proceed (HAMILTON 1964). This principle has now achieved seminal recognition by many psychologically oriented investigators who are not, by tradition, accustomed to think in biological terms. Unfortunately, the acceptance of this profound evolutionary principle, which is most clearly applicable to sub-human species, did not promote an evident desire for the assimilation of neuroscientific research into human psychology.

Meanwhile, within ethology, behavioral genetics and comparative neuroscience there has existed a long and practical tradition of evolutionary thinking that continues to remain isolated from modern evolutionary psychology. There is no intellectually coherent reason for keeping the important findings of these fields un-integrated. Together, these disciplines can help create a balanced view of how the human mind was constructed. Empirical evidence indicates that the human mind was created through evolutionary shaping of ancient mammalian brains (MACLEAN 1990). Focusing on these ancestral emotional functions of the brain, to the extent that they are still represented in existing species, provides a unique empirical platform for thinking about the adaptive foundations of the human brain/mind (NESSE 1990; PANKSEPP 1982, 2000a-e).

We believe that the essential character of the human mind was laid down to a substantial extent within very ancient (i.e., subcortical) emotional and motivational neurochemical systems that we share with many other animals. Modern cladistic analyses of ancestral descent permitted by DNA, RNA and protein sequencing, along with the specification of neural systems in which such molecules are found, has dramatically increased our ability to uncover homologous brain functions across all mammalian species that have been studied. It is within the subcortical systems of the brain that the anatomical, neurochemical and functional homologies among

mammalian brain/minds are most striking (MA-CLEAN 1990; PANKSEPP 1998a). It is also within these homologous brain areas where the most definitive human brain/mind 'modules' will be found. If we do not consider these shared proclivities, we will be led astray in trying to identify the abilities that have emerged from the unique higher brain functions of our species-namely from our cortico-cultural 'thinking cap'. The organization of the neocortex, although still constrained by many unknown genetic rules (e.g., KEVERNE et al. 1996; VANDERHAE-GHEN, et al. 2000), may be much more of a generalpurpose computational device than modern evolutionary psychologists have been willing to concede. Of course, there is abundant room for debate on most of these issues, but hopefully not of the kind that is disengaged from substantial segments of the relevant evidence.

From animal brain research, we know that there are a great number of special-purpose emotional operating systems in the mammalian brain (PANKSEPP 1998a). It may be that much of the potential explanatory power imparted by evolutionary scenarios will be found in the details of the robust and widespread influence that those systems have throughout mammalian brains. The possibility is remote, however, that many unique and detailed epistemological engravings of sociobiological strategies (i.e., modules) exist within the human neocortex. Moreover, the likelihood is high that many human behavioral tendencies, consistent with inclusive-fitness dictates, emerge as functions of individual experiences. Once a basic emotion has been aroused, the mind is wonderfully filled with cognitive processes that can be fertile breeding grounds for unseemly sociobiological strategies (i.e., epigenetically derived 'modules'). Yet, we must remember that many of these emotionally charged cognitive manifestations are driven by the sub-cortical emotional systems that exist in all mammalian brains.

The exploration of emotional systems is a major challenge that is recognized by many evolutionary theorists (NESSE 1990; BUSS 1999; COSMIDES/TOOBY 2000), but, rarely is existing brain evidence incorporated into such discussions. For instance, the adaptive 'fear' module postulated by COSMIDES/TOOBY (2000) does not adequately recognize one 'fear system' that has already been characterized in the brains of other mammals (PANKSEPP 1982, 1990a; GRAEFF 1994; ROSEN/SCHULKIN 1998). The fear module envisioned by COSMIDES and TOOBY appears to be a master module that coordinates the activity of the many smaller modules dedicated to cognition and

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autonomic regulation. In fact, the type of fear 'module' that has been revealed by animal brain research appears to have come into existence long before any sophisticated cognitive capacities existed (PANKSEPP 1990a, 1998a). From the way Cosmides and Tooby appear to envision matters, the modularization of fear came after the existence of rather sophisticated cognitive capacities. Their fear module's main purpose is to simultaneously recruit and coordinate cognitive activities during fearful situations, so that the likelihood of an adaptive behavioral response is maximized. In fact, the experimentally demonstrated neuro-emotional systems are extensive, widely-ramifying subcortically situated circuits which posses the intrinsic capacity to modulate and synchronize a large variety of relevant brain and bodily resources. Evolutionary psychologists appear to be seeking specific socio-emotional modules among higher brain functions where the predominant functions may only be general-purpose cognitive/thinking mechanisms.

Only after a great deal of development can the cortex regulate emotional states by creating higher meanings through deliberation over fitness concerns. This view is quite similar to E. O. WILSON's suggestion at the introduction of *Sociobiology*, where he states that the genetically provided "emotional control centers flood our consciousness with all the emotions", not only "to promote the happiness and survival of the individual, but to favor the maximum transmission of the controlling genes" (1975, pp3-4). We now know an enormous amount about these ancient affect-generating, fitness-regulating systems-the "ancestral voices of the genes", to share the felicitous phrase of BUCK (1999). Unfortunately, that knowledge has yet to penetrate the sociobiology revolution that continues presently under the banner of evolutionary psychology.

The Plasticity of Language Cortex in Human Brain

We believe that some currently fashionable versions of evolutionary psychology are treading rather close to neurologically implausible views of the human mind. Although the lower reaches of all mammalian brains contain many intrinsic, special-purpose neurodynamic functions (e.g., basic motivational and emotional systems), there is no comparable evidence in support of highly resolved genetically dictated adaptations that produce socio-emotional cognitive strategies within the circuitry of the human neocortex.

Although there is substantial neuro-evolutionary evidence for the emergence of certain special abilities such as language (DEACON 1997; PINKER 1997), we still do not know with any assurance that such uniquely human abilities emerged from de novo genetic shaping of cognitive structures or from the re-molding of preexisting adaptations (i.e., exaptations). It is certainly possible that language emerged within a spandrel of evolving multimodal brain complexities selected to generate internal imagery necessary for reflective consciousness, rather than being a deeply ingrained adaptation that emerged from evolutionary sculpting of the fine details in cortico-communicative neural circuits (GOULD 1991). The availability of extra general-purpose 'computational space' in the cortex may have been sufficient to allow language to 'emerge' without the guidance of specific evolutionary selective pressure. As CLARK (1997) put it, language may have adapted to the emerging complexities of the brain rather than the other way around. Although once language did emerge, it most certainly provided new social environments for both biological and cultural evolution (DEACON 1997). However, the result of such selective pressures, we would assume, was to dedicate more cortical tissue towards general-purpose symbolic processing. Once there was an urge to communicate and some new intersubjective pragmatics (e.g., social intent and social gestures), language may have been guided by cultural evolution as much as by natural selection. In any event, the traditional view that language is a discrete, genetically-dictated specialization residing unconditionally in BROCA's and WERNICKE's areas (a simplification that CHOMSKY himself never accepted) has been crumbling for some time now (DEACON 1997). The reason the receptive aspects of speech find their natural home in WERNICKE's Area may largely be because that part of the neocortex is simply the brain's most multimodal area for integrating information coming from the external senses.

Although such radical degrees of revisionism may seem unlikely from certain popular points of view (e.g., PINKER 1994,1997), it is certainly not a perspective that has been falsified, and thus, should not be scientifically neglected. There are many lines of evidence that commend the view that recent human brain evolution provided the context for the emergence of a very general and flexible form of intelligence (e.g., PLOMIN 1999; SPENCE/FRITH 1999). Much of what traditional evolutionary psychology conceives to have been modularized in recent brain evolution may simply reflect our multi-modal capacity to conceptualize world events symbolically and to relate them to primitive affective feelings that reflect specific fitness concerns. Our massive memorial capacity then allows us to project these feelings and associated thoughts forward and backward in time, as well as onto other minds. There have surely been other remarkable evolutionary advances in the way ancient emotional systems interact with more recent cognitive processes (WIMMER 1995), but empirical knowledge remains meager (PANKSEPP 2000b,d,e). Indeed, without assimilating existing brain evidence, evolutionary psychology and psychology in general will remain on weak evidential footing with regard to the basic genetically-dictated psychological tendencies that guide the behavior of our species (PANK-SEPP 1990b, 1998a).

Neuro-foundational Issues the Evolution of the Brain/Mind

We subscribe to the view advocated by Paul MACLEAN (1990): the human brain is a structure consisting of distinct evolutionary layers, with many more homologies existing in the lower strata of the brain than in the higher cortico-cognitive layers. Our ancient reptilian basal ganglia and paleomammalian limbic system harbor many homologies, in comparison to the enormous species divergences at neocortical levels. Primary process consciousness is obviously based on subcortical circuits (DAMASIO 1999; PANKSEPP 1998a, 1998b). Hence, we doubt if it will be possible to reveal the intrinsic nature of higher aspects of the human brain/mind without first having a solid understanding of the lower aspects-the archetypal emotional-motivational processes that all mammals share

Although rats and humans diverged in evolutionary history some 80 million years ago, there is evidence that we continue to share some remarkably similar emotional and motivational urges-evidence for an ancestral mind-if we simply consider all the available evidence (PANKSEPP 1998a). At present, it remains possible that most of the higher aspects of the human brain/mind arise largely from the interaction between general-purpose neural systems of the multimodal cortical association areas and the very basic life experiences encoded by more ancestral emotional/mind systems that all mammals share. This is not to say that there won't be many mismatches between the ancient operating systems of the human brain and the modern environments in which we currently live (PANI 2000).

In our estimation, 'minds' started to exist when the evolved complexities of the nervous system allowed organisms to know more than is contained within their reflexive responses to the world (GOD-FREY-SMITH 1996). In other words, the existence of 'mind' can be inferred whenever a substantial amount of the variability in the behavior of organisms needs to be understood with reference to the intrinsic, evolved 'representational' abilities of the brain. For instance, the ability to experience affect may be an essential antecedent to foresight, planning, and thereby willful intentionality. We place 'representational' in quotes to highlight our suspicion that the central dogma of cognitivism may be deeply misleading when it is applied to many fundamental brain functions, which may intrinsically seek meaning by dynamically 'grasping' the world (Freeman 1999; PANKSEPP 2000b).

In short, 'mind' represents our shorthand way of talking about the more creative ways that brains reach out into the world in their attempts to make sense of internal imbalances and environmental circumstances that can help alleviate those imbalances. In our estimation, the human mind, as well as all other mammalian minds, are fundamentally built upon ancient emotional and motivational value systems that generate affective states as indicators of potential fitness trajectories (DAMASIO 1999; PANKSEPP 1998a, 2000b,e).

By considering the knowledge that has been derived from other animals, we are ready to share an alternative vision of evolutionary psychology that is based solidly on our deep ancestral heritage. Such sources of evidence have been neglected in recent discussions of evolutionary epistemology because many investigators are understandably hesitant to deal with the difficult issue of cross-species comparison. Indeed, this has proved to be a most troublesome approach as the tendency of too many investigators has been to simply remain at the behavioral level, instead of considering the underlying causal (i.e., brain) mechanisms. Our ontological bias is as follows: We take the naturalist-pragmatist's view that all aspects of mind supervene upon the material functions of the brain (for the seminal discussion of supervenience, see KIM 1993). Although mind may not be simply reduced to neurophysiological functions, due to the genetic and neuroscientific revolutions, we can finally begin to understand the intrinsic nature of the human mind by scientifically exploring its lower, ancestral manifestations.

During the past decade, the functional architecture of the cognitive brain/mind in other mammals—the evolved dynamics of 'the great intermediate net' that intervenes between inputs and

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outputs-has become a topic of vigorous discussion (BUDIANSKY 1997; PANKSEPP 1998a; FREEMAN 1999; TO-MASELLO 1999; HAUSER 2000). This recent cycle of intellectual activity has the strength to become a solid foundation for understanding the types of mechanisms that evolution truly built into the human brain. Now that there is a growing acceptance that we are thoroughly biological in both mind and body, and that the foundations of psychology make no sense except in an evolutionary framework (paraphrasing DOBZHANSKY's famous statement), let us be constrained by the evidence rather than captivated by the sea-swell of possibilities. In short, we believe that all too many 'stories' of evolutionary psychology may be scientifically explained by the interaction between basic emotional systems and the unique general-purpose intellectual abilities that human beings possess. If so, the foundations of 'human nature' will boil down to an 'animal nature' that was solidified in evolution long before the Pleistocene.

