Language and Communication:
Comparative Perspectives

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Animal Language Research Needs a Broader Comparative and Evolutionary Framework

Peter L. Tyack

In 1960, Jane Goodall went to live with chimpanzees in their natural habitat like an anthropologist living with some tribe of forest people. It took her years to gain the trust of her subjects, but eventually she and those who followed were able to get close enough to watch these apes interact with each other and with humans (Goodall, 1986). Since 1947, animal psychologists have taken the equally radical step of raising chimps as part of their families in order to see how well chimps could learn human language (Hayes, 1951). Both kinds of study bear promise for the study of animal cognition, but each has suffered from a peculiar insularity. Psychologists have studied for decades how well chimps can learn artificial or human languages, scarcely interacting with the parallel inquiries into the social behavior, parental care, and communication systems of wild chimps. Progress in animal cognition will be much faster if psychological and cognitive studies of animal behavior develop tighter links with biological disciplines of ethology, neurobiology, and behavioral ecology (Kamil, 1988; Snowdon, 1983). Kummer, Dasser, and Hoyningen-Hüne (1990) point out that cognitive ethologists have much to learn from psychology's emphasis on proximate mechanisms, on behavioral development, and on experimental methods. On the other hand, cognitive ethology emphasizes the larger context in which all behavior is embedded. It can contribute a strong tradition of emphasizing function and evolution of animal behavior, and of methods to study animals in their natural environments. In order to understand the evolutionary origins of animal cognition, we require a synthesis of these two disciplines.

The cooperation of biologists and psychologists studying foraging behavior has a synergy that accelerates scientific progress. Behavioral ecologists have developed formal models of how foragers can optimize the costs and benefits of foraging (e.g., Stephens & Krebs, 1986). Data from animals feeding in the wild and in controlled experiments are consistent with complex foraging strategies. Optimal foraging models have been taken up by comparative psychologists in attempts to test more specifically the proximate mechanisms by which animals follow or approximate decision rules (e.g., Kamil & Roitblat, 1985). While food-reinforced conditioning was a staple of comparative psychology, optimal foraging finally provides a theory that allows the integration of data describing how contingencies of food reinforcement affect subsequent behavior with the typical ecological problems faced by a species. Evolutionary biologists have also targeted new areas little explored by comparative psychologists. For example, W. D. Hamilton described the evolutionary importance of kinship in animal social behavior (Hamilton, 1964). This has stimulated behavioral and cognitive research into the proximate mechanisms for kin recognition in animals. These collaborations show great promise for elucidating the evolutionary origins of specific cognitive skills and mechanisms.

Similar collaborations have been less productive in the study of language and communication in animals. The controversy accompanying the interpretation of animal language experiments should be no surprise. It does not just stem from the religious and ideological intensity with which some humans guard the separation between human and animal. If linguists and psychologists cannot agree about how we learn and generate the language of our own species, questions of comparing animal language to human language can only be less well formulated. Part of the problem lies in a history of divergent goals between psychologists and linguists. There has been a strong tradition within psychology of seeking to minimize the building blocks of psychological theory to a few general principles associating sensory stimuli and behavioral responses. Although this theory in principle could describe complex behavior, few linguists have been taken with such parsimony; they would much rather trade in associationism for a richer theory that is more practical for working with language.

7. A Comparative and Evolutionary Framework

THE EVOLUTION OF DOMAIN SPECIFIC COGNITIVE PROCESSES

During the past decade or so, there has been a trend within psychology away from an exclusionary insistence on general principles of learning, memory, and intelligence. Rather than viewing learning or memory as content independent, more psychologists have been willing to consider domain-specific intelligences (Cheney & Seyfarth, 1990; Gardner, 1983) or innately specified cognitive modules (Fodor, 1983). The domain specific view emphasizes that learning may be channeled by innate predispositions to facilitate the solution of particular problems. For an example that ranchers have known as bait shyness, some animals are more likely to associate a taste or smell than a sound with becoming sick, even hours later, and this may help them learn to avoid noxious food after only one exposure (Garcia & Koelling, 1966). This view is more consistent with an evolutionary view[1] and is more easily integrated than general theories of learning with both the neurobiological and ethological views of cognitive processes. The classic ethological studies of learning, such as imprinting, orientation, and avian song learning, are domain specific. The neural substrates that birds use to learn song are better understood than substrates for more general learning abilities. Auditory information from the ears projects to nuclei involved in song processing. These nuclei project to integrative nuclei which project to motor nuclei driving the syrinx, thus closing the loop of vocal control.

Sensory perception clearly involves domain-specific cognitive processing. Visual information flows along clear pathways between brain areas specialized for vision. Lesions of these areas involve vision-specific deficits. Just as some stimuli may more easily associated with some responses, some stages of visual processing are more accessible than others. Animals cannot be trained to identify stimulation of one retinal cell rather than another. Visual information is processed to represent features of objects in the world before most integration with nonvisual information. Different areas of visual cortex in cats map different functional representations of visual features. These specialized mechanisms appear to be necessary for solving the complex problem of extracting meaningful representations of the outside world from stimulation of the retinal surface.

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[1] However, see Lieberman (1991) concerning problems reconciling a strong modular view with evolutionary theory.

Human language has been proposed as another candidate for treatment as a modular cognitive system (Fodor 1983). Many linguists argue that humans have a language acquisition module in the brain, which is activated during a critical period of development and is required to enable the acquisition of language given the limited and unsystematic exposure to speech that children have. Lieberman (1991) debates both how independent language is from other cognitive processes, and whether we must inherit a universal grammar in order to learn language. However, most linguists appear to agree that humans rely on a combination of both general and specialized processes to perceive and generate phonemes, words, and sentences. When humans parse phonemes, they rely on some auditory processes shared with other mammals and other more species-specific linguistic processes (Kuhl, 1987). As with vision, specific neural substrates are defined for many language abilities. For example, damage to Broca's area of cerebral cortex is associated with Broca's aphasia, which is characterized by deficits in speech and syntax. An aphasia characterized by difficulties in naming rather than syntax or vocal control of speech sounds is associated with damage to Wernicke's area of cortex.

If the development, production, and comprehension of language depend in humans on a somewhat idiosyncratic collection of specialized cognitive processes and neural circuits along with more general ones, then this raises questions about animal language. When animals are trained with language, are we testing whether they have similar specialized circuits to perform similar tasks, or are we forcing them to use more general-purpose cognitive systems? Areas homologous to Broca's and Wernicke's area have been identified for some primate species (Deacon, 1988), but it is unclear how involved these areas are either in natural communication or in trained performance for animal language experiments. No such homologous areas have been identified for birds or marine mammals. Species in both of these taxa use vocal learning in their natural systems of communication. It is unknown whether animals in animal language experiments use neural circuits analogous to those used by humans for language.

The training in language experiments may on the other hand enlist primarily general learning and cognitive abilities. The further such experiments diverge from homologies with human language and its underlying neural circuits, the more strained the language analogy becomes. To the extent animals are trained using domain-independent learning, animal language experiments would better be framed as animal thought experiments. This view would emphasize the role of training in facilitating an animal's ability to report internal states by communication. Even Fodor (1983), who emphasizes the modularity of the mind, argues that there must also be domain independent central mechanisms that integrate representations from the different domains.

Even if animal language experiments are viewed as a window on central mechanisms, investigators must search carefully to find the right match between natural communication abilities and the artificial language training. Each species may require careful tailoring of an artificial language in order to open the communication channel fully. I would argue that the only way to make sense of these questions is to perform a broad evolutionary comparison of language-specific capabilities and more general cognitive capabilities as evolutionary traits. We must go below surface similarities of trained language acts to investigate how these languages are acquired and processed. Convergences between domain specific views of cognition, neural studies of cognitive function, and the ethological views of cognitive capabilities as adaptations may facilitate the required interdisciplinary efforts. However, it is critical to bear in mind that cognitive capabilities in animals including *Homo sapiens* have been shaped by evolution.

Evolution is a historical process, and a science of evolution must use different methods from sciences such as physics that aim for general laws. If behavior and cognition derive from evolutionary processes, then the quest in psychology for context independent laws of learning may be ill-founded. Evolution does not proceed like an engineer who can start new designs from scratch and whose choices for subunits are only limited by his purchasing power. Evolution must work with the materials that are at hand, and this often leads to a messy mixture of parts that originally served different purposes. Old parts may be changed to take on new functions, and these may function in parallel with new parts. Lieberman (1991) emphasizes that some of the neural building blocks for human language stem from brain circuits evolved in our reptilian ancestors, while others are found in the expanded neocortex that evolved recently in our species. Some of these neocortical circuits may have evolved specifically to serve linguistic functions.

