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ADAPTATION VERSUS PHYLOGENY: THE ROLE OF ANIMAL PSYCHOLOGY IN THE STUDY OF HUMAN BEHAVIOR

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ABSTRACT: Advocates of Darwinian approaches to the study of behavior are divided over what an evolutionary perspective is thought to entail. Some take "evolution-mindedness" to mean "phylogeny-mindedness," whereas others take it to mean "adaptation-mindedness." Historically, comparative psychology began as the search for mental continuities between humans and other animals: a phylogenetic approach. Independently, ethologists and now behavioral ecologists have placed far more emphasis on the niche-differentiated mental abilities unique to the species being investigated: an adaptive approach. We argue that the output of complex, dynamical systems can be dramatically changed by only minor changes in internal structure. Because selection acts on the consequences of behavior, the behavioral output of the psyche will be easily shaped by adaptive demands over evolutionary time, even though the modification of the neurophysiological substrate necessary to create such adaptive changes may be minor. Thus, adaptation-mindedness will be most illuminating in the study of cognition and behavior, whereas phylogeny-mindedness will be most illuminating in the study of their neurophysiological substrates. Similarly, a phylogenetic approach to cognition and behavior is likely to cause one to overlook our most interesting, complexly designed species-typical traits, whereas using animal psychology to exfoliate general principles of behavioral ecology represents our best hope of understanding humanity's many zoologically unique characteristics.

Darwin, with the publication of the *Origin of Species* (1859) and the *Descent of Man* (1871), united the human and the animal worlds into a single system by proposing an explanation for species' characteristics, including their similarities and differences from each other, in terms of the operation of intelligible natural causal processes. By tying all animals together in a single tree of descent, Darwin made the study of every species relevant to the study of every other species. Animals drawn from different species are separated only by phylogenetic distance; character differences separating different phylogenetic groups were produced either by chance, or they were driven by niche-differentiating selection pressures.

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This scientific account of the nature of living things embedded human characteristics in the world of natural cause and effect, and constituted a radical attack on the nearly universally accepted doctrine of total human singularity: the idea of humans as a special divine creation, or as outside of nature, or as subject to principles—supernatural or otherwise—totally alien to those operating in the rest of the world. Darwin's departure was so radical that the human sciences are still trying to come to terms with it, and the debate about human singularity remains with us today. The guise in which this debate continually re-emerges changes—from claims about reason, or intelligence, or language, or learning, or emergent social processes, or the superorganic nature of human culture—but the attachment to the idea of humans as subject to entirely unique principles is, to this day, the centerpiece of persisting, anti-Darwinian arguments (e.g., Durkheim, 1962; Kroeber, 1952; Sahlins, 1976). Implicit in the Darwinian revolution is the recognition that however interesting and endearing we humans might be to ourselves, we are simply one species out of an entire ocean of species; if humans are not the product of unique principles, if we are simply one causal outcome in a larger scientific landscape, then there is potentially a general and principled science that encompasses the entire animal world (Darwin, 1871; Williams, 1966; Staddon, 1988; Tooby & De Vore, 1987).

There are three positions one might take on human singularity. The first is that humans are not unique, but rather are typical animals (e.g., Skinner, 1938, 1953, 1957; see also Macphail, 1987). Although this view is clearly true when humans and nonhuman animals are compared along certain dimensions, such as in terms of their biochemical and cellular processes, for many other dimensions such a view is difficult to sustain, given human agriculture, machine tools, VCRs, ping pong, nonsense verse, deconstructivist architecture, and so on. Much of manifest human behavior appears to be qualitatively different from that of other animal species.

A second possible position derives from traditional religious and philosophical views, echoed in modern form throughout the social sciences (e.g., Descartes, 1977; Durkheim, 1962; Evans-Pritchard, 1954; Geertz, 1973; Kroeber, 1952; Radcliffe-Brown, 1977; Sahlins, 1976): that humans are so singular, so incomparable, that they are either outside of nature, or at least a natural phenomenon *sui generis*, governed by their own special and incommensurate laws. More precisely, this position is that humans may (or may not) be legitimate objects of scientific study, but that the principles that created them or that govern them are unique, not derived from or applicable to any other species—that humans cannot be analyzed with conceptual tools other than those specially devised for understanding them. This, of course, means that that evolution is irrelevant, and that other animals are irrelevant, separated from humans by an unbridgeable gulf (Sahlins, 1976).

