

EVOLUTIONARY PSYCHOLOGY, ADAPTATION, AND THE EVOLUTION OF LANGUAGE: IS THERE A NEED FOR COMPARISON?

Mark A. Krause
University of Tennessee, USA

ABSTRACT: A general assumption held by evolutionary psychologists is that a reference point for examining the origins and evolution of human psychological adaptations exists within a time range beginning roughly two million years ago. Scenarios for explaining the evolution of human psychological processes often allude to possible selection pressures encountered by hominids during this time. Unfortunately, comparative psychology and ethology are relatively absent from much current evolutionary psychological thought. Selective pressures that existed during the putative environment of evolutionary adaptedness may have predated the origin of hominids. Based on examples of the evolution of communication, this paper offers another approach to discovering the origins and evolution of psychological traits, with the aim of modifying a potentially misleading assumption of evolutionary psychology.

"The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (Darwin, 1871, p. 128).

Comparative psychology has confirmed Darwin's assertion in so many ways. The mental differences among humans and the "higher animals" are largely of degree, although some evolutionary discontinuities exist for which we may never find capacities, rudiments, or vestiges in other species. Despite some of its historically limited focus (Beach, 1950), comparative psychology is at a theoretical advantage over many other fields of psychology by virtue of its relationship to evolutionary theory. Evolutionary psychology is a relatively recent attempt to synthesize evolutionary biology with the

Address correspondence to Mark A. Krause, Department of Psychology, 307 Austin Peay Building, University of Tennessee, Knoxville TN, 37996, USA.

theoretically bereft field of psychology [see Tobach (1995) for a historical discussion of both evolutionary and comparative psychology]. Psychology as a whole is not woven together with a general theory such as natural selection, which, since its inception, has united most of the various subfields within the biological sciences. As Buss (1995) stated "...psychologists assume that the human mind is a whole and integrated unity, no metatheory subsumes, integrates, unites, or connects the disparate pieces psychologists gauge with their differing calipers " (p. 1).

Although Darwinian thought has often been applied to human behavior, it has not brought the field of psychology together across all of its subdisciplines. The chance that some natural theory applies only to humans is vanishingly small. Thus human behavior, in all of its complexity, should be explicable in evolutionary terms. Specifically, natural selection could serve as a metatheory that unites psychology, which would not necessarily alter the sub-theories that are currently scattered across the discipline, but could possibly increase (or constrain) their explanatory power.

Evolutionary psychologists often remind us that our current suite of behavioral characters evolved under conditions quite different from those of the present day, and that an ancient point of reference is needed wherein original selective pressures can be considered. By embracing natural selection as a unifying theory, evolutionary psychologists present themselves with two general questions; namely, what is the historical origin of the trait in question and what is its function? These questions are generally answered using the concepts of an "environment of evolutionary adaptedness" (EEA), and "adaptationism". Specifically, the EEA was the setting in which the human evolutionary drama was played out during the Pleistocene epoch. Most humans have dispersed and rapidly altered their surroundings to degrees that render them virtually incomparable to regions inhabited during the EEA. However, behavioral patterns and thought processes that were adaptive during this time period (and the settings therein) remain firmly embedded in human psychology.

There is often a link between the historical origin and function of a trait, but, according to many, the two should be recognized as potentially separate (e.g., Gould, 1991; Gould & Lewontin, 1979). This topic has a long history of debate within the biological sciences [see Allen, Bekoff, and Lauder (1998) for a compilation of various perspectives on adaptationism]. Although adaptationism is an important concept for evolutionary psychology, the focus of this paper is less on

the concept of adaptationism itself, and more on pinpointing the origins of the putative adaptations hypothesized by evolutionary psychologists.

