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ANIMAL COMMUNICATION AND EVOLUTION[1]

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Marc Hauser has written a book called *The Evolution of Communication.* I can best summarize the book's scope and immediately reveal my prejudice for its success by quoting my endorsement on the book jacket:

> The study of Animal Communication is a diverse endeavor encompassing disciplines from physics and chemistry to psychology and linguistics, traversing neurobiology, behavior and evolution along the way. No one treatment of this field could be definitive. Hauser has sampled it, however, to produce a treatment that encompasses both the subject's richness and its subtleties, and that is exquisitely clear in its presentation. This work can serve as an undergraduate text, an introduction to the novice researcher and a reminder to others of us of the initial excitement that drew us to this area of study.

Although evolution is prominently highlighted in its title, this book strives for a more diverse audience of neuroscientists, animal behaviorists, psychologists, and linguists, as well as evolutionary biologists. It enthusiastically introduces each topic, reviews the research methods used to address various hypotheses, and copiously illustrates the results of numerous case studies. Sometimes the details overwhelm, but when Hauser discusses unfamiliar topics, I was more than grateful for them. For example, Hauser (as well as Pinker 1994) has done a great service for nonlinguists who want to understand Chomsky's thoughts on language evolution by sparing us the ordeal of plowing through Chomsky in its dense and jargon-laden original. Thus the book's exposition is best suited to the nonexpert; due to the book's breadth, however, most readers would be classified as non-experts much of the time. I am sure that there are few who are even conversant with, let alone expert on, all of the topics that are reviewed here, a small sampling of which include: various philosophies and theories of the mind, psycholinguistic studies of language acquisition in children, ecological sources of selection on acoustic transmission, hormonal correlates of bird song control, and the influence of sexual selection and species recognition on the evolution of communication systems.

Despite the book's title, there are many topics that are outside the immediate interests of most evolutionary biologists. But Hauser has two not-so-hidden agendas here. One is to convince the readers of the virtues of a multidisciplinary analysis of communication guided by Tinbergen's famous "four questions." The other is to argue strongly for an evolutionary continuum between animal communication and human language. The book's hallmark is that it encompasses a diversity of topics from often unrelated disciplines, while managing to maintain coherence by reference to these two goals, and it does so in a manner both entertaining and informative.

Prior to considering the content of *The Evolution of Communication* in more detail, it is necessary to consider the book's coverage. This is a book primarily about how vertebrates communicate in the visual and acoustic domains. In keeping with the spirit of a multidisciplinary analysis, Hauser justifies this coverage by wanting to concentrate on those communication systems that have been subject to a rather broad scope of investigations. Therefore, within vertebrates, for example, there is little about olfactory communication in mammals or electrical communication in fishes. Thus omitted are some of the most elegant analyses of neural and endocrine mechanisms in communication (Heiligenburg 1991). The restricted taxonomic scope also deprives the readers of a rich literature. There is little about insects. Thus, the readers again miss elegant studies of neural bases of signal recognition (Huber 1990); a proposal of how neural central-pattern generators could result in the tightly coordinated signal-receiver systems that guide species recognition in crickets (Bentley and Hoy 1972; Doherty and Hoy 1985); the role of communication in hybrid zones of grasshoppers (Ritchie et al. 1992); the complicated and surreptitious coevolution of signal and receiver in the *Photuris-Photinus* fireflies in which females mimic the signals of heterospecific females to lure and then dine upon mate seeking males (Lloyd 1984), and the debated role of the *per* locus in *Drosophila* courtship song and mating preferences (Kyriacou et al. 1992; Hall 1994).

These limitations are not oversights but result from organizing the text around Tinbergen's four questions. Also, there is a matter of economy. At nearly 600 pages and 1500 references (including a quite detailed index—an item that appears to be an afterthought in many other books), this book is already a large undertaking. An alternative would have been to concentrate on nonhuman animal communication; drop the emphasis on integrative studies; and omit the discussions of a universal generative grammar, the creolization of pidgins in both spoken and sign languages, the ontogeny of infants' concepts of cause and effect, and the various forays into the theory of mind. That would have been one approach. Hauser chose a more ambitious and unique one in which he explicitly attempts to bring human language into the context of animal communication and evolution. For me, Hauser made the right choice. But as I suggested at the outset of this essay, no one treatment of this field can be definitive. Hauser's book should be viewed as a compliment to, rather

[1] *The Evolution of Communication.* Marc D. Hauser. 1996. MIT Press, Cambridge, Massachusetts. 592 pp. ISBN 0-262-08250-0. HB $55.00.

than a replacement for, other reviews of animal communication.