The third view is that humans have many unique, zoologically unprecedented properties that make us unlike any other species, but that this is not because humans are the product of unique principles particular to humans, but rather because we are the product of a unique combination of general evolutionary principles, which act across the field of animal life. Other forms of life also manifest zoologically strange features, such as the eusocial insects, with their separate castes linked to their bizarre genetic systems (Wilson, 1971). Yet, understanding them proved generally illuminating to our understanding of evolutionary principles, such as kin selection, that apply to all animals (Alexander, 1974; Hamilton, 1964; Williams & Williams, 1957; Williams, 1966; Wilson, 1975). By looking at each species as a unique combination of general evolutionary principles, it is possible to deduce what these natural causal principles are, and to see how, in each instance, they fit together in a unique, yet fully comprehensible way (Alexander, 1971, 1974; Tooby & DeVore, 1987).

Darwin himself, along with his contemporaries, realized that the most controversial of his claims was that the evolutionary perspective applied with equal force to the psychological as well as the physiological (Darwin, 1873). Since Descartes, educated belief was quite willing to hold that the physical body was a machine, subject to physical law, and that animals were automatons, like the water-powered robots in the gardens of Louis XIV. It was mental phenomena, believed to exist only in humans, such as reason, emotions, goal-seeking, language, and culture, that were separated off by religious belief and Cartesian dualism into the extra-physical, extranatural domain of the soul, the mental, the psychical (Descartes, 1977). It was this dualism that Darwin's much misunderstood concept of mental continuity was addressed to, and indeed was intended to refute: the dualistic claim that mental phenomena in humans represented a qualitatively different essence, a spiritual agency, constituting an abyss that evolutionary explanations could not bridge (Darwin, 1873). Darwin argued that mental faculties were explicable in the same evolutionary terms that accounted for the origin of species and the acquisition of their physiological characteristics—a position that Alfred Russell Wallace, co-originator of the theory of natural selection, was not willing to endorse: Wallace (1904) felt that human mental faculties required supernatural explanation. [Darwin's doctrine of mental continuity was subsequently overliteralized by early comparative psychologists into the idea that all animals existed on a linear continuum, with only quantitative differences in their capacities (see Hodos & Campbell, 1969, and Lockard, 1971, for a critical discussion of this issue; see Macphail, 1987, for a post-behaviorist defense of the doctrine of mental continuity)]. So Darwin's achievement was more than just the principled unification of the human, animal, and plant worlds: It was

also the principled unification of the mental and physical worlds, joining the mental and physical characteristics of humans and other animals into the same system of causation, created by mechanistic evolutionary principles. This allowed a radical transformation of biology and psychology as sciences (Dawkins, 1976; 1986). Instead of being descriptive, particularistic sciences, fueled by unguided observation, the cataloguing of phenomena, and the inductive, atheoretical search for regularities, biology and psychology could be seen as grounded in an elegant set of mechanistic evolutionary principles that provided a causal explanation of how each species acquired its distinctive characteristics—its design.

Since Darwin's time, despite the appealing prospect of a powerful, general, evolutionary psychology, evolutionary approaches to psychology have waxed and waned in popularity several times, with, for example, the long behaviorist interregnum, motivated by the anti-Darwinian belief that learning and environmentalist influences somehow insulate behavior from evolutionary shaping and analysis (Skinner, 1953; Boakes, 1984). As evolutionary-oriented psychologists ourselves, we hope that finally, evolutionary psychology has arrived on the scene permanently, anchored this time by a deeper and more balanced understanding of the nature-nurture issue (Daly & Wilson, 1983; Lehrman, 1970; Lorenz, 1965; Marler and Hamilton, 1966; Mayr, 1974; Staddon, 1983; Symons, 1987; Tinbergen, 1951; for discussion, see Cosmides & Tooby, 1987; Tooby, 1985; Tooby & De Vore, 1987; Tooby & Cosmides, in press), and by more comprehensive and useful models of the evolutionary process (e.g., Hamilton, 1964; Williams, 1966; Dawkins, 1976, 1982).