Criticisms of the adaptationist program notwithstanding (Gould & Lewontin, 1979), ethology has profited greatly by assuming that many behavioral and cognitive capabilities are similar to morphological or physiological adaptations. While the design features of cognitive adaptations may be more difficult to identify than those for an eye or a wing, this point of view would suggest that some cognitive capabilities are honed by evolution to develop specific functional skills. This functional view stresses that if one wants to understand an adaptation, whether cognitive, behavioral, or morphological, one must understand both the problems it evolved to solve and the building blocks available to a phylogenetic lineage for achieving the solution. Adaptations in the Darwinian sense evolve through natural selection of different genotypes, and ethologists have traditionally focused on innately determined behaviors. However, learning mechanisms may evolve in just the same fashion. Genetic predispositions may even guide learning for those species that require learning for behavioral development. Imprinting and song learning in birds are classic ethological examples, and many linguists argue that language acquisition in humans is guided by similar predispositions. Many of the most complex behavioral and cognitive skills involve sensitive periods for learning, extended periods of development, and may even require training by or observation of parents and other conspecifics. The interplay of innate factors with development and learning will be particularly complex for higher cognitive functions, but this does not free them from the evolutionary process.

If we are to understand the evolution of cognitive processes in animals and humans, four basic biological questions must be explored. While these questions must be answered for the study of any kind of adaptation, they were identified as the backbone of classical ethology (Tinbergen, 1951). The four avenues of exploration are mechanism, development or ontogeny, function, and evolution. Tinbergen argued that the isolation of behavioral scientists studying proximate explanations of behavior from those studying the ultimate evolutionary causes impeded both avenues of study. Studying a learning mechanism without understanding its function is like trying to solve how a clock works without knowing what the clock is for (Cosmides & Tooby, 1987). On the other hand, simply matching contemporary behavioral acts to those predicted by a model of an adaptive problem provides only a caricature of an evolutionary analysis.

Whereas individual behavioral acts may have obvious consequences for natural selection, it is perilous to overemphasize the stage on which natural selection plays so much that one loses sight of the fact that individual acts of behavior do not evolve. Between their ears, animals carry sophisticated mechanisms to select information from their environment, compare this to past information and internal states, and respond with strategies to achieve goals. These mechanisms filter a bewildering array of potential environmental inputs to produce an equally complex and variable array of behavioral responses. Classical ethology provides examples of tight linkages between fixed action patterns that are elicited by an innate releasing mechanism when a feature detector is triggered by a particular suite of environmental cues. However, one cannot assume that the evolution of behavioral mechanisms always proceeds by linkages so tight between situation and response that one can ignore intervening sensory and cognitive mechanisms.

There are many situations where selection may favor more opportunity for an animal to modify its responses based on its environment. Students of birdsong have suggested a threshold in song repertoire size may exist, beyond which it is cheaper to build a mechanism to learn to imitate songs rather than to encode the acoustic structure genetically. Given the enormous variety of situations an animal may encounter throughout its life and the variety of appropriate responses depending on its condition, the potential simplifications of cognitive mechanisms more flexible than the fixed-action-pattern/innate-releasing-mechanism link should be obvious. Tierney (1986) reviewed neurobiological evidence that also questions assumptions that individual behaviors are programmed by specific genes and that more canalized behaviors are simpler, less costly, and phylogenetically primitive to less canalized behaviors. There are other classes of novel or unpredictable situations that may require learning and other plastic forms of cognition. Many individual animals encounter situations that are unpredictable for their population or species. Even if an animal inherits a sophisticated ability to navigate, it is likely to have to learn where home is. Optimal foraging studies show that, even though a species may have a limited range of prey species and distributions, each individual can improve its foraging behavior by tailoring it to the conditions prevailing at any one moment. On the other hand, trial and error learning may not be the algorithm of choice for avoiding a deadly predator, because one may not survive the first trial. Depending on these kinds of considerations, a behavior may be selected to be more or less canalized.

Many authors have argued that the social environment of hominids may have been particularly important for the evolution of human intelligence and even consciousness. If hominids lived in groups where success demanded both cooperation and competition with the same individuals, this could have led to particularly unpredictable social strategies and counter-strategies, creating something of an arms race for intelligence in the sense of abilities to forecast the outcome of interactions (Humphrey, 1976). Animals that form individual specific social relationships and that face a similar tension between competition and cooperation in reciprocal relationships may also encounter selective pressures to evolve more complex forms of social cognition. Cooperation that is maintained by taking turns with asymmetric costs and benefits requires the players to monitor for cheaters who take the benefits of cooperation but do not reciprocate and pay the costs when their turn is due (Axelrod, 1984; Trivers, 1971). There is evidence that humans have evolved domain specific cognitive processes to analyze these social interactions. Cosmides (1989) made sense out of otherwise puzzling deviations of humans from the rules of formal propositional logic by suggesting that when humans evaluate social contracts, their behavior deviates from logic in order better to detect cheaters. Her results suggest that when humans reason about social problems, their thought may be guided by Darwinian algorithms to solve these adaptively important problems.

Analysis of the evolution of behavior cannot evade study of cognitive mechanisms. The study of sociobiology suffered from attempts to bypass this level of understanding to find a shortcut to understanding the evolution of behavior. On the other hand, because adaptive mechanisms must evolve from parts initially often serving other functions, the mechanistic details of proximate solutions to adaptive problems are often obscure. The functional cognitive level is required to link these two widely separate levels of understanding. Physiology plays a critical role relating organ structure to organ function. Physiologists lump complex suites of anatomical and biochemical features to form more readily interpretable functional descriptions such as digestive or circulatory systems. The study of cognitive processes provides a similar functional language to bridge the gap between the details of a neural mechanism and the behavioral function(s) it serves (Cosmides & Tooby, 1987). Tinbergen (1951) was correct to reject the lack of integration between these often separate disciplines and to "argue the necessity of studying both causation and adaptiveness" (p. 152).

The general problems of studying adaptation are compounded by several difficulties specific to cognition. It is difficult enough to discriminate genetic and environmental influences on developmental maturation, and learning adds yet another layer of processes by which the environment can alter behavioral traits. One must both investigate the range of environments in which the functional trait can develop and also investigate how flexible the developed trait is to fine tuning through learning in particular environments. Cognitive mechanisms that generate adaptive behavior in an animal's normal environment may generate maladaptive behavior in other environments. The very sensitivity of flexible mechanisms to environmental change and novelty may render them vulnerable to derailing in environments very different from those in which they evolved.

Darwin (1859/1979) appreciated that natural selection can lead to the evolution not just of beautifully designed bodily traits such as eyes or a wings but also of behavioral traits that function so well as to seem intelligent and purposive. Darwin (1871/1981) also recognized that selection is not limited to individual behaviors, but may favor the evolution of higher mental faculties such as intelligence and intentionality to the point of self-awareness in humans. It requires great care to discriminate animals whose individual behaviors merely appear goal directed from animals that reason intelligently to achieve their goals. Here is where experimentation with artificial and novel problems is most useful. It is ironic that experiments training animals with artificial languages have been framed more as language experiments than as experiments to gain access to more general cognitive processes such as intentionality, intelligence, or even awareness. While language-like skills may open a window on these general cognitive processes, there is a strong tradition emphasizing that human language itself is not a general skill but has many idiosyncratic and species-specific features.

One way to test whether animal species have adaptive specializations in particular cognitive skills involves broad comparative analysis of both the skill and its underlying neural structures. For example, Shettleworth (1990) reviewed data on differences among birds in spatial memory related to whether they store food or not. The hippocampus has been implicated in spatial memory in both birds and mammals, and Krebs (1990) showed that two regions of the hippocampus are enlarged in food storing species. Comparative analysis also reveals strong associations between song learning in birds and its neural substrates. For example, male marsh wrens (*Cistothorus palustris*) in western North America produce about four times as many different songs as the eastern subspecies (Kroodsma & Verner, 1987). There is a well-defined song perception and control system in the brains of songbirds, and it expands in volume and capability during the song season. The song control nuclei in western marsh wrens are larger than in eastern marsh wrens (Kroodsma & Canaday, 1985). Male-male competition appears to be higher in western versus eastern marsh wrens, and natural selection appears to have favored the evolution of larger song repertoires and investment in larger neural structures in the western subspecies. Marler (1990) emphasized the synergy between behavioral and neural studies of song development in birds. Extensive data indicate that specific areas of the human brain are involved in different linguistic functions, but little attempt has been made to compare homologous structures in different species involved in animal language studies. This is critical for determining whether so-called language skills in other species are homologous or analogous (in the evolutionary sense) to those of our own species (Deacon, 1988).

Detailed investigation of the interplay between innate and environmental factors in development is critical for understanding the evolution of cognitive traits. We need to attend more to how animals acquire traine language skills-what forms of training are necessary and sufficient. One of th striking features of language aquisition in humans is how little formal trainin children get when they solve arguably the most complex intellectual task of thei lives. By focusing on the data children receive and their performance as the acquire language, one can rule out some possible models of languag comprehension and production. As children learn a language, their errors[2] (i.e. "runned" for ran) reveal that they are not just imitating grammatica constructions by rote, but that they try out grammars approximating norma usage. Even though seldom corrected for making ungrammatical sentences, most children converge on a productive grammar that seldom generates sentences recognized by adults as ungrammatical. Pinker (1984) argues that given this lack of correction, the only way children can acquire a well-formed grammar is by innate restraints on which grammars are considered. If only a subset of the grammars that could describe adult language is learnable by children, then the learnability constraint can be used to narrow the search for which grammars humans actually use.