Tinbergen's Four Questions and Integrative Science of Communication

Animal behavior, of which much of animal communication is a subset, is a field that lacks a single unifying concept because its studies address the phenomenon at different levels of analysis. Tinbergen (1963) brought some organization to this field when he proposed a method for unifying the diversity of studies in animal behavior. The four questions, as modified and summarized by Hauser (p. 2), address the following issues: (1) Mechanistic—understanding the mechanisms (e.g., neural, physiological) underlying the expression of a trait; (2) Ontogenetic—determining the genetic and environmental factors that guide the development of a trait; (3) Functional—looking at a trait in terms of its effects on survival and reproduction (i.e., its fitness consequences); and (4) Phylogenetic—unraveling the evolutionary history of the species so that the structure of the trait can be evaluated in light of ancestral species.

These questions provide the outline of Hauser's attempt to unify the study of animal communication, which in this work includes human language. Reviewing the field of communication in the context of such an all-encompassing array of questions presents its own difficulties. Doing so in an integrative nature, in which Tinbergen's questions are not merely descriptors of unrelated studies but a protocol for integrating levels of analysis, is even more onerous.

Animal Communication and Human Language

The Evolution of Communication consists of eight chapters. The second, "The Evolution of Communication: Historical Overview," gives us some appreciation for the various views of the biology of human language and animal communication. This short introduction sets the tone and the agenda for the rest of the book, and as such deserves comment.

Hauser reviews the contributions of three biologists as being critical to shaping how we currently view animal communication. One, of course, is Darwin; his *The Expression of the Emotions in Animal and Man* is the first treatment of the evolution of behavior and still appears to offer many insights into the issue. The others are John Smith and Peter Marler. Smith has written extensively on the relationship between message and meaning, but it is Marler's studies that have defined the field for many of us. Key are Marler's studies that are relevant to human language. First and foremost are his investigations of song acquisition in birds. For some oscines, song learning is restricted to a sensitive period during which the songs of tutors are memorized and later used as templates or models to which birds compare their own developing song during a period of song crystallization. If there is not a model, then the young do not develop true song. If there is a model, but no way to compare that model to the developing song (e.g., birds are deafened), again no song develops. Bird song acquisition is strikingly analogous to some stages of language acquisition in infants. Both are characterized by an improvisational or babbling stage, the importance of auditory feedback, and the appearance of an "instinct to learn," perhaps akin to Chomsky's notion of a universal, generative grammar (see below). The latter concept was before its time in animal behavior, a field plagued with the overly simplistic nature-nurture diatribe. Marler's suggestion of an instinct to learn is enlightened in its recognition of gene-by-environment interactions as a more productive paradigm than the categorical debate of genes versus experience. This emphasis also has parallels to Chomsky's assertion that "Language learning is not something that a child does; it is something that happens to a child placed in an appropriate environment. . ." (cited in Hauser 1996, p. 594).

Another one of the major contributions of Marler and his colleagues is the demonstration that animal signals can be referential. Some social scientists have been enamored with identifying uniquely human attributes: tool use, self awareness, and language were some of the most popular. Language, however, is composed of several components that involve the production, reception, and perception of signals (Hockett 1960). The specific relation of human language to the external world had been thought diagnostic of language. Unlike the growl of a dog, which Darwin and most others viewed as a mere expression of the animal's emotional state, language is referential—by Hauser's definition, "it is reliably associated with the occurrence of X." When we consider that vervet monkeys and chickens have separate calls for terrestrial and aerial predators, let alone the clear symbolism imbedded in the honey bee's dance, then we have identified a key component of language present in animals. Categorical perception is another feature that was held to be dear to humans. But we now know that not only can chinchillas and quails categorically partition synthetic continua of human phonemes, but rats and even crickets (Wyttenbach et al. 1996) rely on categorical perception to decode natural sounds.

