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Nonhuman Primate Communication

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Abstract.

Nonhuman primates produce a large number of communicative signals, especially in the auditory channel, and these calls function in a wide range of contexts including mating, alarm, food discovery, affiliative social relationships, and aggressive competition. In this chapter, we explore the information encoded in these signals and the perceptual decoding of and response to the signal. An understanding of primate signal design, in combination with studies of signal perception, reveal an exceptionally rich communicative repertoire, while pointing the way to future questions concerning the mechanisms underlying call production and categorization.

Introduction

All primates live in social groups. Some, like orangutans, live a largely solitary life, but come together for mating, aggressive competition, and offspring care. Others, such as chimpanzees, live in large communities, but on a day to day basis exist in small ephemeral parties. Independent of group size and composition, monkeys and apes engage in a wide variety of social and non-social activities including the discovery of food, the detection of predators, inter-group encounters, group movement, play, grooming, aggressive attacks, coalitions, submissive retreats, and reconciliatory actions designed to redress imbalances in a relationship. In principle, one can readily imagine the adaptive significance of a signaling system capable of informing others of these various activities. Of particular use would be a vocal system designed to convey such information in the absence of any other contextual information. Such a system would enable Monkey A to inform Monkey B of the location, movement and type of predator, and monkey B would be able to decode this information and more, including the fact that monkey A is a member of the same species, same group, is high ranking and male. This hypothesis about adaptive design is only partly accurate. Nonhuman primates do produce vocalizations in a variety of contexts, and listeners do extract considerable information from the signal. But there are significant constraints on the kind of information conveyed and the kind of information extracted. These constraints are both internal (peripheral and central processing mechanisms) and external (habitat, climate, distance to receivers, competing acoustic signals) to the animals themselves.

Students of animal behavior have long argued over the proper definition of communication (Hauser, 1996; Bradbury and Vehrencamp, 1998; Owings and Morton, 1998). Early theories, centered primarily in classical ethology, focused on the veridical transmission of information from sender to receiver. One variant of this view borrowed from engineering, and in particular Shannon-Weaver information theory. Communication was said to occur if a receiver's uncertainty about an event was reduced by the information transmitted in the sender's signal. Critics of this information perspective emerged with the sociobiology revolution. Dawkins and Krebs (1978) argued that a veridical signaling system was invadable by a mutant who generated the same signal but with a different, and deceptive motivation. Thus, for example, if an aggressive signal was designed to convey information about the probability of escalating aggression, then a mutant who always signaled the highest level of aggressive intent, but was bluffing, would always win because receivers would readily back down. Thus, so Dawkins and Krebs originally argued, the adaptive function of communication is for signalers to manipulate the behavior of receivers. This view was quickly criticized for being signaler-centric. Dawkins and Krebs responded by modifying their original model to include both manipulative signalers and skeptical receivers. Thus, communication evolves as an arms race in which selection favors signals designed to manipulate the behavior of receivers for fitness gains, and counter-selection favors receivers that distinguish between truths and lies.

Riding along with this selfish-gene perspective was Zahavi's (Zahavi, 1975) handicap principle, often interpreted as a specific explanation for mating behavior, but originally proposed as a general theory of signaling. For Zahavi, signals provide veridical information about the signaler if, and only if, there are costs to signaling relative to current condition, and the capacity to generate such cost-bearing signals is heritable. Although there have been several empirical examples supporting Zahavi's intuition (e.g., stotting in gazelles, courtship displays in several bird species), it is also clear that honesty can emerge in the absence of significant costs. For example, a series of studies by Fitch and colleagues indicate that physical constraints anchor honesty in the absence of costs (e.g., the length of the vocal tract correlates with body size which provides, via formant frequency dispersion, an honest indicator of size (Fitch, 1997).

All of these definitions of communication have pros and cons, and most side step the cognitive mechanisms underlying both the production and perception of communicative signals. For purposes of exposition, we borrow from these different definitions and focus on what we see as the most empirically tractable aspects: the information encoded in the signal, the transmission medium, and the perceptual decoding of and response to the signal (Fig 1).