Unfortunately, however, there are fundamental differences in what an evolutionary perspective is thought to entail, generating substantial confusion. Two of the most important evolutionary principles accounting for the characteristics of animals are (1) common descent, and (2) adaptation driven by natural selection. Some take "evolution-mindedness" (Symons, 1987) to mean "phylogeny-mindedness," the search for phylogenetic continuities implied by the inheritance of homologous features from common ancestors. Others take evolution-mindedness to mean "adaptation-mindedness," the search for adaptive design, which usually entails the examination of niche-differentiated mental abilities unique to the species being investigated. Historically, comparative psychology began as the search for mental continuities between humans and other animals (Lockard, 1971; Hodos & Campbell, 1969): a phylogenetic approach that persists, in some measure, to the present (e.g., Boakes, 1984; Macphail, 1987). Independently, ethologists (subsequently joined by behavioral ecologists and many modern comparative psychologists) have placed far more emphasis on animal psychology as case studies in adaptive design (e.g., Alcock, 1989; Daly & Wilson, 1983; Dewsbury, 1984; Gould, 1982; Krebs & Davies, 1984; Staddon, 1988; Tinbergen, 1951; see discussion in Tooby & DeVore, 1987). The phylogeny-

minded tend to believe that the study of animal psychology provides observations that directly parallel human mental processes (Macphail, 1987), whereas the adaptation-minded tend to believe that the psychology of each species is distinct, and that direct leaps from one species to another are speculative and unfounded.

One can see the interplay of these sentiments in the ape-language controversy: Half of the scientific audience cheers for the apes, hoping they can duplicate human linguistic feats, while the other half is confident that the apes' linguistic abilities will prove very limited. The phylogeny-minded form the apes' cheering section: They reason that if a human can learn a language, then our nearest relatives should be able to do so as well. The adaptation-minded are skeptics in the ape language controversy: They (correctly) see the acquisition of a language as a species-specific mental ability, requiring highly complex and specialized cognitive mechanisms that are not likely to be shared by other primates, who were not selected to participate in communication through linguistic behavior (Chomsky, 1975).

Animals from different species are similar to each other in psychological architecture because of (1) common inheritance, (2) the same selection pressures operating on different species, or (3) both. Animals from different species differ in psychological architecture because of (1) independent descent, (2) the operation of different selection pressures on different species, or (3) random divergence. Both adaptive and phylogenetic components of the evolutionary approach have value, but their relative validity depends on exactly what level of psychological investigation they are applied to.

To understand why this is so, it is necessary to deal with the issue of the complexity and domain-specificity of psychological mechanisms. As we and others have argued elsewhere (Cosmides & Tooby, 1987; Rozin, 1976; Symons, 1987), an evolutionary perspective leads to the conclusion that although the psyche has some domain-general mechanisms, it must also include many domain-specific, function-specific mechanisms. This view draws support from artificial intelligence, whose history has largely been the history of discovering that information-processing procedures must be very complex indeed if they are to perform even very simple tasks (e.g., moving around a half a dozen blocks in a small area; see, e.g., Boden, 1977; Brown, 1987; Minsky, 1986; Cosmides & Tooby, 1989). Work in cognitive science and artificial intelligence (AI) has shown that mechanisms capable of solving even supposedly simple real-world cognitive tasks must contain very complex "innate" prespecified procedures and/or information, matched narrowly to the structural features of the domains within which they are designed to operate (Marr, 1982; Chomsky, 1975, 1980; Fodor, 1983). AI programs are complex and function-specific because the world is itself complex in ways that are not logically analyzable or deducible without an enormous amount of a

priori knowledge: In order to solve a task, you must already know a great deal about the nature of the circumstances in which the task is embedded. Of course, for "natural intelligence," as opposed to artificial intelligence, the origin of such necessary *a priori* knowledge and procedures is readily understood: Hundreds of thousands of generations of exposure to recurrent adaptive problems selected for minds that came preequipped with mechanisms tuned to solving those problems (Cosmides & Tooby, 1987).

The process of adaptation through natural selection is what constructs mental mechanisms, with their functional characteristics; common descent can only conserve them. Adaptations evolve in response to selection pressures, some of which are very general (such as the requirement to see, or to function in three-dimensional space), whereas others can be ranked as increasingly specific, down to those selection pressures that act uniquely on a single species. Adaptations, consequently, will range from those that many species hold in common, to those held by some, to those specific to a single species. For these reasons, the adaptive approach often, but by no means always, involves claims of niche-differentiated mental abilities unique to the species being investigated. Shepard's (1984) work on the mental representation of motion in space, or Staddon's (1987) work on learning as inference, for example, represent the analysis of universal selection pressures general to the psychology of different animal species. Language acquisition, production, and comprehension, on the other hand, are the result of selection pressures that have only impinged on humans, although the function language serves for humans may reflect selection pressures that are broader in scope. This is why adaptation-minded evolutionists are so skeptical of expansive claims about the linguistic abilities of apes: Language was simply not part of their social environment, and clearly requires complex, specialized, innate psychological mechanisms, as Chomsky (1975, 1980) has so persuasively argued.