On the language side, Hauser begins by reviewing the views of Chomsky, which suggest that there is a strong genetic component to language acquisition, that language is a uniquely human quality, and that natural selection played no role in the emergence of human language. This view is contrasted, on the other extreme, with that of an emerging paradigm in evolutionary psychology, cleverly and forcefully argued by Pinker (1994) in his immensely popular *The Language Instinct*. Evolutionary psychologists argue that language is indeed an instinct, as Chomsky suggested, but that natural selection is clearly the only agent that can be implicated for the existence of such a complicated design.

The data presented in favor of Chomsky's view of a language instinct are that children master a complex combinatorial system of parsing words into meaning without explicit instruction from others, and that language acquisition occurs most efficiently during an early sensitive period. The phenomenon of creolization is often cited to support this assertion. When adults of different languages are forced together, a nongrammatical communication system emerges—a protolanguage or pidgin. But when the adult's pidgin interacts with the child's universal generative grammar, a true grammatical language emerges—a creole. The classic example of creolization is from the Hawaiian sugar plantations. When slaves from various language groups were forced into work camps, a pidgin was used for communication, but when the slave's children were exposed to that pidgin they developed a creole. Language development is not restricted to the acoustic domain. When the Sandanistas began formally instructing the deaf in sign language in Nicaragua, those who learned signing later in life exhibited a pidgin. A creole sign language, with all the subtleties and complexities of a spoken language, was acquired when young deaf children were exposed to the pidgin.

Those of us working in nonhuman communication cannot help wanting to see the types of critical data that Marler and colleagues have provided for an instinct for song learning in birds. But studies of human language, thankfully, do not have the luxury of experimental intervention. Instead they must rely on the natural, albeit cruel, experiments of children in slave camps, those deprived a hearing early in life, and the "wolf children," who were tragically raised in social isolation. Considering some of the limitations of language research, creolization seems to be credible evidence for a language instinct. Other data in support of Chomsky's language instinct, such as the recent attention to a "grammar gene," seem to be misplaced, however. There might be an inherited language deficit as reported by Gopnik (1990), but this is hardly evidence for Chomsky's long-lost grammar gene, despite some exaggerated interpretations of this finding (Szathmary and Maynard Smith 1995).

There might be little debate in some quarters about a human language instinct, but what about the other notion—that natural selection is responsible for the evolution of language. There are several tacts to this argument. One is that of continuity. The existence of animal antecedents of some components of human language suggests it is less likely that all of the components of language emerged de nova in humans. Referential signals might be homologous in some primates and humans. Categorical perception is evidenced in some birds, mammals and insects, hardly evidence for uniqueness. This evidence by itself might not argue strongly for a role of natural selection, but it picks away at Chomsky's foundation—that language is a uniquely human attribute. Perhaps this is true when all of its components are considered in toto, but not when they are considered in isolation. The next advances in demonstrating animal antecedence of language components might come from the neurosciences. Some of the striking aspects of language neurobiology are left-hemisphere dominance and the existence of localized areas of the brain (Broca's and Wernicke's areas) involved in language. Although there are anatomical homologs of Broca's and Wernicke's areas in primates, these are not functional homologs. The increasing use of brain-imaging techniques, however, could reveal more detailed analysis of human function that might be profitably extended to other primates.

Thus, there are data available to evaluate the notion of animal antecedents for language, but to argue more specifically for a role of selection in guiding the evolution of language in humans is more difficult. One argument from evolutionary psychologists comes from complexity of design. Language involves quite specific morphologies of the sound production mechanism, localized areas of the brain for language, and the fantastic feats accomplished by every child who has ever learned to speak. Could we expect this to evolve without natural selection playing some role (see also Szathmary and Maynard Smith 1995)? Perhaps not. There are many selective advantages that might have favored language. Sexual selection seems to be an obvious force, but these arguments are based on the force of logic rather than data. This is rather unsatisfying when compared to the wealth of hard data on how the brain functions in language.

Animal Communication and Evolution

I have commented extensively about Hauser's treatment of human language evolution because this is less familiar to most evolutionary biologists. These comments should not imply that Hauser's book treats animal communication only as a potential antecedent to language. This is far from the case. This book serves as a wonderful and broad introduction to animal communication in the narrow sense.