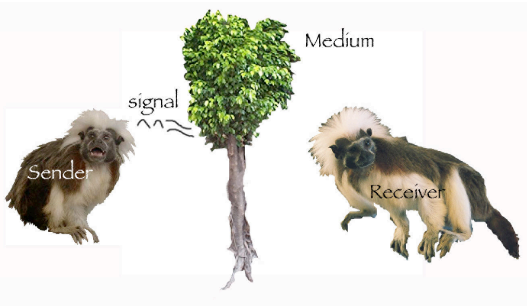

Figure 1. *The basic structure of communication systems. Shown are the four central elements that comprise communication: the sender emits a signal that travels through a medium to a receiver. Shown is a vocal communication in which the signal is a vocalization and the medium is a forested environment.*

In the present manuscript, we focus our discussion on communication in nonhuman primates (see chapters of this volume for similar discussions of other taxonomic groups). We focus on vocal communication because there has been considerably more progress for this sensory channel in primates than for all others. This is largely due to the fact that the analytical techniques for analyzing the signal and testing its perceptual significance in primates are far more sophisticated than for the visual, tactile or olfactory channels. We begin with a discussion of call context, focusing on three functional problems: food, sex, and anti-predator alarm. We then focus on the potential for signalers to convey information about individual, sex, and group identity, and the capacity for receivers to decode this information. We end this chapter with a discussion of some pressing gaps in our understanding and the need to develop new analytic tools and comparative data sets.

Call Context

Primates produce an astonishing array of vocalizations—from the simple, tonal phees of the common marmoset (Fig 2,a), to the spectrotemporally complex syllable sequences of the chimpanzee pant hoot (Fig 2,b), to the moving formants found in rhesus monkey girneys (Fig 2,c). There is enormous variability in the spectrotemporal structure of different call types within species and in the acoustic properties of particular calls within and between individuals. These observations raise two questions: to what extent is the variability in signal morphology behaviorally relevant and how shall we go about quantifying call morphology? One method is to chart the association between social and ecological situations and call morphology. More recent work has extended these earlier findings to explore the possibility that, like human words, primate vocalizations have the capacity to pick out salient objects and events in the environment, and convey this information to listeners. We focus here on functional aspects of these calls, leaving aside discussion of their cognitive substrates.

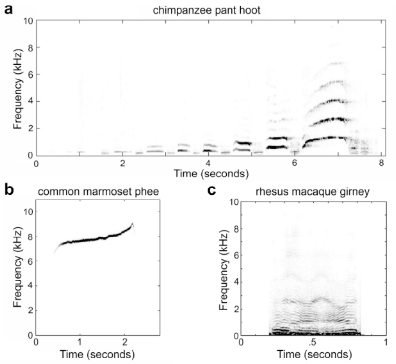

Figure 2. *Spectrograms show inter-species variation in the acoustic structure of primate vocalizations. For each spectrogram, the X-axis shows time and the Y-axis shows frequency. Depicted are a) chimpanzee pant hoot, b) common marmoset phee, and c) rhesus monkey girney.*

Food

Many primates produce distinct calls when discovering or eating food. Call rate appears to correlate with hunger in rhesus macaques (*Macaca mulatta*), with food preference in cotton-top tamarins (*Saguinus oedipus)*, with amount of food and location in toque macaques (*M. sinica*), and with amount of food and whether that food is divisible in chimpanzees (*Pan troglodytes*). In addition, distinct vocalizations for low quality/common and high quality/rare foods have been observed in rhesus macaques (Hauser, 1996).

Rhesus macaques not only produce acoustically distinct vocalizations for low and high quality food items, they also appear to recognize these categories. In a habituation-discrimination experiment (Hauser, 1996), habituation was shown to transfer between two high quality food call types ('warbles' and 'harmonic arches') despite the fact that they are acoustically distinctive; this suggests that both calls are classified as falling within the same functional category. Information in rhesus food calls was shown to be relevant to conspecifics in another context as well (Hauser, 1996). Experimenters observed individual rhesus following discovery of food. Discoverers produced food calls 45% of the time. However, because of the density of the population, other conspecifics detected the food discovery 90% of the time. On average, vocal discoverers consumed more food than silent discoverers because silent discoverers, when detected, were often chased away from the food or aggressively attacked. Similar results have also been observed in white-faced capuchins (*Cebus capucinus*) (Gros-Louis, 2004).

