12th Altenberg Workshop in Theoretical Biology 2005

THE EVOLUTION OF COMMUNICATIVE CREATIVITY
From Fixed Signals to Contextual Flexibility

7-10 July 2005

organized by D. Kimbrough Oller and Ulrike Griebel

Konrad Lorenz Institute
for Evolution and Cognition Research
Altenberg, Austria

The topic

The study of flexibility in communication systems in a wide variety of animals is offering new perspectives on the special forces that may have favored the evolution of language, with its omnipresent and seemingly unlimited flexibility. A variety of birds, marine mammals, New World monkeys, and even certain invertebrates show notable capabilities to break free from the fixed signaling patterns that have been so much the focus of description in classical ethology. A useful summary of the selection forces that favor steps toward contextual flexibility can now be provided, a summary that places in perspective speculations about the forces that may have guided hominid evolution toward spoken language.

Research in human infant vocal development also provides invaluable clues about the first steps of vocal communication that may have been taken by ancient hominids as they became differentiated from the primate background. In particular, human infants, during the first half-year of life, develop capabilities to produce vocalizations with a remarkable degree of contextual flexibility, apparently surpassing all the other primates and perhaps all other mammals. Since spoken language requires vocal contextual flexibility in all its aspects and functions, it appears that an extremely early step in hominid evolution, establishing a necessary foundation for later evolution of language, was the emergence of contextually flexible vocalization.

Philosophical work on communication and its origins along with modeling and simulation have vastly increased our view of possible sources and routes in the emergence of language. An important focus for such work is the formal conditions under which systems of communication can break free from the bonds of fixed signaling, the primary mode of vocal communication in the primates. Developing an understanding of these formal conditions is crucial in understanding the evolution of language.

Program

PERSPECTIVES ON CONTEXTUAL FLEXIBILITY

Ulrike Griebel Evolutionary Forces Favoring Contextual Flexibility: The Role of Deception and Protean Behavior
Kim Oller Contextual Flexibility in Infant Vocal Development and the Earliest Steps in the Evolution of Language

ROOTS OF LANGUAGE

Terrence Deacon On the Empty Space where we Expected to Find a Language Template: How a Complex Cognitive Function Evolved by Off-Loading Epigenetic Control
Brian MacWhinney The Linking of Recursion to Perspective-Taking
Kurt Hammerschmidt Neurobiological Constraints of Vocal Production in Primates and Other Mammals

PRIMATE CONTEXTUAL FLEXIBILITY

Michael Owren Integration of Production and Response Mechanisms as a Key Feature of Context-Independent Vocal Communication
Charles Snowdon Contextually Flexible Communication in Neotropical Primates
Josep Call How Apes use Gestures: The Issue of Flexibility
Jessica Flack A Potential Signaling Innovation in Primate Communication: The Role of Context in Signal Semantics

OTHER ASPECTS OF CONTEXTUAL FLEXIBILITY

Brenda McCowan Measuring Diversity, Flexibility and Complexity in Human and Nonhuman Animal Communication Systems
Stan Kuczaj The Role of Play in the Evolution and Ontogeny of Contextually Flexible Communication
Ron Schusterman Pinniped Vocal Learning
Martine Hausberger Social Life and Communication: Contextual Flexibility of Fixed Rules
Robert Lachlan Gene-Culture Coevolution in Bird Song

PHILOSOPHICAL PERSPECTIVES

Kim Sterelny Language, Evolution and Niche Construction

MODELING

Gert Westermann Flexible Communication from Interacting Constraints: A Connectionist Model
David Krakauer Universal Regularities in the Evolution of Biological Signals

Abstracts

JOSEP CALL
call@eva.mpg.de
Max Planck Institute for Evolutionary Anthropology
Deutscher Platz 6, D-04103 Leipzig

How Apes use Gestures: The Issue of Flexibility

Fixedness and emotional-boundedness were previously thought to be prominent features of animal communication. However, recent research on vocal and gestural communication has challenged this traditional view. Focusing on apes, I will show that flexibility is one of the defining features of their gestural communication. Such flexibility is manifested in a number of ways such as, for instance, contextual freedom. Ape gestures have no one-to-one correspondence between signals and functions (or contexts). Apes use single gestures in multiple contexts and a single context is served by multiple gestures. Tomasello et al. (1994) found that 38% of the chimpanzee gestures were used in more than one context by individuals. Likewise, the number of contexts served by a single gesture varied from five to one depending on the individual. In addition to this dissociation between signals and functions there are three other aspects that make ape gestural communication particularly flexible. First, apes combine gestures into sequences, usually as a way to engage unresponsive recipients. Second, they can acquire gestures outside their natural repertoire to request things from others, which in some cases entails referring to items that are not currently present.
Finally, they can adjust the sensory modality of their gestures to the attentional state of the recipient. This means that apes use visual gestures preferentially when others can see them whereas tactile gestures are used regardless of the attentional state of the recipient. Moreover, confronted with a recipient who is not bodily oriented to them (so that she cannot see them) they can use a number of strategies to get her attention such as using tactile gestures, walking around the recipient to face her directly or producing auditory signals.
Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. Primates, 35, 137-154.

