7th Altenberg Workshop in Theoretical Biology 2001

EVOLUTION OF COMMUNICATION SYSTEMS

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organized by D. Kimbrough Oller and Ulrike Griebel

The topic

The study of communication systems and their evolution has benefited from efforts within a wide variety of disciplines. On the one hand, recent theoretical progress in animal communication and related empirical research have yielded rich perspectives on the forces that guide the emergence of communicative displays in species ranging from invertebrates, to birds, to primates. Research has also demonstrated that birds, dolphins, and apes are capable of learning to utilize important features of human communication in circumstances where systematic training is applied.

In addition, the study of human communicative development has produced new perspectives on the flexibility of the human mind and new suggestions about the constraints on possible patterns of evolution for complex and flexible communicative systems. For example, work in artificial intelligence and connectionism is providing increasingly significant simulations of human communicative abilities, simulations that offer important tests of the plausibility of proposed theories of language function, and that also provide empirical proof regarding the power of relatively simple theoretical constructions to characterize some of the rich capabilities of human language users. Further, research on human infant vocal development has recently offered perspectives on ways that communicative systems can possess properties greatly surpassing those found in non-human systems while at the same time being severely restricted when compared to mature human languages.

The workshop's topic is the evolution of communicative systems of a broad range. The comparison among these, and the development of frameworks in which such comparison can be fruitfully made, is of paramount importance in the study of the evolution of communication.

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Abstracts

JELLE ATEMA
atema@bu.edu
Marine Biological Laboratory
Boston University Marine Program
Woods Hole, MA 02543, USA
phone: +1 508 289 7499
fax: +1 508 289 7950

Chemical Communication Signals

Most sensory signals travel rapidly from source to receiver through the medium. With their nearly instantaneous presence this results in predictable spatial patterns. The unusual aspect of odor signals is that they travel rather slowly and primarily with not through the fluid medium, be that air or water. Odor dispersal is commonly linked with hydrodynamic dispersal of fluid momentum. Hydro-(and aero-) dynamic stimuli have similarly chaotic properties. This physical constraint has profound consequences for senders and receivers of chemial signals. Whereas odor can convey highly specific identification of the source of release, locating that source by odor alone is so difficult that many animals use additional sensory information for tracking.

Odor specificity originates with molecular and mixture complexity. The evolutionary process of ligand-receptor interactions takes place at all levels of biological organization. One might define life by this chemical recognition process. Pheromones constitute a specific subset of this molecular recognition process. Defined as communication signals they are subject to "cheating" as any other communication signal. Urine signals are interesting because they may contain not only pheromones but also automatic safeguards against cheating. Individual recognition may have evolved to maintain stable dominance hierarchies; it is based frequently on chemical signals that may be genetic, dietary and/or bacterial in origin. Receptor physiology can provide narrowly tuned filters that can make chemical signals "private" communication channels.

Dispersal of chemical signals is accomplished through molecular diffusion and fluid flow; the latter has been described as eddy diffusion. Molecular diffusion is essential over cellular distances including those involved in chemoreceptor processes. Interanimal distances are typically larger and here eddy difusion is essential. Animals releasing odor must rely on currents and often generate these themselves. Natural currents in the environment provide the next steps of dispersal. Odor plumes are only statistically predictable. Spatial patterns of mean concentration can be derived and some slowly moving animals may use that information. Faster animals appear to derive directional information more quickly from gradients of small plume features. Their chemoreceptor cells are dynamically tuned to such features. Since eddy dispersal includes dispersal of momentum generated at the source it is logical to expect bimodal processing of chemical and hydrodynamic signals. The resulting tracking behavior is Eddy Chemotaxis.

ROBIN . M. DUNBAR
rimd@liverpool.ac.uk
School of Biological Sciences
Nicholson Building
University of Liverpool
Liverpool L69 3GS, England
phone: +44 151 794 5917
fax: +44 151 794 5094

The Transition from Primate to Human Communication Systems

Human communication systems presumably have their origins in the communication systems of non-human primates, but the processes by which evolution from one to the other has actually happened remain obscure and the subject of heated debate. I shall focus on the role that communication has in facilitating the bonding of social groups in Old World monkeys and apes, and the role that language/speech might have played (and may still play) in meeting that requirement in modern humans.