Predators

Many primates produce alarm calls in response to predators. Several species, including Barbary macaques (*M. sylvanus*), chacma baboons (*Papio hamadryas*), ring-tailed lemurs (*Lemur catta*), redfronted lemurs (*Eulemur fulvus rufus*), Verraux's sifakas (*Propithecus verreauxi verreauxi*), Diana monkeys (*Cercopithecus diana*), and most famously, vervet monkeys (*C. aethiops*) (Cheney and Seyfarth, 1990), produce acoustically distinctive alarm calls to different predators. Vervets living in Amboseli National Park, Kenya, produce acoustically distinctive alarm calls to large felines (leopards, etc; Fig 3,a), large raptors (martial eagles and crowned eagles; Fig 3, b), snakes (pythons and mambas; Fig 3, c), baboons, and some humans (e.g., the Maasai who occasionally hunt or threaten them). What information is transmitted in these signals? Two criteria must be met for an alarm vocalization to transmit information about a specific predator as opposed to predators or fearful stimuli more generally: 1) the vocalization must be evoked by the presence of the specific predator, and not by any other stimuli and 2) playback of the vocalization alone must be sufficient to produce the same response as the presence of the predator. If these two criteria are met, the alarm call is considered 'functionally referential' (Marler*, et al.*, 1992), that is, it functions as if it conveys information regarding a specific predator. Studies on vervet monkeys, ring-tailed lemurs and Diana monkeys provide evidence for functionally referential alarm calls. We focus here on the Diana monkey as this work has included some of the most detailed perceptual experiments to date.

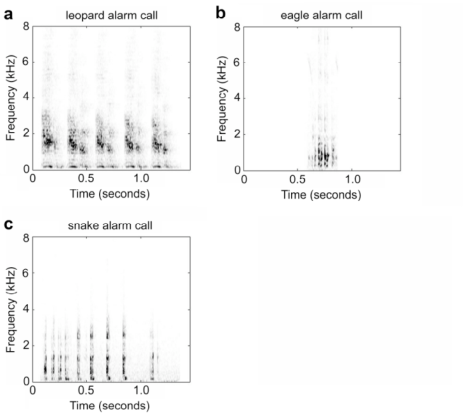

Figure 3. *Spectrograms of the three major vervet monkey alarm vocalizations. For each spectrogram, the X-axis shows time and the Y-axis shows frequency. Shown are the species-typical alarm calls produced in response to a) leopards, b) eagles and c) snakes.*

Diana monkeys live in small single male, multi-female groups. Female Diana monkeys produce eagle alarm calls in response to playbacks of both crowned eagle shrieks and male Diana monkey eagle alarm calls and produce leopard alarm calls to playbacks of both leopard growls and male leopard alarm calls (Zuberbuhler*, et al.*, 1997). Because male alarm calls and the calls of the predator that elicits them are acoustically distinct, the commonality in the females' response suggests that what is driving the response is the commonality of referent. Further evidence for this comes from an elegant priming study in which responses to the acoustic and referential features of the calls were assessed (Zuberbuhler*, et al.*, 1999). In the study, a priming stimulus was presented, followed five minutes later by a probe stimulus (see Figure 4). The prime-probe pairs fell into three categories: the baseline condition, in which the prime and the probe were identical (e.g. both leopard growls), a test condition, in which the prime and the probe differed in acoustic structure but had identical referents (e.g. a male leopard alarm call followed by a leopard growl), and a control condition in which the prime and the probe differed in both acoustic structure and referent (e.g. a male leopard alarm call followed by an eagle shriek). In the baseline condition females produced significantly fewer alarm calls to the probe than to the prime while in the control condition females responded strongly to both the probe and the prime. Habituation therefore occurs when prime and probe share both referential and acoustic features, and does not occur when they share neither referential nor acoustic features. The response of females to the test condition, in which prime and probe share referential but not acoustic features, was similar to that in the baseline condition: females produced significantly fewer alarm calls to the probe than to the prime, suggesting that they were attending to the referential features of the probe.

Mating

A wide variety of primates produce vocalizations in the context of mating. These vocalizations are typically referred to as copulation calls, and are produced immediately before, during or following copulation. In some species it is the male who produces copulation calls, in other species the female emits the vocalizations, and in a handful of species both sexes produce copulation calls (Hauser, 1996). Because of the variability in the vocal behavior surrounding copulation calls, the functional significance of this class of vocalizations has been difficult to ascertain. However, some similarities exist between species that suggest these calls are likely to play a role in mating behavior. For example, copulation calls are acoustically distinctive within the repertoire, carry information about individual identity, and are often produced at high intensities. These properties enable group members to identify and localize the caller, as well as the context. Although copulation calls have been investigated in a wide range of species, including Old World monkeys and apes, the most detailed work concerning the function of these calls comes from studies of Barbary macaques.