THE MODULAR MIND

The brain, like any other bodily system, is material that is altered via natural selection. The pervasive influence this has on behavior is obvious. However, an appropriate model for brain architecture is required, as an understanding of the brain remains vague in comparison to other bodily systems. Evolutionary psychologists have adopted Fodor's (1983) "modular" model of the brain. Generally, the architecture of a modular brain consists of discrete neural units whose functions are fairly specific; and although the topographical layout of these units may be scattered throughout the brain, their manifest behavior and thought patterns are much less diffuse. That is, they are "domain specific", which contrasts with an alternative view that the brain as a whole is relatively unconstrained and remains relatively free to adapt to individual circumstances. The development of the modular brain model fits with a shift from the view that psychology must limit its focus to measurements of stimulus input and behavioral output, to a cognitive perspective. Tooby and Cosmides' (1992) review of the past century of social science in general shows that a new model of the mind, as well as an increasing appreciation for the role of biological processes in behavior, represent a backdrop for an evolutionary psychology.

FITNESS GOALS AND ADAPTATIONISM

One noteworthy point of departure taken by evolutionary psychologists from say, sociobiologists, is the moderate stance taken on fitness "goals". Rather than view humans as "fitness strivers", evolutionary psychologists such as Tooby and Cosmides (1990) propose the terms "adaptation executors" and "mechanism activators" as more appropriate descriptors. These terms integrate the modular and adaptationist perspectives into the conceptual framework of the field. Modern day human activities such as consuming fatty foods and smoking are not suggestive of a fitness-maximizing organism, and viewing pornography is a reproductive dead end. Buss (1995) maintains that such non-fitness promoting tendencies are products of evolved mechanisms from ancestral humans, and the conditions that elicited

them in ancestral humans fundamentally differ from those of modern day humans. According to Buss (1995), to suppose otherwise is to commit the "sociobiological fallacy", which confuses the nature of the psychological mechanisms employed by modern humans with their historical origins.

Among the problems of proposing adaptive explanations concerns the difficulty in testing what a given trait is adapted for. Because the EEA is not repeatable, difficulties arise in testing hypotheses of the historical origins of human cognitive processes. This difficulty, of course, is not unique to this situation but pervades evolutionary biology in general. The current utility of psychological traits may have their origins in other traits, or may be byproducts of a combination of other traits. Also, the EEA concept implies that the origins of much of human cognition arose during a specific period. This may be true for much of human cognition, but findings in comparative psychology and ethology suggest that the historical origins of many human behaviors have their beginnings in times predating the Pleistocene. Thus the selective factors involved in the evolution of human cognitive adaptations, or at least the foundations upon which they were built, may not be the same as some of those hypothesized by evolutionary psychologists, or, if certain selective pressures were relatively constant, they may have predated the Pleistocene. This potential problem can be illustrated by using examples from the evolution of language.

THE "LANGUAGE INSTINCT"

The evolution of language is a topic of great interest to evolutionary psychologists (Bickerton, 1998; Pinker & Bloom, 1992). Human languages differ in some important ways from the communication systems evolved in other species. The human brain has expanded and reorganized considerably through the hominid lineage, and the capacity to acquire a symbolic language evolved to its current state of complexity during this period (Deacon, 1997). The specific selective factors that shaped human language have proven difficult to identify. The Australopithecines probably did not speak, as their brains were not much larger than the brains of modern day apes. However, over a 2-million year period, the threefold size expansion of the human brain and its increased prefrontalization are most likely what allowed a symbolic language to evolve. Symbolic speech and gesture merge with other modes of communication, such as nonverbal and emotional

signals, but also remain separated by several degrees from nonlinguistic forms. Many other species have the capacity to communicate nonverbally and through vocal calls, but these systems are often viewed as qualitatively different from language because, among other things, they may only be elicited by immediate environmental cues and are involuntarily produced. (However, these points of view are becoming less fashionable in light of various findings reviewed below). Human language can be controlled voluntarily, can refer to past, present, and future events, and follows structural rules which combine a finite number of sound units into a potentially infinite array of sentences. Also, the combination of these units allows for the expression of thought and symbolic reference. Thus meaning is expressed in human languages which, according to some (Deacon, 1997), represents the widest chasm separating human language from nonhuman communication.