In chapters 3–7 Hauser adheres to Tinbergen's questions in reviewing animal communication. Chapter 3 sets the stage for a multidisciplinary attack on the subject. In successive chapters he reviews neurobiological processes, ontogeny, adaptive design, and psychological aspects of signal processing. Chapter 8 summarizes Hauser's philosophy by arguing for a "socioecologically sensible neuroscience," and the use of experimental techniques that allow more ready comparison of communication systems across taxa. Throughout these chapters Hauser promotes his second agenda—the fruits of Tinbergen's research design.

An animal can drive a neighbor into sexual heat or aggressive frenzy merely by modulating air as it flows from the lungs. What is involved? There are structures implicated in signal production that function solely for this purpose, while others have been recruited from their evolved functions, like respiration, to aid in the task of communication. The signal that the receiver detects is not the same one sent by the signaler—signals degrade, attenuate, and interact with other sounds in the environment. The challenge to the receiver, then, is to extract biologically meaningful information imbedded in background. To do this, the receiver uses peripheral receptor organs, various areas of the brain, and cognitive processes to decode the sound. Finally, the signal elicits a behavioral response, an effect that is influenced by the biases in the receiver system as well as its hormonal and experiential milieu.

Much of this process can be viewed profitably as a problem in engineering. This is an approach that has been successful in neuroethological studies, as exemplified by Capranica's studies of "Neural coding in the bullfrog's auditory system—a teleological approach" (Frischkopf et al. 1968). But evolution and selection are not teleological. Furthermore, optimality approaches might not be ideal for fully describing the function and evolution of a communication system.

Some features involved in sound production, for example, have certainly evolved under selection to perform that function—the larynx and syrinx of terrestrial vertebrates are examples. But to produce sound, air must be expired from the lungs across a vibrating membrane in the larynx. The rate and force at which this can be accomplished influences the sound that is coupled to the environment. It would be foolhardy to ignore the more general and ancestral function of respiration and assume that this process has been derived to optimize signal production. This is true also in insects, such as *Drosophila*, in which movement of wings and muscles adapted for flight are involved in calling (Bennett-Clark 1971), and in which a gene involved in biological rhythm, the *per* locus, is also thought to influence call patterns in the love song (Kyriacao et al. 1992, Hall 1994).

Even if signal design is not constrained by other physiological functions, there might be additional selection on signal structure generated by the environment. In anurans, for example, the same call often appears to function in both short- and long-distance communication. Since calls usually exhibit differential frequency attenuation with distance, the design features optimal for short distance communication are not the same as in long distance.

Constraints on animal communication might be most apparent in the receiver end of the communication dyad. Animals use their sensory systems, including peripheral end organs, the central nervous system, and cognitive processes, to detect and perceive signals. But these systems have evolved under a variety of selection forces to accomplish other functions. For only one example, the necessity for some fiddler crabs to detect prey approaching over the horizon has caused the evolution of specific arrangements of the ommatidia in the eyes, which in turn favor males which erect vertical structures at the burrow (Christy and Salmon 1991). There might also be more general features of neural-cognitive systems that constrain signal reception. Hartshorn (1973) and Searcy (1992) have argued that complex repertoires in song birds might release the auditory system from sensory habituation, and a series of studies using neural networks have shown that biases for both elaborate and symmetrical stimuli (Enquist and Arak 1993, 1994; Johnstone 1994) might be an unintended consequence of selection or learning. In fact, some aspects of music appreciation in humans might even derive from general sensory properties. Zentener and Kagan (1996) recently showed that four-month-old infants show greater attention to consonance over dissonance in music, supporting Helmholz's (1954) claim that such judgements are based on innate properties of the auditory system.

The evolutionary history of a taxon is known to have a critical influence on the forms of signals displayed. This interest in historical effects is exemplified in earlier ethological studies by Lorenz's (1941) comparative analysis of duck displays. More recently, however, has been the acknowledgment that the signal-receiver dyad has an evolutionary history that can critically influence the response properties of the receiver. Thus it has been found that females have preexisting preferences for traits that sexual selection favors in other taxa but are absent in their own; when swords are added to platyfish they are preferred by female platys, a preference similar to that shown by swordtail females for their own naturally sworded males (Basolo 1990). History also has a predicted effect on strength of biases for heterospecific calls in túngara frogs (Ryan and Rand 1995).