	Prime	**Probe**
Baseline	*Eagle shriek*	*Eagle shriek*
	Leopard growl	*Leopard growl*
Test	*Eagle alarm call*	*Eagle shriek*
	Leopard alarm call	*Leopard growl*
Control	*Leopard alarm call*	*Eagle shriek*
	Eagle alarm call	*Leopard growl*

Figure 4. *Outline of the experimental design used in Zuberbuhler et al. 1999. This experiment consists of two trials (prime/probe) for each of the three test conditions (baseline/test/control). For these experiments, the prime stimulus was presented first, followed by the probe stimulus. The logic here is that if the information provided to the subjects is similar in both the prime and probe trials, then subjects should show a response to the prime stimulus, but not the probe stimulus. If, however, the information is different, subjects should show similar levels of response in both trials.*

Barbary macaques live in social groups consisting of multiple males and females. Their mating system is typically classified as polygynous, with both males and females mating with multiple individuals. During copulation, females produce acoustically distinct copulation calls. Because these calls can be heard from several meters away, it was proposed that they could function to incite competition between males (Hamilton and Arrowood, 1978). Such competition could occur either through direct male-male competition, with the winner of a fight gaining access to a female, or through sperm competition from mating with multiple males in a short period of time. To address this issue, Semple (Semple, 1998) conducted a series of field playback experiments. Results indicated that males were more likely to approach females following the playback of her copulation call relative to controls suggesting that copulation calls functioned to alert males that she was currently in estrous. Further, when two males were in the vicinity of the playback, only the more dominant male approached. These data provided evidence for both types of competition because although males were drawn to females after hearing her copulation calls (potentially leading to increased sperm competition), dominant males gained greater access to these females than lower ranking males (consistent with male-male competition). Further experiments showed that the Barbary macaque copulation calling system consisted of another layer of complexity. Analyses showed that copulation calls produced during peak estrous were acoustically distinct from those calls produced early in the estrous cycle (Semple and McComb, 2000). Following this analysis, Semple and McComb conducted a playback experiment in which peak estrous and early estrous copulation calls were broadcast to males. Results revealed that male subjects were more likely to approach females following playback of calls produced during peak estrous than those produced early in the estrous cycle, thus confirming that the acoustic differences between calls produced at these two periods of estrous were both perceptible and meaningful to male macaques. Overall, these data provide evidence that the Barbary macaque copulation call is a salient acoustic cue that plays a significant role in modulating male mating behavior.

Caller Identity

In this section, we focus on three layers or levels of identity: individual, sex, and group. Major research questions in this area are 1) what are the necessary and sufficient acoustic features associated with an individual's acoustic signature, and 2) to what extent do listeners recognize specific individuals, their sex, or their group identity based on particular features of the signal?

Individual

It has long been known that individual identification based on an acoustic signal is technically possible—in the same way that genetics and environment combine to produce individually distinctive faces, all individuals have individually distinctive voices. However, whether a conspecific can identify an individual based purely on a vocal signal depends on several factors. One important factor is purely perceptual: the listener's auditory system simply may not be sensitive enough to detect the individual distinctiveness in a vocalization. Another factor is the specific vocal signal involved: just as some vocalizations appear to be designed to be either difficult or easy to localize (Marler, 1955), vocalizations appear to vary in their degree of individual distinctiveness. One candidate for the acoustic basis of individual recognition in primate vocal signals is the spectral patterning introduced by vocal tract filtering. The spectral peaks introduced by the vocal tract have been shown to be individually distinctive across two very different calls (coos and grunts) in the rhesus macaque (Rendall*, et al.*, 1998). The vocal tract filtering hypothesis is supported by the observation that screams, calls that do not display prominent vocal tract filtering peaks, are also less individually distinctive in playback experiments. However, other experiments in rhesus and pigtail macaques (Gouzoules*, et al.*, 1984; Gouzoules and Gouzoules, 1990) have found individual recognition with screams, raising the possibility of a different, or at least an additional, acoustic substrate for individual recognition. Another candidate for individual recognition is the degree of acoustic variability within and between calls (Fitch*, et al.*, 2002).