CAPABILITY VERSUS SKILL

Most animal language researchers tend not to examine the training process and responses of animals during training as much as has been exploited by students of human language acquisition. However, the natural tendency for teachers to take credit for the performance of their pupils is evident. Some animal language experiments reveal cognitive abilities not shown for the same species in the wild. Many researchers conclude that their language training has created cognitive skills not present in wild conspecifics (Herman, 1980; Premack, 1983; Savage-Rumbaugh, Lawson, Smith, & Rosenbaum, 1983). Certainly some aspects of the skills trained in the laboratory differ from those developed in nature, but we are just beginning scratch the surface of animal cognition, and are certainly in no position to argue for the creation in the lab of fundamental cognitive abilities that are not expressed in the wild. To clarify this distinction, I distinguish between a capability, or a faculty capable of development, and a skill, or a fully developed ability to perform a particular task.

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[2] The errors children make as they learn a language can help reveal the kind of grammar they are trying out. If artificial languages included the exceptions so typical of natural language, similar errors would help demonstrate that animals actually are applying syntactic rules.

Although it is often more practical to study animals in captivity, few ethologists would not feel the need to verify captive results in the wild. On the other hand, anyone who has attempted to study chimps, parrots, or dolphins in the wild knows how hard it can be simply to find them, much less uncover their mental abilities, while trying to keep up with them in their own habitat. Under these circumstances, if one does not find strong evidence for the existence of a cognitive capability, one cannot conclude that this is strong evidence for the absence of the capability. We know less about the cognitive skills developed by animals in the wild than in the laboratory, so I think it dangerous to assume that a skill discovered in the lab does not have an undiscovered counterpart in the wild. I expect negative results to be the norm in studies of animal cognition. The cognitive ethologist must turn poorly controlled naturalistic observation into a convincing demonstration of a cognitive capability, and the comparative psychologist must select the appropriate age, sex, species, and match of artificial conditions in order to tap selective attention and domain specific intelligences evolved to solve particular problems.

Language acquisition in humans can be modified by many environmental factors. Behavioral development may also be disrupted by artificial conditions in other species that also rely on learning during prolonged periods of parental care. For example, white-crowned sparrows (*Zonotrichia leucophrys*) do not learn songs from tape recordings after 50 days of age, but they continue to learn songs if given the chance to interact with live tutors (Baptista & Petrinovich, 1986). The ethologist is far more likely to expect the fullest development of cognitive capabilities through the process of behavioral development with conspecifics than through being raised and trained by humans, no matter how intelligent and devoted the trainers are. This is not to say that people cannot train specific skills that are not seen in the wild, just that an animal's cognitive capabilities are likely to be most finely tuned to developing functional skills in the environment in which they evolved (for a psychologist's development of this point for humans, see Bowlby, 1969).

PROBLEMS IN APPLYING LANGUAGE ANALOGIES TO ANIMALS

Psychological tests are notoriously culture bound (Cole & Scribner, 1974). If it is difficult for psychologists to rate the cognitive abilities of a human who is from a different culture and speaks a different language, how much more difficult is it for humans to know that they correctly understand what skills are used in the performances of a different species? This is particularly problematic when a psychologist compares the language-like performance of a trained animal to a linguistic gloss of the same performance. Precisely what an animal needs to know or do in order to perform successfully is seldom obvious, and the surface similarity of the linguistic gloss to the performance may be more misleading than helpful. If the animal does correctly respond to the command JUMP OVER FRISBEE, does it really understand JUMP as a verb or FRISBEE as a grammatical object? At what point does the language analogy become inappropriate?

Ethologists have confronted similar problems when they attempt to draw parallels between human language and natural communication in animals (Snowdon, 1990). For example, early work on the development of song in birds emphasized that, as in humans, the young must hear the sounds of conspecific adults during a critical period in order to develop normal song (e.g., Marler, 1970). Babbling in humans and subsong in birds both appear to reflect a process in which the young match their own vocal output to an internal auditory template. Subsequent work on birdsong reveals enormous variety in development in different species. Although some species match some aspects of language development in humans, other closely related species show completely different patterns. Although lateralization of brain function has been demonstrated for both bird song and human language, the structures involved are by no means homologous. Early parallels between birdsong and language may have been overgeneralized and overenthusiastic.

The power of animal language experiments may be unnecessarily limited if researchers only compare animal use of artificial languages to human use of natural human languages. A comparative approach to understanding the evolution of language capabilities requires not just comparing each animal group to humans, but rather comparing all combinations of phylogenetically and ecologically related taxa. Human language involves a complex and idiosyncratic mixture of perceptual, cognitive, and motor capabilities. It is unlikely that many other species have exactly the same mixture, or use the capabilities in precisely the same way. Furthermore, animals are typically conditioned to learn artificial languages using controlled training protocols. Human children learn the rules of human language with far less controlled input and less formal training. The comparative use of linguistic terms such as syntax simplifies interpretation of animal language research to the popular press, but it may force an inappropriate analogy between a subsystem of human language with an animal system involved in some very different task. Clear progress in further animal language research will also benefit from a more careful analysis of the specific cognitive capabilities and training required to acquire and to use the artificial language.

For example, all human languages can create an unlimited number of utterances out of a few tens of morphemes by using syntax to rearrange phonemes into words and sentences. There are no data indicating this level of syntactic rearrangement of phoneme-like chunks of signals in any animal, but other animals can order signals into complex series. Both accomplished songbirds, such as the long-billed marsh wren (*Cistothorus palustris*, Verner, 1976) and the humpback whale (*Megaptera novaeangliae*; Payne, Tyack, & Payne, 1983), can produce organized strings of hundreds of signals (individual songs in the wren, song units in the whale) lasting tens of minutes before they repeat. Songs of both birds and whales are reproductive advertisement displays. Their structure appears to have evolved through sexual selection involving male-male competition and female choice of a mate. Male songbirds can increase the acoustic complexity of their display through large song repertoires, and some even produce structured sequences of many songs within their repertoire. Experimental studies show that songbird females of some species tend to prefer males with larger song repertoires. Individual humpback whales do not have large song repertoires at any one time, but all of the whales singing on a breeding ground slowly change the song over time. The song changes so pervasively that after several years, no sounds are left unchanged. Because the same whales still use these different songs in the same interactions, it appears that this variation in the acoustic structure of song does not reflect changes in the message in any linguistic sense (Tyack, 1981). Rather, humpbacks appear to use song change as birds use large song repertoires: to increase the acoustic complexity of their advertisement display.

In human language, syntax is intimately tied to the semantic content of the message. Some animal songs clearly have syntax-like ordering, but not necessarily with a semantic component. It may make no more sense to compare these songs to language than to compare the marks on a peacock's tail to some strange hieroglyphic writing. As Darwin (1859/1979) appreciated, advertisement displays may better be compared to the aesthetic domain than the linguistic. Music may be a more appropriate analogy (if not evolutionary homology) than language for song in birds and whales. Gardner (1983) argued for differences in the cognitive processes and neural structures that mediate the production and comprehension of music compared to language. In right-handed humans, language is lateralized primarily in the left hemisphere of the brain, while most musical abilities are lateralized in the right hemisphere. These two processes can function independently; exposure to tones interferes with recall of a tune much more than exposure to verbal stimuli (Deutsch, 1975). Many autistic children or aphasic adults with severely compromised language have excellent musical abilities. Some animal species may have evolved sophisticated syntactic capabilities with no parallel development of semantics or other specifically linguistic abilities. If one were to train these animals in a language paradigm, the research might never uncover their highly developed abilities to learn complex sequences of sounds.

Another problem with testing linguistic models of animal behavior involves radically different standards for demonstrating the applicability of linguistic terms. If an animal language experiment yields results that deviate from random in the direction predicted by a formal linguistic model, the experimenter typically states that the animal understands the model. However, the skeptic may compare the same performance to humans and conclude that the results are negative. Random expectations are a particularly weak straw man in animal behavior, so it would be better to allow several stronger models to compete in this kind of experiment. However, there is little benefit in splitting hairs over whether particular patterns of animal cognition are distinguishable from human cognition. This is particularly true because what we know of human cognition is a moving target. For example, while babbling was initially thought to involve a process of matching vocal articulation to an auditory template, recent studies of manual babbling in deaf infants indicates that babbling may represent a more amodal expressive language capability (Petitto & Marentette, 1991). Rather than argue whether an animal has "true" babbling, syntax, or whatever, we would do better to focus on which particular models best fit the performance of each species.

Distinguishing between good alternate models is much more difficult than comparison to a null hypothesis of random behavior. Even for human language, linguists cannot agree which formal models of grammar best predict our language production. For animal communication, this problem extends well beyond fine details separating similar models. For example, in order to test whether animals can learn syntactic rules, an artificial language with a formal syntax may be taught to animals. Either their utterances or their responses to sequences of commands may be used to test whether the animals have learned the grammar. Typically these grammars are simple and non-recursive, and may simply involve serial learning of a chain of tokens.