The adaptive functions of various animal communication systems, such as calls associated with predators, food, and conspecific mating or competition, are perhaps easier to identify than for human language. It is difficult to imagine an evolutionary scenario wherein fitness advantages accrued to those capable of using symbolic reference; much more so than it is to recognize the adaptive function of mating calls. Many linguists consider language to be an innate feature of human cognition, but do not offer explanations as to what function(s) language serves. In contrast to this, Pinker (1994) and Pinker and Bloom (1992) consider the expression of complex thoughts, rich in meaning, to have been of adaptive value among early hominids, where cooperation, as well as cheater detection, were of great importance. As Pinker and Bloom (1992) state "...humans, probably early on, fell into a life-style that depended on extended cooperation for food, safety, nurturance, and reproductive opportunities" (p. 483). According to this view, language allowed for an unlimited expression of thought and those with at least rudiments of the capacity presumably found themselves at a reproductive advantage over those more inclined to simply grunt.

According to evolutionary psychological points of view, whatever the adaptive functions of symbolic language, be it for cooperation, social manipulation, etc., the advantage was bestowed upon its users during the EEA. However, similar selective pressures for communication clearly existed prior to the EEA. Pre-hominid species presumably also "fell into" lifestyles where cooperation for food, safety, nurturance, and reproductive success were better attained by communicating. It is difficult to imagine these needs suddenly arose for

humans only during the EEA. While various features of language may be unique to humans, foundational components such as meaning and intentionality are present in the communication of other extant species. It is these capacities upon which a significant part of human language may have been built. Therefore, a time period and setting different from the EEA might be a better place to look to discover the evolutionary origins of language.

Those who take a hard-line view of language definitions tend to define language in ways that disqualify nonhuman communication as comparable (e.g., Bickerton, 1998; Pinker, 1994). Many comparative psychologists, on the other hand, view human language as built upon a mental substrate existing among nonhuman species (mostly primates). The use of grammar, for example, is often considered an ability that evolved along the hominid lineage with no comparable ability to be found among primate vocalizations. However, Savage-Rumbaugh et al. (1993) found that a bonobo chimpanzee making use of lexigram symbols was capable of generalizing syntactical rules to novel situations and grasped differences in meaning due to changes in the grammatical structure of sentences. Reference, meaning, and intentionality are present in many primate calls. That these communicative properties are present supports the view that several aspects of human language are built upon abilities originating prior to the origin of the hominid line.

Ape language research has been largely ignored (and criticized) by several evolutionary psychologists (Bickerton, 1998; Pinker & Bloom, 1992; Plotkin, 1998). Apes taught to use gestural signs or artificial languages have revealed some similarities between human and nonhuman language, yet many differences remain. However, the existing similarities should not be summarily dismissed. They require careful examination if the aim is to trace the evolutionary history of human language, especially when there is consideration of the mental abilities necessary for it, and the selective pressures that influenced them. Plotkin (1998) asserts that "What the ape language studies do seem to share with experiments on the likes of 'mind-reading' and 'self-awareness' in other apes is a prejudiced stance among many primatologists who want to see such 'upper'-level human cognitive abilities in other primates, and hence make inflated claims for what their studies show" (p. 127). Such a view will not hasten the progress that can be made in tracing the evolution of language. Conversely, the unwillingness on the part of many to take into account nonhuman primate research leads to inflated claims about the uniqueness of human

language. The results of ape-language projects are indeed germane to the question of language origins. However, evaluating the selective pressures and functions associated with language evolution may best be done from a more naturalistic perspective. Regardless of what ape-language studies have or have not told us about human language, a more applicable approach to the subject comes from ethological research on animal communication.

THE ETHOLOGY OF REFERENCE

Reference is one aspect of human language that is shared with nonhuman species. Reference can take a variety of increasingly complex forms: mimetic, proxy, and conceptual (Allen & Saidel, 1998). Mimetic reference occurs when a response is elicited by a stimulus that resembles the referent. For example, angler fish attempt to lure prey by "mimicking" food typically eaten by their own unsuspecting prey. This is not a "higher-level" of reference because no intentionality is necessary on the part of the signaler and the signal is in no way arbitrary with respect to the context (see below for further discussion on intentionality). A proxy referential signal elicits the same response as the actual referent itself (Allen & Saidel, 1998). The anti-predator alarm calls of many bird, rodent, and primate species are proxy referential in that they may refer to a particular predator, and the signal is perceptually paired with the stimulus. Conceptual reference is the most stimulus-removed of the three forms of referential communication, and occurs when a signal refers to something external with no expectation of a response that is normally evoked by the referent. When we speak of objects or events that are not immediately present we are using conceptual reference.