TERRENCE DEACON
deacon@sscl.berkeley.edu
Biological Anthropology and Linguistics
UC Berkeley, USA

On the Empty Space where we Expected to Find a Language Template: How a Complex Cognitive Function Evolved by Off-Loading Epigenetic Control

In order to attempt an explanation of the unprecedented language competence of humans, linguists and evolutionary psychologists have postulated the existence of an extensive innate knowledge of language structure. The evolution of this innate template is often attributed to a biological implausible hopeful-monster mega-mutation or else an evolutionary scenario in which this "language module" is progressively built up by a process like the Baldwin Effect or Waddington's genetic assimilation.
I show that these latter processes suffer from previously unrecognized limitations that render any claims that they promote nativization of acquired knowledge or cognitive habits highly dubious. But accepting these limitations and tracing out the more likely consequences (e.g. "masking" -- the reverse of what Baldwin imagined would happen) we can discern a far more powerful effect that I call 'parallel distributed selection' (PDS, on the analogy of parallel distributed processing computation). I show that PDS serves to promote increasing epistasis (gene-gene interdependency) and increasing functional synergies while offloading some control of phenotype construction onto extragenomic constraints and processes. The mechanisms and consequences of this process are traced via biological examples (including a birdsong study showing the evolution of increasing "syntactic" complexity, increased

learning, and involvement of additional brain systems in the absence of selection and due to *degradation* of an innate song template) and multi-agent evolutionary simulations (showing how and why the process works this way).
It is concluded that it may be more accurate to conceive of the human language adaptations (plural) as roughly analogous to a photo-negative of an innate language template, and that they have evolved in part due to genetic and neurological de-volution. A surprising implication is that even if a language template were to have appeared fully formed in hominid brains at some earlier point in evolution, over time this template would have become spontaneously degraded, and an increasingly larger fraction of the determination of language structure would have been offloaded onto symbolic communication processes and their reliable emergent structural consequences.
The PDS effect is generalizable to many evolutionary contexts involving phenotypic plasticity, extra-organismic dependencies, complex functional synergies, or codependence (as in symbiosis and social cooperation), at all levels of biological organization.

JESSICA C. FLACK
jflack@santafe.edu
Santa Fe Institute
1399 Hyde Park Road
Santa Fe, New Mexico 87501, USA

A Potential Signaling Innovation in Primate Communication: The Role of Context in Signal Semantics

We are interested in the role that context plays in signal semantics, and how contextual shifts in signal usage might facilitate communication about increasingly abstract social referents, such as roles in relationships. Here we address the possibility that an innovation occurred in animal communication when primates began using unidirectional dominance signals, which arose in the agonistic context to signal yielding (immediate behavior), in peaceful settings to communicate subordination (agreement to a pattern of behavior). We explore the possibility that the invention of these special dominance signals allowed the formation of new types of social relationships, marked by a qualitatively greater degree of affiliation, cooperation, and repair mechanisms, and less frequent conflict.

ULRIKE GRIEBEL & D. KIMBROUGH OLLER
ugriebel@memphis.edu
The University of Memphis, Department of Biology,
Ellington Hall, 3700 Walker Avenue, Memphis, TN 38152

Evolutionary Forces Favoring Contextual Flexibility: The Role of Deception and Protean Behavior

There is a huge gap between the complexity of communication in human and non-human animals. In the non-human case, signals and functions tend to be few and show very limited contextual flexibility, whereas in humans, signals are of indefinitely large number, have a multitude of functions, and mapping from form to function and vice versa shows a huge degree of contextual flexibility. In an attempt to understand the evolution of human communicative flexibility, we have to look at other species. There seem to be very specific circumstances and only a limited number of evolutionary pressures that favor selection for variability and complexity in animal communication systems. Perhaps the most important one is sexual selection which appears to have created big and flexible repertoires in animal groups such as birds, pinnipeds and whales. Another very strong evolutionary force to diversify communication is created by complex social living circumstances. We find large repertoires and flexible communication signals in social species such as cetaceans, certain species of primates, and also in several species of social birds. Another possible selection force could be parental selection where communication has to be diversified to attract parental investment, which might play an important role e.g. among some new world monkeys.