Demonstration that an animal's performance is closer to that predicted by a grammar than by a random model does not provide a strong test of whether the animal is using the grammar. Animals may produce what appear to be highly significant sequences of vocalizations when there is no contingency between one vocalization and the next. In a study of natural sounds from wild dolphins, Markov analysis of a transition matrix for dolphin vocalizations showed significant deviations from random (Solow & Tyack, 1990). In animal language terms, this would appear to support the hypothesis that dolphins organize their vocalizations in a finite state or simple chaining type of grammar. However, if one separates the sequences into different behavioral states, in this case fast travel and slow travel, then the sequences appear random within each state. The data are completely consistent with the interpretation that the probabilities of each vocalization are conditionally dependent on behavioral state and are completely independent of the preceding vocalization. If one ignores or does not know about the behavioral states, and if one only tests a model assuming serial dependence, then one could easily mistakenly "confirm" a sequential grammatical model where in fact there may be no serial dependence of any sort.

VOCAL LEARNING AND IMITATION

Given the difficulties in both defining and testing for the presence of such general abilities as language or syntax for comparative analysis, it may help to focus on more specific cognitive capabilities that may be components of higher level processes. Demonstrating the presence or absence of component capabilities in different species will also facilitate the search for optimal study animals for particular problems. It is easier to specify capabilities with better defined input/output relations than language. There is also strong reason to target specific learning abilities that foster or allow language acquisition in humans. One such capability that appears to be very limited among animals is vocal learning: the capacity to modify what one says on the basis of what one hears. This capacity is clearly necessary for human speech. While four families of birds are capable of vocal learning, no terrestrial nonhuman mammal has been unequivocally shown to modify its vocal repertoire based on what it hears. Many primates are skilled at "aping" or imitating gestures and expressions, but despite decades of intensive research, there is no strong evidence for any vocal learning in nonhuman primates (Newman & Symmes, 1982). Imitation has been identified as particularly important in the acquisition of language and other aspects of culture that are not trained and shaped by overt reinforcement (Lieberman, 1991).

The absence of vocal learning has been a robust result from some animal language experiments. For example, it appears that one cannot teach a chimp to speak, even if it is raised at home from a very young age (Hayes, 1951). One explanation is that chimps are anatomically incapable of producing some human speech sounds (Lieberman, 1984), but this failure may also reflect a more central inability. Vocal learning is one of the skills necessary for speech, that appear to have evolved de novo in our hominid ancestors. Just as comparison of language in deaf and hearing humans can help address the question of how easily language can be divorced from the vocal channel in humans (Klima & Bellugi, 1979; Meier, 1991; Petitto & Marentette, 1991), so comparisons of language-like communication in species capable or incapable of vocal learning may address the same question across species.

Although it is not clear precisely how to specify and test for animal analogs of linguistic concepts such as syntax, vocal learning is well defined in terms of input and output. However, testing for vocal learning in the development of natural sounds is time-consuming and difficult. One way to target promising taxa is to look for species that can imitate manmade sounds. If an animal can imitate a sound that is not normally part of its repertoire, then it must have learned to modify its normal vocalizations to match the model. Animals that have evolved this rare capability may use it in developing their natural vocalizations. Even though we know little about vocal development in most marine mammal species, there are a surprising number of reports of marine mammals imitating manmade sounds: Hoover, a harbor seal at the New England Aquarium, imitated human speech well enough to have a recognizable New England accent (Ralls, Fiorelli, & Gish, 1985). Captive dolphins from many aquaria have been reported to learn to imitate computer generated tones and pulses (e.g., Richards, Wolz, & Herman, 1984; Sigurdson, this volume, chapter 8). Logosi, a beluga whale at the Vancouver Aquarium, was able to imitate his own name (Eaton, 1979). These reports include both seals and whales, which have different terrestrial ancestors. Presumably, this means that both groups independently evolved this capability.

It is difficult to differentiate learning from maturation, especially if all members of a species develop similar repertoires (Tinbergen, 1951). For example, young vervet monkeys produce calls higher in pitch than those produced by adults (Seyfarth & Cheney, 1986). As the young monkeys grow older, these calls become more similar to those of adults. This could simply be a result of growth of the vocal tract rather than a consequence of learning. It would be easier to test for vocal learning in species where different individuals produce different sounds.

The bottlenose dolphin (*Tursiops truncatus*) is perhaps the most promising marine mammal species for the study of vocal learning. These dolphins have a global distribution and number in the tens of thousands in the coastal waters of the southeastern United States. Hundreds of bottlenose dolphins also live in captivity, where their vocalizations and acoustic environment can be studied in great detail. Bottlenose dolphins have also been the subject of many cognitive experiments including animal language experiments at the Kewalo Basin Marine Mammal Laboratory in Honolulu (Herman, Richards, Wolz, 1984). Since the mid 1960s, it has been known that captive bottlenose dolphins produce individually distinctive pure tone sounds called signature whistles (Caldwell & Caldwell, 1965). Unlike the click sounds used for echolocation, which are processed in midbrain areas such as the inferior colliculi, whistles are processed in the cerebrum, particularly temporal cortex (Bullock & Ridgway, 1972). These whistles function both to broadcast individual identity and to maintain contact between individuals such as between mothers and calves.

One puzzling question to me as an ethologist was why dolphins appear to have evolved highly developed skills of vocal mimicry when they tend to produce only one highly stereotyped whistle. Do dolphins use vocal learning and imitation in the development of their natural vocalizations? If so, when and in what contexts? Sigurdson (this volume, chapter 8) suggests that even during training for mimicry, bottlenose dolphins may only actively imitate or match acoustic models for limited periods of time under limited circumstances. I have taken two approaches to studying vocal learning and imitation in bottlenose dolphin whistles. One involves finding situations where one can identify the vocal repertoire of individual dolphins repeatedly in the wild. The other studies the vocal repertoires of captive dolphins during social interaction.

SIGNATURE WHISTLES IN WILD DOLPHINS

Randall Wells of the Chicago Zoological Society (Brookfield Zoo) and Woods Hole Oceanographic Institution has been studying wild bottlenose dolphins near Sarasota, FL since 1970 (Wells, Scott, & Irvine, 1987). Dolphins in this area have distinctive marks that allow most individuals to be identified. In this coastal habitat, individual dolphins often have such predictable home ranges that one can set out each day to look for particular animals. Wells has resighted some individuals for decades and knows several generations of matrilineal ties.

One of my graduate students, Laela Sayigh, and I have worked with Wells to study the signature whistles of these wild dolphins. It is seldom possible to determine which dolphin makes a whistle when they are swimming freely, so we record them when they are restrained in a net corral. When the dolphins are held in the corral, we can attach underwater microphones, or hydrophones, to their heads with suction cups. This is not a very natural context for these animals, but it allows us to sample the results of normal whistle development among wild dolphins. Moreover, dolphins swimming freely within the net corral or recorded immediately after release produced whistles very similar to those produced while they were restrained.

Whistles have been recorded from many of the Sarasota dolphins over a period of 15 years. These recordings confirm that wild dolphins, like captive ones, produce individually distinctive signature whistles, and that signature whistles are stable for over a decade (SayighB, Tyack, Wells, & Scott, 1990). Sayigh has concentrated on studying whistle exchanges between dolphin mothers and their young calves. When a mother-calf pair in the net corral was ready for processing, we restrained the pair together. Typically, one of the pair was held in shallow water while the other dolphin was being measured in a rubber raft. The animals were always in acoustic contact even when they could not see one another. Mothers and their calves typically started a well-defined whistle exchange as soon as they were restrained.

Young dolphins both in the wild and in captivity have variable whistles when born, but develop a stereotyped signature whistle within the first year of life. David and Melba Caldwell have recorded whistles from captive dolphins on the day they were born, but these whistles remain faint, "quavery," and unstereotyped for 4-6 months (Caldwell & Caldwell, 1979). Sayigh has recorded similar whistles while following wild mothers and calves, but one can seldom be sure which dolphin produces which whistle under these circumstances. The whistles of wild calves can be recorded using contact hydrophones from when they are first caught at an age of 1 year until well after they leave their mothers at ages typically ranging from 3 to 6 years. Analysis of whistles from over 40 mother-calf pairs shows that by the first year of age, wild calves have developed a stereotyped whistle pattern that remains more or less fixed over subsequent observations as many as 10 years later (Sayigh et al., 1990). This is similar to the pattern reported for captive dolphins (Caldwell, Caldwell, & Tyack, 1990).

When she compared whistles from male and female calves, Sayigh discovered that almost all of the female calves developed whistles that were very different from those of their mothers, but most of the male calves developed whistles that were remarkably similar to their mother's whistle. This sex differences in signature whistle structure may reflect differences in the life histories of males versus females. In Sarasota, when a young adult female first has a calf, she tends to associate with a group of adult females including her own mother. If the grandmother and daughter with calf (not to mention other related females within the same group) had similar whistles, it could be difficult for a young calf to maintain contact with its mother. Males, on the other hand, disperse from their natal group. There may thus be little advantage for males to develop signature whistles different from their mothers. There may even be benefits to allowing recognition of relationships between mother and son or between brothers. Recognition of mother-son relationships could limit inbreeding. Adult males form coalitions that compete with other males for access to females (Connor, Smolker, & Richards, in press); recognition of brother-brother relations might facilitate the role of kinship in mediating interaction within and between coalitions.