Although language offers many important selective advantages that allowed ancestral hominids to overcome the constraints on group size imposed by the time costs of social grooming, it nonetheless is a poor alternative to social grooming for more intimate types of relationship. Social grooming seems to work through its ability to stimulate the production of endogenous opioids, thereby creating a direct pharmacological reinforcement for an effective relationship. Speech, because it acts at a distance, lacks that direct bonding mechanism. I will review evidence to suggest that the deliberate stimulation of laughter during conversation was coopted to fill this vacuum.

W. TECUMSEH FITCH
tec@wjh.harvard.edu
Department. of Psychology
Harvard University
Rm 982 William James Hall
33 Kirkland St., Cambridge MA 02138
phone: +1 617 496 6575
fax: +1 617 495-3728

Evolving Honest Communication Systems: Production Constraints and "Mother Tongues"

The study of the evolution of communication has been strongly influenced in recent decades by the theory of handicaps, introduced by Zahavi and formalized by Grafen and others. Despite its value, the "handicap principle" makes several assumptions that limit its generality. These limitations are quite relevant to the evolution of vertebrate communication systems, especially human language. First, by ignoring the mechanisms of signal production, the theory overlooks the numerous ways in which signal production is constrained by physics, physiology and anatomy. Such constraints can have a powerful impact upon the details of signal design, making certain signals easy to produce and others nearly impossible.

When the factors underlying these "production constraints" are causally related to biologically important qualities (e.g., size, sex, species, or quality), the mechanism of signal production can enforce honest communication: honesty becomes the default in the absence of specific selection against it. I illustrate this point with the example of acoustic cues to body size. Second, handicap theory assumes conflict among individuals, and thus has little to say about situations in which signaler and receiver have common interests. This is particularly common in communication among kin, where low-cost honest signals can be evolutionarily stable. Because many visual and acoustic signals are low cost (the "conspiratorial whispers" of Krebs and Dawkins), the main costs associated with signaling are not physiological, but rather those fitness costs associated with accidental sharing of information with non-kin.

Thus, honest low-cost signaling systems are most likely to evolve in compact groups that
1) have a high-level of relatedness, and
2) are spatially separated from groups of unrelated individuals. I will argue that kin-selected "mother tongues" provide an excellent model for the evolution of human speech: the prototypical cheap, honest signal.

PETER GÄRDENFORS
Peter.Gardenfors@lucs.lu.se
Lund University Cognitive Science
Kungshuset
S-222 22 Lund, Sweden
phone: +46 46 2224817
fax: +46 46 2224817

Cooperation and the Social Emergence of Meaning

Humans are the only animals who can plan for future needs. I will argue that symbolic communication evolved in order to plan for future cooperation. A consequence of this position is that the social meanings of symbolic expressions emerge from the cooperation between individuals. I will discuss how constraints on semantic representations evolve through processes of cooperative sharing of knowledge and plans. As a paradigm case, I describe pragmatic settings of referential communication and provide a model of how the roles of names, nouns and adjectives can be explained by a process of abstraction that is based on principles of cognitive economy. The process is driven by strain on memory as a cost and efficiency of communication (identifying a referent) as benefit.

WILLIAM F. HARMS
billharms@billharms.com
3621 37th Ave. West
Seattle, WA 98199, USA
phone: +1 206 352 7851

Primitive Content and Representational Pluralism

The standard "propositional attitude" account of language meaning does not do justice to animal communication, nor does it facilitate the comparison of human and animal languages. Functional or teleosemantic theories of meaning offer an alternative which promises to explain not only what animals are saying, but also how the content of their language can be captured in ours.