In this paper we also explore the role of additional possible evolutionary forces that stem from a deceptive function of signaling: false signaling, protean (unpredictable) behavior and camouflage. It seems that deception can create new and different uses for former fixed signals even in invertebrates. Some species of fireflies have evolved a mechanism to learn the communication signals of the females of other species and use them deceptively to prey on the males of these species. Caribbean reef squid have evolved a very flexible system of color patterns on their skin which they use in camouflage as well as in social communication. In this species the need to hide in the open water has produced flexible production of body patterns to avoid potential predators: protean behavior. They also use disruptive patterns and mimetic behavior in other circumstances. This flexibility in pattern production is also seen in the social context where it also appears to be used with a deceptive function. Males and females are capable of using the entire signaling repertoire of the species and are thus able to falsely portray themselves as being members of the other sex.
In hominid evolution probably most of these forces have played a significant role at some point in time, and several of them are still involved at present. We suspect that particularly strong roles were played by sexual and parental selection at the point of the hominid divergence from the primate background.

KURT HAMMERSCHMIDT
kurt.hammerschmidt@dpz.gwdg.de
Deutsches Primatenzentrum (DPZ)
Arbeitsgruppe Kognitive Ethologie
Kellnerweg 4, 37077 Göttingen, Germany

Neurobiological Constraints of Vocal Production in Primates and Other Mammals

Human language is learned in terms of both vocal production and comprehension. From a comparative view, this raises the question to what extent other primate or mammal species are capable of vocal learning. Recent ontogenetic studies have revealed age related changes in the acoustic structure of nonhuman primate calls. But most of these changes seem to be related to more simple maturational factors, such as growth, or the ability to produce a constant subglottal pressure while vocalizing. Studies with cross-fostered or acoustically deprived animals showed that an acoustic model is not necessary to produce calls which fall within the species specific range. The conclusion that the general neural motor patterns are mainly innate is in line with conditioning experiments, which showed that only basal acoustic features, like duration or the repetition of elements, can be trained.
These findings are supported by neurobiological studies which have shown that monkeys, in contrast to humans, lack a direct connection of the motorcortex to the laryngeal motoneurons. In addition, comparative studies have found a phylogenetic trend in the projections of the motorcortical tongue area. This is of interest because the tongue is the most important organ in the differentiation of phonemes. Studies have found an increasing strength of the cortico-motoneuronal connection from non-primate mammals to non-human primates and humans.
The inability to generate new vocal patterns does not exclude a certain degree of vocal plasticity. Many nonhuman primates showed a life-long high degree of variability in their vocal types. This variability seems to be the foundation for convergence processes, like vocal accommodation or action based learning, which could lead to a certain degree of vocal differentiation within the same species. However, the neurobiological mechanisms of these convergence processes are not known.
Despite the relatively limited number of studies, it seems that most other mammal species have a similar lack of flexibility in vocal production. This is well documented for several rodent species. But also carnivores and ungulates seem to have similar restrictions. The exceptions are species like marine mammals that have a vocal production system which clearly differs from the standard mammal vocal production apparatus.

MARTINE HAUSBERGER
martine.hausberger@univrennes1.fr
Université de Rennes 1
UMR 6552 Ethologie-Evolution-Ecologie, Campus de Beaulieu,
F-35042 Rennes Cedex, France

Social Life and Communication: Contextual Flexibility of Fixed Rules

Communication among members of a social group requires several factors to be efficient: the signal must be heard by a partner, it must be adapted to this partner and to the interaction context, and the social stake it carries must be clear. The idea that communication rules must be shared by interlocutors has been specified and widely investigated in human social psychology. Failure to respect these rules can induce the end of an exchange between interlocutors. In other words, the two partners must share common rules that require a fixed basis. On the other hand, adaptation to context and audience requires a certain level of interactivity in vocal exchange that has to be attuned for social circumstances.
We will see here, at different phylogenetic levels, from birds to humans, how this balance has been found, and how examples can in turn give insights into the processes underlying communication pragmatics. We develop three examples of communication rules: 1) vocal use according to the status of the relationship between interlocutors; 2) flexible expressions produced by one interactor according to the interlocutor's social status; 3) flexible timing of vocal expressions in order to foster and maintain turn-taking.
The capabilities that foster these kinds of expression are powerful ones that are adaptable to a complex and changing social circumstance and have evolved in species that have complex social structures and in different phylogenetical groups.

DAVID C. KRAKAUER
krakauer@santafe.edu
Santa Fe Institute
1399 Hyde Park Road
Santa Fe, New Mexico 87501, USA

Universal Regularities in the Evolution of Biological Signals

The origin of all complex forms of adaptive organization from genomes, cells, multicells to societies, rely on coordination brought about through the exchange of signals. Signals vary according to composition, mechanisms of production and interpretation and local ecology. Signals also vary in their information capacity, susceptibility to noise and generative power. I survey the evolution of biological signals at multiple spatial scales, from signal transduction at the cellular level to human grammar. I focus on those regularities that have emerged at every level, such as discrete combinatorial alphabets, and on those factors contributing to transitions to more expressive forms of communication.