Let us now highlight seven specific 'sins'—flaws in epistemic strategies—we must critically consider before a fully synthesized evolutionary psychology can emerge and prevail in the brain/mind sciences. This summation of shortcomings will be followed by a seven exemplars of how knowledge of sub-cortical functions that humans share with other animals can help solve many of the basic fitness issues that evolutionary psychology has sought to clarify in our own species.

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Some of what follows repeats points already made (allowing each complaint to be read independently), which hopefully will only serve to reinforce their importance for the emergence of more substantive and lasting viewpoints in this field. Indeed, we shall see that many of the 'sins' reflect variants of the failure of evolutionary psychology to conceptualize adequately the emergence of various basic emotional and motivational systems in the mammalian brain and general purpose, cortico-cognitive abilities in the higher reaches of the human brain/mind.

1. Are there really Pleistocene sources of current human social adaptations?

Although all evolutionists recognize that existing organisms are living historical 'texts' that reflect past evolutionary passages, empirically we can only work effectively with the here and now brain/mind processes that are mixtures of evolutionary handme-downs and experiential blossoming. We can directly observe little more than strands of DNA, the proteins they help create, and the resulting developmental progression that takes place in specific environments. As is recognized by most, all historical/ functional issues are largely hidden from any direct analysis. Since we have no time machine that can promote a reasonably credible analysis of specific phases of our ancestral past, the types of psychological adaptations that evolution provided must be extrapolated from a direct analysis of brain/mind processes that presently exist in other creatures. We can attempt to estimate the emergence of various general principles only to the extent that we have established credible brain structure/function relationships in many related species, and we should only believe narratives where convergent lines of evidence point in the same direction.

It seems to us that much of brain evolution during the Pliocene and Pleistocene eras was based upon the rapid expansion of general-purpose cortico-computational space (which permitted the emergence of foresight, hindsight and language) rather than on any fine-grained molding of special-purpose socioaffective mechanisms. Most special-purpose mechanisms in the brain, of which there are many in subcortical regions, evolved long before humans emerged as contenders for the top 'predator' position in the feeding hierarchy. Although those ancient special-purpose systems surely constrained subsequent brain/mind evolution in our line of ascent, we have barely started to fathom the resulting evolutionary epistemology-the 'affect logic'-that can come to exist within the higher reaches of the human brain (SCHAND 1920; WIMMER/CIOMPI 1995; SEGAL/WEISFELD/WEISFELD 1997: BOROD 2000: PANK-SEPP 2000b,d).

Although many evolutionary psychologists are wisely backing away from creative speculations concerning the role of specific Pleistocene EEAs that are assumed to have been conducive to the selection of various psychological abilities, it might be wise to have a moratorium on such potentially idle speculations until what is already known about the functional organization of mammalian brains is integrated into evolutionary psychological thinking. Also, as noted earlier, animal husbandry practices and many behavior genetics experiments have indicated that it takes no more than a half dozen generations of selective breeding for robust temperamental differences to be induced into animal lines (Scott/FULLER 1965; SEGAL 1999). Hence, we should

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not resist considering the possibility that a significant amount of phenotypic variability in human temperaments and intrinsic cognitive styles have been created by reproductive isolation or 'caste' precipitated assortative mating (FREEDMAN 1979; SEGAL et al. 1997), but such work should be done and communicated with a deep sense of responsibility for human sensitivities. The effects that can obviously be demonstrated, have multiple explanations and they will account for very little in our fundamental understanding of 'human nature'. Indeed, most of the genetically selected differences that have been documented are probably a matter of selection for differential emotional and motivational sensitivities and responsivities rather than any qualitative differences in underlying psychological 'kinds'. Some people may simply never really understand the concept of color because they are color-blind; others may simply not understand 'emotions' because their emotional systems are not as strongly developed as those of others. In any event, our remarkable similarities to other mammals, especially at an emotional/affective level, should not be underestimated. However, we should also recognize that different species, and perhaps different lines of the human family, have dispositionally and developmentally distinct patterns of emotional and motivational expressions (to put an incredibly complex topic in shorthand).

2. Excessive species-centrism in evolutionary psychology

Evolutionary psychology remains enthralled by the human species. Although this species-centrism is understandable considering the anthropocentric biases of most modern schools of psychology, it creates enormous shortcomings in our ability to tackle basic issues of human brain/mind evolution. Many of our basic values and ways of ascribing affective meaning to events may be based on primitive brain processes that are homologous in all mammals. If so, we should be able to effectively study these processes in animal models. A highly restricted focus on human issues is bound to be less productive than judicious integration of demonstrable evolutionary antecedents in our conceptual structures (PANKSEPP 1998a). Recognition of the ancient emotional systems may help frame many of the ideas of evolutionary psychology in more archetypal, evolutionary terms. This may be a more fertile way to understand the primordial sources of our essential affective abilities and emotional tendencies.

We do not believe that it makes intellectual sense to follow a fundamental specism in evolutionary psychology, where human proclivities are commonly discussed independently of what we share with other creatures. There is a profound continuity in the subcortical neuro-mental processes among all mammalian species, especially with respect to deep emotional-motivational issues. If we do not fully recognize these shared processes, we can easily construct intellectual houses of cards by solely considering the final products of human socio-cultural life. Despite what some culturologists and social constructivists believe, the modern human mind is still tethered to ancestral animal minds. But, as they also claim, most of what we outwardly do is obviously constructed from our massive and highly generalized intellectual abilities interacting with cultural contexts. Of course, there are bound to be perceptual canalizations that are unique to humans (e.g., PER-RETT et al. 1998; PENTON-VOAK/PERRETT 2000). In any event, brain/mind evolution during the past few million years probably operated mostly by generating new general-purpose regulatory mechanisms that could flexibly solve the endogenously generated affective dictates aroused by the ancient emotional systems we share with many other animals.

3. The sin of adaptationism

Little needs to be said on this issue, since we have all become sensitized to the flaws of Panglossian thinking (GOULD/LEWONTIN 1979), and the necessary mechanistic and conceptual distinctions have been acknowledged (e.g., BUSS et al. 1998). In any event, if we do share a variety of basic emotional and motivational systems with all other mammals, there surely should be little doubt that those systems reflect profound cross-species adaptations. However, difficulties become more apparent when we come to consider the evolution of higher cognitive abilities. Since the emergence of massive, generalpurpose cortical space, exaptations and spandrels have arisen everywhere we look (GOULD 1991). In this conceptually tricky territory, it is easy to imagine intrinsic brain/mind patterns that appear to be evolutionarily engraved in the higher regions of the brain, whereas in reality there are only social and cultural cortico-constructions that are simply tethered to more primitive attentional, motivational and emotional systems. Ancient emotional systems are able to imbue 'cold' perceptions with 'hot' affective charge. Thus, we must reconsider which higher intellectual tools and perceptual proclivities actu-

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ally reflect inherent tendencies of the higher reaches of the brain as opposed those arising from learning.

Within the neocortical reaches of the brain, we suspect data-constrained scholars may only agree that all mammals have the ability to perceive objects and events, to compute temporal passages of time between events, to navigate through objects in space (HAUSER 2000; SILVERMAN et al. 2000), and perhaps several other species-typical resource holding capacities (e.g., KANWISHER 2000; PENTON-VOAK/PERRETT 2000). Unfortunately, evolutionary psychology, rather than deriving most of its impact from a discussion of such general cognitive capacities, typically entices us with the allure of much juicier emotional and motivational stories that color human life. However, at present, there is very little evidence for those types of discrete cortico-cognitive adaptations, even though we can anticipate that special forms of affect logic-'centers of gravity' for emotioncognition interactions-emerge in higher brain areas developmentally (SCHAND 1920; FRIDJA 1986; WIMMER/CIOMPI 1995; CIOMPI, 1997; PANKSEPP 1989 2000b). Although sociobiological modular possibilities may certainly exist in the higher regions of the human brain/mind, it is essential to try to demonstrate them rather than to simply argue for their existence based upon commonly observed phenotypic expressions. Many of the postulated cognitive adaptations, upon closer examination, may simply turn out to be emergent properties of development and culture (GOULD 1991; SCHAFFNER 1998).

4. The sin of massive modularity

After the reign of general-purpose behaviorism/ associationism was declining, FODOR (1983) opened up the Pandora's box of innate faculties by simply accepting what to most was obvious-that there are brain/mind modules for all of our basic sensory/perceptual and motor processes. However, we can now be equally confident that there is also a great amount of general-purpose computational space (heteromodal tissues). The phenotypic expression of complex mental and behavioral tendencies can be generated by so many different mind-brain processes that any ascription of intrinsic modularity to human association cortex must presently be deemed intuition-trading rather than evidencebased argumentation (SAMUELS 1998). Although it may be possible that some unique genetically-channeled resource-holding mechanisms related to social-emotional needs do exist in higher areas of the brain (e.g., systems for monitoring attractiveness, greediness, degree of social reciprocity and commitment, as well as 'mind-reading' tendencies), it should be the responsibility of each investigator who posits such modules to plot out credible strategies for revealing their inherent nature. Without that and with the recognition of general purpose intelligence mechanisms in the brain, it may be wiser to accept as a default assumption that most socio-modular functions are simply due to epigenetic emergence. Of course, this makes the search for ingrained socio-emotional systems of the brain even more interesting (CARTER/LEDERHENDLER/KIRK-PATRICK 1999).

The traditional position, certainly not negated by available evidence, is that most higher cortico-cognitive functions are epigenetically created by the experiences of organisms. Although there is abundant evidence for the emergence of neural complexities that permitted language and a general increase in propositional intelligence (SCHEIBEL/SCHOPF 1997), there is presently no clear evidence that new and refined emotional modular functions emerged in the human brain/mind during the past several million years of human brain evolution. Indeed, when humans have strong affective experiences, higher cortical regions tend to shut down (DAMASIO et al. 2000; FISCHER et al. 2000). Although it is certainly possible that modules for social affiliation, empathy, pride and various other resource holding capacities emerged within the massive neocortical mushrooming that occurred in our line several million years ago (NESSE 1990), it is as easy to envision how such sociobiological processes may emerge from the interaction of basic emotional systems with higher general-purpose propositional abilities. Indeed, our facility with general-purpose representational abilities (e.g., internal imagery and language) may have been as important in generating such emergent adaptive processes as any type of special-purpose epistemological engravings within the expanding neocortex.

Obviously, adaptive behavior can be genetically, experientially and culturally guided. The genetic components of adaptive behavior can only be distinguished by especially stringent criteria. As BUSS and colleagues (1998) have enumerated, but have not yet empirically resolved, genetically ingrained adaptations can be identified by specific criteria such as "complexity, economy, efficiency, reliability, precision and functionality" (p536), but learning can also provide these results. In our estimation, such conceptual criteria can only be cashed out by more rig-

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orous developmental-neurobehavioral approaches than have yet to be implemented by evolutionary psychologists. In any event, the simple postulation of genetically-dictated modules, especially in higher areas of the human brain, may end up being a regressive 'phrenological' strategy rather than a progressive paradigm based on real brain circuit analysis.

We should not forget that it took the better part of brain evolution to create the subcortical systems of the mammalian brain, while the expansion of the cortex was remarkably rapid, guided probably by a small number of genetic regulatory changes. Morphometric analysis suggests that the higher brain as a whole enlarged, with no clear indication for specialized modular development, at least at the gross anatomical level (FINLAY/DARLINGTON 1995). Let us recall that the 'chips' of the human cortex—the columnar structures containing approximately 3,000 neurons each—are very similar throughout the brain and also from one mammalian species to another. These features are suggestive of highly generalized (almost 'random access', chip-type) computational devices.