If a species is analyzed at the level of total behavioral output, and viewed as an integrated system, then species look very different from one another, and reasoning from species to species appears conjectural. For example, the early literature on territoriality or aggression (Ardrey, 1966; Lorenz, 1966¹), which reasoned from the behavior of a scattered handful of species to human violence and warfare, had little to recommend it. Similarly, anthropological models of human evolution have been led seriously astray by the series of animal models that have been proposed: baboons, or chimpanzees, or hunting dogs behave in a certain fashion, and therefore it was asserted that early humans did as well (Tooby & DeVore, 1987).

¹In fairness, it should be pointed out that this popular book (Lorenz, 1966) was very uncharacteristic of Lorenz's other work, in which he carefully explored and documented species-specific adaptation.

However, behavioral output is the combined simultaneous output of all psychological mechanisms activated in an animal at the time: A change in any one mechanism may affect the combined interacting output, making this level the most variable between species. Consequently, the only kind of analysis that makes this kind of approach valid is one that matches different species' behavior against selection pressures, finding regularities in their relationships, as in behavioral ecology (see, e.g., Clutton-Brock & Harvey, 1979). Behavioral ecology is the study of selection pressures, and of the behaviorally-described adaptations that have evolved in response to them.

However, if one drops below the level of total behavioral output, and as one decomposes the psyche into different psychological mechanisms, continuities (and discontinuities) from one species to another become far more apparent. Substantial design complexity is required to solve most specific adaptive problems, and this necessary complexity has several implications for whether the study of animal behavior is relevant to the study of human behavior:

1. Because selection tends to work step by step, complex systems take time to evolve, and wholly new psychological mechanisms do not appear rapidly. The amount of complex psychological adaptation to a problem will be proportional to the length of time selection has been operating, as well as the intensity of the selection pressure. For example, mother-infant relations are considerably more ancient than father-infant relations, and so mothers can be expected to have more specialized and reliable psychological mechanisms than fathers (Tooby & DeVore, 1987). Many human maternal psychological mechanisms may be shared among apes, or monkeys, or even mammals (e.g., oxytocin release during birth triggering imprinting of the mother on the neonates; Konner, 1982). On the other hand, significant paternal care is a human evolutionary novelty within the great ape lineage, and hence is an adaptively-driven, niche-differentiated selection pressure operating to produce psychological mechanisms unique to human males. However, paternal care, though recent in the sense of having emerged after the human lineage split off from the other great apes, may still be several million years old. Language is another case of a post-divergence psychological capacity. Very recent developments, such as agriculture, cities, or contraception, can be expected to have called forth no new psychological mechanisms or complex adaptations, because they have not existed long enough for selection to act (Symons, 1987; Cosmides & Tooby, 1987).

2. The requirement of complex design for effective psychological mechanisms means that, once a problem has been solved in an evolutionary lineage, the psychological mechanism generally will be retained, passed on to all descendent lineages. Just as with physical organs, mental organs (Chomsky, 1980) can show substantial structural continuity from species to species. This is what makes psychological experi-

mentation on one species valuable and illuminating for related species. Such continuity from species to related species will be present to the extent that the mechanism evolved prior to their phylogenetic divergence, and to the extent that the selection pressures responsible remain constant from species to species. Over time, mechanisms may indeed be modified or refined, but it is relatively unlikely that such mechanisms will be rapidly or completely supplanted. This has particular application to humans, where an entire range of standard adaptive functions, like eating, parenting, mating, and so on, have been widely held to have been entirely supplanted by equipotential, culture-learning mechanisms (Geertz, 1973; Kroeber, 1952; Sahllins, 1976). Anthropologists frequently claim that although humans may behave in certain respects like closely related species, it is for entirely different, "cultural," reasons (Sahllins, 1976).

3. If psychological architecture involves an intricate series of very complex, domain-specific mechanisms, then adaptation-mindedness is more important if the level being examined is behavior or the cognitive structure of the mechanisms regulating behavior. Correspondingly, phylogeny-mindedness may be more important in examining the physiological and neurological substrates of behavior. This is because the output of complex, dynamical systems can be completely altered by only minor changes in internal structure (Sparrow, 1982). Where output of a system is determined by the combinatorial interaction of many subsystems, changing any part of the interaction can completely change the output behavior of the system: Turning off the ignition of the car, or turning the steering wheel, or changing the diameter of one wheel, or removing the distributor, does not incrementally alter the behavior of the car; it changes its behavior qualitatively and dramatically.