Proxy reference is probably the most ubiquitous form of referential communication found among nonhuman organisms, although evidence for conceptual reference does exist among language-trained apes. The alarm calls of vervet monkeys (*Cercopithecus aethiops*) are considered to be proxy referential. Specific calls are produced in response to certain predators (snakes, eagles, and leopards). These monkeys also emit different calls when they move into open areas, when encountering another monkey troop, and during aggressive interactions with conspecifics. Cheney and Seyfarth (1988) consider these calls to have meaning to vervets, and that they respond to the calls based on the semantic differences that are reflective of the discreteness of the calls

(see below). These vocalizations are not hard-wired from birth, but rather follow a developmental course relying on both maturational and experiential factors (Hauser, 1989; Seyfarth & Cheney, 1986). Vervet monkeys must learn to discriminate both among and within different predator types. Young vervet monkeys, for example, emit calls for aerial predators when the stimulus might actually be a non-threatening bird; but this response is eventually extinguished. Vervet monkeys also appear capable of recognizing the calls of individual group members, and are sensitive to the reliability of an individual's calls within referent categories (e.g., predators vs. conspecifics).

Proxy reference requires an element of shared attention. If the signal is an alarm call, the recipient may simply look in the vicinity of the caller in an attempt to discover the specific location of the predator. Or, the recipient may look in the direction toward which the caller is looking. This has not been experimentally manipulated in field settings (but see Cheney & Seyfarth, 1982), but several nonhuman primate species evince the capacity to follow gaze directions of humans or conspecifics in laboratory experiments (Emery, et al., 1997; Povinelli & Eddy, 1996; Tomasello, Call, & Hare, 1998). Joint visual attention, an advanced form of gaze following, is thought to facilitate the development of language in human infants (Bruner, 1983; Goldfield, 1990). Captive chimpanzees with various rearing histories engage humans in bouts of joint attention when communicating the location of objects by pointing (Krause & Fouts, 1997; Leavens & Hopkins, 1998). However, this appears to serve an imperative function and differs from the declarative pointing often seen in human infants, which functions to show objects and events to others. Regardless, the requisite behaviors for shared attention are present in both human and nonhuman, and their relationship to language acquisition in the former is indeed critical. Humans have expanded upon this capacity by engaging in joint visual attention as a mode of acquiring vocabularies. However, the selective pressures for engaging in shared attention in primates, at least, existed prior to the hominid split. From a developmental perspective, the evolution of human language owes much to the ability to engage in joint visual attention.

CATEGORICAL PERCEPTION OF SPEECH AND SOUND

Speech comprehension requires that the listener is capable of categorically discriminating phonemes. For humans as well as

nonhumans, categorical perception of non-phonemic sounds also occurs. Macaques, chinchillas, sparrows, and mice all show evidence for categorical perception of speech sounds as well as of sounds made by conspecifics (see Evans & Marler, 1995 for review). Therefore, the capacity to receive and categorize auditory stimuli, a fundamental requirement for the comprehension of speech, preceded the evolutionary onset of speech. Similar to speech, vocal call perception is lateralized to the left hemisphere in many mammalian and avian species (see Hauser, 1996 for review). Therefore, the neural adaptations for vocal processing may be phylogenetically ancient. Vervet monkeys are capable of categorizing alarm calls, but the meaning these calls may have to the animals is a different issue. Whether animals base their responses to vocalizations on meaning has further implications for the evolution of language.