Although functional specialization must have emerged as cortical columns proliferated and interconnected in increasingly complex ways, there is presently little empirical data, aside from certain perceptual and motor/action processes (e.g., VANDER-HAEGHEN et al. 2000), that any types of functional psychological strategies emerged in the cortex via natural selection. Perhaps the identification of the learned inputs into the headwaters of the fear circuitry in the amygdala (LEDOUX 1996), and the reward-association learning circuits of the frontal lobes (ROLLS 1999) might be taken as exemplars, but they may also reflect general learning principles operating in higher brain areas to which intrinsic subcortical emotional circuits project (PANKSEPP 1998a).

Put another way, the relatively homogeneous columnar organization of the neocortex is not straightforwardly compatible with any highly resolved, genetically-governed, modular point of view. Indeed, functional studies suggest a vast plasticity in many of the traditionally accepted cortical functions. For instance, visual cortex can be destroyed in fetal mice, and visual ability will emerge in adjacent tissues (see DEACON 1990, 1997). Accordingly, the heteromodal cortex of the human brain may be better conceptualized as a general purpose cognitive-linguistic-cultural 'playground' for regulating the basic affective and motivational tendencies that are organized elsewhere. In this view, cognitive processes are 'tools' or 'handmaidens' for helping regulate the more basic life concerns.

5. On the conflation of emotions and cognitions

Common human subjective experiences highlight how massively emotional feelings and cognitive attitudes are intermeshed. Clearly cognitions can easily become 'charged' with emotional values. This has led some (e.g., PARROT/SCHULKIN 1993; COSMIDES/TOOBY 2000) to ignore the evidence that the basic emotional circuits of the brain emerged much earlier in brain evolution than the higher cognitive capacities. For those not accustomed to neuro-evolutionary thinking, the 'ancientness' of basic emotional systems is supported by their medial and caudal locations in the brain (DAMASIO et al. 2000; PANKSEPP 1998a), as well as the dating of neurogenesis in the underlying brain zone (i.e., the timing of the fetal development of brain systems seems to parallel the historical pattern of their phylogenetic origin).

In short, the classic distinction between emotional and cognitive processes is sustained by abundant data indicating that the two can be dissociated functionally and anatomically (e.g., ZAJONC 2000; PANKSEPP 1990c, 2000b). Even though emotions and cognitions obviously interact massively, there is no scientifically sound reason to conflate the two, especially in subcortical realms where the power of affect seems to be elaborated (OLMSTEAD/FRANKLIN 1997; PANKSEPP 1998a, 1998b, 2000b) However, perhaps more important for the present argument is the issue of whether genetically guided cognitive specializations exist in higher regions of the neocortical apparatus to generate higher order emotions such as jealously, shame, guilt, pride, etc. There may well be such intrinsic higher 'centers of gravity' (e.g., in subareas of the frontal lobes) for the blending of basic emotional impulses (WEISFELD 1997; DAMASIO 1999; ROLLS 1999; PANKSEPP 1982, 1989), but at present, there is no critical neurodevelopmental evidence to adjudicate how such functions actually emerge. Although there may well be abundant genetically governed canalizations for such processes, it is still equally likely that most are created through cognitive learning and other developmental processes guided fundamentally by the affective power of basic emotional circuits concentrated in subcortical regions of the brain.

6. The absence of credible neural perspectives

Although there is increasing talk of neural circuits for cerebral modules, especially since evolutionary psychology became a compelling view in cognitive

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neuroscience (e.g., PINKER 1997; TOOBY/COSMIDES 2000). Yet, none of the proposed sociobiological modules have coalesced with established neural realities. In this context, it is remarkable that evolutionary psychology continues to neglect evidence concerning the basic socio-emotional systems of the mammalian brain that have been studied for many years in animal models (e.g., note the absence of existing neuroscience work in a recent chapter by COSMIDES/TOOBY 2000 which is juxtaposed to a summary of such work by PANKSEPP 2000a).

Instead of a solid confrontation with the brain, there is abundant talk of computational-representational views which ignore the fact that many neuroscientists are not convinced that such informationprocessing metaphors provide much that resembles an accurate perspective on how the brain creates meanings (Freeman 1999). Perhaps the higher cortical systems are 'computational' by some stretch of the digital information processing metaphor, but the subcortical reaches that mediate emotions and motivations are not. Subcortical systems generate many neurochemically-specific mass-action effects in the brain where the patterning of action-potentials carry no psychological or behavioral 'codes', but their population frequencies do control the intensity and patterning of specific action tendencies. We should never forget that the capacity to simulate certain brain functions in a digital processor does not mean those computations reflect physiological realities. Also, we should at least consider that many brain functions are created not simply by digital informational codes but by 'volume-conduction' types of analog mechanisms (explaining why 'pressure' and 'energy' metaphors have been so popular in emotion and motivation research).

Although we do not want to distance ourselves completely from the potential utility of computational approaches for understanding the brain (e.g., MAUK 2000), we should remember that brain 'computations', even in the higher cortical regions, are probably vastly different than those that transpire in digital computers. Biological brains contain massive internally generated background activities that help establish spontaneous, self-organizing, non-linear dynamic capacities of which digital 'brains' seem incapable (FREEMAN 1999; LEWIS/GRANIC 2000). In other words, the foundations of mind are fundamentally 'embodied' by organic processes that are impossible to compute except in the most superficial ways. The exploitation of ever-popular computational-informational metaphors may not really be instructive for understanding the essential organic underpinnings of the human mind. A realistic confrontation with the biology of neural systems most assuredly will. Of course, considering the power of computer algorithms to superficially model essentially anything, it is understandable why many continue to be enticed by traditional computational metaphors.

7. Anti-organic bias or the computationalist/ representationalist myth

Let us consider the previous 'sin' from the perspective of recent flirtations by evolutionary psychologists with proximal mechanistic analyses (e.g., TOOBY/COSMIDES 2000). Evolutionary psychology, as most other forms of cognitive psychology, has been inspired by computer science rather than the molecular biology/neuroscience revolutions of the past three decades. Indeed, at times, it seems that practitioners of evolutionary psychology have an active aversion to organic perspectives. They talk about the brain simply as a modular computational device. Although that view has also been pushed forward by many cognitive neuroscientists, an equally credible alternative is rarely discussed: Much of mental life is fundamentally organic. The only reason the brain-mind appears to be computational is because nerve cells fire action potentials, yielding a surface similarity to SHANNON-WIENER type informational principles (CAMPBELL 1982). However, we could view those microscopic elements of neural activity as mere 'stitches' within a more dynamic, amplitude modulated neural fabric of mind that must be understood fundamentally in organic terms. From this view, action-potentials simply provide the necessary mass-action effects to generate a more global neurodynamic fabric of the mind. The molding and shaping of the populationdynamics arising from ensembles of neurons may be more important in generating a substantive understanding of mind, than is the search for discrete digital codes of action potentials in individual neurons.

We should certainly remember that no sophisticated digital 'neuronal code' for psychological processes has yet been found via a study of action potentials. At best, we have some impressive neuronal correlates for some sensory and perceptual processes, but an equally impressive amount of evidence that specific neurochemical patterns in the brain can create basic psychological states (PANKSEPP 1986b, 1993, 1998a). One could argue that processes such as emotions could be instantiated by any of a

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variety of neurochemistries or computational devices, but at present that is an empty promissory note and a view (Dare we call it 'dustbowl cognitivism'?) that does not encourage the search for practical knowledge that could link up with basic human and clinical issues, although recent developments in evolutionary medicine and psychiatry certainly do have potential (e.g., NESSE/WILLIAMS 1974; STEVENS/ PRICE 1996; MCGUIRE/TROISI 1998).

Just to highlight how remarkably ingrained is the bias against the organic brain, we note that in How The Mind Works, PINKER (1997) shares a vivid description of the computational bias. He describes a scenario of information transfer in which one person says something into a telephone receiver, and the 'information' then gets successively converted from nerve cell and muscle activity; to air pressure oscillations (i.e., auditory signals); to electrical signals traveling down wires; to electrochemical reactions within a silicon medium and subsequently back in the completely reverse order. The receiving brain converts this 'information' into a vocal response that can be perfectly and reliably conveyed to a companion sitting on the couch. PINKER then makes the point that the information remained unaltered and in perfect form, independent of the medium in which it traveled. This view almost completely ignores the simple fact that the brain has actively created 'meaning' out of sensory events. Few ideas have been put forward about how this is achieved.

By contrast, an esteemed hands-on neuroscientist working on such profound issues has noted that "The only patterns that are integrated into the activities of the brain areas to which the sensory cortices transmit their outputs are those patterns they have constructed within themselves. In colloquial terms, the ingredients received by brains are not direct transcriptions of impressions from the environment inside or outside the brain. All that brains can know has been synthesized within themselves" (FREEMAN 1999, p93, our emphasis). Although we do not suggest that auditory and visual information is not strongly restrained by computational algorithms at the neuronal level, we do assert that, at present, computationalism has added no fundamental understanding to how the brain generates emotions and motivations.

Nevertheless, PINKER uses his example to explain why neuroscience deserves less merit than information/computational theories in attempting to study mind. Yet, he fails to emphasize that the only entities that have ever been demonstrated to possess mind are those that possess neurally- (as opposed to silicone-) based brains. To rephrase a previous point, it is a mistake to believe something is biologically real simply because one can computationally simulate the shadow of an end result. Until someone discovers facts to the contrary, we should continue to acknowledge that there is something remarkably special about the organic brain medium. Abundant examples exist that would be very hard to explain from any existing computational view, but can easily be explained by the organic properties of brain tissue. Thus, it is certainly premature and unwise, for any science of the mind to neglect the brain, as is still too common in evolutionary psychology and most of psychology, in general. (ROBINS et al. 1999).

In sum, from a neuroscience perspective, there is certainly no paucity of sins in current evolutionary psychology. Hubris and reification of verbal concepts are not in short supply. Fortunately, only a few have had the temerity to claim that their speculations are providing the conceptual structures that can effectively guide future neuroscience investigations (TOOBY/COSMIDES 2000). So far evolutionary psychology has only been effective in framing stochastic predictions in terms of presumed distal evolutionary adaptations guided largely by Hamilton's concept of inclusive fitness. However, now that evolutionary psychologists are persistently talking about 'mechanisms' [e.g., note the use of that term three times in the introductory paragraphs of a fine paper by BUSS (2000) on the evolutionary nature of happiness], they need to invest vigorously in the underlying causal and supervenience issues rather than simply making computational assumptions concerning the nature of the underlying processes.

Now that sophisticated brain imaging devices and samples of anatomically well-characterized brain-damaged individuals are available, we anticipate that evolutionary psychologists will attempt to cash out their claims using neuroscientific approaches. However, since those approaches are not likely to yield anything but correlative data, it is bound to be a rocky road toward any substantive understanding of the underlying mechanisms. Thus, we strongly urge the discipline to cultivate good relations with various animal brain research traditions that can help them reveal, in some reasonable detail, the underlying causal mechanisms. To facilitate this hope, we now share some of the intriguing possibilities from animal brain research that can help evolutionary psychology ground itself in a more catholic empirical tradition.

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Seven Solutions from Neuroevolutionary Psychobiology

In this section, we highlight seven specific examples, from a vast pool of available evidence, of how existing behavioral and affective neuroscience research can clarify some of the basic neural underpinnings of major problem areas in evolutionary psychology. These examples also help highlight how the interactions between ancient brain emotional systems and general purpose cortico-cognitive abilities can contribute insight into how we might proceed to solve some of the fascinating, but often self-evident (i.e., folk-psychological), human tendencies that evolutionary psychology has helped bring to the intellectual foreground (e.g., see Table 1, BUSS et al. 1998). Although there are a large number of options to choose from, most come from the senior author's long-term research program into the fundamental nature of mammalian emotions. Since evolutionary psychology has such a unique and highly delimited epistemological agenda, these ideas may have little impact on those who already have well-established positions in the field. However, we offer this 'sampler' for all scholars who are seeking a comprehensive understanding of the ancestral roots of 'human nature'.