The strength of *The Evolution of Communication* is that it delves into all of these subjects and gives the uninitiated a useful introduction to neural processing, the structure of sound-producing structures, environmental attenuation, and adaptations of communication. It treats these topics not in isolation but as components of a general biology of communication, which might have been a more fitting title for the book.

My purpose in this review has been twofold. One was to consider the degree to which Marc Hauser's *The Evolution of Communication* succeeds. And in my view, it is most successful. The other was to introduce some aspects of this field to readers of *Evolution* not familiar with it. Animal communication is a critical component of many fields in evolution, such as sexual selection, species recognition, kin recognition, reinforcement, hybridization, coevolution, behavioral and population genetics, and systematics. Many researchers acknowledge this and incorporate some components of animal communication into their studies. Most, however, have not been exposed to any formal or organized overview of the field, and for a long time none was available. With *The Evolution of Communication* we now have an extensive treatment of this active and exciting field that encompasses much of biology and is especially relevant to evolution.

Literature Cited

Basolo, A. L. 1990. Female preference predates the evolution of the sword in swordtail fish. Science 250:808–810.
Bentley, D. R., and R. R. Hoy. 1972. Genetic control of neural network generating cricket song patterns. Anim. Behav. 20:478–492.
Bennet-Clark, H. C. 1971. Acoustics of insect song. Nature 234: 255–259.
Christy, J. H., and M. Salmon. 1991. Comparative studies of reproductive behavior in mantis shrimp and fiddler crabs. Am. Zool. 31:329–337.
Doherty, J., and R. R. Hoy. 1985. Communication in insects III. The auditory behavior of crickets: some views of genetic coupling, song recognition, and predator detection. Q. Rev. Biol. 60:453–472.
Enquist, M., and A. Arak. 1993. Selection of exaggerated male traits by female aesthetic senses. Nature 361:446–448.
———. 1994. Symmetry, beauty and evolution. Nature 372:169–170.
Frischkopf, L. S., R. R. Capranica, and M. H. Goldstein Jr. 1968. Neural coding in the bullfrog's auditory system—a teleological approach. Proc. I.E.E.E. 56:969–980.
Gopnik, M. 1990. Feature-blind grammar deficit and dysphasia. Nature 275:344–346.
Hall, J. C. 1994. The mating of a fly. Science 264:1702–1714.
Hartshorn, C. 1973. Born to sing. Harper and Row, New York.
Heiligenburg, W. 1991. The neural basis of behavior: a neuroethological view. Annu. Rev. Neurosci. 14:247–267.
Hemholz, H. V. 1954. On the sensations of tone as a physiological basis for the theory of music. Dover, New York.
Hockett, C. F. 1960. The origin of speech. Sci. Am. 203:88–96.
Huber, F. 1990. Nerve cells and insect behavior-studies on crickets. Am. Zool. 30:609–627.
Johnstone, R. A. 1994. Female preference for symmetrical males as a by-product of selection for mate recognition. Nature 372: 172–175.
Kyriacou, C. P., M. L. Greenacre, M. B. Ritchie, and B. C. Byren. 1992. Genetic and molecular analysis of the love song preferences of *Drosophila* females. Am. Zool. 32:31–39.
Lorenz, K. 1941. Comparative studies of the motor patterns of Anatinae. Stud. Anim. Hum. Behav. 2:14–18, 106–114 (translated by R. Martin 1971).
Lloyd, J. E. 1984. On deception, a way of all flesh, and firefly signalling and systematics. Oxf. Surv. Evol. Biol. 1:48–54.
Pinker, S. 1994. The language instinct. William Morrow, New York.
Ritchie, M. G., R. K. Butlin, and G. M. Hewitt. 1992. Fitness consequences of potential assortative mating inside and outside a hybrid zone in *Chorthippus parallelus* (Orthoptera: Acrididae):

implications for reinforcement and sexual selection theory. Biol. J. Linn. Soc. 45:219–234.

RYAN, M. J., AND A. S. RAND. 1995. Female responses to ancestral advertisement calls in the túngara frog. Science 269:390–392.