MEANING AND PRIMATE VOCALIZATIONS

Cheney and Seyfarth (1988) correctly maintain that "Humans make judgments about the similarity or differences between words on the basis of an abstraction, their meaning" (p. 477). Cheney and Seyfarth (1988) reasoned that if two vervet monkey calls have similar meanings, monkeys should transfer habituation from one played-back call to another if the initial call comes from an unreliable monkey (that is, no observable referent is present when the call is played). Their results suggest that indeed vervet monkeys judge the relationship between calls based on meaning. Their habituation to one type of aggressive call transferred to another type of aggressive call made by the same (unreliable) monkey. Therefore, vervet monkeys may classify physically dissimilar calls into meaningful categories. The ability to assess calls based on meaning by nonhuman organisms suggests that the requisite cognitive capacities existed prior to the origin of hominids.

Syntax makes human language perhaps the most complex, and the least constrained, of all animal communication systems. The devices and rules used to convey meaning make for an infinite level of productivity and are among the hallmarks of human languages. Did the intense need for cooperation and nurturance result in selection for an original, infinitely productive grammatical language? Selection for the ability to use syntax was potentially quite strong during the EEA. However, this may have been built upon more ancient abilities that existed prior to Hominids. According to Mitani and Marler (1989),

male gibbon songs vary by duration, frequency range, minimum and maximum frequency, start and end frequency, and inflection. Similar types of call variation in chimpanzees and bonobos exist as well (Hohmann & Fruth, 1994; Mitani, Hasegawa, Gros-Louis, & Marler, 1992). Although simplistic and motivationally limited, many primate vocalizations involve the combination of various elements that potentially vary in meaning according to their structure. Whether primate calls have anything remotely similar to syntax remains to be firmly established.

INTENTIONAL COMMUNICATION

Whether primates mean to signal is a separate issue from whether their signals have meaning. Neurological studies of animal communication systems frequently show that more ancestral brain regions control vocal behavior. It follows from this that primate calls, for example, are only evoked by the presence of certain stimuli and motivational states, and are not under voluntary control. The fact that vervet monkeys use referential calls and appear to understand the meaning of these calls is suggestive of intentionality, but is not unequivocal evidence for it. Tomasello and Call (1997) offer two additional criteria for distinguishing intentional from non-intentional communication - "flexibility of use and use in socially sensitive ways (i.e., audience effects)" (p. 252). As previously noted, the ontogeny of vervet alarm calls is somewhat flexible. Although young vervet alarm calls are acoustically adult-like, their appropriate usage is largely based on experience. Anecdotal evidence also suggests that vervet monkeys use their calls deceptively, but this may be a type of "functional" deception, rather than "tactical" deception (Cheney & Seyfarth, 1990), which requires the attribution of false beliefs.

The presence of conspecifics may determine whether vervet monkeys, and even squirrels (Sherman, 1977), and chickens, vocalize. Vervet monkeys typically do not alarm call unless others are close by (Cheney & Seyfarth, 1990). Similarly, the humble domestic chicken is more likely to emit predator alarm calls when in the vicinity of hens, than when quail or an empty cage are nearby (see Evans & Marler, 1995 for review). While these results should be interpreted with caution, they may indicate that various animal vocalizations are controlled voluntarily. The gestural communication of great apes shows much stronger evidence of intentional communication among

nonhuman organisms. However, most of these studies are conducted in laboratories under controlled experimental conditions. Often these subjects have had extensive contact with human caregivers, which, although informative in many ways, compromises their ethological validity (see Tomasello & Call, 1997 for review and extensive discussion). Regardless, there is strong evidence for intentional communication among captive apes, and although it may not be regularly expressed in the same variety of ways in natural situations, support is lent to the notion that communication could be done intentionally prior to the hominid line.

THE COMPARATIVE METHOD AND COMMUNICATION

The comparative method has become a very useful tool for examining the phylogeny of behavior (Burghardt & Gittleman, 1990; Martins, 1996). The comparative method could be well applied to studies of human and nonhuman communication, and could provide a systematic way of identifying the fundamental similarities and differences between animal communication systems. Extensive treatments of the evolution of language that include comparative psychological viewpoints can be found in Velichkovsky and Rumbaugh (1996) and Krasnegor, Rumbaugh, Schiefelbusch, and Studdert-Kennedy (1991).