In general, the meaining-content of a signal or representation is the combination of two sorts of maps or conventions. Extensional conventions determine under which external conditions a signal is correct or what a symbol stands for, i.e, truth-conditions or reference. Intensional conventions involve standards for correct causal or inferential processes within a representational system, e.g. what follows from or justifies a signal or representation. The standard assumption of combinatorial syntax as a prerequisite for any language allows only one way in which intension and extension can be combined (the propositional way), to the extent that it is commonly claimed that "intension determines extension." However, functional analyses of simple signaling systems (Millikan 1984, Skyrms 1996) demonstrate that intensions and extensions can be combined quite arbitrarily, depending on the function of a signaling system. For example, warning cries can take states of affairs as their extensions and direct behavioral consequences (instead of other signals) as their intensions. This simple kind of "tracking-and-motivating" content can be understood as biologically primitive, and is typically not translatable across species boundaries, since translation requires the preservation of both extension and intension. Nonetheless, once the structure of primitive content is understood, we can use our own language (extensionally) to specify both extension and intension of animal signals, thus capturing (though not translating) their content.

JAMES R. HURFORD
jim@ling.ed.ac.uk
Language Evolution and Computation Research Unit
Department of Theoretical and Applied Linguistics
University of Edinburgh

Adam Ferguson Building
Edinburgh EH8 9LL, Scotland, UK
phone: (0131) 650 3959
fax: (0131) 650 3962

The Neural Basis of Predicate Argument Structure

Vision and audition research in primates and humans shows two independent neural pathways; one locates objects in body-centered space, the other attributes properties, such as colour, to objects. In vision these are the dorsal and ventral pathways. In audition, similarly separable "where" and "what" pathways exist. PREDICATE(x) is a schematic representation of the brain's integration of the two processes of delivery by the senses of the location of an arbitrary referent object, mapped in parietal cortex, and analysis of the properties of the referent by perceptual subsystems.

The brain computes actions using a few "deictic" variables pointing to objects. Parallels exist between such non-linguistic variables and linguistic deictic devices. Indexicality and reference have linguistic and non-linguistic (e.g. visual) versions, sharing the concept of attention. The individual variables of logical formulae are interpreted as corresponding to these mental variables. In computing action, the deictic variables are linked with "semantic" information about the objects, corresponding to logical predicates.

Mental scene-descriptions are necessary for practical tasks of primates, and pre-exist language phylogenetically. The type of scene-descriptions used by non-human primates would be reused for more complex cognitive, ultimately linguistic, purposes. The provision by the brain's sensory/perceptual systems of about four variables for temporary assignment to objects, and the separate processes of perceptual categorization of the objects so identified, constitute a preadaptive platform on which an early system for the linguistic description of scenes developed.

RUFUS JOHNSTONE
raj1003@hermes.cam.ac.uk
Department of Zoology
Downing Street
Cambridge, CB2 3EJ, UK
phone: +44 (0) 1223 336685
fax: +44 (0) 1223 336676

Game Theory and Animal Communication – When is Honesty the Best Policy?

Communication entails interaction between at least two individuals – signaller and receiver – whose evolutionary interests need not coincide. Game theory, with its emphasis on strategic interaction and conflict resolution, is thus a useful tool with which to analyse the evolution of animal signalling behaviour. Here, I review the conflicts of interest that may arise in communication, and consider how they may be resolved. I focus in particular on the problem of honesty: how can informative communication persist when signallers stand to gain by deceit? Game theoretical models provide a clear formalisation of this problem, and can also suggest possible solutions. I consider both the influential 'handicap principle', which claims that honesty is maintained by signal cost, and more recent analyses, which suggest that cheap yet reliable communication may also be possible. I conclude by considering the limitations of the game theoretical approach, and how it may be related to other perspectives on communication.