This sex difference suggests that calf whistles are modified as a consequence of exposure to the mother's whistle. Males modify their initially unstereotyped whistles to become more like those of their mother, while females modify their initially unstereotyped whistles to become more distinct. The two sexes may inherit different predispositions for learning their signature whistles. Any alternative explanation that rules out vocal learning would have to model how the X chromosome from the father triggers the formation of a new and distinctive whistle structure in a young female, while the Y chromosome from the father limits the young male to produce a whistle structure encoded in the mother's contribution to its genes. The simplest genetic model would posit that whistle structure is an X-linked additive trait. Male calves, with only one X chromosome from the mother, would inherit their whistle structure from the mother, while the whistles of female calves would be influenced by the X chromosomes from both parents. Wells is currently establishing paternities of calves in the Sarasota population, and we will compare whistles of mothers, fathers, and calves in order to test these competing hypotheses.

Sayigh and I are also conducting a series of playback experiments to test whether mothers and their independent calves recognize each others' signature whistles. When in the net corral, dolphins can be gently restrained by hand, and their position with respect to a playback speaker and other dolphins can be controlled. Dolphins responded strongly to some playbacks, both vocalizing and turning toward the playback speaker. We are using a matched pair design in which each of two mothers (or calves) are played the same stimulus tape containing whistles of one of their calves (or mothers), then the other. The prediction is that dolphins will show a stronger response to the whistles of the animal with which they shared a strong bond than to the matched animal. Similar tests are being conducted for bonds other than the mother-calf bond.

VOCAL IMITATION IN ADULT CAPTIVE DOLPHINS

Even before the Caldwells' pioneering work on signature whistles, many studies reported that dolphins use whistles to establish vocal or physical contact with one another (McBride & Kritzler, 1951; Wood, 1954). Captive dolphins whistle when separated and respond to whistles either by whistling themselves or by approaching the whistler. As we observed with wild dolphins, captive females and their young calves will exchange whistles until reunited. Data from both captivity and the wild strongly indicate that individual-specific social relationships are very important to bottlenose dolphins. Even when other animals in the group are also whistling, a mother and calf, for instance, presumably can use their signature whistles to find one another.

It has been difficult to investigate the social functions of signature whistles because it is so difficult to tell which dolphin is whistling underwater, even within a small captive group. I developed a small telemetry device, called a *vocalight* (Tyack, 1985), and a miniature computer data logger (Tyack & Recchia, 1991) to overcome this obstacle. Either device is attached to a dolphin's head or back with a suction cup. The vocalights are made in a variety of colors. Every time a dolphin produces a sound, its vocalight lights up. If several animals are in a pool, each can be equipped with a vocalight that produces a different color. To identify which dolphin has made a particular sound, a poolside observer simply calls out the color that was illuminated when the sound was heard. Both the whistles (recorded underwater with hydrophones) and the observers' identifications are recorded simultaneously for later analysis. It is difficult for an observer to follow more than two or three dolphins simultaneously, so dataloggers are used for larger groups. We attach a datalogger to each dolphin to record the level of sound 20 times/second for up to 45 minutes. The dataloggers are synchronized to a time code recorded simultaneously with both audio and video records from the pool.

The vocalights were first used with two captive bottlenose dolphins named Scotty and Spray at Sealand, a marine park in Brewster, MA, on Cape Cod. Here the dolphins could be studied while they were interacting in the water, rather than recorded in air or in isolation as had been typical for earlier studies of signature whistles. Scotty and Spray each produced a stereotyped whistle very much like the signature whistles described by the Caldwells. However, the Caldwells reported that signature whistles made up over 90% of the whistle repertoire of each bottlenose dolphin, yet only 48% and 67% of the whistle samples from Scotty and Spray, respectively, were their own signature whistles (Tyack, 1986). Both Scotty and Spray produced highly variable whistles and each also produced whistles almost identical to the presumed signature whistle of its poolmate. The most common whistle from each animal was its signature whistle, but each imitated the other's whistle at rates near 20%. The male, Scotty, produced more imitations than Spray, and both listening and inspection of spectrograms indicate that his imitations of Spray's signature whistle were more precise than Spray's imitations of Scotty's whistle. Scotty was recorded 2 years after Spray died, and when Spray was not present, he whistled less frequently, produced shorter whistles, and did not imitate Spray's whistle (Tyack, 1991).

In considering possible functions for imitation of signature whistles, I was helped by data from a foray by an ethologist to Louis Herman's marine mammal lab at Kewalo Basin. For several years, Herman used acoustic cues as well as gestural cues for language training with his dolphins. When Douglas Richards joined Herman's lab, he already had ethological experience studying acoustic communication. After Richards joined the lab, they showed that the dolphins not only responded to the acoustic cues as commands, but they also were imitating them quite precisely. Similar imitation had been reported earlier (e.g., Caldwell & Caldwell, 1972).

As Sigurdson (this volume, chapter 8) points out, these whistle mimicry results suggest a useful medium for dolphin language research focussing on signal production as well as comprehension. Even though apes failed at vocal imitation, ape language researchers were so committed to establishing a two-way communicative link with their subjects that they switched to gestural communication. It is ironic that the animal language research on marine mammals has not taken advantage of their imitative capabilities to establish two-way use of an artificial vocal communication system. Once training problems are overcome, the kind of system being developed by Sigurdson should allow humans to listen and respond to the dolphins as well as vice versa.

Richards et al. (1984) showed that a dolphin can be trained to label arbitrary objects by imitating arbitrary manmade sounds. When they gave a dolphin the command to imitate a sound, they would simultaneously play the model sound and hold up an object associated with that sound. For example, for the tune of "Mary had a little lamb," one might show a frisbee, and for "Row, row, row your boat," one might show a pipe. After the dolphin got used to this, they started occasionally to show the object but not to play the model sound. In order to respond with the right sound, the dolphin had to remember which sound was associated with which object. After sufficient training, the dolphin succeeded in learning how to label each manmade object with an arbitrary manmade tune.

I am currently testing the hypothesis that imitated signature whistles are also vocal labels used as names, and that untrained dolphins imitate whistles of particular individuals in order to call them. This shares an obvious analogy with the research on imitation of manmade sounds. The vocal labeling study by Richards et al. demonstrates that dolphins have the cognitive capabilities required to use signature whistles as names. If dolphins do imitate signature whistles to name a particular individual, they must be able to make similar associations between each dolphin in their group and the appropriate signature whistle. We are currently using the dataloggers to study the precise behavioral contexts when captive dolphins produce their own signature whistles and when they imitate the signature whistles of others. We are also investigating the responses of other dolphins when a dolphin produces its own whistle, imitates the whistle of the listener, or imitates the whistle of some other dolphin. Neither study addresses the question of how referential is the use of these vocal labels (Savage-Rumbaugh, 1986; Savage-Rumbaugh Rumbaugh, Smith, & Lawson, 1980;).

DO DOLPHINS IMITATE SIGNATURE WHISTLES TO CALL SPECIFIC INDIVIDUALS?

We also have consistent evidence for vocal imitation of signature whistles among the wild dolphins of the Sarasota community. These dolphins tend to imitate the whistles of animals with whom they share strong social bonds. Mothers and calves have been recorded to imitate one another, as do pairs of adult males that have formed a coalition and are almost always sighted together. The signature imitation research is in progress, but I describe preliminary data from one whistle exchange that illustrates how dolphins may use signature whistles to call specific individuals. This exchange was recorded on 21 June 1984, before we had adopted the policy of processing calves together with their mothers during the temporary captures in Sarasota. This whistle exchange occurred between a dolphin in the processing raft and one of five that were in the net corral. The whistles from the animal in the raft were recorded using a suction cup contact hydrophone, all other whistles were recorded from one hydrophone in the water approximately 6 m from the raft and up to 80 m from the furthest part of the net corral.

Six dolphins were encircled in the net corral. The first one to be put into the raft was Nicklo, a 34-year-old adult female. Nicklo maintained a stable whistle rate of approximately 18 whistles/minute throughout her time in the raft. This rate was higher than that of any of the animals in the net corral. Nicklo produced over 520 signature whistles, 39 variant whistles, and no imitations during the first half of her hour in the raft. Halfway into the recording, measuring, and sampling process, Nicklo began imitating the signature whistle of Granny, the oldest dolphin in the corral (40 years old in 1984). During the second half of the hour, Nicklo produced 472 signature whistles, 47 imitations of Granny, and 6 variant whistles. Nicklo continued to imitate the signature whistle of Granny until she was released from the raft. She did not imitate the signature whistle of any other animal in the group, including her own 3.5-year-old female calf. As the oldest female in the group, Granny was most likely to have had experience with this new and potentially threatening situation, and on this basis would be most likely to be of assistance.

Signature whistles from the 5 dolphins in the net corral were also analyzed. Because these were recorded together on the same underwater channel, we were not able to identify which dolphin made which whistle, and thus would not have been able to detect imitation of whistles among these dolphins. Furthermore, another mother had signature whistle contours so similar to her 3.5 year old male calf that we did not attempt to discriminate between them. None of the animals in the corral imitated the whistle of Nicklo.