SEARCY, W. A. 1992. Song repertoire and mate choice in birds. Am. Zool. 32:71–80.

SZATHMARY, E., AND J. MAYNARD SMITH. 1995. The major transitions in evolution. Nature 374:227–232.

TINBERGEN, N. 1963. On aims and methods of ethology. Z. Tierpsychol. 20:410–433.

WYTTENBACH, R. A., M. L. MAY, AND R. R. HOY. 1996. Categorical perception of sound frequency by crickets. Science 273:1542–1544.

ZENTNER, M. R., AND J. KAGAN. 1996. Perception of music by infants. Nature 383:29.

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A BIG BOOK AND A SMALL BOOK ON SELECTION[1,2]

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Selection. The Mechanism of Evolution and *The Basics of Selection* are two versions of the same book. The first is a lengthy treatise, which is clearly intended primarily for graduate students and researchers in evolutionary biology. The second is an abridged version that is more suitable for a less-specialized audience, such as advanced undergraduates. I will focus on the longer work, as it is probably of greater interest to readers of *Evolution*.

R. A Fisher started *The Genetical Theory of Natural Selection* with the remark that "Natural selection is not Evolution." In the introduction to *Selection*, Graham Bell states provocatively that "Evolution is the development and maintenance of complex organization that functions appropriately in given conditions. There are many forces that hinder evolution—mutation, sampling error, immigration, and so forth—but selection is the only process that *causes* evolution" (p. xix). It is quite an achievement to be more Fisherian than Fisher, and people who conduct DNA sequence comparisons will be surprised by the notion that the fixation of neutral nucleotide substitutions does not constitute evolution. But this assertion certainly leaves the reader without any illusions as to the scope of this book, one of the longest on evolutionary biology to appear in recent years. Indeed, its coverage is even narrower than the title and these remarks suggest. It is concerned mainly with selection experiments, in which either the direction of natural selection is controlled by the experimenter, or in which artificial selection is applied to traits of interest. Bell's avowed reason for this is that "it is only through selection experiments that the mechanism of evolution can be studied directly" (p. xxi).

The first chapter starts by explaining the basic principles of selection on self-replicating molecules, which is where it presumably all started. Bell uses the results of the Qβ RNA virus system to illustrate processes such as correlated responses to selection, the stepwise incorporation of individual changes to achieve more perfect adaptations, and the element of historical contingency inherent in evolution by selection and random mutation. All of this is very well done, and thoroughly clears away most of the major misconceptions about the nature of selection. Chapter 2 deals with the nature of selection on single characters in more complex systems, with very detailed reviews of artificial selection experiments for a variety of traits and of the artificial evolution of novel metabolic functions in bacteria, with a much briefer account of some of the classic studies of selection in the wild. The interaction between selection and genetic drift is treated qualitatively, as are a number of special topics such as the effect of genetic recombination on the response to selection.

Chapter 3 is concerned with selection on multiple characters, with considerable emphasis on the concept of trade-offs between life-history traits, and on the evolution of the rate of genetic recombination as a correlated response to selection on phenotypes controlled by the genes in question. Genotype × environment interactions in fitness traits are discussed at great length (pp. 310–382), and the chapter concludes with a discussion of levels of selection. The much briefer Chapter 4 treats selfish genetic elements, which propagate themselves within the host genome, even at the expense of reducing the fitness of their hosts. Experiments on the propagation of transposable elements and segregation distorters are the major focus of attention. Chapter 5 is another long one (pp. 434–580), and deals with density-dependent and frequency-dependent selection and selection on host-pathogen relations. It concludes with the argument that the "Red Queen" process of continual coevolution between hosts and parasites *must* be the explanation for the evolution and maintenance of sex and recombination, but without offering any strong evidence that favors this model over its rivals. The final chapter is on sexual selection which Bell defines

[1] *Selection. The Mechanism of Evolution.* Graham Bell. 1997. Chapman and Hall, New York. xxii + 699 pp. ISBN 0-412-05521-X. HB $75.

[2] *The Basics of Selection.* Graham Bell. 1997. Chapman and Hall, New York. ISBN 0-412-05531-7. PB $37.50.

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