The thought experiments of Valentino Braitenberg (1984) elegantly demonstrate that the behavioral output of complex, dynamical systems analogous to psychological mechanisms can be radically modified by minor changes in internal structure. In his book, *Vehicles: Experiments in Synthetic Psychology*, Braitenberg systematically explores the properties of simple "vehicles" (organisms) that consist of sensors connected to motors, and shows the richly intricate behavioral complexity that can emerge from even very simple structures. Step by step he shows how the behavior of these simple vehicles can be radically refashioned by an incremental change in a motor's threshold of activation, by a shift in the relative sensitivity of sensors, by changing the function relating stimulus intensity to motor speed from monotonic to nonlinear, by adding internal connections, and so forth. The more sensors and internal connections the vehicles had, the more a minor change in a subcomponent would transform the final behavioral output of the system in complex and interesting ways.

This finding translates directly from engineered or imagined systems to biological ones. Small lesions or the administration of minute quantities of drugs may have striking effects on behavior. Embryological processes are notorious for their sensitivity (Gilbert, 1985; Gould, 1977). In fact, even in fully matured and developmentally stabilized organisms, it is difficult to find psychological mechanisms that do not display this general characteristic. For example, entire constellations of behaviors can be turned on or off in rats by the relative balance of two neurotransmitters, norepinephrine and serotonin, a process that can be experimentally manipulated by a minor drug-induced change (Ellison, 1979). These experimental manipulations could be heritably duplicated by, for example, a shift in the thresholds at which these neurotransmitters act. According to Ellison, serotonin-depleted rats engage in behaviors that are typical of rats "out in the world"—feeding, fighting, watching for predators, and so on. In familiar environments, serotonin-depleted rats spend more time out of their burrows: they eat more food and take their meals more frequently, they are hyperactive and exploratory, and they become hyperaggressive and competitive, especially at feeding time. In novel environments, they appear "frightened and paranoid": they are hypervigilant, they "freeze" frequently, and they try to stay out of sight. In contrast, norepinephrine-depleted rats act somewhat like rats who are at rest, safe in their burrows. In a familiar environment they tend to stay in their burrows, and when they do venture out they are inactive, are the last to come to feedings, underconsume food, and tend to lose battles, gradually falling to the bottom of the dominance hierarchy. In novel environments they do not show the predator-wariness of the serotonin-depleted rats: they are not vigilant, they rarely "freeze," and they do not hide.

In this case, a chemical switch turns entire suites of behaviors on and off, modulating a (normal) animal's behavior in adaptively appropriate ways. Once such switches have evolved, however, relatively modest modifications in them can form the substrate for substantial subsequent evolutionary change. A case can be made that the evolutionary divergence of the spotted hyena (*Crocuta crocuta*) reflects such a process (the following discussion is based on Alcock, 1989: pp. 207-209; Ewer, 1973; Gould, 1982: pp. 463-466; Gould, 1981; Kruuk, 1972; Racey & Skinner, 1979; and Stewart, 1987).

Female spotted hyenas present a constellation of traits, both behavioral and morphological, that are unusual in the mammalian world. Unlike the typical mammalian pattern, and more importantly, unlike all other hyena species, female spotted hyenas are larger than the males, lead their clans in hunting and territorial defense, and tend to dominate the males, even those that are slightly larger than themselves. In addition, the female's clitoris and labia are enlarged and folded such that

they resemble the penis and scrotum of the male hyena. As a result, the two sexes are difficult to distinguish by appearance.

It appears that this entire constellation of traits, which represents a marked departure from the typical mammalian pattern, may have evolved in substantial measure via a modification of a simple chemical switch. Unlike other hyenas, which live in small groups and hunt small game, spotted hyenas live in large clans of up to 100 individuals, hunt large game, and compete fiercely for meat from the animals they kill. Stewart (1987) has argued that these factors have selected intensively for aggressive, dominant females. Because androgens, such as testosterone, regulate aggressivity and dominance in mammals, Ewer (1973) hypothesized that female spotted hyenas would have a high level of androgens in their blood. This proved to be the case: in the spotted hyena, the blood androgen level of females is equal to that of males (Racey & Skinner, 1979).