Regardless of the specific substrate, there are many *a priori* reasons for thinking that primates would benefit from the ability to recognize the identity of a vocalizer: 1) many primates live in dense cover and are often out of sight of group members, 2) success in the social domain often depends on support from conspecifics (particularly kin), and 3) an acoustic signal is better suited to eliciting support from social partners than a visual signal because acoustic signals can travel in 360 degrees and over large distances. Individual recognition by voice has been elegantly demonstrated in vervet monkeys.

Vervet monkey females remain in their natal troupe while males emigrate. Each troupe, therefore, consists of several groups of closely-related females. Alliances between close kin during agonistic encounters are common and have repercussions in terms of maintenance of dominance rank, access to scarce resources and reproductive success. When a juvenile vervet vocalizes during an agonistic encounter, its mother often intervenes to support her offspring. Cheney and Seyfarth (1980) took advantage of this behavior to test whether or not vervet females could recognize the vocalization of an individual juvenile. They began by locating three females whose juvenile offspring were out of sight. They then recorded the behavior of the three females before and after playback of the recruitment scream of the juvenile offspring of one of the females. They showed that although all three females responded to the playback by looking in the direction of the concealed playback speaker, the mother of the juvenile whose call had been played responded with a significantly shorter latency and longer duration (Fig. 5) than did the other two, 'control', females. Interestingly, the control females were also more likely to look at the mother after playback. These two pieces of data together suggest that vervet females are able to recognize the individual who produced a particular vocalization.

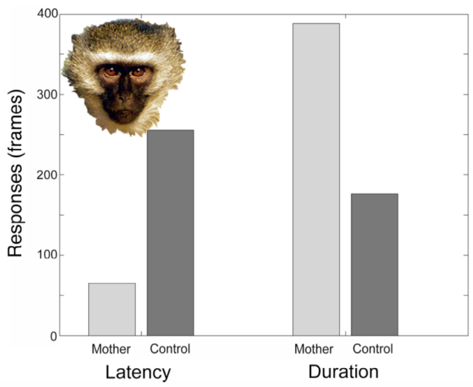

Figure 5. *Bar graph showing results from individual recognition playback experiments in vervet monkeys. In each playback, juvenile screams were played back to the juvenile's mother and two control females who also had offspring. Results show that mothers responded with a faster latency and with longer looks than control females. The y-axix plots responses in frames [18 frames/second]. Redrawn from Cheney & Seyfarth (1980).*

Similar abilities have been shown using a variety of methodologies in yellow baboons (*P. cynocephalus*), rhesus macaques, Barbary macaques (where it has been shown to emerge as early as 10 weeks of age), pygmy marmosets (*Cebuella pygmaea*), chimpanzees, grey-cheeked mangabeys (*Cercocebus albigena*), squirrel monkeys (*Saimiri sciureus*) and cotton-top tamarins (Snowdon, 1986).

Sex

As with many aspects of primate behavior, sex differences exist in primate vocal behavior. Sex differences emerge both in the overt behavior associated with vocalizations, as well as the acoustic structure of the vocalizations themselves. Producing vocalizations with sex differences may be crucial for animals such as primates that must navigate complex social systems. Being able to determine an individual's sex without having experience with that individual is likely to provide one with cues about how and whether to interact with an animal before coming into physical or visual contact with the individual. Although the acoustic differences between male and female primates are often reported, little is known about the perceptual salience and behavioral relevance of this information.

Recently, researchers have begun to address this issue using different experimental techniques. In a study of wild baboons, Rendall and colleagues (Rendall*, et al.*, 2004) recorded grunts, a close distance affiliative call. Acoustic analyses showed that the fundamental frequency and the first three formant frequencies were lower in males than females suggesting that these acoustic differences could potentially be used to determine the sex of a caller. To test this possibility, Rendall and colleagues trained captive baboons to discriminate between exemplars of male and female grunts in a psychophysical experiment. Results indicated that subjects successfully discriminated between grunts produced by males and females suggesting that this could be accomplished using the natural acoustic differences present in the vocalizations. While these data show that the animals are able to perceive a difference between male and female calls following training, they do not address whether the animals are able to do this naturally. Evidence of spontaneous discrimination is critical for making arguments about whether information about the caller's sex is used in natural behavioral interactions. This gap in our understanding was recently addressed in a study of captive cotton-top tamarins.