1. A general purpose foraging system

The mammalian brain contains a powerful subcortical system that can generate the seeking of resources essential to survival (ROBINSON/BERRIDGE 1993; PANKSEPP 1981, 1982, 1986a, 1992, 1998a). This socalled expectancy/SEEKING or 'wanting' system has been the focus of work for decades, typically guided by discrete behavioral hypotheses of reward, reinforcement and more recently pleasure. Now, an increasing number of investigators, taking their lead from ethological rather than behaviorist analyses, are recognizing that this a generalized system for foraging-a system that provides a goad with no fixed goal for exploratory/investigatory activity. This system is capable of helping construct goaldirected behavior patterns based on the confluence of bodily need states, environmentally accessible reward objects, and contextual contingencies. In evolutionary terms, this system could be conceptualized as a generalized positive appetitive 'resource holding potential' system that monitors and promotes fitness issues by instigating vigorous exploratory-seeking activities (PANKSEPP/KNUTSON/ BURGDORF 2001).

We will not attempt to even allude to the remarkable behavioral neuroscience work that has been done on this system (for a recent review see IKEMOTO/ PANKSEPP 1999), but we highlight this circuitry simply as one example of a variety of widespread subcortical emotional systems shared by all mammals (and probably some other animals). This system has broad implications for a large number of appetitive behaviors that can vary considerably depending on the contexts encountered by such animals. It also surely controls a diversity of human/animal aspirations and desires.

This brain process also helps establish confirmation biases in organisms-coaxing them to behave with causal 'convictions' when only correlations exist in perceptual inputs (for a summary of the relevant 'auto-shaping' literature, see PANKSEPP 1981, 1982, 1986b). We suggest that much of evolutionary psychology, indeed much of science, proceeds on the inductive inferences made by such forward-looking, experience-expectant brain processes. Unfortunately, many resulting conclusions constructed in the aroused cortico-cognitive spaces of the mind turn out to be delusional from formal logical perspectives. We urge evolutionary psychologists to ponder the implications of this general-purpose motivational system for the ways they are seeking to understand 'human nature'. We also would suggest that functionally dedicated subcortical systems for RAGE, FEAR, LUST, CARE, PANIC and PLAY be considered as foundational (PANKSEPP 1998a) for the creation of many of the socio-emotional 'modules' that are currently being entertained. The general point is that despite such dedicated systems for emotions, human behavior and the underlying brain systems are much more plastic than evolutionary psychologists commonly emphasize.

2. General-purpose neurochemical systems for regulating all psycho-behavioral tendencies

Consider just one neurochemical system: Ascending brain serotonin circuits arising from two compact midbrain cell groups ramify widely throughout the forebrain. Through a diversity of distinct receptors, these networks modulate all emotional and motivational process in all mammalian species in essentially similar ways (PANKSEPP 1986a, 1998a). In general, when serotonin is high, mammals appear more relaxed, satisfied and confident. They are less likely to initiate aggression, but also less likely to back down during social confrontations (see McGUIRE/TROISI 1998). Humans respond likewise

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(KRAMER 1993; KNUTSON, et al. 1998). Similar behavioral patterns, modulatory functions, cellular characteristics (autoinhibition) and diffuse projection patterns have also been documented in invertebrate serotonin systems (HUBER/DELAGO 1998; HEINRICH et al 1999; KRAVITZ 2000).

Since such neurochemical issues are probably the most credible means of confirming homologies between animals and humans (PANKSEPP 1986b, 1993, 1998a), let us dwell on this issue at some length: In order to clarify whether domain-specific brain modularity is a physical reality, evolutionary psychology as well as the neurosciences must rely on the existing evidence of brain structure and function to support all claims that attempt to elucidate how the brain/ mind operates. Historically, the most thoroughly studied neural systems have been amine-modulatory systems that utilize small amino acid derivatives (dopamine, norepinephrine, serotonin) as neurotransmitters. Evidence from these well-studied systems provides a suitable foundation for brain/mind theorizing in evolutionary psychology. The group of neurochemicals that are utilized by these systems (collectively referred to as biogenic amines) are present in the nervous systems of many animal groups, including molluscs, annelids, crustaceans, and all mammals. Most neurons that produce biogenic amines reside in discrete clusters of cell bodies that are situated near the midline of the nervous system. Their projections stretch over large areas of neural tissue and release chemical messages diffusely, rather then through information-specific synaptic transmissions. In essence, functions of amine-modulatory systems have remained highly conserved across a remarkably wide range of species.

Instead of producing neuronal activity per se, this type of global release regulates ongoing nerve cell activity by changing the response properties of large neuronal ensembles. Amine-modulatory systems have been indicated as key elements in the regulation of a broad range of appetitive behaviors in every species studied. For example, calcium-calmodulin kinase II knock-out mice exhibit marked decreases in serotonin release from the raphe nuclei (i. e. the serotonin-producing cells in the mammalian brain) and have been shown to be less fearful in situations where animals normally exhibit heightened fear responses (e.g., foot shocks, fear conditioning, 'openfield' tasks, re-engaging aggressive conspecifics). Heterozygous mutants are also much more aggressive in various behavioral paradigms (CHEN et al. 1994). Even more notable from the present perspective is the role of biogenic amines in a wide range of human

psychological abnormalities. Serotonin-modifying drugs can treat depression, anxiety, hyper-aggressive tendencies and eating disorders (BITTAR/BITTAR 2000).

Alterations in this widespread neuro-modulatory system produce effects that span across large behavioral repertoires. The close association between these systems and global arousal, attentional and appetitive states should make us dubious about any suggestion that would ever attempt to ascribe unique human brain/behavioral propensities to these systems. The basic plans of these neural networks were established long before humans existed. Although these chemistries also came to regulate the types of higher brain tissues that emerged in the humanoid line during the Pleistocene, there is no indication that biogenic amines ever evolved to participate in anything more than non-specific modulation of all attentional, cognitive and emotional functions, albeit at times in remarkably subtle ways. For instance, KRAV-ITZ (1988, 2000) has proposed that aminergic modulation may function to recruit adaptive behaviors over contra-adaptive behaviors. Unlike the computationally resolved cognitive models that evolutionary psychology suggests underlie mind and behavior, the amine-'spritzer' systems tend to support a more general, organic explanation where global, neurochemically induced field-dynamics set the tone for what the brain is likely to produce.

For 'modular' evolutionary arguments to work, we have to be able to specify how selection pressures can mold specific neural circuits. All perceptual and cognitive specificity appears to be driven by a few excitatory and inhibitory amino acids (e.g., glutamate, GABA), and it is very hard to envision how genetics could mold the detailed wiring of those systems, but easy to imagine having different amounts of such computational networks in different areas of the neocortex. We believe that humans simply have much more of such brain tissue than other animals, without it being uniquely dedicated to any specific inclusive-fitness functions. Admittedly, there are bound to be some preferred modes of information transmission within such cognitive networks (i.e., canalizations or forms of preparedeness guided by functionally dedicated systems of deeper parts of the brain), but most of the higher results are bound to be dramatically shaped by the individual experiences of each person.

By comparison, it is easy to envision how various peptide modulatory systems that we share with the other animals are more dedicated for specific evolutionary ends. There is now abundant evidence that neuropeptide systems can modulate very specific

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emotional and motivational tendencies (e.g., as reviewed by PANKSEPP 1986, 1993, 1998a). Working together with such ingrained emotional and motivational systems, the intensity of whose influence could easily be modified by genetic selection, higher cognitive systems can surely be epigentically molded more readily by differential fitness demands that vary with individual environmental exigencies. This is not to say that emotional systems do not also change with experience; they certainly do (PANKSEPP 2001) and with many cognitive consequences (LIU et al. 2000).

3. General mammalian mechanisms of kin selection

Although a great deal of discussion in sociobiology and evolutionary psychology has been premised on the nature of social relationships (e.g. inclusive fitness, altruism, kin-recognition—see HAMILTON 1964; WILSON 1975), for over a quarter of a century these disciplines have remained silent about how proximal mechanisms in the brain might control such processes. Although there is abundant talk about 'mechanisms', acknowledgement of the abundant ongoing neuroscience work on such issues is rarely offered. Meanwhile, behavioral neuroscientists have been making considerable progress in understanding these processes by studying brain functions related to the emotions of separation distress and attachment (PANKSEPP 1989/1999). Among the neural systems that are especially important in the mediation of social attachments are brain opioids, oxytocin, glutamate, norepinephrine and probably prolactin (INSEL 1997; NELSON/PANKSEPP 1998; PANK-SEPP 1998a). Just one of many noteworthy findings is that kin-appreciation in male mice is mediated by the release of endogenous opioids (D'AMATO 1998), and the tolerance that occurs in opioid synapses, and hence social bonds, could easily help explain inclusive-fitness related changes in social strategies (PANKSEPP 1998a). Surprisingly, evolutionary psychologists have exhibited little interest in integrating or advancing such findings, even though there is direct and rather profound implications for their scientific agendas.

4. On the nature of play, power, tickling and friendship

Powerful social control systems for playful engagement exist in subcortical regions of the brain, and their functions are beginning to be systematically dissected (VANDERSCHUREN, et al. 1997; PANKSEPP, et al. 1984; PANKSEPP 1993b). These systems allow higher brain regions, perhaps via recently discovered 'mirror neurons' (RIZZOLATTI et al. 1996; GALLESE/ GOLDMAN 1998), to establish and solidify social strategies that have enormous implications for the structuring of animal societies. Adult relations, including alliance-friendship patterns, may arise as a result of the high degree of activity in social engagement systems during juvenile development. The desire to engage in such activities is communicated in various ways that are not well understood, but discoveries such as play vocalizations, that may have more than a passing resemblance to primitive forms of human laughter (KNUTSON et al. 1998; PANKSEPP/BURGDORF 1999 2000), may help open the door to systematic studies of how positive social emotions regulate the construction of personality differences, as well as social systems (PANKSEPP 2000e).

A study of these systems also has implications for seemingly distant concepts such as anticipatory eagerness (BURGDORF et al. 2000), the cravings that accompany drug addictions (PANKSEPP et al. 2001) and the nature of current social problems such as the increasing incidence of attention-deficit, hyperactivity disorders (PANKSEPP 1998c). The underlying evolutionary pressures that have molded such basic mammalian play systems should be of foundational importance for understanding the underlying nature of many inclusive-fitness concepts in evolutionary psychology.

5. Male sexual jealousy and potential neurochemical therapies

The fact that males are defensive over reproductive opportunities has been repeatedly noted in the human and animal behavior literature. We finally have animal models that suggest subcortically situated vasopressin systems are critically involved in such processes (WINSLOW et al. 1993). Male voles become highly aggressive toward intruders after a single sexual experience with a specific female. However, if their brain vasopressin signals were immobilized with receptor antagonists, a maneuver that does not compromise copulatory success, the males do not exhibit offensive behavior toward intruders. Conversely, the mere experience of elevated brain vasopressin in the presence of a female conspecific, but in the absence of sexual contact, is sufficient to establish the aggressive attitude toward 'intruding' males. In contrast, there is a parallel line of investigation that indicates oxytocin can pro-

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mote maternal care and increase friendly relations among individuals (CARTER 1998; NELSON/PANKSEPP 1998). These types of subcortical processes appear to be essential for the emergence of positive social relations, which may be of foremost importance for the development of a 'mechanistically' sound and clinically productive understanding in evolutionary psychology. For instance, if there are deep evolutionary homologies in these systems, we anticipate that orally-effective vasopressin antagonists might eventually be designed to combat male sexual jealousy and related forms of male irritability.