Selection for dominant, aggressive females via the modification of this chemical switch appears to have had an interesting side-effect: the development of a sham penis and scrotum in females. Testosterone is the agent responsible for masculinizing mammalian embryos: the same embryonic tissue will develop into a penis and scrotum, or into a clitoris and labia, depending on whether it is exposed to high levels of testosterone during the critical developmental period. Because a pregnant spotted hyena has (phylogenetically) unprecedented levels of androgens in her blood, the female fetuses she carries are bathed in androgens, and, as a consequence, develop external genitalia of a male, as well as an array of other phenotypic properties phylogenetically and developmentally more characteristic of males. In comparison, the adult females of other hyena species have low blood androgen levels, and their daughters do not develop male-like characteristics such as greater size, aggressiveness or sham penises and scrotums (Racey and Skinner, 1979). Once present, the ancestral female spotted hyena's sham genitalia were further elaborated by natural selection, and they are now used in the kind of communicative social displays characteristic of all male hyenas.

We are not arguing that all of the integrated adaptively organized traits that differentiate spotted hyenas from their closest relatives were brought about by a single change. Given the evolutionary time available to improve and elaborate adaptively organized systems of traits after speciation, and the improbability that a single change could yield exactly the outcome necessary, it would be very surprising if a single change were all that was involved. There are undoubtedly many additional modifications throughout the design of the spotted hyena's inherited phenotype that were tuned and elaborated through subsequent selection acting on its psychology and morphology. For example, the female mimicry of the male genitalia appears to be too perfect to have been brought about entirely by androgen induction. Nevertheless, there is substantial evi-

dence suggesting that the major avenue of change was a simple modification in the level of circulating androgens in adult females.

Thus, a minor quantitative change in the internal structure of ancestral spotted hyenas—a change in the level of blood androgens—may have been primarily responsible for a dramatic transformation in the behavior, the psychology, the social system, and even the morphology, of the female spotted hyena, differentiating it not only from its phylogenetically closest relatives, but from the mammalian baseline as well. One can see in this account that in terms of the social system and its associated behaviors, spotted hyenas seem drastically transformed from their phylogenetic baseline, both local (other hyenas) and global (other mammals). Yet, the more their design is decomposed into physiological subcomponents, the more continuity appears, until the essence of their divergence can be traced to a rather modest modification in their developmental physiology. If a single change at the physiological level can accomplish so much, what can many minor changes at the physiological level cumulatively accomplish at the behavioral level?

A system as complex as a mammalian psyche has many interacting parts, providing a wealth of potential changes, and a change in any one can change the final behavioral output (Tooby & Cosmides, *in press*). Because selection acts on the consequences of behavior, the behavioral output of the psyche will be easily shaped by adaptive demands over evolutionary time, even though the modification of the innate neurophysiology necessary to create such adaptive changes may be comparatively minor. As Ernst Mayr points out, even in tracking the truly massive aggregate changes from a reptilian ancestor to a bird or mammal descendent, “we are astonished at how few are truly new structures. Most differences are merely shifts in proportions, fusions, losses, secondary duplications, and similar changes that do not materially affect what the morphologist calls the plan of the particular type” (Mayr, 1976 pp. 96). The power of such modifications undercuts arguments about phylogenetic constraint (Gould & Lewontin, 1979) made at the adaptive and behavioral levels: The vast differences in social behavior between humans, chimpanzees, orangutans, and gorillas is eloquent testimony to how little phylogeny constrains the adaptive differentiation of psychologies among even closely related species. Because combinatorial interaction magnifies the impact of changes on output, the sculpting influence of selection will be strongly felt on behavior and on psychological mechanisms described in terms of functional design. Reciprocally, even striking behavioral differences between related species may be traced to relatively minor changes in underlying neurophysiological arrangement.

Thus, by specifying what “level” or kind of biological phenomena are involved, the controversy over the relative freedom of selection to create adaptive design versus the limiting role of phylogenetic constraint (Dawkins, 1982; Gould & Lewontin, 1979; Williams, 1966) may be clarified

(as may the otherwise well-explored issue of the relative role of homology and analogy in evolutionary analyses; Atz, 1970). We suggest that the nature of complex design makes the search for continuities among animals (including humans) helpful and illuminating at the neurophysiological level, where structural homologies are easily recognizable and readily traceable through related species. However, it is only adaptation-mindedness, and more specifically, the analysis of niche-differentiating species-specific selection pressures, that can illuminate the zoologically unique features of any species' psyche, including our own.