Cotton-top tamarins produce a species-specific vocalization called a combination long call (CLC) when separated from group members. This long distance, multi-syllabic vocalization typically elicits antiphonal calls and approach behavior from conspecifics. Acoustic analyses of CLCs showed that male calls consisted of significantly shorter syllables than female calls. To test the perceptual and behavioral salience of these acoustic differences, Miller and colleagues (Miller*, et al.*, 2004) conducted a phonotaxis experiment. In phonotaxis experiments, subjects are presented with vocalizations from two speakers situated equidistant from subjects and scored for which speaker is approached first. In the first experiment, subjects were presented with naturally produced exemplars of male and female CLCs. Subjects showed significant preference to approach female CLCs suggesting that they could discriminate between the sexes of the caller. When the syllable durations were then manipulated to be identical, subjects no longer showed this behavioral bias, suggesting that syllable duration is a critical feature in sex recognition. Building on this result, a second experiment tested whether the basis for sex differences in CLCs was due to perceptual biases in signal receivers. In this experiment, subjects were first presented with CLCs from animals of the opposite sex in which the syllable durations were manipulated to be at the high and low end of the naturally produced range. Results showed that whereas males showed a preference for female calls with the longest syllable durations, females preferred male calls with the shortest syllable durations. When the syllable durations were manipulated to be outside the naturally produced range, this preference persisted suggesting that sensory biases may impose selective pressure on the structure of CLCs.

Group membership

Similarities in the spectrotemporal properties of vocalizations within primate social groups have been shown in a variety of species: chimpanzees, Barbary macaques, pigtail macaques (*M. nemestrina*), rhesus macaques, cotton-top tamarins, and mouse lemurs (*Microcebus murinus*). These acoustic similarities are called different things by different authors: dialects, vocal signatures or vocal accommodation (Fischer, 2002). However, they all may serve the purpose of signaling current group membership. This may be particularly useful in species in which group membership is relatively fluid, or in species, such as most of the Old World monkeys, in which there are many different kin groups within a single troupe.

A group level signature has been shown in the chimpanzee's pant hoot. This vocalization, which consists of a an introductory phase of long tonal syllables, a build-up phase with shorter elements, a loud and high frequency climax phase and a short let down phase (See Fig 2, b), is a long distance vocalization used by males to maintain contact between allies. Mitani and Gros-Louis (Mitani and Gros-Louis, 1998) recorded pant hoot choruses between a variety of males in Mahale Mountains National Park in Tanzania. They observed that the pant hoots of males that chorus together are more similar to each other than when they are chorusing with other males, providing a potential cue for current alliance membership. Variation in pant hoot structure was also shown by Marshall and colleagues (Marshall*, et al.*, 1999), who described the introduction of a spectrally distinct pant hoot syllable (the 'Bronx cheer' or 'raspberry' variant) by a single individual into a captive colony of chimpanzees. Finally, Crockford and colleagues (Crockford*, et al.*, 2004), have observed variation in pant hoot structure between neighboring chimpanzee communities, but not between isolated communities. These authors suggest that groups that are within acoustic contact actively modify their vocalizations to make them distinctive, allowing community allegiance to be detectable at a distance.

However, all studies on group-specific signatures to date have been observational. It is still an open question whether these signatures are meaningful to receivers, though it seems likely, given that the tendency to produce such signatures appears to be widespread among primates. Demonstrating the salience of such signatures, however, will be challenging, as any discrimination based on a group-specific signature might also be supported by individual recognition. It will therefore be necessary to create synthetic calls in which a signature at the individual level is maintained, while the group level signature is manipulated.

Future directions

Primate senders can clearly transmit a variety of information to primate receivers. This information can range, as we have discussed, from information about the sender's location, size, or sex, to information about an external object, such as quality of food or predator type. In addition, other experiments have shown that signalers can convey information about dominance rank, degree of risk in an agonistic encounter, call bout termination and contact with another conspecific group. Given the richness of information transfer, what are the next steps in the study of primate vocal communication?