MAGNUS S. MAGNUSSON
msm@rhi.hi.is
Human Behavior Laboratory
University of Iceland

Sudurgata 26, IS-101 Reykjavik, Iceland
phone: +354 525 4585
fax: +354 562 5219

Repeated Patterns in Behavior and Some Other Biological Phenomena: The T-System and its Corresponding Detection Algorithms

Even if largely unnoticed by humans for countless millennia, human behavior is highly structured as the development of alphabetic coding of verbal behavior and consequent intensive analysis of the records has born out suddenly but unmistakably during the very last tiny fraction of human existence. The existence of much more hidden structure could thus be expected.

While real-time and nonverbal aspects were typically excluded from linguistic studies it is recognized that human communication is a context sensitive real-time process, i.e., a deeply entangled time dependent system of both verbal and non-verbal elements. However, the methodological simplifications due to the technical difficulty of capturing and analyzing complex dynamic systems before the invention of video and computers are now loosing their justification and behavioral scientists are faced with data comparable in complexity to that of, for example, molecular biology and genetics where the development of adequate computerized pattern detection methods based on relevant structural models is now a vital concern. A similar effort seems urgently needed regarding the analysis of the structure and function of human behavior and communication.

In the view, the present paper thus presents a system of time patterns types, called the t-system, especially developed for more than two decades for the detection of recurrent hierarchical/syntactical patterns in real-time behavior records considered as multivariate point processes. recurrence of some sets of event-types and/or patterns such that the elements occur in a particular order and with time distances between them that are significantly similar between repetitions. Some derived terms are the t-marker, which is an element of a t-pattern that rarely occurs outside it and thus indicates (marks) its occurrence. Positive (or negative) t-associates of particular t-patterns are behaviors that are significantly likely (or unlikely) to occur within or around them. The respective extreme cases are called the t-satellite and the t-taboo. The t-packet is a t-pattern with its associates and it has attraction and repulsion zones around it within which its positive/negative associates, respectively, are significantly likely or unlikely to occur. A t-composition refers to the sub-set of non-overlapping alternating t-patterns (or t-packets) that best covers the behavioral stream in which they were detected.

The specially developed detection algorithms are implemented in the Theme computer program. The basic t-pattern detection algorithm searches for "critical interval" relationships between pairs of occurrences time series indicating the co-occurrence of two event-types and/or detected patterns within the same larger repeated pattern. The algorithm uses a bottom-up, dynamic programming, unsupervised learning approach, where the simplest patterns are detected first while more complex patterns are detected as patterns of simpler patterns up to any level decided by the data. The t-pattern concept allows gradual detection of the most complex patterns (and avoiding combinatorial explosion) through pattern competition where only the most complete version of each pattern survives as partial versions are deleted.

The use of these behavioral models and methods has begun in bio-informatics, i.e., for the discovery of structure in proteins and DNA. The first results seem promising and results from the analysis of both behavioral and molecular structure will be presented.

JENNIFER MATHER
mather@uleth.ca
Department of Psychology and Neuroscience
University of Lethbridge
Lethbridge, AB, Canada T1k 3M4
phone: +1 403 329 2423
fax: +1 403 329 2555

Cephalopod Skin Displays: From Concealment to Communication

The skin of Cephalopod molluscs is a superb structure for visual display formation. Elastic chromatophore sacs contain yellow, red or brown pigment, and the direct neural connections to each set of extensor muscles assures fine spatiotemporal control of the animals' appearance. This is assisted by reflective irridophores and leucophores in deeper skin layers which reflect the surroundings, and by postures of body and arms. The system probably evolved for as anti-predator concealment, and skin appearance produces a variety of concealing devices. Background matching and disruptive patterning, both in whole and on parts of the skin surface, as well as quick temporal shifts in appearance, will be discussed as cephalopod camouflage devices.