STAN KUCZAJ
s.kuczaj@usm.edu
The University of Southern Mississippi
Hattiesburg, MS 39406-5025, USA

The Role of Play in the Evolution and Ontogeny of Contextually Flexible Communication

Play is a ubiquitous characteristic of the young of many species, and this apparent universality has led to considerable speculation about play's ontogenetic functions and evolutionary origins. Although the specific roles of play in individual development have yet to be unequivocally determined, play has been suggested to facilitate cognitive development, social development, and language development.

For example, play has been hypothesized to be important in the ontogeny of contextually flexible thought. According to this view, play provides contexts in which an individual's behaviors are free from normal consequences (unless a predator or rival happens to take advantage of the play situation), and as a result encourages young organisms to create novel experiences for themselves and to learn from these experiences and from the novel experiences produced by others during play. As a result of the opportunities afforded by these sorts of experiences, play helps the young to develop the requisite cognitive skills for creative thinking and problem solving.
If contextually flexible thought is necessary for contextually flexible communication, then play may indirectly contribute to the emergence of contextually flexible communication by virtue of play's effect on requisite cognitive abilities. Play may also contribute to contextually flexible communication in more direct ways. Human infants and young children play with language sounds and structures as they acquire their native tongue, and there is some evidence to suggest that the young of other species engage in sound play as they acquire their vocal repertoire.
For the purposes of this talk, I wish to distinguish play with sound and/or language from other forms of play. Although I recognize that all communication is not necessarily language, that language need not be vocal, and that language and communication involve behaviors, for the sake of convenience I will refer to all play that involves language or vocal communication signals as language play and to all play that is not language play as behavioral play.
How similar are behavioral play and language play? Both typically occur in contexts that free the player from normal consequences, and so promote flexibility, exploration, and discovery. However, the two types of play differ in a number of ways, including the influence of peers on play complexity. Much of human children's early language play occurs while they are alone, and this solitary play seems to drive increasing complexity on its own accord. Although young children also engage in solitary behavioral play, the complexity of behavioral play is facilitated by the opportunity to observe and interact with peers much more so than is complexity of language play. In order to ascertain the significance of play for contextually flexible communication, it is essential to better understand the roles of peers in the behavioral play and language play produced by humans and other species.
In this talk, I will explore the possibility that play evolved to enhance behavioral flexibility, the relationship of behavioral flexibility and contextually flexible communication, and the relative roles of peers and adults in shaping a young organism's behavior and thought. The intrinsically reinforcing nature of play insures that players will work to perfect behaviors used during play, and so provides a mechanism through which individuals can acquire skills that have allowed their ancestors to survive. In addition, the freedom inherent in play contexts may help organisms acquire behavioral and communicative flexibility as they learn to disassociate one-to-one correspondences between individual functions and individual forms. The extent to which species differences in contextually flexible communication are related to differences in behavioral play and language play may help to determine the manner in which the human capacity for language became unique.

ROBERT F. LACHLAN
lachlan@rulsfb.leidenuniv.nl
Behavioural Biology, Institute of Biology, Leiden University,
PO Box 9516, 2300RA Leiden, The Netherlands

Gene-Culture Coevolution in Bird Song

Birds from many species socially learn their songs very accurately from conspecifics. A large body of empirical research has described how song learning affects the variety and distribution of song-types within and between populations. Compared to genetically transmitted signals, learned bird songs are much more variable within a population, and they also tend to vary over much shorter distances. Despite this, there is little evidence that different song-types have different functions. In some species, females prefer males with many different song-types, while in others males react differently to rivals that share song-types with them. But in many species, cultural evolution of song can be modeled as an analogy of genetic drift. In these cases, the question of why bird song is so variable is unanswered.
I will describe several models that explore this issue using the concept of gene-culture coevolution: the interaction between genetic and cultural evolution. The 'genes' in most of these models underlie the perceptual predisposition birds seem to have to recognize their own species' songs. These models indicate that cultural evolution itself creates a selection pressure for less restrictive predispositions, as

well as accelerating divergence in these predispositions. In contrast, models of conformity in bird song (where birds favour those with whom they share song-types) suggest a selection pressure for less variation in song.