In order to test whether the whistles of Nicklo became synchronized with whistles from any of the dolphins in the net, we tallied how often each kind of whistle from Nicklo occurred within the same 3 second window as whistles from each of the dolphins in the net corral. The time window was chosen to be short enough that dolphins seldom produced more than one whistle per window. The only whistles that synchronized with Nicklo were the signature whistles of Granny during the period immediately after Nicklo started imitating Granny's signature whistle. A caveat is in order regarding statistical analysis of these windows. Successive whistles from the same dolphin are seldom independent, but depend on both what kind of whistle came before and how long ago it occurred. Therefore, treatment of successive 3 second windows as independent may inflate the sample size of independent observations for statistical analysis.

These data clearly support the prediction of the signature labeling hypothesis that a dolphin will show a differential response following imitation of its signature whistle. Before Nicklo first imitated Granny's whistle, there was no temporal association between Granny and Nicklo whistles. As soon as Nicklo started imitating Granny's whistle, Granny and Nicklo whistles were strongly associated. Granny showed a higher response to Nicklo's imitations of her own whistle than to Nicklo's signature whistle. The association between Granny and Nicklo whistles was stronger than that of Nicklo and any other dolphins in the net, including Nicklo's own calf. Nicklo thus imitated the whistle of the oldest dolphin in the group (perhaps the most able and likely to help her), and only that dolphin responded to the imitations. Some of Nicklo's imitations preceded and some followed Granny's production of her own signature whistle. This demonstrates that Granny did not just respond to imitation and Nicklo did not just imitate Granny immediately following a Granny whistle.

Although dolphins can play with imitating novel sounds, they harness learning primarily to develop stable whistles. It may seem counterintuitive to use flexibility in the service of developing a stable sound, but this is how humans learn words. People who speak a language must share the same referents to words, but the precise sounds we use are learned and arbitrary. English speakers learn to say *house*, while French speakers say *maison*. If dolphins learn to develop their signature whistles and learn to imitate the whistles of others in order to name them, then learning allows a remarkably open-ended system of communication in these social animals.

ETHOLOGICAL SUGGESTIONS FOR ANIMAL LANGUAGE RESEARCH

When comparative psychologists want to study a particular cognitive skill in the laboratory, they would do well to search the animal kingdom for taxa that solve similar problems. For studies of spatial memory, animals such as nutcrackers (*Nucifraga* sp), which store and retrieve tens of thousands of seeds per year, might be more promising than species such as pigeons (*Columba livia*), which seldom are faced with spatial memory problems of similar magnitude (Shettleworth, 1990). If animal language research is taken as an attempt to study how the communication skills of animals can be modified by learning, then the selection of apes, dolphins, parrots, and sea lions makes some sense. All four groups are highly social, with relatively long periods of parental care, and with well developed imitative capabilities. Any species where the young are taught would also be a promising candidate for animal language research.

More careful examination of behavioral development in young animals raised by their own parents may also target particular age or sex classes as optimal for language training. In most songbird species, males provide more evidence for vocal learning than females, and they learn best during critical periods of development. Data on whistle imitation suggest that male dolphins might be better subjects for the study of vocal imitation than females. Not only does a male calf in the wild tend to learn his signature whistle by imitating his mother, but also the imitations of adult males appear more precise than those of adult females. The captive male Scotty produced more frequent and more accurate imitations than did the female Spray (Tyack, 1991). However, both sexes do show strong evidence for vocal learning, and females can produce quite accurate imitations.

Animal language training may be improved by closer matching to development of natural communication systems in each species. There are obvious problems with starting training after a critical period for learning has passed, but there are more subtle problems as well. Cognitive capabilities may be channeled to solve particular tasks by perceptual limitations, selective attention, domain-specific intelligences, and motivational factors. Close feedback between laboratory experiment and field work are of obvious utility for matching an experimental protocol to an animal's capabilities. I discuss four different ways in which better matches may be developed: stimuli used in artificial languages, training techniques, context of testing, and more emphasis on the communicative and expressive elements of artificial languages.

Care must be taken to match artificial languages to the perceptual and motor abilities of the subjects. It is by now obvious that the inability of chimps to speak says little about their language abilities. While they are physically incapable of producing many speech sounds, they can learn and use manual gestural languages. Perceptual limitations are not so obvious, but may be equally important. For example, it appears that discrimination of the human speech sounds /pa/ from /ba/ relies in part on a categorical perception that is shared among mammals, whereas humans use specially evolved mechanisms to parse sentences in normal speech (Kuhl, 1987). For artificial languages to proceed beyond minimal complexity, they must rely on features that animals can discrimate rapidly with little error. If discrimination of /pa/ from /ba/ relies on auditory processing shared among most mammals, this may be a useful feature for artificial languages, but if humans require special mechanisms to parse phoneme strings within speech, artificial languages for other species may require special attention for more discriminable features. Attention to the natural signals of each species may help identify such features. For example, the coo calls of Japanese macaques (*Macaca fuscata*) divide into groups with early or late maxima in frequency, and these two classes of coo occur in different contexts (Green, 1975). Japanese macaques discriminate this feature with ease, while closely related species require extensive training for the same discrimination (Zoloth et al., 1979).

Some psychologists choose highly artificial settings or stimuli for tests. If the experimental protocol requires novel objects or contexts, then artificiality may be advantageous, but many animals may perform best on problems similar to those for which their cognitive capabilities evolved. If students of artificial intelligence want to program a robot to find, identify, and manipulate things, they could simplify their task by narrowing down the robot's symbol set and outside world to very few different kinds of simple geometrical shapes that do not move about on their own. It is by no means certain that training an animal to use a formal language describing a similar static and highly constrained object world is simpler for the animal than a more natural world. Perceptual abilities are likely to be tuned to an animal's natural environment. Pigeons learn to form "complex" natural concepts of visual images of water, trees, or even one individual human, just as quickly as "simple" geometric shapes (Herrnstein, Loveland & Cable, 1976). Psychologists may have to search carefully to find the right match of settings and stimuli in order to open a communication channel and gain access to more general cognitive abilities of different species.

Animal language researchers would do well to match their training techniques to observations of how their subjects acquire their own natural systems of communication. Some communication skills may be learned better through social reinforcement than food reinforcement. Animal language training in parrots advanced only after application of an innovative social modeling paradigm in which a human alternated with the parrot in responding to spoken English (Pepperberg, this volume, chapter 11). As has been reported for white-crowned sparrows learning song from conspecifics, more intense social interaction with tutors may engage learning processes that are otherwise hidden (Baptista & Petrinovich, 1986).

Selection of naturalistic settings for experimental testing may also improve performance. For example, Terrace, Saunders, and Bever (1979) trained a chimpanzee (*Pan troglodytes*) to sign using American Sign Language. The chimp was trained and tested by many different people during controlled test sessions in a small bare room, under the assumption that this impoverished environment would minimize distractions and cueing. They concluded that the chimp seldom signed spontaneously and that many of the chimp's multisign utterances were cued by the trainer. The regularities in the chimp's multisign utterances were thus as likely to be a consequence of the trainers' understanding of syntax as the chimp's. However, this same chimp was later tested in both Terrace's restrictive testing environment and while interacting and playing with people. In the Terrace test setting, the chimp primarily responded to the trainer, but in the more relaxed setting, most of the signs were spontaneous and only

11% were imitations (O'Sullivan & Yeager, 1989). After the fact, Terrace (1979) concluded that motivation to sign had been a problem in his study and that the chimp would have made better progress if his sign training had been more integrated into communication throughout the day rather than limited to formal sessions in an impoverished environment.

If pigeons can easily form a concept of an individual person, if parrots can learn language skills most easily by role playing with a human, and if chimps show more communicative use of signs while playing with people, then this suggests that more explicitly interactive use of human-animal relationships might further animal language research. As we learn more about the social behavior of species involved in animal language research and about how their communication mediates social interaction, there will be more opportunity for humans to intervene both with playback experiments and for humans to play roles interacting with animals as more active agents. Close observation of captive primates (e.g., de Waal, 1989) and field experiments with wild primates (e.g., Cheney & Seyfarth, 1990) reveal that monkeys and apes know and communicate a surprising amount about their complex social relationships. If the social domain is a primary one for communication and cognition in these species, then animal language researchers would do well to develop a richer repertoire for manipulating and communicating about their interspecies social relationships.

An ethologist with an evolutionary and cognitive beat may find it difficult to interpret experiments in which an animal is trained with an artificial language to communicate about an artificial object-oriented world constructed by humans. How can he or she integrate the observation that, say, a chimp or a parrot can label a triangle or square and tell us what color a ball is? How can one compare to natural observations, experiments where people train animals to produce or understand strings of commands, such as GO THROUGH A HOOP, after earlier exposure only to different requests such as JUMP OVER A FRISBEE? The ethologist interested in the adaptive functions of particular cognitive skills is more interested in how animals develop representations of and communicate about their own natural world, including their social world.