But what happens when this ultra-flexible system is used for deliberate communication? Two instances of skin signals to conspecifics in Sepioteuthes will illustrate. Female Sepioteuthis display a pale-mantle dark-rim Saddle as an indication of sexual interest to potential mates. As their reproductive interest wanes, and to less attractive suitors, females modulate the signal by paling less and less of the mantle. This modulation with motivation change is also true for Octopus cyanea males' sexual display. A second example is the Sepioteuthis male Formal Zebra striped display. This ritualized contest of two males has relative positions, visual patterns and signal intensities, accompanied by arm positions and standardized winners and losers. It represents a formalized contest which is the end result of signal escalation. These instances of Cephalopod skin pattern communication use different extents of the spatiotemporal modulation and accompanying postures presumably developed for camouflage from potential predators and show how the animals can take a system evolved for interspecies communication and adapt it to signal to conspecifics.

RUTH G. MILLIKAN
ruth.millikan@uconn.edu
Department of Philosophy
U-54, University of Connecticut
Storrs, CT 06269-2054, USA.
phone: +1 860 486 4592
or: +1 860 429 1284

On Reading Signs; Differences Between Us and the Others..

When discussing what signs animals can understand or might learn to understand, it is important to have right in center stage an explicit theory of mental representation, and to consider what kinds of mental representations these animals might possess. If there are certain kinds of signs that an animal cannot learn to interpret, that might be because it cannot discriminate the signs, or it might be because the decoding is too difficult for it. These problems might be solved by using another sign system, say, gestures rather than noises, or perhaps icons positioned on a keyboard. But a more interesting reason the animal might fail to understand the sign is that it lacks mental representations of the necessary kind. It is incapable of representing mentally what the sign conveys. I am going, very quickly, to sketch a theory of mental representation and of the most basic varieties of mental representation. Then I will talk about some uses that we humans make of signs and why it is likely that the content of some of these signs is impossible for other animals to grasp.

I had better begin with a disclaimer. "Mental representation," in my vocabulary, has nothing to do with consciousness. I am not going to talk about what is before or within animals' conscious minds. Mental representations have to do only with the mechanics of behavior control, how this control is accomplished, presumably, neurologically. The theory I will offer could be viewed, for example, as a clarification and embellishment of Gallistel's ideas on mental representation.

D. KIMBROUGH OLLER
kimoller@maine.edu
Department of Communication
Sciences and Disorders
University of Maine, 5724 Dunn Hall
Orono, ME 04469-5724, USA
phone: +1 207 581 2036
fax: +1 207 581 2060

Underpinnings for a Theory of Communicative Evolution

To address the comparison of communication systems in a variety of species and to form the basis for a lasting system of interpretation of relationships among communicative systems, it is necessary to establish a general theory of the ways that systems of communication can evolve. It has been my hypothesis for some time that evolution of systems of communication is constrained by a progression of necessary steps toward elaboration and increasing communicative power. According to the reasoning, the steps can be specified as "properties", or "design features", of possible communicative systems, and because these properties are necessary components of powerful function, they may be able to provide a firm basis for comparison of communication across species and for characterization of the level of complexity and richness of various communication systems. The properties can also be thought of as "capabilities", that evolving organisms must command in order for their communicative systems to attain given levels of power in communication.

The challenge, if my hypothesis is on target, is to specify the nature of each elemental property of potential communicative systems as well as the presuppositional relationships among the properties. This is a partially terminological problem (because different scientists often use technical terms in individual ways, and confusions abound based on such differences in usage), but more fundamentally the problem is one of determining the functional limits on each of the properties, the boundaries that differentiate one property from another. The hypothesis implies that such boundaries should indeed be determinable, and consequently that when the enterprise of definition has progressed to some significant degree, there should emerge a lasting consensus about features of evolution of communicative systems in a very wide variety of species, and indeed in an indefinitely large range of possible species. The characterization of properties and their hierarchy should endure because the properties, if the hypothesis is correct, are real aspects (not just contrivances developed by individual thinkers) of the infrastructure of communication systems.