Initially primate vocal repertoires were characterized as either "discrete" or "graded". Discrete vocal repertoires contain calls whose spectrotemporal features are distinct from one another, while graded systems are those in which there are intermediate forms between many of the calls types. One problem with this sort of distinction is that a sparsely sampled (either in terms of total number of calls recorded, or type and complexity of social contexts observed) graded system will look like a discrete system. More critically, describing a system as graded or discrete assumes that the experimenters estimation of the relevant acoustic parameters matches those of the species under study. Selection of appropriate acoustic features is implicit in identifying call types and critical to asking experimentally rigorous questions. This task is complicated by the fact that primate vocalizations are extremely variable, both within and between individuals. How do we determine what variation is meaningful? Historically vocalizations have been analyzed based on features that are obvious in a spectrogram. Unfortunately, there is no guarantee that the acoustic features that are obvious to a human observer in a spectrogram are features that are behaviorally meaningful to a non-human primate (Owren and Linker, 1995). We are therefore faced with a three-fold problem: 1) what features exist in the vocalizations? 2) Of these features, which features are behaviorally relevant? and 3) Are these features perceived as discrete or graded? Addressing question 1 requires analysis techniques suitable to the high-dimensional and variable nature of primate vocalizations. Addressing questions 2 & 3 requires behavioral experiments in which identified features are tested for behavioral relevance.

Mathematical methods designed to uncover the low-dimensional structure embedded in high dimensional data have been developed in a variety of fields and some, such as multi-dimensional scaling (MDS) and principle components analysis (PCA), have been adopted by bioacousticians. However, there are two drawbacks to these methods, one in implementation and one inherent to the analytic techniques themselves. The implementation problem is that researchers usually carry out the feature extraction by hand,

and then use these handpicked features in the analysis (thus exposing the results to bias). This problem can be mitigated, however, by selecting a large number of uncorrelated features for analysis. The second problem is more critical, namely that both MDS and PCA require a large number of high quality recordings to be effective. Until recently such data sets have been rare in the primate literature, because of the difficulty of recording vocalizations in normal social contexts.

In the past there has often been a tradeoff between the quality of the recording and the naturalness of the social situation—it is no accident that some of the best studied vocalizations are either very loud, common vocalizations (like alarm calls) or calls that can be elicited by isolation (e.g. the CLC of the cotton-top tamarin or the isolation peep of the squirrel monkey). The short range vocalizations of primates living in large social networks, with the most potential for information transmission of a high degree of complexity, are often the most difficult to record and then test experimentally. To extend our investigations to the rest of repertoire, we need a method for collecting large, high quality data sets, particularly of rare and quiet vocalizations. Advances in radiofrequency transmitters, making them both smaller and more affordable, now allow the possibility of recording large numbers of calls from freely behaving animals, both in captive colonies and in the wild. The advantages of such systems are 1) high quality recordings of clearly identified callers are possible because the microphone is attached to the animal, 2) recordings can occur during all social contexts, 3) a large number of recordings can be collected automatically and 4) if all members of a social group carry transmitters, information about call sequencing and bout structure can also be collected. Such systems, in conjunction with observations of behavioral context, will allow a deeper look into nonhuman primate vocal behavior.

Finally, researchers must begin to recognize the limitations of current perceptual tests. Most playbacks elicit a simple orienting response associated with a particular reaction time and duration—the robust behavioral responses elicited by alarm calls, or the antiphonal calling to contact calls, are relatively rare. Following the lead of researchers working on other non-primate systems, including frogs, birds, and humans, single playback experiments must be extended to include habituation-dishabituation procedures, phonotaxis, inter-active playbacks, and physiological measures (e.g., heart rate, skin conductance, neural recordings) to complement orienting responses.

Natural vocal communication offers a privileged window into primate mental processes, but studies of primate vocal communication to date have focused on the transmission of relatively simple types of information. However, primates produce a richness of vocalization in a diversity of contexts. This variation suggests that a considerable amount of information is potentially encoded and decoded about the signaler's motivational and affective state and the nature of the social and ecological environment. As the field of primate vocal communication advances to include more complex types of information transmission, the study of primate vocal communication has the potential to offer insight into the cognitive substrates underlying the primate mind.