By comparison, orally-effective oxytocin agonists should promote feelings and attitudes of nurturance, and thereby promote many higher psychological reasons for being less aggressive. Genetic manipulations along these lines have already modulated the social temperament of animals (YOUNG et al. 1999). One relevant finding in modern evolutionary psychology is that females tend to have better social memories than males (SALMON/DALY 1996), and in that context it is worth noting that mice whose oxytocin gene has been disabled exhibit deficient social memories (Ferguson et al. 2000). Both of these findings contribute powerful support for a general mammalian 'brain's eye' view in evolutionary psychology, as females have more oxytocin activity in their brains than males. In this context it is also noteworthy that female rats, just like their human counterparts, exhibit better social memories than males (BLUTHE/DANZER 1990).

6. Beauty, sexual attraction and mate selection

The manner in which facial expressions and bodily gestures help elicit, communicate, and regulate affective states is a central issue of both ethological and evolutionary psychological approaches to animal and human behavior. Although there are many cortical perceptual processes related to the detection of beauty, sexual attractiveness and reproductive fitness (for recent reviews, see JOHNSON 1999; BOROD 2000), a key issue is whether such perceptual mechanisms can operate independently of the socio-sexual circuits that exist subcortically. We simply do not know at present, but we suggest that the ability of various perceptions to regulate such desires and aversion (e.g., PERRETT, et al. 1998) is based very much on how they link up to subcortical socio-sexual circuits. (PFAFF 1999). We would be surprised if any higher perceptual 'modules' for social attraction in humans could operate effectively without connections to the types of basic subcortical emotional systems that have already been clarified in other species (PANKSEPP 1998a).

In this context, we also note the many recent animal studies that have highlighted how mate attraction may be mediated by signals of reproductive fitness (e.g., WELCH et al., 1998; GIL et al 1999). The inclusive-fitness based predictions that have been confirmed by population genetical and behavioral ecological points of view are truly remarkable (e.g., ELLEGREN et al. 1996; KOMDEUR 1997; Johnsen et al. 1998; SHELDON/ELLEGREN 1998). Although these studies highlight the fact that various species-typical perceptions are involved in mate choice within all species, we must again wonder whether these inputs operate independently of the subcortical socio-sexual motivational circuits that share a high similarity in all vertebrates. Although little is known about the brain mechanisms that mediate such adaptive socio-sexual strategies as noted above, we suspect that the primitive, genetically dictated affective brain systems are essential in all mammals (PANKSEPP 1998a).

7. Affect, sociopathy and the primordial self

We believe that studying how affective states are generated by the brain will be critical for understanding how evolution guides various behavioral strategies in humans and animals (PANKSEPP et al. 2000). The existence of various emotional and motivational feelings, along with general-purpose learning systems, can provide practically all the types of adaptive behavioral strategies that have been discussed by evolutionary psychologists (e.g., BUSS 1999). If this viewpoint is correct, then we have no alternative, but to make the study of affect a primarv concern in evolutionary psychology. Although this principle appears to be recognized by the majority of investigators, in our estimation this cannot be achieved in any deep sense without assimilating evidence from brain research in related animals.

For instance, subcortical emotional systems are decisive in the way organisms spontaneously comport themselves socially. Sociability can be modulated powerfully by a great number of subcortical brains systems (NELSON/PANKSEPP 1998), with the most detailed analyses having been conducted on the differential expression of oxytocin and vasopressin systems in voles exhibiting very different social temperaments (for review, see INSEL 1997, 1998). It is expected that even human sociopathy (for review see MEALEY 1995), is modulated by similar sys-

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tems, even though critical evidence for such issues is not yet available. Of course, there are bound to be gradients of sociopathy, some of the milder versions being simply based upon the normal variability of primitive emotional urges in our species coupled with deficient higher forms of consciousness. For instance, rape by human males, thought by some to be an adaptive human reproductive strategy (see THORNHILL/PALMER 2000), is more likely to be based on strong testosterone driven erotic and dominance urges in males, coupled with emotional insensitivity (e.g., deficient frontal lobe functions) and inadequate moral socialization. To the best of our knowledge, higher cerebral 'modules' have not evolved to promote such nefarious behavioral tendencies, even though one can envision how diminished frontal lobe functions (e.g., diminished guilt, shame, empathy and sympathy) could be reproductively advantageous in certain primitive environments. In short, it is easy to construct credible neuronal hypotheses of how tendencies toward social insensitivity, sexual coercion and agonistic tendencies could emerge from the interaction between basic emotional systems and general-purpose neocortical processors that are able to learn a vast number of context-dependent behavioral strategies.

However, to the best of our knowledge, the neocortex is not the source of affective experience (PANK-SEPP 1998a, 2000b). Rather, raw emotional feelings emerge from ancient brain systems in ways that are just beginning to be understood in humans (Heath 1996; DAMASIO, et al. 2000). For instance, a primordial form of 'self-representation' that can generate basic bodily expressions and emotional feelings was probably laid down deep in the brainstem. Of course, the full resolution of affective feelings (cerebral feelings and sentiments) surely emerges through the dynamic interactions of higher brain systems that regulate emotional states (DAMASIO 1999; PANKSEPP 1998a, 1998b). Evolutionary psychology needs to consider such possibilities, if it is to make substantive contributions to its fundamental 'mechanistic' concerns.

The Evolution of Behavior and Developmental Views in Psychology

All of what we have proposed now needs to be grounded in other key intellectual traditions. At somato-phenotypic levels, the power of genetic influences in guiding the construction of bodies and behavioral repertoires has long been affirmed by animal-husbandry practices. The heritability of temperament has also been confirmed by abundant work from behavioral-geneticists (SCOTT/FULLER 1965; FREEDMAN 1979; PLOMIN et al. 1997; HAMER/ COPELAND 1998; SEGAL 1999). Furthermore, modern neuroscience has verified the existence of homologous brain mechanisms by its demonstration of abundant structural, neurochemical and functional similarities throughout the brains of all mammals (for overview PANKSEPP 1998a).

However, when we begin to speculate about the functional organization of the higher aspects of mind-the 'natural kinds' of the cortico-cognitive brain-we proceed at our own peril if we do not fully assimilate the *developmentalist challenge*—that structure-function relations do not simply emerge from DNA codes, but as much from the many interactions between genetic information, environmental information and the ontogenetic experiences of individuals (TINBERGEN 1972; OYAMA 1985/2000; GRIFFITHS 1997). All Evolutionary Psychological endeavors should recognize that genes do not directly control mind or behavior, but only the proteins and developmental patterns that help construct specific types of brains. Equally important is the recognition that genes and brains can only operate within environmental constraints (OYAMA 1985/2000). These stipulations will help temper radically reductionistic agendas in evolutionary thinking that simply cannot work. They are also a potential saving 'grace' for our apparent proclivity to misuse genetic knowledge.

Such assertions are not offered to simply acknowledge the inextricable roles of nature and nurture in all aspects of behavior, but to highlight the fact that apparent 'natural kinds' can be produced developmentally, as well as linguistically. Due to the intrinsic ambiguities that result from our impoverished knowledge about the developmental causes of individual differences in animals, the chasm from genes to final psychobiological product cannot be credibly bridged through any form of genetic determinism, especially in humans. At the same time, the power of genetic information as a key arbiter in the construction of specific brain/mind functions (at least within 'normal' environmental constraints) should not be underestimated. In this context, most of the half-truths of previous generations in claiming that there were 'genes for behavior', may in retrospect, be ascribed simply to sloppy, short-hand forms of communication that should have only been advanced with the proviso: the developmental processes operating during ontogenesis must always be given their due (TINBERGEN 1972; OYAMA 1985/2000). This

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should be repeated as a mantra whenever one begins to fall into the trap of ascribing any form of genetic determinism to psychological matters.

Such intellectual constraints must be heeded consistently in our currently immature brain/mind sciences, where the natural order of psychological processes has to be theoretically inferred rather than directly visualized. Because of such ambiguities, there has been a long-standing and persistent resistance in psychology and behavioral neuroscience to viewing the hidden brain/mind functions as inborn faculties. Learning, guided by still mysterious reinforcement-reward processes, has continued to be accepted as the main agent of behavioral control and plasticity. As a result, the issue of how many reinforcement-reward processes and related worldgrasping mechanisms actually exist in the brain, not to mention whether they were internally experienced, remains largely undiscussed in both modern behavioral psychology and neuroscience. Now, partly because of the inroads made by evolutionary psychology (BARKOW et al. 1992; BUSS 1999) and Affective Neuroscience (PANKSEPP 1998a), there is a growing taste for such possibilities.

Since evolutionary psychology established relations with cognitive neuroscience (PINKER, 1997), a few attempts at cross fertilization have emerged (e.g., TOOBY/COSMIDES 2000). However, even with the current revolution in functional brain imaging, which seems like a blessing for visualizing intrinsic brain functions (and hence, some believe, the historical record of past adaptations), we should proceed cautiously, continually constrained by converging evidence, rather than accepting direct genetic adaptations behind every consistent phenotypic trend or brain difference that is documented with new imaging technologies (TOGA/MAZZIOTTA 2000). Since evolutionary psychologists are likely to begin using such technology in the near future, they should appreciate the many problems that accompany such approaches.

At present, brain imaging only provides a low-order, ghostly image that something of importance may be transpiring somewhere in the brain. There are, no doubt, many 'false positives' and perhaps even more 'false negatives' due to the many technical constraints that exist in such studies. No form of human brain imaging, by itself, can assure us that what is being observed is a 'natural kind'—a brain/ mind process that is strongly dictated by the way genetic factors help direct the function of certain brain circuits. Also, brain-imaging studies only provide neural correlates of psychological functions. Traditional animal studies, where brain systems are directly manipulated, as well as neuropsychological studies following cases of human brain damage and stimulation, provide better causal evidence of the functional characteristics within brain organization. Obviously, causal studies provide the best evidence upon which a scientifically sound evolutionary psychology can be built.

Some 'Prescriptions'

The aim of this paper was to critique some of the prominent views in evolutionary psychology, and to share an alternative perspective that is grounded in the ethological and comparative psychoneurological traditions that have long acknowledged the importance of natural selection in constructing the behavioral and psychological capacities of all animals. The current appeal and danger of evolutionary psychology arises from its unflinching willingness to utilize extreme modes of adaptationist thinking about the human mind, without critically distinguishing genetic adaptations from epigenetically emergent phenomena. Although the HAMILTONIAN (1964) concept of inclusive-fitness has turned out to be the most compelling evolutionary priniciple of the 20th century and an apt guide for ecological research on the social preferences of many species, those types of behavior patterns have not yet been shown to arise from genetically ingrained neural circuits in the higher regions of the human brain/mind.

We should not forget that in most mammals, including humans, social-bonds are learned to a great extent. Although social learning is based upon primitive social-emotional systems that all mammals share (PANKSEPP et al. 1978, 1980, 1984, 1985, 1988, 1994) and is surely under robust genetic control (SCOTT/FULLER 1965; PLOMIN et al. 1997; PANKSEPP/ BURGDORF/GORDON 2001), everything that mature humans do is filtered through their higher neural capacity for flexible 'intelligent' action. Perhaps all too many individuals utilize those capacities largely for their own selfish ends, but it is important to emphasize that the nature of the higher regulatory systems in humans does permit many alternative courses of action. Although our psychological tendencies are tethered to ancient emotional concerns, we can individually entertain options of our own making. Also, there are group-dynamics operating in our lives and in the ongoing procession of evolution that have barely been envisioned (LUMSDEN/ WILSON 1981; SOBER/WILSON 1998). Animals exhibit non-ge-

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netic modes of inheritance (e.g., LIU et al. 2000), and such trans-generational effects provide a changing social fabric that has enormous implications for the way we conceptualize evolutionary canalizations. Surely, differential survival of groups may lead to differential survival of brain mechanisms that only operate efficiently in groups. Such effects may emerge more rapidly via group selection than by individual selection. At the very least, these issues remain more open, especially in humans, than some selfish gene advocates would like to believe.

