

Chapter 9

**AN AFFECT-CONDITIONING MODEL OF
NONHUMAN PRIMATE VOCAL SIGNALING**

Michael J. Owren¹

*Department of Psychology
Reed College*

Drew Rendall

*Department of Psychology
University of Pennsylvania*

ABSTRACT

We outline a model of nonhuman primate vocal behavior, proposing that the function of calling is to influence the behavior of conspecific receivers and that a Pavlovian conditioning framework can account for important aspects of how such influence occurs. Callers are suggested to use vocalizations to elicit affective responses in others, thereby altering the behavior of these individuals. Responses can either be unconditioned, being produced directly by the signal itself, or conditioned, resulting from past interactions in which the sender both called and produced affective responses in the receiver through other means.

In this view, the social relationship between the sender and the receiver is an important determinant of what sorts of responses can be elicited and, hence, which calls are used. For instance, a sender that is subordinate to, or otherwise has little power over a given receiver also has little opportunity to use its calls

¹Correspondence to: Michael J. Owren, Department of Psychology, 224 Uris Hall, Cornell University, Ithaca, New York 14853. Voice: (607) 255-3835; fax: (607) 255-8433; email: mjo9@cornell.edu.

as predictors of negative affective responses. It therefore relies primarily on vocalizations that have unconditioned effects. We refer to such calls as squeaks, shrieks, and screams, and propose that sounds of this general type should occur in acoustically variable streams—thereby maximizing unconditioned affective responses in the receiver while minimizing habituation effects. If the sender is dominant to the receiver, in contrast, it has ample opportunity to pair threatening calls with negative outcomes and can routinely induce and subsequently elicit conditioned affective responses. Such responses result from experiences in which the sender has produced individually distinctive vocalizations prior to attacking or otherwise frightening the other animal. As a given receiver routinely hears many such calls, the identity of the sender is the most important predictor of upcoming events and this animal's individually distinctive acoustic cues play a primary role in mediating any conditioning that occurs. Vocalizations used as conditioned stimuli must therefore carry salient, discrete cues to individual identity. We argue that individually distinctive cues based on vocal-tract filtering are best suited to this role, and refer to such sounds as sonants and gruffs.

Sonant and gruff calls should also be used by both dominant and subordinate senders in order to elicit positive conditioned responses. Such calls might occur, for instance, when an animal approaches a subordinate individual for grooming and attempts to decrease its fear during the approach. A subordinate animal should pair such calls with grooming or other positive outcomes when interacting with a dominant, thereby being able to elicit positive conditioned responses in that individual on other occasions.

The affect-conditioning model suggests that nonhuman primate vocalizations need not have “meaning” in the sense of transmitting referential information from a sender to a receiver. This approach may thereby provide a unified conceptual framework in which a number of issues related to the structure of vocal repertoires, acoustic features of calls, repetition and variability in vocalizations, and the evolution of such signals can be understood. In emphasizing the ability of the sender to mold the affective state of the receiver through simple conditioning processes, the model underscores the inherent asymmetry of these two roles. This imbalance is suggested to be an important factor in the evolution of more sophisticated cognitive mechanisms, which allow receivers to modulate their own behavioral responses to calls by evaluating the significance of such signals in a flexible, context-dependent fashion.

INTRODUCTION

The vocal behavior of nonhuman primates (hereafter primates) has been examined from a variety of perspectives (e.g., Todt, Symmes, & Goedecking, 1988; Zimmermann, Newman, & Jürgens, 1995), producing progress on a range

theoretical issues. Within this diversity, however, a smaller number of themes have tended to recur. For instance, a number of studies have been geared toward showing that primate calls can be referential—encoding information that is transmitted from sender to receiver. It has been of particular interest to demonstrate that the referents in question can be objects, events, or circumstances from the external environment (see Gouzoules, Gouzoules, & Ashley, 1995, and Cheney, 1996, for recent reviews). Such work has led to important advances in understanding animal cognition, helping to uncover both impressive capabilities and unexpected limitations in various species (e.g., Cheney & Seyfarth, 1990). However, the excitement over evidence of human-like symbolism in the communication of both primates and other animals has also distracted attention from other important aspects of signaling (e.g., Owings, 1994).