BRIAN MACWHINNEY
macw@cmu.edu
Department of Psychology, Carnegie Mellon University
5000 Forbes Ave.
Pittsburgh PA 15213, USA

The Linking of Recursion to Perspective-Taking

Human language capacities emerged not as a single evolutionary event, but as a result of a series of cumulative adaptations across millions of years, each of which produced a new evolutionary platform. The unlinking of signals from specific functions emerged through the entrainment of the vocal system by the gestural system. This entrainment led to a far greater cortical control over vocal production in hominids than in monkeys or apes (Tucker, 2002). As Donald (Donald, 1991, 1998) and Dunbar (Dunbar, 1998) have argued, this increased flexibility gave rise to a system of mimetic communication with a primarily social function. I will argue that this system, although flexible, was non-analytic and non- conventionalized.

It is likely that this mimetic system arose first in homo erectus and then gave rise in homo sapiens to proto-language. This transition depended on the loosening of the bond between signal and function as our ancestors began to compose words from phonological segments. Through the development of first phonological and then lexical combinations, the link between the symbol and the referent became more fully subject to control through cognitive simulation.

The development of a loosened bond between symbol and referent opened up a pathway for integrating two preexisting currents in hominid cognition. These two currents are perspective-taking and recursion. The skills of perspective taking and perspective switching had been undergoing elaboration in the context of mimetic communications. Although the perspective-taking system is largely in place in all primate, the linking of perspective-taking to vocal signals required a further decomposition of Gestalt mimetic gestures into components and then the development of a system of grammatical markings to indicate perspective flow and shift.

The development of methods for marking perspective shift relies on the second pre-existing current in hominid cognitive evolution. This is the ability to make recursive use of actions, primarily in a spatial context. Recursive spatial cognition is important in navigation, hunting, and tool use.

Recursion in language relies crucially on the operation of item-based patterns (MacWhinney, 1982). These patterns serve to link lexical items through their affordances and expectations. Sentences are composed by recursive combinations of item-based patterns. Neither recursion nor perspective-taking are unique to language. However, availability of a vocal systematics brought these two pre-existing systems into closer contact, facilitating rapid co-evolution. This co- evolution then led to major advances in perspective-taking that built on the linguistic infrastructure to compose higher level cognitive simulations, social structures, socialization patterns, and plans.

Donald, M. (1991). Origins of the modern mind. Cambridge, MA: Harvard University Press.
Donald, M. (1998). Mimesis and the Executive Suite: missing links in language evolution. In J. R. Hurford, M. G. Studdert-Kennedy & C. Knight (Eds.), Approaches to the evolution of language. New York: Cambridge University Press.
Dunbar, R. (1998). Theory of mind and the evolution of language. In J. R. Hurford, M. G. Studdert-Kennedy & C. Knight (Eds.), Approaches to the evolution of language. New York: Cambridge University Press.
MacWhinney, B. (1982). Basic syntactic processes. In S. Kuczaj (Ed.), Language acquisition: Vol. 1. Syntax and semantics (pp. 73-136). Hillsdale, NJ: Lawrence Erlbaum.
Tucker, D. (2002). Embodied meaning. In T. Givon & B. Malle (Eds.), The evolution of language out of pre-language (pp. 51-82). Amsterdam: Benjamins.

BRENDA McCOWAN
bmccowan@vmtrc.ucdavis.edu
Veterinary Medicine Teaching & Research Center
Population Health & Reproduction
School of Veterinary Medicine, University of California, Davis
18830 Road 112, Tulare, CA 93274, USA

Measuring Diversity, Flexibility and Complexity in Human and Nonhuman Animal Communication Systems

The nature and complexity of nonhuman animal communication systems in comparison to human languages is not well understood, partly as a result of methodological limitations but also because of differences in perspective among scientists on how nonhuman animal communication systems function and are structured. For example, robust evidence is lacking for two language-like characteristics thought to underlie communication complexity, syntax and symbolism, among systems of animal communication. Two alternatives could explain this lack of evidence: (1) nonhuman animals do not possess these human-specific adaptations in communicative capacity or (2) effective methods for deciphering the nature and complexity of communication systems have not been fully developed or applied to the communication systems of nonhuman animals. If the latter is the case, direct evidence for truly referential or symbolic communication will unlikely surface in nonhuman animal systems until a broader perspective is taken on strategies for measuring communication structure. For example, the very methods by which we study communication systems in animals almost necessarily negates discovery of symbolic communication because we tend to study the production of a signal in relationship to the specific context in which it occurs. Yet in symbolic systems, communication signals can refer to objects and events that are not physically present in the immediate environment and thus this method of 'connecting signal to context' diminishes our ability to measure the degree to which nonhuman animals exhibit contextual flexibility and complexity in their communication systems. Yet many nonhuman animal communication systems are comprised of signals that are not strongly connected to particular contexts, and it may be here where we can begin to develop and examine questions about contextual flexibility and complexity in nonhuman animals.
Recent research by mathematical modellers of human language indicates that a necessary condition for symbolic communication to evolve is the development of a nested or 'syntactical' communication structure (e.g., conditional dependencies of communication units on each other). It has been argued that, after a certain point, lexicon expansion alone cannot keep pace with the amount of information requiring transmission with increasing message complexity. Therefore one approach toward deciphering the nature and complexity of nonhuman animal communication systems would be to examine the communication systems of nonhuman animals precisely as that, "a system", by categorizing signals into types based upon signal structure, not context, and then calculating the degree and composition of structural nesting under different conditions, which can be conducted by estimating global lexical co-occurrence and temporal dependencies among signals produced in communicative sequences. Information theory, along with other mathematical tools, can measure the degree of structural nesting in addition to other aspects of repertoire and signal structure which can then be used in combination to provide quantitative comparative measures of the diversity, flexibility and complexity of communication systems both within and across species. Presenting data from both humans and nonhuman models, I will discuss how predictions on the structure and organization of nonhuman animal communication systems can be made using these types of measures in light of behavioral ecology and evolutionary theory. I will also address important methodological issues such as signal sampling, signal structure and signal categorization, pertaining to the use of these tools in analyzing nonhuman animal communication systems. Finally, I will discuss the utility of this systems approach to the study of nonhuman animal communication toward increasing our understanding of the evolution of social intelligence and complexity in humans and nonhuman animals.