With the emergence of high culture and high intelligence in our species, group selection may operate in human societies in ways that few have considered in the past few decades. We must remember that in humans, within the context of cultural evolution, biological evolution can move along much more rapidly than it does in animals who do not cognitively conceptualize their place in nature (CHAGNON/ IRONS 1978; NEEL/WARD 1970). As Dan FREEDMAN, one of the first modern evolutionary psychologists, put it, "Sewall WRIGHT (1940)... consistently made the point that the same gene varies in its effect and action depending on the genes in its company... Wright has demonstrated mathematically that competition between individuals can be insignificant when compared with competition between families or competition between populations" (1979, p5). Although the classic 'group-selection' views of WYNN-EDWARDS (1962) have been widely held in disrepute (e.g., DAWKINS 1976), ever since HAMILTON (1964) introduced the compelling concept of inclusive-fitness, human mental and cultural evolution has in fact created extraordinary opportunities for alternative modes of evolutionary change. Modern genetic engineering is only the most blatant recent example of this claim. It could be argued that such possibilities are only little waves on the great sea of evolutionary progression, but perhaps it is a bit more in creatures like ourselves that have been endowed with a massive random-access type of general-purpose intelligence. To some yet unfathomed extent, we have been liberated from the crucible of a mindless biological emergence. This point is commonly acknowledged by many humanistically oriented scholars, but all too rarely by evolutionary psychologists.

At least for the human species, the excesses of selfish-gene type inclusive-fitness heuristics now need to be tempered by what we already know about mammalian and human brain/minds. Evolutionary psychology, along with the other variants of the discipline, have all too often neglected causal scientific understanding of the underlying brain processes shared by all mammals by continuing to prefer descriptions of surface processes which they believe are directly related to presumably recent human evolutionary issues. However, can we credibly utilize phases of recent human brain evolution that have left essentially no historical traces as a basis for our theorizing? Can imaginary evolutionary scenarios be used as a crystal ball to the real pre-historic EEA's that molded our brain/minds? To what extent should we consider tenuous 'modular' visions of human brain/mind evolution when more credible non-modular alternatives are already available? How do we adjudicate among the contending views? How do we incorporate the strikingly relevant evidence culled from our fellow animals into the exceedingly anthropocentric modes of thought that characterize so much of present day psychology? How shall we accept our animal heritage without demeaning our vast intelligence?

In our estimation, the type of psychological functions that evolutionary psychologists speak of, arise largely from the utilization of very old emotional capacities working in concert with newly evolved inductive abilities supported by the vast general purpose neocortical association areas. Although there are bound to be certain manifestations of emotional and motivational tendencies within these newly evolved regions of the human brain/mind, the massive modularity thesis entertained by evolutionary psychologists remains, except for certain well-accepted sensory-perceptual processes, far fetched and inconsistent with what we presently know about the higher reaches of the human brain/mind. It will rapidly become a circular discipline if it comes to rely exclusively on fMRI-type brain-imaging data for its neurological conjectures. What types of evolutionary engravings have, in fact, occurred in higher cortical areas remain anyone's guess. Processes such as the social use of our eyes, facial expressions, rhythmic gestures and prosodic intonations for instrumental purposes—perhaps even musical ability—are bound to be prominent dimensions of higher brain functions (e.g., EKMAN 1998; BOROD 2000; Emery 2000), but such general issues are too rarely considered in mainstream evolutionary psychology.

It is good to see the discipline moving toward an eager confrontation with the brain (TOOBY/COSMIDES 2000), but it should pay attention to both higher and lower brain/mind functions, cultivating a research tradition that considers matters at all relevant levels. It is among the higher cortical functions, that learning, plasticity, and epigenetically emergent software functions prevail. Investigators should be especially

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cautious about concluding what was or was not constructed by natural selection during recent brain evolution within the human species. Likewise, it is at the cortical level that we cannot extrapolate readily from the animal data. Among those recently evolved brain areas there was abundant opportunity for massive evolutionary divergence (DEACON 1997). However, we should remember that those higher systems simply cannot work without the support of the basic subcortical systems we share with our fellow animals. If critical neuro-cognitive experiments eventually demonstrate the existence of geneticallydictated, special-purpose cognitive/affective modules in the higher reaches of the human brain-mind, all humans committed to an accurate description of our species' nature should be delighted to accept them into the pantheon of scientific evidence. However, as long as no compelling neurobehavioral evidence is provided, we should continue to regard distal adaptationist stories of human evolution, even when supported by some preliminary correlative evidence, as simply another aspect of the wondrous carnival of human fancy.

In our estimation, animal brain research will be more decisive in giving a clear scientific picture of how human social behaviors are guided by past evolutionary forces. What those vast cerebral expansions that emerged during the Pleistocene probably provided was a vast symbolic capacity that enabled foresight, hindsight, and the brain-power to peer into other minds and to entertain alternate courses of action, thereby allowing humans to create the cultures that dominate our modern world.

Conclusions

Why was serious scrutiny of mental processes based on the DARWINIAN framework so greatly delayed in the brain/mind sciences? Historically, it was partly due to the embarrassment of phrenology-where mental faculties were related, with the most trifling evidence, to the shape of cerebral structures inferred from craniometry. In a similar vein, we must now wonder whether modern brain imaging is also giving us many false conclusions (especially abundant false negatives) based on modest biophysical changes in cerebral blood flow and oxygenation. The visually impressive statistical maps of brainimaging, with their islands of color suspended on ghostly MRI images of the brain, do not do justice to the actual neurodynamics that create mind. They provide only one approximation that must be supplemented by many other techniques.

With the possibility of real neuropsychological understanding, we may also need to question the potentially misleading 'saving grace' of the computational-computer revolution that has allowed investigators to readily create distorted digital views of psychological processes which are fundamentally analog in nature. As the search for heuristic computational algorithms came to be deemed a more worthy scientific enterprise among cognitive psychologists (CUMMINS/CUMMINS 2000), the possibility of a mature and fully substantive evolutionary psychology diminished. To discover what types of specialpurpose adaptive functions evolution truly created within our brain/minds, there is no substitute for integrative cross-species brain research. We are only at the beginning of that grand intellectual journey.

A discipline that is as exceedingly anthropocentric as modern evolutionary psychology is likely to make a variety of preventable mistakes if it does not fully immerse itself in neurobiological, phylogenetic and ontogenetic issues. Our impression is that the most visible form of modern evolutionary psychology is currently pursuing a rash course of over-interpretation of the human condition, simply because the inclusive-fitness idea is so tremendously compelling.

Although we subscribe fully to the idea that natural selection gave rise to the rudiments of our fundamental neuro-mental apparatus, we are disappointed by the fact that current evolutionary psychological thought (not to mention that in most of psychology) is not guided by what we already know about the neurology of emotional and motivational processes in the brains of related animals. It is equally sad to see clear disregard for the likelihood that much of our neocortex is based upon generalpurpose engineering principles rather than genetically guided modules. A top-down cognitive view may be deluded by the many emergent epigenetic specializations of the *adult* neocortex. The study of primitive emotional systems in other mammals provides a variety of parsimonious 'bottom up' tools for decoding the developing neural landscapes of higher mind functions in humans. Since the evolution of subcortical systems was probably guided by straightforward inclusive fitness issues, we anticipate that a great deal of our higher cognitive apparatus is still affected by similar influences, but certainly not in any inherently modularized ways.

What makes humans unique, perhaps more than anything else, is that we are a linguistically adept story-telling species. That is why so many different forms of mythology have captivated our cultural

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communicate with each other.

Evolutionary psychology and sociobiology are

such attractive scientific views (e.g., FREEDMAN 1979;

SCOTT 1989; SEGAL et al. 1997) that they need to be

carefully cultivated and constructed as accurately as

possible, continually constrained by genetic and

cross-species brain evidence from our fellow animals

rather than by the sea-swell of imaginary neuropsy-

chological possibilities in humans. If we continue to

imaginations since the dawn of recorded history. Evolutionary psychologists also have many intriguing stories to tell, but if we are committed to a deep evolutionary view, their current speculations should not be accepted as credible foundations for our fundamental nature. The only massive cortical modules we should be convinced of at the present time are our vast linguistically based foresight and hindsight abilities, which mediate our compulsion to tell tales to each other. Incidentally, the basic urge to speak to each other may be closely linked to anterior cingulate and adjacent frontal lobe tissues which appear to mediate certain types of pain, feelings of separa-

tion distress and thereby social sensitivities (MACLEAN 1990; PANKSEPP 1998a; MAY-BERG/MCGINNIS 2000; VOGT/ DEVINSKY 2000; VOGT/SIKES 2000). Clearly, something very interesting is happening to the social-emotional realm in these brain tissues that are of great importance in controlling our motivation to

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proceed without considering all the available evidence, we will only produce more of the polarizedviews that have been endemic to this troubled corner of evolutionary thought. Now that we have a real
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tion, we may become mired in

myth making rather than re-

maining on the shores of

sound scientific inquiry.

Note

We dedicate this paper to the memory of our esteemed colleague John Paul SCOTT (1909–2000) who first coined the term 'sociobiology' for a series of joint sessions of the American Society of Zoologists and the Ecological Society of America held initially at the AAAS meeting of 1946—a series that eventually led to the organization of the American Animal Behavior Society. Paul's research was the first to systematically analyze the heritability of behavioral tendencies in a mammalian species, specifically, temperamental differences among different strains of domesticated dogs (see SCOTT/FULLER 1965). We appreciate the realistic tradition of rigorous and respectfully complex evolutionary scholarship he promoted at BGSU and around the world.

References

- Barkow, J./Cosmides, L./Tooby, J. (eds) (1992) The Adapted Mind. Oxford Univiversity Press: New York.
- Betzig, L. (ed) (1997) Human Nature: A Critical Reader. Oxford University Press: New York.
- Bittar, E. A./Bittar, N. (2000) Biological psychiatry. JAI Press: Stamford CT.
- Bluthe, R. M./Danzer, R. (1990) Social recognition does not involve vasopressinergic neurotransmission in female rats. Brain Research 535: 301–304.
- Borod, J. C. (2000) The Neuropsychology of Emotion. Oxford University Press: New York.
- Brown, D. E. (1991) Human Universals. New York: McGraw-Hill.
- Buck, R. (1999) The biological affects: A typology. Psychological Review 106: 301–336.
- Budiansky, S. (1998) If a Lion Could Talk: Animal Intelligence

and the Evolution of Consciousness. The Free Press: New York.

- Burgdorf, J./Knutson, B./Panksepp, J. (2000) Anticipation of rewarding brain stimulation evokes ultrasonic vocalizations in rats. Behavioral Neuroscience 114: 1–8.
- Buss, D. M. (1999) Evolutionary psychology: The new science of the mind. Allyn and Bacon: Boston.
- Buss, D. M. (2000) The evolution of happiness. American Psychologist 55: 15–23.
- Buss, D. M./Haselton, M. G./Shackefortd, T. K./Bleske, A. L./ Wakefield, J. C. (1998) Adaptations, exaptations, and spandrels. American Psychologist 53: 533–548.
- Campbell, J. (1982) Grammatical Man: Information, Entropy, Language and Life. Simon and Schuster: New York.
- Carter, C. S. (1998) Neuroendocrine perspectives on social attachment and love. Psychoneuroendocrinology 23: 779– 818.
- Carter, C. S./Lederhendler, I./Kirkpatrick, B. (eds) (1999) The

Evolution and Cognition | 127 | 2000, Vol. 6, No. 2

Integrative Neurobiology of Affiliation. MIT Press: Cambridge MA.