Jolly (1972) and Parker and Gibson (1979, 1990) originated the field of Comparative Developmental Evolutionary Psychology (CDEP). Comparative studies of language are one focal point of this approach. In addition to this, the non-linguistic, cognitive development of humans and nonhuman primates are treated as amenable to comparison; an approach that dates at least back to James Mark Baldwin's (1894) initial speculations and empirical studies. Based on their early review and initial model derived from comparative data, Parker and Gibson (1979) conclude that the common ancestor of humans and great apes "...displayed rudimentary forms of late sensorimotor and early preoperational intelligence similar to that of one- to four-year-old children" (p. 367). Based on Parker (1996) and Parker and Gibson (1979), there is a trend toward greater sensorimotor complexity as the hominid line is reached. Cognitive development has not been a major focus of evolutionary psychological research thus far, but the field will be better informed if results from CDEP studies are considered and the comparative method used. This will also require practitioners to loosen

the theoretical confinement posed by the EEA concept.

Evidence for categorical perception of speech, reference, meaning, and intentionality exists in several nonhuman communication systems (Allen & Bekoff, 1997; Hauser, 1996). This has potentially significant implications for the evolution of human language. A complex system like human language can and should be broken down into the elements that comprise it. The main point here concerns which of these elements existed prior to the hominid line. The EEA may be too simplistic and confining as a concept that can adequately reflect the complexity of the origins and evolution of language and human cognition. I second Daly and Wilson's (1995) assertion that "Comparative evidence can ...aid us in better characterizing the adaptive functions of particular attributes in a focal species, such as *Homo sapiens*" (p. 37).

CONCLUSION

Thus far I have not dealt much with how the behavioral comparisons made above corroborate with neuroanatomical characteristics of human and nonhuman brains. The cortical representation of language in humans, and in that of nonhuman communication systems, have previously been compared in the attempt to determine whether language has an evolutionary basis in homologous brain regions of other species (Deacon, 1991). The vocalizations of well studied species such as squirrel monkeys and macaques are largely controlled by the midbrain, diencephalon and limbic regions (Deacon, 1991). The perception of vocal signals, however, occurs in higher cortical regions of nonhuman primate brains (Rauschecker, Tian, & Hauser, 1995). One challenge to comparative neuroanatomists is to discover the neural units that give rise to specific aspects of language and communication that humans and nonhuman animals share. The edited volume by Steklis and Raleigh (1979) and Hauser's (1996) *Evolution of Communication* review much of the work done in this area.

The modular model of the brain has been incorporated into much evolutionary psychological theory. The applicability of this model to many psychological processes is potentially extensive. However, the original application of Fodor's (1983) "Modularity of the Mind" was specific to human language (and somewhat to visual perception). Evolutionary psychologists might overextend this model and infer the existence of modules for nearly every thought process and behavior

studied. The appeal of the modular brain model is clear, as it offers a material on which selection can act that is both unitary in function, yet integrated within the nervous system. However, it is important to remember that both evolutionary and comparative psychologists are typically measuring behavior and thought processes, and not modules per se. The existence of modules themselves is based on inference. This is not necessarily misleading, but it seems important to resist allowing the proverbial tail to wag the dog.

Some evolutionary psychologists imply that language is adaptive by virtue of its vast complexity (Pinker & Bloom, 1992). In other words, why would something so complex evolve if it had no adaptive value? I am in agreement with this position. However, this does not explain what language is adapted for or why it originated. As previously mentioned, Pinker and Bloom (1992) consider the unlimited expression of thought facilitated by language to be crucial to developing cooperation among its users. Furthermore, according to this view, language is a fairly recent phenomenon that originated among Pleistocene hominids. In examining the origins of language with greater accuracy, it seems necessary to specify which Pleistocene hominids were the adaptive language users (and was there only one EEA?). Potts' (1996) discussion on EEA related topics is a great source to consult for descriptions of ancestral environments, and it suggests that there was tremendous environmental variability encountered by human groups during this time. Finally, the notion that language evolved under selection pressures for communicating and cooperating with others seems much too general. Richardson (1996) has made a similar point, and discusses various criteria that should be implemented when an evolutionary explanation for an adaptation is needed. Among these criteria is that an independently established phylogeny should be used so that convergent and shared characters are recognized.