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REFERENCES

- Alcock, J. (1989). *Animal behavior: An evolutionary approach. (fourth edition)*. Sunderland, MA: Sinauer.
- Alexander, R. D. (1971). The search for an evolutionary philosophy of man. *Proceedings of the Royal Society of Victoria*, 84, 99-120.
- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology & Systematics*, 5, 325-383.
- Ardrey, R. (1966). *The territorial imperative*. New York: Atheneum.
- Atz, J. W. (1970). The application of the idea of homology to behavior. In Aronson, L. R., Tobach, E., Lehrman, D. S. & Rosenblatt, J. S. (Eds.), *Development and evolution of behavior*, pp. 53-74. San Francisco: Freeman.
- Boakes, R. A. (1984). *From Darwin to behaviorism: Psychology and the minds of animals*. London: Cambridge University Press.
- Boden M. (1977). *Artificial intelligence and natural man*. New York: Basic Books.
- Braitenberg, V. (1984). *Vehicles: Experiments in synthetic psychology*. Cambridge, MA: MIT Press.
- Brown, F.M. (1987). *The frame problem in artificial intelligence*. Los Altos, CA: Morgan Kaufman.
- Chomsky, N. (1975). *Reflections on language*. New York: Random House.
- Chomsky, N. (1980). *Rules and representations*. New York: Columbia University Press.
- Clutton-Brock, T.H., & Harvey, P.H. (1979). Comparison and adaptation. *Proceedings of the Royal Society of London (B)*, 205, 547-565.
- Cosmides, L. & Tooby, J. (1987). From evolution to behavior: Evolutionary psychology as the missing link. In Dupre, J. (Ed), *The latest on the best: Essays on evolution and optimality*, pp. 227-306. Cambridge, MA: MIT Press.
- Cosmides, L. & Tooby, J. (1989). Evolutionary psychology and the generation of culture, Part II. Case study: A computational theory of social exchange. *Ethology and Sociobiology*, 10, 51-97.
- Daly, M. & Wilson, M. (1983). *Sex, evolution, and behavior. (second edition)*. Boston: Willard Grant Press.
- Darwin, C. (1859). *On the Origin of Species*. London: Murray.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: Murray.
- Darwin, C. (1873). *The expression of the emotions in man and animals*. New York: Appleton.

- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Dawkins, R. (1982). *The extended phenotype: The gene as the unit of selection*. Oxford and San Francisco: W. H. Freeman.
- Dawkins, R. (1986). *The blind watchmaker: Why the evidence of evolution reveals a universe without design*. New York: Norton.
- Descartes, R. (1977). *The essential writings*. New York: Harper & Row.
- Dewsbury, D. (1984). *Comparative psychology in the twentieth century*. New York: Van Nostrand Reinhold.
- Durkheim, E. (1962). *The rules of the sociological method*. Glencoe, Illinois: Free Press.
- Ellison, G. D. (1979). Chemical systems of the brain and evolution. In Oakley, D. A. & Plotkin, H. C. (Eds.), *Brain, behaviour and evolution*, pp. 78-98. New York: Methuen.
- Evans-Pritchard, E. E. (1954). *Social anthropology*. Glencoe, Illinois: Free Press.
- Ewer, R. F. (1973). *The carnivores*. Ithaca, NY: Cornell University Press.
- Fodor, J. A. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.
- Geertz, C. (1973). *The interpretation of cultures*. New York: Basic Books.
- Gilbert, S. F. (1985). *Developmental biology*. Sunderland, MA: Sinauer.
- Gould, J. J. (1982). *Ethology: The mechanisms and evolution of behavior*. New York: Norton.
- Gould, S. J. (1977). *Ontogeny and Phylogeny*. Cambridge, MA: Harvard University Press.
- Gould, S. J. (1981). Hyena myths and realities. *Natural History*, 90, 16-24.
- Gould, S. J. & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist program. *Proceedings of the Royal Society of London*, 205, 581-598.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology* 7, 1-52.
- Hodos, W. & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review*, 76, 337-350.
- Konner, M. (1982). *The tangled wing*. New York: Holt, Rinehart, & Winston.
- Krebs, J. R. & Davies, N. B. (1984). *Behavioural ecology: An evolutionary approach*. (second edition). Sunderland, MA: Sinauer.
- Kroeber, A. L. (1952). *The nature of culture*. Chicago: University of Chicago Press.
- Kruuk, H. (1972). *The spotted hyena*. Chicago: University of Chicago Press.
- Lehrman, D. S. (1970). Semantic and conceptual issues in the nature-nurture problem. In Aronson, L. R., Trobach, E., Lehrman, D. S. & Rosenblatt, J. S. (Eds.), *Development and evolution of behavior*, pp. 17-52. San Francisco: W. H. Freeman.
- Lockard, R. (1971). Reflections on the fall of comparative psychology: Is there a message for us all? *American Psychologist*, 26, 22-32.
- Lorenz, K. (1965). *Evolution and the modification of behavior*. Chicago: University of Chicago Press.
- Lorenz, K. (1966). *On aggression*. London: Methuen.
- Macphail, E. (1987). The comparative psychology of intelligence. *Behavioral and Brain Sciences*, 10, 645-689.
- Marler, P. & Hamilton, W. J. III. (1966). *Mechanisms of animal behavior*. New York: Wiley.
- Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: Freeman.
- Mayr, E. (1974). Behavior programs and evolutionary strategies. *American Scientist*, 62, 650-659.
- Mayr, E. (1976). The emergence of evolutionary novelties. In: *Evolution and the diversity of life*, pp. 88-113. Cambridge, MA: Harvard University Press.
- Minsky, M. (1986). *The society of mind*. New York: Simon & Schuster.
- Racey, P. A. & Skinner, J. D. (1979). Endocrine aspects of sexual mimicry in spotted hyenas *Crocota crocota*. *Journal of Zoology, London*, 187, 315-326.
- Radcliffe-Brown, A. R. (1977). *The social anthropology of Radcliffe-Brown*. London: Routledge & Kegan Paul.
- Rozin, P. (1976). The evolution of intelligence and access to the cognitive unconscious. In Sprague, J. M., & Epstein, A. N. (Eds.), *Progress in psychobiology and physiological psychology*, pp. 245-280. New York: Academic Press.
- Sahlins, M. (1976). *The use and abuse of biology: An anthropological critique of socio-biology*. Ann Arbor: University of Michigan Press.
- Shepard, R. (1984). Ecological constraints on internal representation: resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychological Review*, 91, 417-447.