- Chagnon, N. A./Irons, W. (eds) (1978) Evolutionary Biology and Human Social Behavior. Duxbury: North Scituate MA.
- Chen, C./Rannie, D. G./Greene, R. W./Tonegawa, S. (1994) Abnormal fear response and aggressive behavior in mutant mice deficient for alpha-calcium-calmodulin kinase II. Science 266: 291–294.
- Clark, A. (1997) Being There: Putting Brain, Body, and World Together Again. MIT Press: Cambridge MA.
- Cosmides, L./Tooby, J. (2000) Evolutionary Psychology and the Emotions. In: Lewis, M./Haviland, J. (eds) The Handbook of Emotions, 2nd edition. New York: Guilford, pp. 91–116.
- Cummins, R./Cummins, D. D. (eds) (2000) Minds, Brains, and Computers: The Foundations of Cognitive Science. Blackwell Publishers: Malden MA.
- D'Amato, F. R. (1998) Kin interaction enhances morphine analgesia in male mice. Behavioral Pharmacology 9: 369– 373.
- Damasio, A. R. (1999) The Feeling of What Happens: Body and Emotion in the Making of Consciousness. Harcourt Brace: New York.
- Damasio, A. R./Grabowski, T. J./Bechara, A./Damasio, H./ Ponto, L. B./Parvizi, J./Hichwa, R. D. (2000) Subcortical and cortical brain activity during the feeling of self-generated emotions. Nature Neuroscience 3: 1049–1056.
- Darwin, C. (1872/1998) The Expression of the Emotions in Man and Animals, 3rd edition. Oxford University Press: New York.
- Dawkins, R. (1976) The Selfish Gene. Oxford University Press: Oxford.
- Deacon, T. W. (1997) The Symbolic Species: The Co-Evolution of Language and the Brain. Norton: New York.
- Deacon, T. W. (1990) Rethinking mammalian brain evolution. American Zoologist 30: 629–705.
- Ekman, P. (1998) Universality of emotional expression? A personal history of the dispute. In: Darwin, C. (1998) The Expression of the Emotions in Man and Animals, 3rd editon. Oxford University Press: New York, pp. 363–393.
- Ellegren, H./Gustafsson, L./Sheldon, B. C. (1996) Sex ratio adjustment to paternal attractiveness in a wild bird population. Proceedings of the National Academy of Science USA 93: 11723–11728.
- Emery, N. J. (2000) The eyes have it: the neuroethology, function and evolution of social gaze. Neuroscience and Biobehavioral Reviews 24: 581–604.
- Ferguson, J. N./Young, L. J./Hearn, E. F./Matzuk, M. M./Insel, T. R./Winslow, J. T. (2000) Social amnesia in mice lacking the oxytocin gene. Nature Genetics 25: 284 – 288.
- Finlay, B. L./Darlington, R. B. (1995) Linked regularities in the development and evolution of mammalian brains. Science 268: 1578–1584.
- Fischer, H./Andersson, J. L. R./Furmark, T./Fredrikson, M. (2000) Fear conditioning and brain activity: A positron emission tomography study, Behavioral Neuroscience 114: 671–680.
- Fodor, J. (1983) The Modularity of Mind. MIT Press: Cambridge MA.
- Freedman, D. J. (1979) Human Infancy: An Evolutionary Perspective. Erlbaum: Hillsdale NJ.
- Freeman, W. J. (1999) How the Brain Makes Up its Mind. Blackwell: London.
- Fridja, N. H. (1986) The Emotions. Cambridge University Press: Cambridge UK.
- Gallese, V./Goldman, A. (1998) Mirror neurons and the sim-

ulation theory of mind-reading. Trends in Cognitive Sciences 2: 493–501.

- Gil, D./Graves, J./Hazon, N./Wells, A. (1999) Male attractiveness and differential testosterone investment in zebra finch eggs. Science 286: 126–128.
- Godfrey-Smith, P. (1996) Complexity and the Function of Mind in Nature. Cambridge University Press: New York.
- Gould, S. J. (1991) Exaptation: a crucial tool for evolutionary psychology. Journal of Social Issues 47: 43–65.
- Gould, S. J./Lewontin, R. C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proceedings of the Royal Society of London B 205: 581–598.
- Graeff, F. G. (1994) Neuroanatomy and neurotransmitter regulation of defensive behaviors and related emotions in mammals. Brazilian Journal of Medical and Biological Research 27: 811–829.
- Griffiths, P. E. (1997) What Emotions Really Are: The Problem of Psychological Categories. University of Chicago Press: Chicago.
- Hamer, D. H. (1998) Living with our genes: Why They Matter More Than You Think. Doubleday: New York.
- Hamilton, W. D. (1964) The genetical evolution of social behaviour (I and II). Journal of Theoretical Biology 7: 1–52.
- Hauser, M. D. (2000) Wild Minds: What Animals Really Think. Henry Holt & Co: New York.
- Heath, R. G. (1996) Exploring the mind-brain relationship. Moran Printing Inc: Baton Rouge LA.
- Heinrich, R, Cromarty S. I./Horner, M./Edwards, D. H/Kravitz, E. A. (1999) Autoinhibition of serotonin cells: an intrinsic regulator sensitive to the pattern of usage of the cells. Proceedings of the National Academy of Sciences USA 96: 2473–2478.
- Huber, R./Delago, A. (1998) Serotonin alters decisions to withdraw in fighting crayfish, Astacus astacus: the motivational concept revisited. Journal of Comparative Physiology A 182: 573–583.
- Ikemoto, S./Panksepp, J. (1999) The role of nucleus accumbens dopamine in motivated behavior: a unifying interpretation with special reference to reward-seeking. Brain Research Reviews 31: 6–41.
- Insel, T. (1997) The neurobiology of social attachment. American Journal of Psychiatry 154: 726–735.
- Johnsen, A./Lifjeld, J. T./Rohde, P. A./Primmer, C. R./Ellegren, H. (1998) Sexual conflict over fertilizations: female bluethroats escape male paternity guards. Behav. Ecol. Sociobiol. 43:401–408.
- Johnsen, A./Andersson, S./Örnborg, J./Lifjeld, J. T. (1998) Ultraviolet plumage ornamentation affects social mate choice and sperm competition in the bluethroat (Luscinia s.svecica): a field experiment. Proceedings of the Royal Society of London B 265: 1313–1318.
- Johnson, V. S. (1999) Why We Feel: The Science of Human Emotions. Perseus Book Group: New York.
- Kanwisher, N. (2000) Domain specificity in face perception. Nature Neuroscience 3: 759–763.
- Keverne, E.B./Fundele, R./Narasimha, M./Barton, S. C./Surani, M. A. (1996) Genomic imprinting and the differential roles of parental genomes in brain development. Developmental Brain Research 92: 91–100.
- Kim, J. (1993) Supervenience and Mind: Selected Philosophical Essays. Cambridge University Press: New York.
- Knutson, B./Wolkowitz, O. M./Cole, S. W./Chan, T./Moore, E. A./Johnson, R. C./Terpstra, J./Turner, R. A./Reus, V. I. (1998) Selective alteration of personality and social behavior by serotonergic intervention. American Journal of Psy-

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chiatry 155: 373-379.

- Komdeur (1997) Extreme adaptive modification in sex ratio of the Seychelles warbler's. Nature 385: 522–525.
- Kraemer, P. D. (1993) Listening to Prozac. Viking: New York.
- Kravitz, E. A. (1988) Hormonal control of behavior: amines and the biasing of behavioral output in lobsters. Science 241: 1775–1781.
- Kravitz, E. A. (2000) Serotonin and aggression: insights gained from a lobster model system and speculations on the role of amine neurons in a complex behavior. Journal of Comparative Physiology A 186: 221–238.
- LeDoux, J. (1996) The Emotional Brain. Simon & Schuster: New York.
- Lewis, M. D./Granic, I. (eds) (2000) Emotion, Self-Organization, and Development. New York: Cambridge Univ. Press.
- Liu, D./Diorio, J./Day, J. C./Francis, D. D./Meaney, M. J. (2000) Maternal care, hippocampal synaptogenesis and cognitive development in rats. Nature Neuroscience 3: 799–806.
- Lumsden, C. J./Wilson, E. O. (1981) Genes, Mind, and Culture: The Coevolutionary Process. Harvard University Press: Cambridge MA.
- MacLean, P. D. (1990) The Triune Brain in Evolution: Role in Paleocerebral Functions. Plenum Press: New York.
- Mauk, M. D. (2000) The potential effectiveness of simulations versus phenomenological models. Nature Neuroscience 3: 649–651,.
- Mayberg, H. S./McGinnis, S. (2000) Brain mapping: the application, mood and emotions. In: Toga, A. W./Mazziotta, J. C. (eds) Brain Mapping :The Systems. Academic Press: San Diego CA, pp. 491–522.
- Mealey, L. (1995) The sociobiology of sociopathy: an integrated evolutionary model. Behavioral and Brain Sciences 18: 523–599.
- McGuire, M. T./Troisi, A. (1998) Darwinian Psychiatry. Oxford University Press: New York.
- Neel, J. V./Ward, R. H. (1970) Village and tribal genetic distances among american indians, and the possible implications for human evolution. Proceedings of the National Academy of Sciences USA 65: 323–330.
- Nelson, E./Panksepp, J. (1998) Brain substrates of infantmother attachment: Contributions of opioids, oxytocin, and norepinepherine. Neuroscience & Biobehavioral Reviews 22: 437–452.
- Nesse, R. M./Williams, G. C. (1974) Why We Get Sick. Times Books Random House: New York.
- Nesse, R. M. (1990) Evolutionary explanations of emotions. Human Nature 1: 261–289.
- Olmstead, M. C./Franklin, K. B. (1997) The development of a conditioned place preference to morphine: effects of microinjections into various CNS sites. Behavioral Neuroscience 111: 1324–1334.
- Oyama, S. (1985/2000) The Ontogeny of Information: Developmental Systems and Evolution. Cambridge, UK: Cambridge University Press (reprinted in 2000 by Duke University Press).
- Pani, L. (2000) Is there an evolutionary mismatch between the normal physiology of the human dopaminergic system and current environmental conditions in industrialized countries? Molecular Psychiatry 5: 467–475.
- Panksepp, J. (1981) Hypothalamic integration of behavior: rewards, punishments, and related psychobiological process. In: Morgane, P. J./Panksepp, J. (eds) Handbook of The Hypothalamus, Vol. 3, Part A. Behavioral Studies of the Hypothalamus. Marcel Dekker: New York, pp. 289–487.
- Panksepp, J. (1982) Toward a general psychobiological theo-

ry of emotions. The Behavioral and Brain Sciences 5: 407–467.