Bibliography:

Books

Bradbury, J. W. & Vehrencamp, S. L. (1998) *Principles of animal communication.*, Oxford, Blackwell

Cheney, D. L. & Seyfarth, R. M. (1990) *How monkeys see the world: Inside the mind of another species.*, Chicago, Chicago University Press

Hauser, M. D. (1996) *The evolution of communication.*, Cambridge, MIT Press

Owings, D. H. & Morton, E. S. (1998) *Animal vocal communication: A new approach*, Cambridge, Cambridge University Press

Articles in Books

Dawkins, R. & Krebs, J. R. (1978) 'Animal signals: Information or manipulation' In *Behavioural ecology* (Krebs, J. R.&Davies, N. B., eds), pp Oxford University Press

Fischer, J. (2002) 'Developmental modifications in the vocal behavior of non-human primates' In *Primate audition: Ethology and neurobiology* (Ghazanfar, A. A., ed), pp 109-125, CRC Press

Marler, P., Evans, C. S. & Hauser, M. D. (1992) 'Animal signals? Reference, motivation or both?' In *Nonverbal vocal communication: Comparative and developmental approaches.* (Papoucek, H., Jürgens, U.&Papoucek, M., eds), pp 66-86, Cambridge University Press

Owren, M. J. & Linker, C. D. (1995) 'Some analysis methods that may be useful to acoustic primatologists' In *Current topics in primate vocal communication* (Zimmermann, E., Newman, J. D.&Juergens, U., eds), pp 1-27, Plenum Press

Snowdon, C. T. (1986) 'Vocal communication' In *Comparative primate biology, vol. 2a, conservation and ecology* (Mitchell, G.&Irwin, J., eds), pp 495-530, Alan R. Liss

Articles in Journals

Cheney, D. L. & Seyfarth, R. M. (1980) Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour* 28,362-367

Crockford, C., Herbinger, I., Vigilant, L. & Boesch, C. (2004) Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology* 110,221-243

Fichtel,C. & Kappeler, P.M. (2002) Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. Behavioral Ecology and Sociobiology, 51: 262-275.

Fitch, W. T. (1997) Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America* 102,1213-1222

Fitch, W. T., Neubauer, J. & Herzel, H. (2002) Calls out of chaos: The adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour* 63,407-418

Gouzoules, H. & Gouzoules, S. (1990) Body size effects on the acoustic structure of pigtail macaque (*macaca nemestrina*) screams. *Ethology* 85,324-334

Gouzoules, S., Gouzoules, H. & Marler, P. (1984) Rhesus monkey (*macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *Animal Behaviour* 32,182-193

Gros-Louis, J. (2004) The function of food-associated calls in white-faced capuchin monkeys, *cebus capucinus*, from the perspective of the signaller. *Animal Behavior* 67,431-440

Hamilton, W. J., III & Arrowood, P. C. (1978) Copulatory vocalisations of chacma baboons (papio ursinus), gibbons (hylobates hoolock), and humans. *Science* 200,1405-1409

Marler, P. (1955) Characteristics of some animal calls. *Nature* 176,6-7

Marshall, A. J., Wrangham, R. W. & Clark, A. P. (1999) Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour* 58,825-830

Miller, C. T., Scarl, J. S. & Hauser, M. D. (2004) Sex-specific sensory biases underlie sex differences in tamarin long call structure. *Animal Behaviour* 68:713-720.

Mitani, J. & Gros-Louis, J. (1998) Chorusing and convergence in chimpanzees: Tests of three hypotheses. *Behaviour* 135,1041-1064

Rendall, D., Owren, M. J. & Rodman, P. S. (1998) The role of vocal tract filtering in identity cueing in rhesus monkey (*macaca mulatta*) vocalizations. *Journal of the Acoustic Society of America* 103,602-614

Rendall, D., Owren, M. J., Weerts, E. & Hienz, R. D. (2004) Sex differences in the acoustic structure of vowel-like vocalizations in baboons and their perceptual discrimination by baboon listeners. *Journal of the Acoustical Society of America* 115,411-421

Semple, S. (1998) The function of barbary macaque copulation calls. *Proceedings of the Royal Society, London* 265,287-291

Semple, S. & McComb, K. (2000) Perception of female reproductive state from vocal cues in a mammal species. *Proceedings of the Royal Society, London* 267,707-712

Zahavi, A. (1975) Mate selection: A selection for a handicap. *Journal of Theoretical Biology* 53,205-214

Zuberbuhler, K., Cheney, D. L. & Seyfarth, R. M. (1999) Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology* 113,33-42

Zuberbuhler, K., Noe, R. & Seyfarth, R. M. (1997) Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behaviour* 53,589-604