D. KIMBROUGH OLLER & ULRIKE GRIEBEL
koller@memphis.edu
The University of Memphis
School of Audiology and Speech-Language Pathology
Memphis Speech and Hearing Center
807 Jefferson Avenue, Memphis, TN 38105, USA

Contextual Flexibility in Infant Vocal Development and the Earliest Steps in the Evolution of Language

The study of human infants in the first six months is offering clues about what the first steps of differentiation from the primate background may have been, as well as hints about what the special selection forces may have been that led hominids alone to make the break toward massive contextual flexibility in vocalization. While the approximately 100 non-human primate species vary notably in vocal flexibility, it appears that the human infant in the first six months of life exceeds all of them. Empirical research from the Univ. of Memphis laboratories illustrates the extent of that flexibility in human infants and provides new tools for future comparison with flexibility in non-human primate vocalization. In particular the research illustrates the emergence of 1) spontaneous variable production of sounds, in both play and face-to-face interaction, 2) contrastive production of sounds as indicated by systematic repetition and alternation of vocal categories seemingly created by the infant, 3) contextually flexible usage of these invented sound categories as seen in production of each of the categories in multiple, sometimes affectively opposite circumstances, and 4) contextually flexible usage where particular sound types are sometimes directed toward a listener and other times not.
Every aspect of spoken language depends on vocal production flexibility. Previous speculation about the evolution of language has focused on many features of language that make human communication unique. These include syntax, word-learning, segmentation of syllables into consonants and vowels, production of canonical (or well-formed) syllables of which words are composed, imitation of canonical syllables, and imitation of precanonical vocalizations. Yet none of these unique characteristics of language would be logically possible (not even imitation) in the absence of vocal contextual flexibility.
In seeking the roots of the human capacity for vocal flexibility, we note that ancient hominid infants were (and modern human infants are) more altricial than any prior primate infant. In addition the infancy/childhood was longer in ancient hominids than in any prior primate. Consequently, we speculate there was a premium among ancient hominid infants on eliciting both immediate and long-term parental investment to an extent that exceeded that in any prior primate. We propose that hominid infants were thus selected precisely for their tendency to produce spontaneous, vocal displays in circumstances of comfort and socialization, displays that indicated their fitness and elicited bonding and commitment from the hominid parents. We suggest that all the subsequent evolutionary steps that led toward language depended upon this initial step where a neurological capability to control vocalization voluntarily and flexibly was selected.

MICHAEL OWREN & MICHAEL H. GOLDSTEIN
mjo9@cornell.edu
Department of Psychology
Cornell University, USA

Integration of Production and Response Mechanisms as a Key Feature of Context-Independent Vocal Communication

Flexibility in communication is often studied from the signaler's perspective, emphasizing the potential to produce signals that are independent of immediate circumstances. However, it is also the nature of communication that individuals play dual roles as both signaler and perceiver, and we argue that facultative flexibility in signal production can be importantly dissociated from flexibility in responding to signals. We further suggest that the degree of dissociation observed across species provides