Applying evolutionary theory to human behavior is a step toward theoretical synthesis - a much-needed direction toward a unified psychology. The comparative method is a powerful tool that can aid evolutionary psychologists in identifying the origins of many other behavioral and cognitive traits. This method might require that some traits be broken down into constituent elements in order to map out their phylogenetic distribution. In addition, it could add scientific rigor to evolutionary psychology, and can circumvent some of the problems associated with assuming that human psychology is a product of selective factors that existed only during the EEA. The collaborative work of evolutionary and comparative psychologists and ethologists

should prove mutually beneficial, and in the end may provide a more accurate view of our own evolutionary past.

ACKNOWLEDGEMENTS

I sincerely thank Colin Allen, Warren P. Roberts, Christine R. B. Boake, and Gordon M. Burghardt for helpful discussions and comments on earlier drafts of the manuscript.

REFERENCES

- Allen, C., & Bekoff, M. (1997). *Species of Mind: The Philosophy and Biology of Cognitive Ethology*. Cambridge, MA: MIT Press.
- Allen, C., Bekoff, M., & Lauder, G. (Eds.). (1998). *Nature's purposes: Analyses of function and design in biology*. Cambridge: MIT Press.
- Allen, C, & Savidel, E. (1998). The evolution of reference. In D. Cummins & C. Allen (Eds.) *The evolution of mind*. Oxford University Press.
- Baldwin, J.M. (1884). *Mental development in the child and the race*. New York: Augustus Kelley.
- Beach, F.A. (1950). The Snark was a Boojum. *American Psychologist*, 5, 115-124.
- Bickerton, D. (1998). The creation and recreation of language. In C. Crawford & D.L. Krebs (Eds.) *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 613-634). New Jersey: Lawrence Erlbaum.
- Bruner, J. (1983). *Child's talk*. New York: Norton.
- Burghardt, G.M., & Gittleman, J.L. (1990). Comparative behavior and phylogenetic analyses: New wine, old bottles. In M. Bekoff & D. Jamieson (Eds.) *Interpretation and explanation in the study of animal behavior* (pp. 192-225). Boulder, CO: Westview Press.
- Buss, D.M. (1995). Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry*, 6, 1-30.
- Cheney, D.L., & Seyfarth, R.M. (1982). Vervet monkey alarm calls: Manipulation through shared information? *Behaviour*, 94, 150-166.
- Cheney, D.L., & Seyfarth, R.M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, 36, 477-486.
- Cheney, D.L., & Seyfarth, R.M. (1990). How monkeys see the world: Inside the mind of another species. Chicago: University of Chicago Press.
- Daly, M., & Wilson, M. (1995). Evolutionary psychology: Adaptationist, selectionist, and comparative. *Psychological Inquiry*, 6, 34-38.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: John Murray.
- Deacon, T.W. (1991). The neural circuitry underlying primate calls and human language. In J. Wind (Ed.) *Language origins: A multidisciplinary approach* (pp. 131-172). Netherlands: Kluwer Academic.
- Deacon, T.W. (1997). *The symbolic species: The co-evolution of language and the brain*. New York: W. W. Norton.