- Skinner, B. F. (1938). *The behavior of organisms*. New York: Appleton.
- Skinner, B. F. (1953). *Science and human behavior*. New York: Macmillan.
- Skinner, B. F. (1957). *Verbal behavior*. New York: Appleton.
- Sparrow, C. (1982). *The Lorenz equations, bifurcations, chaos, and strange attractors*. Berlin: Springer-Verlag.
- Staddon, J. E. R. (1983). *Adaptive behavior and learning*. Cambridge, UK: Cambridge University Press.
- Staddon, J. E. R. (1987). Learning as inference. In Bolles, R. C. & Beecher, M. D. (Eds), *Evolution and learning*, pp. 59-77. Hillsdale, NJ: Erlbaum.
- Staddon, J. E. R. (1988). Animal psychology: The tyranny of anthropocentrism. In Bateson, P. P. G. & Klopfer, P. (Eds), *Perspectives in ethology*. Vol. 8: *Whither ethology?*, pp. 123-135. London: Plenum.
- Stewart, K. J. (1987). Spotted hyenas: The importance of being dominant. *Trends in Ecology and Evolution*, 2, 88-89.
- Symons, D. (1987). If we're all Darwinians, what's the fuss about? In Crawford, C. B., Smith, M. F., & Krebs, D. L. (Eds), *Sociobiology and psychology*, pp. 121-146. Hillsdale, NJ: Erlbaum.
- Tinbergen, N. (1951). *The study of instinct*. New York: Oxford University Press.
- Tooby, J. (1985). The emergence of evolutionary psychology. In Pines, D. (Ed), *Emerging syntheses in science*, pp. 106-122. Santa Fe: Santa Fe Institute.
- Tooby, J. & Cosmides, L. (in press). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*.
- Tooby, J. & DeVore, I. (1987). The reconstruction of hominid behavioral evolution through strategic modeling. In Kinzey, W. G. (Ed.), *The evolution of human behavior: Primate models*, pp. 183-237. New York: SUNY Press.
- Wallace, A. R. (1904). *Man's place in the universe. (fourth edition)*. London: Chapman and Hall.
- Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton: Princeton University Press.
- Williams, G. C. & Williams, D. (1957). Natural selection of individually harmful social adaptations among sibs with special reference to social insects. *Evolution*, 11, 32-39.
- Wilson, E. O. (1971). *The insect societies*. Cambridge, MA: Harvard University Press.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Harvard University Press.