important clues to the ontogeny and phylogeny of context-independent communication.
Although the underlying goal of many animal communication studies over the past 25 years has been to demonstrate similarities between signaling behavior in human and nonhuman mammals, results concerning vocalizations have underscored a series of enduring, fundamental differences. In normative development of human speech, for example, a child quickly comes to show great flexibility both in producing signals and in responding to signals. This ability emerges during the first year, while the infant is engaged in babbling. The earliest vocalizations show little differentiation and while they are context-independent, carry little meaning for perceivers. By six months of age, however, the phonology of babbling has increased greatly in variability, setting the stage for caregivers to respond differentially to their infants' sounds and for infants to learn about the consequences of vocalizing. At the neural level, speech production and perception draw on a wide range of brain structures, including both cortical and subcortical areas of the telencephalon.
Species-typical vocal communication is quite different among other mammals, specifically including nonhuman primates. In monkeys and apes, a fundamental discontinuity in flexibility has emerged between vocal production and responses to vocalizations. For example, development of species-typical vocal production has been found not to depend on auditory input and to occur prior to comprehension of signals produced by others. Call production is also critically emotion-driven, not readily brought under volitional control, and shows a striking lack of intentionality. Neurally, there is little evidence of cortical control of vocalization, with subcortical, midbrain, and hindbrain structures instead playing primary roles. In contrast, responding to vocalizations from others shows great flexibility. Offspring often show a important role of learning in responding to species-typical vocalizations, and come to react quite differently depending on who the vocalizer is, their relationship to that individual, and both immediate and historical signaling contexts. Responses to vocalizations likely involve a wide variety of brain structures and psychological processes, including cortical and subcortical structures mediating both affect and cognition.
Fixed vocal production and flexible responses to vocalizations are thus surprisingly separable in monkeys and apes, relying on dissociated psychological and neural systems. Nonhuman primates do not develop the flexibility in production that characterizes even the prelinguistic vocalizing of human infants. We believe that differences in flexibility between vocalization and response are key both to understanding critical aspects of nonhuman signaling and to constructing a coherent account of human language evolution. To illustrate this perspective, we first examine the construct of signal "meaning" when production and comprehension are dual, non-complementary processes. Second, we argue that the function of early vocal learning in humans is to bridge among disparate neural systems, thereby creating an integrated and flexible medium of vocal communication.

RONALD SCHUSTERMAN
rjschust@ucsc.edu
Research Marine Biologist & Adjunct Professor of Ocean Science
UCSC Long Marine Laboratory
Santa Cruz, California 95060, USA

Pinniped Vocal Learning

Until recently, the litany of comparative ethologists and psychologists stated that vocal communication in mammals is ritualized and not modifiable. Their sound production is thought to be involuntary and only used to express emotions. Their vocal signals were considered automatic and a fixed part of instinctive behavior. Accordingly, mammalian vocal musculature was thought to be constrained and therefore, unable to be operantly conditioned. This was contrasted to the uniqueness of human speech which is available to operant learning and conditioning, i.e. the vocal musculature of humans can readily come under operant control. Therefore, it was held that comparative studies concerning the learned aspects of mammalian vocal communication were a dead end in a search for an evolutionary pathway to human speech. That has all changed now. A number of mammalian taxa, including elephants, bats, and marine mammals as well as several avian taxa show vocal learning at different ages and in a variety of context. In particular, the pinnipeds (seals, sea lions, and walruses) as well as some other marine mammals have showed a surprisingly strong propensity for vocal learning. A good deal of research from the field as well as from the laboratory has shown that these mammals are quite intelligent and are indeed ideal subjects for vocal learning studies. Such comparative research can yield

valuable information about the original and evolution of vocal learning, a skill that is considered so indispensable for the faculty of human speech.
In this paper, we present data from all three pinniped families showing that with food reinforcement, individuals from each of these taxa can learn both simple and complex tasks involving calls used in their natural communication systems. We believe that this kind of vocal usage plays an important role in signalers modifying the behavior of listeners and vice versa. Furthermore, we suggest that kin communication may be a powerful force in the evolution of language. Specifically, we believe that innate distress calling by a pup is modifiable by reinforcing and punishing consequences and becomes highly differentiated during ontogeny. Thus, because the pup is nursed by its mother as a consequence of calling, such vocal emissions become operantly conditioned. Later the stage is set for more differentiated calls in the developing pup as it processes sounds, sights, smells, and touches coming from its mother and other individuals with whom it interacts on the rookery.

CHARLES SNOWDON
snowdon@facstaff.wisc.edu
Department of Psychology
University of Wisconsin
1202 West Johnson Street, Madison, WI 53706-1696, USA