DONALD H. OWINGS
dhowings@ucdavis.edu
Department of Psychology
University of California
One Shields Avenue
Davis, CA 95616-8686, USA
phone: +1 530 752 1673
fax: +1 530 752 2087

Motivation and Emotion are Resources for Self-Interested Communication

This presentation will explore the roles of motivational and emotional systems in communication, emphasizing interactions between parent and offspring. I will begin by discussing similarities between the study of parent-offspring interactions from the perspective of attachment theory, and the study of communication using an assessment/management approach (A/M). Both approaches view organisms as self-interested regulatory systems that use signals to regulate, or manage, the behavior of others. A/M adds the idea that signals work by capitalizing on the psychological assessment systems of signal targets. The combination of the two perspectives raises new questions about the roles of motivation and emotion in communication. Traditional emphases have been on how these psychological processes influence signal production. This presentation will emphasize complementary questions about the

consequences for communication of motivational and emotional processes in the targets of signals. The motivational and emotional systems of others are communicative resources, potentially exploitable as "levers" to use in the management of their behavior.

IRENE PEPPERBERG
impepper@media.mit.edu
The Media Lab
MIT Bldg E15-318, 20 Ames Street
Cambridge, MA 02139, USA
phone: +1 617 253 0364
or: +1 617 253 8337
fax: +1 617 253 6215

The Evolution of Communication from an Avian Perspective

Most studies on the evolution of communication systems devolve into treatises on the evolution of language, and thereby concentrate on the primate lineage. Although direct connections between the communication systems of birds and humans are unlikely—other than those made by the Bwiti tribe in Africa, who claim that Grey parrots (Psittacus erithacus) brought language to humans as a gift from the gods—what is missing in most current studies of the evolution of communication is the concept of parallel lines of evolution. No longer, for example, are papers of Marler and his colleagues on the parallels between birdsong and human language considered central to communication studies; similarly, research that examines what avian species can achieve in the laboratory is often marginalized as artifactual. But, given our knowledge of vocal learning in birds, of the effects of social interaction on such learning, and of their complex cognitive abilities, we cannot ignore the avian line if we wish to determine the evolutionary pressures that purportedly affected the evolution of complex communication systems—particularly vocal systems—and develop theories and models that can be tested.

Although phylogenetically remote from humans, Grey parrots in particular share many cognitive and communicative abilities with humans. On certain tasks, they demonstrate processing abilities comparable to 4 year old humans; they learn very simple vocal syntactic patterns and referential elements of human communication only through social interaction. Moreover, recent studies suggest that, despite their walnut-sized brain that is organized very differently from those of primates, their learning of such elements proceeds in ways similar to those of humans. And, as do humans, Grey parrots engage in solitary sound play (phonetic 'babbling') and also recombine phonemes in the presence of humans to produce new speech patterns from existent ones, implying that theyacoustically represents labels as do humans and that phonetic categories develop in nonhumans. They likely use a two-tube system similar to that of humans to produce their speech. One parrot appears to use anticipatory coarticulation—separates specific phonemes from speech flow and produces these sounds so as to facilitate production of upcoming phonemes—which along with sound play is consistent with top-down processing.. They recombine labels in novel ways to respond to novel situations and transfer their use of such labels across contexts. Greys learn from each other in the laboratory; in the wild they have dialects and alter their calls if they move to a different dialect area. They are long-lived, establish strong pair-bonds, and reside in large groups that may have complex social structure, much like that of primates. Such data suggest that these birds will provide important insights into what abilities were both necessary and sufficient for the evolution of complex cognitive and communicative processes.

CHRIS SINHA
Chris.Sinha@language.sdu.dk
Institute of Language and Communication
University of Southern Denmark
Odense, Campusvej 55
DK-5230 Odense M, Denmark

phone: +45 65 503631
fax: +45 65 932483

From Communication to Language: How (and When) did We Get There?

What distinguishes human natural language from other naturally occurring communicative behaviours and communication systems? An exclusive focus on syntax tends, paradoxically, to minimize the gap between human natural language and non-linguistic modes of communication. In addition to syntactic and morphological complexity, all natural languages also display symbolic complexity (sometimes referred to as "displacement"), cognitive complexity (in terms of conceptualization subsystems) and pragmatic complexity (linked, in the case of performatives, to symbolic complexity).