Study of signature whistles suggests that dolphins use vocal learning and imitation to develop a flexible and open-ended way to communicate primarily about individual-specific social relationships. This contrasts with the marine mammal language experiments, in which dolphins or sea lions are trained to manipulate objects (JUMP OVER HOOP) or to treat people or other dolphins as they do other objects (FETCH BALL [to] PHOENIX). Although these animals clearly can be trained to label objects, to report their presence or absence, and to comprehend sequential commands about objects and actions, all of these experiments use artificial languages as a one-way street to get the animals to perform. This training opens a clear window on some aspects of dolphin or sea lion cognition, but the animals are never given a chance to use the language to alter the contingencies of any human behavior other than tossing a fish. Describing the experiments as "language" experiments thus stretches the usage of language as a communication system. The marine mammal experiments are in this way very different from both the primate (e.g., Savage-Rumbaugh, this volume, chapter 22) and parrot research (Pepperberg, this volume, chapter 11).

The term "animal language" sometimes seems to be used as a cipher for animal awareness. Humans certainly use language to refer to the mental states of themselves and others. Consciousness is required for all but highly unusual language use (and exceptions such as infant speech, talking in ones sleep or talking in hypnosis may more accurately reflect alterations of consciousness rather than its absence). Kihlstrom (1987) identified consciousness primarily as a link of cognition to a representation of the self as either an agent or an experiencer. This would suggest that consciousness is particularly important for the ability it provides of mental scenario building, including the ability to represent ones own performance as others may see it. Alexander (1990) suggested that consciousness evolved to prepare humans for the flow of novel social circumstances for reciprocation that characterize human societies. Language may have evolved in parallel as a way to frame and to manipulate such social understandings. Animals that form individual-specific social relationships and that face a similar tension between competition and cooperation in reciprocal relationships may also encounter selective pressures to evolve more complex forms of social cognition. If consciousness and language coevolved in humans in large measure as a response to human sociality, then higher cognitive functions related to sociality in other animals may have evolved in parallel with abilities to communicate about them. One might expect "animal language" also to frame representations of self and self interest compared to other conspecifics or other elements of the environment.

There is a danger in taking such a formal view of artificial languages and language training that the communicative context is overshadowed. There is a striking lack of overlap between psychological studies of artificial languages and ethological studies of animal communication. Communication is a social phenomenon, and the study of natural communication systems in animals is primarily a study of social behavior. Most animal signals mediate social interactions, yet few animal language studies emphasize the social domain. Animals are more typically trained to use artificial languages primarily to request, describe, or manipulate objects. Researchers following this approach run the risk that their subjects are less able to tap potentially domain-specific communication skills. Animals may be much better at recognizing their mother, have a much richer concept of mother, and be much more motivated to communicate about this kind of natural social relationship than to communicate about discriminating an "x" from a "+."

Language training should not be a purely formal exercise, but should be a tool for opening a two way channel of communication with animals. As with children early on in language development, animals may use signs to obtain favored foods or objects. This may be a useful way to start language training, but it is limited in its communicative scope. Savage-Rumbaugh et al. (1980) suggested that if chimps can get away with being behaviorists, they will, but that they can also engage in symbolic reference if trained to do so. If we create more ways for animals to communicate with us (and possibly deceive us) about desires or plans, including those involving their social environment, and about individuals they associate with, including the trainers, we may both increase their motivation and start to learn more about the social functions of cognition.

Natural animal communication tends to be manipulative and goal oriented. Much of the goal directedness of natural animal behavior is a consequence of adaptation through natural selection of genetically determined behavior patterns. Testing animals under artificial circumstances may help to discriminate whether apparently intentional and intelligent behavior observed under natural conditions represents a "clever" adaptation or an intelligent and intentional animal. If animals can show similar planning in the laboratory using artificial systems of communication, this will help to address these difficult issues of intentionality and intelligence. In the past, the researchers who have been most sensitive to these issues have not been preoccupied with comparisons to human language. Köhler (1925) created experiments to detect insight and to investigate whether chimps appear to understand the problems being solved by other chimps. Menzel and Halperin (1975) showed that captive chimps appear to be able to convey or withold information on the location of hidden objects, apparently intentionally, but the researchers were unable precisely to specify the mode of communication.

In order for animal language research to address these questions, animals should be tested within a social and communicative context. Data both from the natural communication of primates (Cheney & Seyfarth, 1990) and animal language experiments (Bennett, 1978) suggest that animal utterances are more like commands aimed to elicit behavior than like statements aimed to produce or change beliefs in the other party. However, few carefully controlled animal language experiments have given the animals scope for this kind of communication. Humans are disposed to attribute intentions, beliefs, and desires to others, but we have scarce evidence that other animals make similar social attributions. The work of Premack and Woodruff (1978) on whether apes attribute mental states to others and of Woodruff and Premack (1979) on deception suggest that these questions can be addressed by controlled psychological experiments.

Griffin (1981) emphasized that just as language is a medium by which humans can learn about each other's mental experiences, so too animal language training has similar potential for opening a window on the minds of animals. Animal language research has often focused more on narrow comparisons with human language than on these more general cognitive questions. The ability to communicate with people using language is a mixed blessing for cognitive scientists; talking, by itself, may often be a shallow and misleading probe of cognition. A major theme of psychology in this century has been how few of our internal psychological processes are fully accessible for conscious reflection, and how inaccurate the conscious report of human subjects may be. Even in humans, analysis of consciousness cannot proceed independently of nonconscious cognitive processes. Psychological research on humans clearly indicates that nonconscious cognitive processes have impacts on conscious processes and that different cognitive processes are more or less penetrable by conscious thought (Kihlstrom, 1987). However, to the extent that animal language experiments can give us access to intentionality, attribution, and the ability to synthesize information across domains in animals, they will remain important general tools in the study of animal cognition.

It is difficult to integrate animal language experiments into comparative study of the evolution of animal cognition. We require more information on the functions in nature of the cognitive capabilities revealed by these experiments in order to understand their evolutionary origins. It is only by shuttling back and forth between cognitive experiments and observational study that we can hope to understand the full complexity and diversity of animal cognition. The work of Richards and co-workers, for instance, gave me more confidence that dolphins had the cognitive capabilities required to imitate signature whistles in order to label or call other individuals. Conversely, results on the imitation of signature whistles may help comparative psychologists to understand the functions in nature of cognitive skills they have uncovered in the laboratory. Further progress in animal cognition requires a tighter synthesis of the functional and evolutionary studies of organismal biologists, mechanistic study by neurobiologists, and study of development and cognitive processes by comparative psychologists.

REFERENCES

Alexander, R.D. (1990). Epigenetic rules and Darwinian algorithms. *Ethology and Sociobiology,* 11, 241-303.

Axelrod, R. (1984). *The evolution of cooperation.* New York: Basic Books.

Baptista, L. F. & Petrinovich, L. (1986). Song development in the white-crowned sparrow: Social factors and sex differences. *Animal Behavior,* 34, 1359-1371.

Bennett, J. (1978). Some remarks about concepts. *Behavioral and Brain Sciences,* 1, 557-560.

Bowlby, J. (1969). *Attachment.* New York: Basic Books.

Bullock, T. H. & Ridgway, S. H. (1972). Evoked potentials in the central auditory system of alert porpoises to their own and artificial sounds. *Journal of Neurobiology,* 3, 79-99.

Caldwell, M. C. & Caldwell, D. K. (1965). Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature,* 207, 434-435.

Caldwell, M. C. & Caldwell, D. K. (1972). Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. *Cetology,* 9, 1-8.

Caldwell, M. C. & Caldwell, D. K. (1979). The whistle of the Atlantic bottlenosed dolphin (*Tursiops truncatus*) - ontogeny. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals, Vol. 3, Cetaceans* (pp. 369-401). New York: Plenum Press.

Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). A review of the signature whistle hypothesis for the Atlantic bottlenose dolphin, *Tursiops truncatus.* In S. Leatherwood, & R. Reeves (Eds.), *The* *bottlenose dolphin: Recent progress in research* (pp. 199-234). San Diego: Academic Press.

Cheney, D. L. & Seyfarth, R. M. (1990). *How monkeys see the world.* Chica University of Chicago Press.

Cole, M. & Scribner, S. (1974). *Culture & thought, a psychological introduction.* New York: Wiley.

Connor, R. C., Smolker, R. A., & Richards, A. F. (in press). Dolphin alliances and coalitions. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals.* Oxford: Oxfo University Press.

Cosmides, L. (1989). The logic of social exchange: Has natural selection shape how humans reason? Studies with the Wason selection task. *Cognition*, 31, 187-276.

Cosmides, L. & Tooby, J. (1987). From evolution to behavior: evolutionary psychology as the missing link. In J. Dupre (Ed.), *The latest on the be* (pp. 277-306). Cambridge MA: MIT Press.

Darwin, C. (1859/1979). *On the origin of species by means of natural selection* Cambridge: Harvard University Press.

Darwin, C. (1871/1981). *The descent of man, and selection in relation to sex.* Princeton: Princeton University Press.

Deacon, T. W. (1988). Human brain evolution: 1. Evolution of language circuits. In H. J. Jerison & I. Jerison (Eds.), *Intelligence and evolutionary biology*, (pp. 363-381). NATO ASI Series G: Ecological Sciences, Vol. 17, . Berlin: Springer Verlag.