- Panksepp, J. (1986a) The anatomy of emotions. In: Plutchik, R. (ed) Emotion: Theory, Research and Experience Vol. III. Biological Foundations of Emotions. Academic Press: Orlando FL, pp. 91–124.
- Panksepp, J. (1986b) The neurochemistry of behavior. Annual Review of Psychology 37: 77–107.
- Panksepp, J. (1989) The psychobiology of emotions: the animal side of human feelings. In: Gainotti, G./Caltagirone, C. (eds) Emotions and the Dual Brain. Experimental Brain Research, Series 18, pp. 31–55. Berlin: Springer-Verlag.
- Panksepp, J. (1989/1999) Altruism and helping behaviors, neurobiology. In: Edelman, G. (ed) The Encyclopedia of Neuroscience. Boston: Birkhauser, pp. 55–57.
- Panksepp, J. (1990a) The psychoneurology of fear: evolutionary perspectives and the role of animal models in understanding anxiety. In: Burrows, G. D./Roth, M./Noyes Jr., R. (eds) Handbook of Anxiety, Vol. 3: The Neurobiology of Anxiety. Elsevier: Amsterdam, pp. 3–58.
- Panksepp, J. (1990b) Can mind and behavior be understood without understanding the brain?: a response to Bunge. New Ideas in Psychology 8: 139–149.
- Panksepp, J. (1990c) Gray zones at the emotion-cognition interface: a commentary. Cognition and Emotion 4: 289– 302.
- Panksepp, J. (1992) A critical role for 'affective neuroscience' in resolving what is basic about basic emotions. Psychological Review 99: 554–560.
- Panksepp, J. (1993a) Neurochemical control of moods and emotions: amino acids to neuropeptides. In: Lewis, M./ Haviland, J. (eds) The Handbook of Emotions. Guilford: New York, pp. 87–107.
- Panksepp, J. (1993b) Rough-and-tumble play: a fundamental brain process. In: MacDonald, K. B. (ed) Parents and Children Playing. SUNY Press: Albany NY, pp. 147–184.
- Panksepp, J. (1998a) Affective Neuroscience: The Foundations of Human and Animal Emotion. Oxford University Press: New York.
- Panksepp, J. (1998b) The periconscious substrates of consciousness: affective states and the evolutionary origins of the SELF. Journal of Consciousness Studies 5: 566–582.
- Panksepp, J. (1998c) Attention deficit hyperactivity disorders, psychostimulants, and inteolerance of childhood playfulness: a tragedy in the making? Current Directions in Psychological Sciences 7: 91–98.
- Panksepp, J. (2000a) Emotions as natural kinds within the mammalian brain. In: Lewis, M./Haviland, J. (eds) The Handbook of Emotions, 2nd edition. Guilford: New York, pp. 137–156.
- Panksepp, J. (2000b) Affective consciousness and the instinctual motor system: the neural sources of sadness and joy. In: Ellis, R./Newton, N. (eds) The Caldron of Consciousness: Motivation, Affect and Self-organization, Advances in Consciousness Research. Amsterdam: John Benjamins Pub. Co.
- Panksepp, J. (2000c) The neurodynamics of emotions: an evolutionary-neurodevelopmental view. In: Lewis, M. D./ Granic, I. (eds) Emotion, Self-Organization, and Development, pp. 236–264. New York: Cambridge Univ. Press.
- Panksepp, J. (2000d) The neuro-evolutionary cusp between emotions and cognitions: implications for understand consciousness and the emergence of a unified mind science. Consciousness & Emotion 1: 17–56.
- Panksepp, J. (2000e) The riddle of laughter: neural and psychoevolutionary underpinnings of joy. Current Directions

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in Psychological Sciences 9: 183-186.

- Panksepp, J. (2001) The long-term psychobiological consequences of infant emotions: prescriptions for the 21st century. Infant Mental Health Journal (in press).
- Panksepp, J./Burgdorf, J. (1999) Laughing rats? Playful tickling arouses high frequency ultrasonic chirping in young rodents. In: Hameroff, S./Chalmers, D./Kazniak, A., Toward a Science of Consciousness III. Cambridge MA: MIT Press, pp. 231–244.
- Panksepp, J./Burgdorf, J. (2000) 50k-Hz chirping (laughter?) in response to conditioned and unconditioned tickle-induced reward in rats: effects of social housing and genetic variables. Behavioral Brain Research 115: 25–38.
- Panksepp, J./Burgdorf, J./Gordon, N. (2001) Toward a genetics of joy: Breeding rats for 'laughter'. In: Kazniak, A. (ed) Emotions, Qualia, and Consciousness. World Scientific: London (in press).
- Panksepp, J./Herman, B./Conner, R./Bishop, P./Scott, J. P. (1978) The biology of social attachments: opiates alleviate separation distress. Biological Psychiatry 9: 213–220.
- Panksepp, J./Herman, B. H./Villberg, T./Bishop, P./DeEskinazi, F. G. (1980) Endogenous opioids and social behavior. Neuroscience and Biobehavioral Reviews 4: 473–487.
- Panksepp, J./Knuston, B./Burgdorf, J. (2001) The role of emotional brain systems in addictions: A neuro-evolutionary perspective. Addiction (in Press).
- Panksepp, J./Nelson, E./Siviy, S. (1994) Brain opioids and mother-infant social motivation. Acta Paediatrica 397: 40– 46.
- Panksepp, J./Normansell, L. A./Herman, B. Bishop, P./Crepeau, L. (1988) Neural and neurochemical control of the separation distress call. In: Newman, J. D. (ed) The Physiological Control of Mammalian Vocalization. Plenum Press: New York, pp. 263–299.
- Panksepp, J./Siviy, S./Normansell, L. (1984) The psychobiology of play: theoretical and methodological perspectives. Neuroscience and Biobehavioral Reviews 8: 465–492.
- Panksepp, J./Siviy, S. M./Normansell, L. A. (1985) Brain opioids and social emotions. In: Reite, M./Fields, T. (eds) The Psychobiology of Attachment and Separation. Academic Press: New York, pp. 3–49.
- Parrot, W. G./Schulkin, J. (1993) Neuropsychology and the cognitive nature of emotions. Cognition and Emotion 7: 43–59.
- Penton-Voak, I. S./Perrett, D. I. (2000) Female preference for male faces changes cyclically: Further evidence. Evolution and Human Behavior 21: 39–48.
- Perrett, D. I./Lee, K. J./Penton-Voak, I./Rowland, D./Yoshikawa, S./Burt, D. M./Henzl, S. P./Castles, D. L./Akamatsu, S. (1998) Effects of sexual dimorphism on facial attractiveness. Nature 394: 884–887.
- Pfaff, D. W. (1999) Drive: Neurobiological and Molecular Mechanisms of Sexual Motivation. MIT Press: Cambridge MA.
- Pinker, S. (1994) The Language Instinct. Morrow: New York.
- Pinker, S. (1997) How the Mind Works. Norton: New York.
- Plomin, R. (1999) Genetics and general cognitive ability. Nature, Vol. 402 (Suppl): C25–29.
- Plomin, R./DeFries, J. C./McClearn, G. E./Rutter, M. (1997) Behavior Genetics, 3rd edition. New York: W.H. Freeman and Co.
- Rizzolatti, G./Fadiga, L./Gallese, V./Fogassi, L. (1996) Premotor cortex and the recognition of motor actions. Brain Research and Cognition 3: 131–141.
- Robins, R. W./Gosling, S. D./Craik, K. H. (1999) An empirical analysis of trends in psychology. American Psychologist

54: 117-128.

- Robinson, T. E./Berridge, K. (1993) The neural basis of drug craving: an incentive-sensitization theory of addiction. Brain Research Reviews 18: 247–291.
- Rolls, E. T. (1999) The Brain and Emotion. Oxford University Press: Oxford UK.
- Rosen, J. B./Schulkin, J. (1998) From normal fear to pathological anxiety. Psychological Review 104: 325–350.
- Salmon, C./Daly, M. (1996) On the importance of kin relations to Canadian women and men. Ethology and Sociobiology 17: 289–297.
- Samuels, R. (1998) Evolutionary psychology and the massive modularity hypothseis. The British Journal for the Philosophy of Science 49: 575–602.
- Schaffner, K. F. (1998) Genes, behavior, and developmental emergentism: one process, indivisible? Philosophy of Science 65: 209–252.
- Scheibel, A. B./Schopf, J. W. (eds) (1997) The Origin and Evolution of Intelligence. Jones and Bartlett: Boston.
- Scott, J. P./Fuller, J. L. (1965) Genetics and the Social Behavior of the Dog. University of Chicago Press: Chicago.
- Scott, J. P. (1989) The Evolution of Social Systems. Gordon and Breach Science Publishers: New York.
- Segal, N. L./Weisfeld, G. E./Weisfeld, C. C. (eds) (1997) Uniting Psychology and Biology: Integrative Perspectives on Human Development. American Psychological Association: Washington DC.
- Segal, N. L. (1999) Entwined Lives: Twins and What They Tell Us About Human Behavior. Dutton: New York.
- Sheldon, B. C./Ellegren, H. (1998) Paternal effort related to experimentally manipulated paternity of male collared flycatchers. Proceedings of the Royal Society of London 265: 1737–1742.
- Shand, A. F. (1920) The Foundations of Character: Being a Study of the Tendencies of the Emotions and Sentiments. MacMillan and Co: London.
- Silverman, I./Choi, J./Mackewn, A./Fisher, M. Moro, J./Olshansky, E. (2000) Evolved mechanisms underlying wayfinding: further studies on the hunter-gatherer theory of spatial sex differences. Evolution and Human Behavior 21: 201–213.
- Sober, E./Wilson, D. S. (1998) Unto Others. Harvard University Press: Cambridge MA.
- Spence, S. A./Frith, C. D. (1999) Towards a functional anatomy of volition. Journal of Consciousness Studies 6: 11–30.
- Stevens, A./Price, J. (1996) Evolutionary Psychiatry. Routledge: London.
- Thornhill, R./Palmer, C. T. (2000) A Natural History of Rape: Biological Bases of Sexual Coercion. MIT Press: Cambridge MA.
- Tinbergen, N. (1972) Functional ethology and the human sciences. Proceedings of the Royal Society of London, vol. 182B, pp. 385–410.
- Toga, A. W./Mazziotta, J. C. (eds) (2000) Brain Mapping: The Systems. Academic Press: San Diego CA.
- Tomasello, M. (1999) The Cultural Origins of Human Cognition. Harvard University Press: Cambridge MA.
- Tooby, J./Cosmides, L. (2000) Toward mapping the evolved functional organization of mind and brain. In: Gazzaniga, M. S. (ed) The New Cognitive Neuroscience (2nd edition). MIT Press: Cambridge MA, pp. 1167–1178.
- Vanderhaeghen, P./Lu, Q./Prakash, N./Frisen, J./Walsh, C. A./Frostig, R. D./Flanagan, J. G. (2000) A mapping label requaired for normal scale of body representation in the cortex. Nature Neuroscience 3: 358–365.
- Vogt, B. A./Devinsky, O. (2000) Topography and relation-

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ships of mind and brain. Progress in Brain Research 122: 11-22.

- Vogt, B. A./Sikes, R. W. (2000) The medial pain system, cingulate cortex, and parallel processing of nociceptive information. Progress in Brain Research 122: 223–235.
- Winslow, J. T./Hastings, N./Carter, C. S./Harbaugh, C. R./Insel, T. R. (1993) A role for central vasopressin in pair bonding in monagamous prairie voles. Nature 365: 544–548.
- Welch, A. M./Semlitsch, R. D./Gerhardt, H. C. (1998) Call duration as an indicator of genetic quality in male gray tree frogs. Science 280: 1928–1930.
- Weisfeld, G. E. (1997) Discrete emotions theory with specific reference to pride and shame. In: Segal, N.L./Weisfeld, G.E./Weisfeld, C.C. (eds) Uniting Psychology and Biology: Integrative Perspectives on Human Development, pp. 419–443. American Psychological Association: Washington DC.
- Wilson, E. O. (1975) Sociobiology. Cambridge MA: Harvard Univ. Press.
- Wimmer, M. (1995) Evolutionary roots of emotions. Evolution and Cognition 1: 38–50.

- Wimmer, M./Ciompi, L. (1995) Evolutionary aspects of affective-cognitive interactions in the light of Ciompi's concept of 'Affect-Logic'. Evolution and Cognition 2: 37–58.
- Winslow, J. T./Hastings, N./Carter, C. S./Harbaugh, C. R./Insel, T. R. (1993) A role for central vasopressin in pair bonding in monogamous praerie voles. Nature 365: 544–548.
- Wright, R. (1994) The Moral Animal. Academic Press: New York.
- Wright, S. (1940) The statistical consequences of Mendelian heredity in relation to speciation. In: Huxley, J. (ed) The New Systematics. Oxford University Press: New York.
- Wynn-Edwards, V. C. (1962) Animal Dispersion in Relation to Social Behavior. Edinburg: Oliver/Boyd.
- Young, L. J./Nilsen, R./Waymire, K. G./MacGregor, G. R./Insel, T. R. (1999) Increased affiliative response to vasopressin in mice expressing the V1a receptor from a monogamous vole. Nature 400: 766–768.
- Zajonc, R. B. (2000) Feeling and thinking: closing the debate over the independence of affect. In: Forgas, J. P. (ed) Feeling and Thinking: The Role of Affect in Social Cognition. Cambridge University Press: New York, pp. 31–58.