In this paper I develop the case that these dimensions of complexity are emergent consequences of the representational function of language, itself definitional, as proposed by Karl Bühler, of the distinction between SIGNALS and SYMBOLS. I argue that Bühler's signal-symbol distinction is, in terms of psychology of language, a more useful semiotic classification than the better known Peircian triadic classification, inasmuch as icons may be viewed as a species of symbol, and linguistic symbolization is in most cases iconically motivated and always indexically situated.

I propose an account of language evolution based upon the representational development of prelinguistic, intentional communication in contexts of intentional, intersubjective joint reference. The model presented is one in which intentional reference becomes conventionalized and elaborated in processes of semanticization and grammaticalization, about which we know a great deal in the context of historical language change. I discuss the role in language evolution of the niche of infancy, and suggest that the model is compatible with a "late emergence" scenario for evolutionary modern natural languages.

CHARLES SNOWDON
snowdon@facstaff.wisc.edu
Department of Psychology
University of Wisconsin
1202 West Johnson Street
Madison, WI 53706-1696 USA
phone: am: +1 608 262 3974
phone: pm: +1 608 262 1040
fax: +1 608 262 4029

Social Processes in the Evolution of Complex Cognition and Communication

Recent popular treatments of human language and cognition proposing species-specific language instincts or cognitive modules are essentially neo-creationist (or Pan-creationist, if they admit the cognitive skills of some chimpanzees) models that are fundamentally at odds with evolutionary theory. Although often couched in evolutionary theory (in terms of species-specific adaptations) the models often fail to acknowledge any continuity between human and nonhuman animals and provide unsatisfactory hypotheses for what adaptive changes have led to the evolution of human traits so apparently different from those of other species.

The challenge is to develop models that acknowledge what is unique in human cognition and communication while at the same time demonstrating parsimoniously how these traits evolved. Since access to the cognitive and communicative skills of our hominid ancestors is at best sketchy through the archeological record, our best hope for success comes in use of the comparative method with extant species. There are two very different comparative approaches that are possible.

If one views cognition and communication as essentially hard wired neurological processes, then the best models are likely to be those species that are closest to humans in brain size and complexity such as the anthropoid apes or, possibly, cetaceans. Indeed these species display impressive cognitive

accomplishments in tool use, in cultural-specific traits, group coordination in hunting, and possibly in teaching and taking the perspective of others. However, great apes are remarkably silent compared with chattering humans (and many other more vocal species) and therefore, to date, we have little information on the communication skills of apes to rival what we know of their cognitive skills.

An alternative approach is to view cognition and communication not as hard-wired processes but socially-constructed. By this approach our best hope for understanding complex cognition and communication is to look at species with similar social structure. Recently Sarah Blaffer Hrdy has argued (Mother Nature) that the available evidence suggests that humans are cooperative breeders. Thus few mothers can raise infants successfully without assistance from others. Both mothers and allo-mothers contribute to the nurturing and education of human infants. A direct corollary of this argument is that other cooperatively breeding species might display more complex cognitive and communicative skills and that these skills would be socially constructed.

Among nonhuman primates only marmosets and tamarins are cooperative breeders. Although they are phylogenetically remote from humans, there is much similarity in their social structure and infant rearing. Marc Hauser and his colleagues have demonstrated remarkable cognitive skills in tamarins. In addition, there is evidence of social learning of new skills and avoidance of noxious foods not seen in other monkeys, as well as imitation. Evidence from food sharing supports the idea that adults teach infants about food. Infant "babbling" in marmosets leads to improved communication skills. Marmosets show dialects in different populations and adults alter call structure when joining new groups. There are simple grammars and referential signaling. All of these findings suggest that at least some cognitive and communicative processes might emerge from species with social structure and rearing conditions similar to humans.