- Emery, N.J., Lorincz, E.N., Perrett, D.I., Oram, M.W., & Baker, C.I. (1997). Gaze following and joint attention in Rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, *111*, 286-293.
- Evans, C.S. & Marler, P. (1995). Language and animal communication: Parallels and contrasts. In H.L. Roitblat & J-A Meyer (Eds.) *Comparative approaches to cognitive science*. Cambridge: MIT Press.
- Fodor, J.A. (1983). *The modularity of mind*. Cambridge: MIT Press.
- Goldfield, B.A. (1990). Pointing, naming, and talk about objects: Referential behaviour in children and mothers. *First Language*, *10*, 231-242.
- Gould, S.J. (1991). Exaptation: A crucial tool for an evolutionary psychology. *Journal of Social Issues*, *47*, 43-65.
- Gould, S.J., & Lewontin, R.C. (1979). The spandrels of San Marcos and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, B*, *205*, 581-598.
- Hauser, M.D. (1989). Ontogenetic changes in the comprehension and production of vervet monkey (*Cercopithecus aethiops*) vocalizations. *Journal of Comparative Psychology*, *103*, 149-158.
- Hauser, M.D. (1996). *The evolution of communication*. Cambridge: MIT Press.
- Hohmann, G., & Fruth, B. (1994). Structure and use of distance calls in wild bonobos (*Pan paniscus*). *International Journal of Primatology*, *15*, 767-782.
- Jolly, A. (1972). *The evolution of primate behavior*. New York: Macmillan.
- Krasnegor, N.A., Rumbaugh, D.M., Schiefelbusch, R.L., & Studdert-Kennedy, M. (Eds.). (1991). *Biological and behavioral determinants of language development*. New Jersey: Lawrence Erlbaum.
- Krause, M.A., & Fouts, R.S. (1997). Chimpanzee (*Pan troglodytes*) pointing: Hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology*, *111*, 330-336.
- Leavens, D.A., & Hopkins, W.D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, *34*, 813-822.
- Martins, E.P. (Ed.) (1996). *Phylogenies and the comparative method in animal behavior*. New York: Oxford University Press
- Mitani, J.C., & Marler, P. (1989). A phonological analysis of male gibbon singing behavior. *Behaviour*, *106*, 20-45.
- Mitani, J.C., Hasegawa, T., & Gros-Louis, J., & Marler, P. (1992). Dialects in wild chimpanzees? *American Journal of Primatology*, *27*, 233-243.
- Parker, S.T. (1996). Using cladistic analysis of comparative data to reconstruct the evolution of cognitive development in hominids. In E.P. Martins (Ed.) *Phylogenies and the comparative method in animal behavior* (pp. 361-398). New York: Oxford University Press.
- Parker, S.T., & Gibson, K.R. (1979). A developmental model of the evolution of language and intelligence in early hominids. *The Behavioral and Brain Sciences*, *2*, 367-407.
- Parker, S.T., & Gibson, K.R. (Eds.). (1990). *"Language" and intelligence in monkeys and apes*. New York: Cambridge University Press.
- Pinker, S. (1994). *The language instinct: How the mind creates language*. New York: Morrow and Company.
- Pinker, S., & Bloom, P. (1992). Natural language and natural selection. In J.H. Barkow,

- L. Cosmides, & J. Tooby (Eds.) *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 451-493). New York: Oxford University Press.
- Plotkin, H. (1998). *Evolution in mind: An introduction to evolutionary psychology*. Cambridge: Harvard University Press.
- Potts, R. (1996). *Humanity's descent: The consequences of ecological instability*. New York: Avon Books.
- Povinelli, D.J., & Eddy, T.J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, 61 (3, Serial No. 247).
- Rauschecker, J.P., Tian, B., & Hauser, M.D. (1995). Processing of complex sounds in the macaque nonprimary auditory cortex. *Science*, 268, 111-114.
- Richardson, R.C. (1996). The prospects for an evolutionary psychology: Human language and human reasoning. *Minds and Machines*, 6, 541-557.
- Savage-Rumbaugh, E.S., Murphy, J., Sevcik, R.A., Brakke, K.E., Williams, S.L., & Rumbaugh, D.M. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, 58 (3-4, Serial No. 233).
- Seyfarth, R.M., & Cheney, D.L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, 34, 1640-1658.
- Sherman, P.W. (1977). Nepotism and the evolution of alarm calls. *Science*, 197, 1246-1253.
- Steklis, H.D., & Raleigh, M.J. (Eds.). (1979). *Neurobiology of social communication in primates: An evolutionary perspective*. New York: Academic Press.
- Tobach, E. (1995). Comments on the present status of comparative psychology. *Polish Psychological Bulletin*, 26, 203-229.
- Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55, 1063-1069.
- Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375-424.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J.H. Barkow, L. Cosmides, & J. Tooby (Eds.) *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19-136). New York: Oxford University Press.
- Velichkovsky, B.M., & Rumbaugh, D.M. (Eds.). (1996). *Communicating meaning: The evolution and development of language*. New Jersey: Lawrence Erlbaum.