Contextually Flexible Communication in Neotropical Primates

Forty years ago, W. John Smith (1965) first proposed that context was important in understanding animal signals. His perspective was that the repertoires of most animals were limited and hence a specific signal must be used in multiple contexts. Subsequent advances in acoustic analyses led to findings of much larger signal repertoires with subtle variations within broad structural categories often being specific to narrow contexts. The cognitive revolution in Psychology led those studying animals to discover referential signals correlated with specific types of objects or contexts leading to conclusions that these signals might be “proto-words”. However, alternative explanations such as intensity or urgency of response could account for some apparently referential signals.
Although the resemblance of referential signals to “proto-words” has an appealing cognitive parallel to human language, contextual flexibility might be seen as greater challenge for both communicator and receiver. Contextual flexibility requires both communicator and receiver to go beyond a simple one to one mapping of signals and contexts. How can one use an existing repertoire in response to novel situations in a way that is effective to both parties? What type of neuronal circuitry is needed to interpret the meaning of signals given in multiple contexts? What is the role of development, of social experience or social status in interpreting and responding to signals?
All New World primates are arboreal and face challenges of communication through dense vegetation. All species studied to date rely significantly on vocal signaling and many species have well-developed chemical signal systems too. Considerable evidence for contextual flexibility has emerged from captive and field studies especially studies of cooperatively breeding marmosets and tamarins. Among several examples are the following: the use of alarm calls typically given to predators upon encountering familiar foods made noxious; the use of food associated vocalizations with inanimate prey but not animate prey in both wild capuchin monkeys and captive marmosets; the use of mobbing calls by captive tamarins to cleaning equipment used by animal care staff but not to a natural predator- a boa constrictor.
Flexibility appears in developmental contexts. Adult tamarins use a repeated and intense version of food-associated calls when making food transfers to infants. Infant tamarins produce highly variable chirp vocalizations in many contexts that only gradually become differentiated into the 8 distinctive forms used by adults. Infant pygmy marmosets “babble” and those that “babble” more when young have an early transition to adult call structure than those who “babble” less. Adult marmosets also “babble”, but in contexts of conflict and aggression, not seen when infants “babble”.
Social status affects both production and response to signals. Certain types of calls are not given in adult form by reproductively subordinate tamarins living in a natal group, but the calls appear in adult form within matter of days when social status has changed. Unmated pygmy often combine a long call vocalization with food-associated calls when they discover food but mated marmosets do not. Single or paired adult male common marmosets respond to the odors of a novel, ovulating female with a rapid increase in testosterone but fathers do not.

Evidence for contextual flexibility is found in several species, in multiple modalities and provides a means for monkeys to communicate effectively with others in novel contexts, and to adjust communication to changes in ontogeny and social condition. Skillful use of contextual flexibility in communication provides considerable advantages over more fixed mappings of signals and contexts.

Supported by MH29775.
Smith, W. J. (1965) Message, meaning and context in ethology. American Naturalist, 99, 405-409.

KIM STERELNY
Kim.Sterelny@vuw.ac.nz
Philosophy Program
Victoria University of Wellington
PO Box 600
Wellington, New Zealand

Language, Evolution and Niche Construction

Richard Lewontin, and more recently John Odling-Smee, Kevin Laland and Mark Feldman, have argued that evolutionary theorists need to recognise the active role of organisms in partially making their own environment. Organisms partially construct their own niches. This is especially true of humans and our recent ancestors. The problem of the evolution of language is and remains brutally difficult, but I shall explore the consequences for our theories of the evolution of language of this reconceptualisation of evolutionary theory. I shall argue that the niche construction perspective changes our view on (i) honest signalling in language and the limits on such signalling; (ii) the way agents cope with the informational requirements of learning and using language, and (iii) the evolution of compositionality. In particular, in discussing the evolution of compositionality, I shall argue that the "iterated learning" framework of Kirby and others, in idealising away from the active role of agents in learning language, probably misconstrues the adaptive dynamics of the evolution of compositionality.

GERT WESTERMANN
gwestermann@brookes.ac.uk
Department of Psychology
Oxford Brookes University
Oxford OX3 OBP, UK

Flexible Communication from Interacting Constraints: A Connectionist Model

A flexible repertory of communicative elements can be seen as emerging from the interacting constraints of innate predispositions, a learning mechanism, and a structured environment. Connectionist models can serve as a tool to explore such constraints and their effects on the resulting communication system. I will present a simple connectionist model of sensorimotor integration in the development of vowel repertories. In this model, an initial babbling phase establishes a basic vowel repertory for perception and production based on linking articulatory parameters with their resulting sounds. This initial mapping between two topological maps is modified by the added environmental constraint imposed by the vowel system of the ambient language. This system suggests that the final repertory represents a trade-off between internal and external constraints.
I will extend the idea of a mutually constraining interaction between topological maps to the well-studied emergence of a shared vocabulary in language evolution. I will argue that if a topology is assumed both in meaning space (that is, similar meanings are represented close together) and in form space (that is, similar sounding words are represented close together), a common lexicon can develop more effectively. This view suggests that early in language evolution a form of sound symbolism might occur which subsequently develops into a more arbitrary mapping between form and meaning, due to the competing constraints of topology preservation and distinctiveness maximization.