Although there are obvious differences in "hardware", the similarities in the "software" of social interactions may provide a fruitful focus for developing evolutionary models of human cognition and communication. (Supported by USPHS Grants MH29775 and MH00177)

LUC STEELS
steels@arti.vub.ac.be
Artificial Intelligence Laboratory
Vrije Unversiteit Brussel
Pleinlaan 2, Building G, Floor 10
Room 724, B-1050 Brussels, Belgium
phone: +32 (2) 629 37 00
fax: +32 (2) 629 37 29

The Cultural Co-Evolution of Language and Meaning

Recently important advances in the hardware and software architectures of autonomous robots have made it possible to tackle how non-trivial forms of communication could emerge in groups of artificial agents. But this requires that we have good theories on what components are required for communication, how the relevant knowledge is learned, and how a group of agents can reach consensus without global control nor pre-given language structures. I will discuss a number of concrete experiments on the emergence of shared sound repertoires, lexicons, meaning repertoires, and grammar. Some of the underlying theses are that
(1) the architecture needed for natural language like communication is non-modular and holistic,
(2) language and meaning co-evolve,
(3) coherence arises through self-organisation,
(4) neither language nor its underlying conceptualisation is strongly genetically determined.

PETER L. TYACK
ptyack@whoi.edu
Biology Department MS-34
Woods Hole Oceanographic Institution
Woods Hole MA 02543, USA
phone: +1 508 289 2818
fax: +1 508 457 2134

The Role of Sexual Selection, Echolocation, and Individualized Contact Signals in the Evolution of Vocal Learning in Birds and Mammals, with Special Reference to Marine Mammals

Most animals that communicate acoustically cannot modify the acoustic structure of their vocal output based upon auditory input. Only a few scattered animal taxa have evolved abilities of vocal learning. Humans use highly developed skills of vocal learning in the development of music and language, but there is little evidence of production learning in other primates. Among other animals, vocal learning has been studied most extensively in birds, particularly the oscine songbirds (Passeriformes). Among mammals, the only species with convincing evidence of learning to modify frequency parameters of vocalizations are the horseshoe bat, *Rhinolophus ferrumequinum*, harbor seal, *Phoca vitulina*, humpback whale, *Megaptera novaeangliae*, beluga whale, *Delphinapterus leucas*, and the bottlenose dolphin, *Tursiops truncatus*.

Vocal learning allows most songbirds to develop more complex advertisement displays. Sexual selection is thus one candidate for the evolution of vocal learning in species that learn advertisement displays, including songbirds, humpback whales, and some seals. Echolocation may have selected for vocal learning in echolocating species such as bats and dolphins. However, vocal learning is also implicated in maintenance of social bonds in many species, such as songbirds, parrots, dolphins, and humans, which learn to imitate contact calls of social partners.

The best evidence for vocal learning in dolphins stems from imitation of whistle vocalizations, which are used as an individual-specific contact call. Dolphins maintain individualized social relationships in which individuals appear to recognize one another and keep an individual-based history of interaction. Constraints on individual recognition in the sea may have provided a strong selective pressure for vocal learning. Many terrestrial animals learn distinctive visual features or voice cues for individual recognition. Diving mammals need to use acoustic signals for recognition at a distance, but cannot use voice cues because gas-filled vocal tracts change shape under changing pressure. Marine mammals that rely upon individual recognition for complex social relationships have therefore had to evolve specialized signature signals. Bottlenose dolphins have strong individual-specific social relationships within fluid fission-fusion societies. Vocal learning is important for the development of individually distinctive signature whistles, which dolphins use to maintain contact with specific individuals. Vocal imitation is also used for whistle matching among adults. Whistle matching appears to play a role in affiliative interactions in a way that appears similar to vocal accommodation in humans and other animals. As individual dolphins form social bonds, their whistles may converge.

Several different selective pressures are contenders as causing the evolution of vocal learning: sexual selection for more complex advertisement displays, echolocation, and maintaining individual-specific contact signals. Whatever the initial evolutionary causes for the evolution of vocal learning, vocal learning enables the development of complex open systems of communication with flexibility to match a variety of social functions.