Deutsch, D. (1975). The organization of short-term memory for a single acoustic attribute. In D. Deutsch & J. A. Deutsch (Eds.), *Short term memory* (pp. 107-151). New York: Academic Press.

Eaton, R. L. (1979). A beluga whale imitates human speech. *Carnivore*, 2, 22-23.

Fodor, J. A. (1983). *The modularity of mind.* Cambridge, MA: MIT Press.

Garcia, J. & Koelling, R. A. (1966). The relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123-124.

Gardner, H. (1983). *Frames of mind.* New York: Basic Books.

Goodall, J. (1986). *The chimpanzees of Gombe.* Cambridge, MA: Harvard University Press.

Gould, S. J. & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist paradigm. *Proceedings of the Royal Society of London*, 205, 281-288.

Green, S. (1975). Variations of vocal pattern with social situation in Japanese monkey (*Macaca fuscata*): A field study. In L. A. Rosenblum (Ed.) *Primate behavior*, (Vol. 4, pp. 1-102). New York: Academic Press.

Griffin, D. R. (1981). *The question of animal awareness.* Los Altos, CA.: Kaufmann.

Hamilton, W. D. (1964). The genetical theory of social behavior. *Journal of Theoretical Biology*, 7, 1-52.

Hayes, C. (1951). *The ape in our house.* New York: Harper.

Herman, L. M. (1980). Cognitive characteristics of dolphins. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 363-429). New York: Wiley-Interscience.

Herman, L. M., Richards, D., & Wolz, J. (1984). Comprehension of sentences by bottlenosed dolphins. *Cognition*, 16, 129-219.

Herrnstein, R., Loveland, D. H. & Cable, C. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 285-311.

Humphrey, N.K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology*, (pp. 303-317). New York: Cambridge University Press.

Kamil, A. C. (1988). A synthetic approach to the study of animal intelligence. In D. W. Leger (Ed.), *Comparative perspectives in modern psychology:*

Nebraska symposium on motivation. (Vol. 35, pp. 257-308). Lincoln: University of Nebraska Press.

Kamil, A. C. & Roitblat, H. L. (1985). Foraging theory: implications for animal learning and cognition. *Annual Review of Psychology,* 36, 141-169.

Kihlstrom, J. F. (1987). The cognitive unconscious. *Science*, 237, 1445-1452.

Klima, E. S. & Bellugi, U. (1979). *The signs of language.* Cambridge MA: Harvard University Press.

Köhler, W. (1925). *The mentality of apes.* New York: Harcourt Brace.

Krebs, J. R. (1990). Food-storing birds: Adaptive specialization in brain and behaviour? *Philosophical Transactions of the Royal Society, London. B,* 329, 153-160.

Kroodsma, D. E. & Canaday, R. A. (1985). Differences in repertoire size, singing behavior, and associated neuroanatomy among marsh wren populations have a genetic basis. *Auk,* 102, 439-446.

Kroodsma, D. E. & Verner, J. (1987). Use of song repertoires among marsh wren populations. *Auk,* 104, 63-72.

Kuhl, P.K. (1987). The special-mechanisms debate in speech research: Categorization tests on animals and infants. In S. Harnad (Ed.), *Categorical perception* (pp. 355-386). Cambridge: Cambridge University Press.

Kummer, H., Dasser, V. & Hoyningen-Hüne, P. (1990). Exploring primate social cognition: some critical remarks. *Behaviour,* 112, 84-98.

Lieberman, P. (1984). *The biology and evolution of language.* Cambridge, MA: Harvard University Press.

Lieberman, P. (1991). *Uniquely human.* Cambridge, MA: Harvard University Press.

Marler, P. (1970). Birdsong and human speech: could there be parallels? *American Scientist,* 58, 669-674.

Marler, P. (1990). Song learning: the interface between behaviour and neuroethology. *Philosophical Transactions of the Royal Society, London, B*, 329, 109-114.

McBride, A. F. & Kritzler, H. (1951). Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. *Journal of Mammalogy*, 32, 251-266.

Meier, R. P. (1991). Language acquisition by deaf children. *American Scientist*, 79, 60-70.

Menzel, E. W., Jr. & Halperin, S. (1975). Purposive behavior as a basis for objective communication between chimpanzees. *Science*, 189, 652-654.

Newman, J. D., & Symmes, D. (1982). Inheritance and experience in the acquisition of primate acoustic behavior. In C. Snowdon, C. H. Brown, & M. Peterson (Eds.), *Primate communication* (pp. 259-278). Cambridge: Cambridge University Press.

O'Sullivan, C. & Yeager, C. P. (1989). Communicative context and linguistic competence: The effects of social setting on a chimpanzee's conversational skill. In R. A. Gardner & B. T. Gardner (Eds.), *Teaching sign language to chimpanzees* (pp. 269-279). Albany: State University of New York Press.

Payne, K. B., Tyack, P. & Payne, R. S. (1983). Progressive changes in the songs of humpback whales. *AAAS Selected Symposia Series* (pp. 9-59). Boulder, CO: Westview Press.

Petitto, L. A. & Marentette, P. F. (1991). Babbling in the manual mode: Evidence for the ontogeny of language. *Science*, 251, 1493-1496.

Pinker, S. (1984). *Language learnability and language development.* Cambridge, MA: Harvard University Press.

Premack, D. (1983). The codes of man and beast. *Behavioral and Brain Sciences*, 6, 125-167.

Premack, D. & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1, 515-526.

Ralls, K., Fiorelli, P., & Gish, S. (1985). Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina. Canadian Journal of Zoology*, 63, 1050- 1056.

Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labelling of objects by a bottlenosed dolphin, *Tursiops truncatus. Journal of Comparative Psychology*, 87, 10-28.

Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol.* New York: Columbia University Press.

Savage-Rumbaugh, E. S., Pate, J. L., Lawson, J., Smith, S. T., & Rosenbaum, S. (1983). Can a chimp make a statement? *Journal of Experimental Psychology: General*, 112, 457-492.

Savage-Rumbaugh, E. S., Rumbaugh, D. M., Smith, S. T. & Lawson, J. (1980). Reference: the linguistic essential. *Science*, 210, 922-925.

Sayigh, L. S., Tyack, P. L., Wells, R. S. & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, 26, 247-260.

Seyfarth, R. M. & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behavior*, 34, 1640-1658.

Shettleworth, S. J. (1990). Spatial memory in food storing birds. *Philosophical transactions of the Royal Society, London. B*, 329, 143-151.

Snowdon, C. T. (1983). Ethology, comparative psychology, and animal behavior. *Annual Review of Psychology*, 34, 63-94.

Snowdon, C. T. (1990). Language capacities in nonhuman animals. *Yearbook of Physical Anthropology*, 33, 215-243.

Solow, A. & Tyack, P. L. (1990). Inhomogeneity and apparent organization in animal behavior. *Biometrics*, 46, 837-840.

Stephens, D.W. & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.

Terrace, H. S. (1979). *Nim: A chimpanzee who learned sign language*. New York: Washington Square Press.

Terrace, H. S., Petitto, L. A., Saunders, R. J., & Bever, T. G. (1979). Can an ape create a sentence? *Science*, 206, 891-902.

Tierney, A. J. (1986). The evolution of learned and innate behavior: Contributions from genetics and neurobiology to a theory of behavioral evolution. *Animal Learning and Behavior*, 14, 339-348.

Tinbergen, N. (1951). *The study of instinct*. New York: Oxford University Press.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46, 35-57.

Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology*, 8, 105-116.

Tyack, P. (1985). An optical telemetry device to identify which dolphin produces a sound. *Journal of the Acoustical Society of America*, 78, 1892-1895.

Tyack, P. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: Mimicry of signature whistles? *Behavioral Ecology and Sociobiology*, 18, 251-257.

Tyack, P. L. (1991). Use of a telemetry device to identify which dolphin produces a sound: when bottlenosed dolphins are interacting, they mimic each other's signature whistles. In K. Pryor & K.S. Norris (Eds.) *Dolphin societies: Methods of study*, (pp. 319-344). Berkeley: University of California Press.

Tyack, P. L. & Recchia, C. A. (1991). A datalogger to identify vocalizing dolphins. *Journal of the Acoustical Society of America*, 90, 1668-1671.

Verner, J. (1976). Complex song repertoire of male long-billed marsh wrens in eastern Washington. *Living Bird*, 14, 263-300.

de Waal, F. (1989). *Chimpanzee politics*. Cambridge, MA: Harvard Un
Press.

Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). Structural aspects of
societies. In H. H. Genoways (Ed.) *Current mammalogy*, (vol. 1
247-305). New York: Plenum Press.

Wood, F. G., Jr. (1954). Underwater sound production and concurrent b
of captive porpoises, *Tursiops truncatus* and *Stenella plagiodon*.
Bulletin of Marine Science of the Gulf and Caribbean, 3, 120-1

Woodruff, G. & Premack, D. (1979). Intentional communication in the
chimpanzee: the development of deception. *Cognition*, 7, 333-3

Zoloth, S. R., Petersen, M. R., Beecher, M. D., Green, S., Marler, P., Mo
M., & Stebbins, W. C. (1979). Species-specific perceptual proc
of vocal sounds by monkeys. *Science*, 204, 870-873.