On the one hand, any approach that helps create a common framework for understanding psychological processes in humans and nonhumans is to be encouraged. As the prevailing paradigm for understanding human cognition is based on representation and processing of information, this concept represents a powerful tool that should be applied in animal work as well. On the other hand, the notion of information as a commodity that moves from sender to receiver is obviously metaphorical. Information does not literally reside in the energy of a signal, but represents an emergent property of the combined attributes of the individual producing the signal, the individual perceiving the signal, and the circumstances under which the signal is emitted (e.g., Smith, 1977; also see Owings & Morton, this volume). Approaches that capture other aspects of this complex interactive process are therefore also needed. We suggest, for example, that vocal communication must have originated in unspecialized responses occurring to unspecialized energy transmissions. If so, concepts like information and representation would not apply and it is not clear how information-based communication could evolve from such circumstances. We therefore see a particular need for a framework that includes more fundamental principles—accounting for aspects of communication that preceded information-processing, came to be information processing, and arguably now coexist with information processing.

That framework is not presented here. However, we do outline a model that attempts to account for the basic design and function of primate vocalizations by treating the sounds as stimuli that senders use in order to elicit simple affective responses in receivers. The concepts and terminology involved are borrowed from learning theory, and are meant to capture aspects of the communication process that are not well-characterized by terms like cognition and representation. This approach is consistent with Mason's (1979) distinction between “wanting” and “knowing,” and Owings' (1994) use of “conation” to designate the motivational and emotional processes that impel and guide behavior, but are not “cognition.” Note that the contrast intended is not equivalent to the classic differentiation of *referential* from *motivational* signals. Whereas the

former refers to encoding of relatively specific external designata, the latter analogously includes internal designata, for instance representing the signaler's internal states (see discussion by Marler, Evans, & Hauser, 1992). Both terms are therefore rooted in an informational perspective, which we, initially at least, wish to avoid.

Overview

Our model rests on a number of observations and proposals concerning the social lives of primates, a hypothesized distinction between vocalizations that function to elicit unconditioned and conditioned affective responses, respectively, and the implications of vocal-tract-based sound production for the forms of such signals. For clarity's sake, we first describe the model briefly. Some general issues in primate vocal behavior are then discussed, setting the stage for more detailed exploration of conditioning and acoustic cues to individual identity. We then describe the model, both conceptually and by example, and present some of its implications for the general issues raised in the early going.

Throughout the chapter, we broadly refer to the vocal behavior of "primates." Nonetheless, we recognize that significant variation exists in many aspects of the production, perception, and function of vocalizations among the more than 200 extant primate species. Furthermore, while our proposals have been inspired by a general pattern of social and vocal characteristics exemplified by macaques and baboons, important variation occurs among the species and subspecies of these groups as well. However, as presenting the model requires relatively detailed consideration of some important aspects of both learning theory and sound production, this generic sort of approach seems preferable. We have therefore also chosen to rely on selected and illustrative examples rather than providing a more comprehensive data review, but go on to describe a number of specific, testable predictions.

Characteristics of the Primate Species of Interest

The model is being proposed for species with the following general characteristics. First, the animals live in an environment that affords close visual and auditory contact among individuals. Examples include open or lightly forested areas. Second, the animals live in large, complex, and long-lived social groups that include multiple adult males, adult females, subadults, and offspring. The social relationship of any two individuals is therefore shaped by repeated encounters that routinely occur in the course of everyday activity. Third, stable social hierarchies are present, such that these interactions are marked by dominance-related behavioral asymmetries. Fourth, animals are capable of recognizing

group members (and others) both by their appearance and voice characteristics. Finally, the animals exhibit a complex vocal repertoire that includes tonal and noisy sounds, a range of typical production-amplitudes, significant variability in call acoustics within and among individuals, and variability in the calls used in any given circumstance.

Principles of the Affect-Conditioning Model

Vocalizations Elicit Affective Responses

We adopt the general position that the ultimate function of communication is to influence the behavior of another individual. While such influences can be effected in a variety of ways, vocalizations appear particularly well-suited for this purpose in that they can be used to elicit affective responses in receivers. These responses are hypothesized to benefit the sender by priming or biasing the receiver to behave in a way that is compatible with the caller's best interests. These affective effects occur as unconditioned responses, conditioned responses, or some combination of the two. One potentially important unconditioned response is the simple affective quality that a vocalization may have due to general characteristics of the mammalian auditory system. In other words, some calls are proposed to be inherently noxious or pleasant based on phylogenetically ancient auditory processes that are probably shared by many primates and other mammal species. In addition, unconditioned and broadly differentiated affective responses may occur to various calls due to more recent specializations that may be species- or genus-specific. For instance, calls used in affiliative contexts by a given species are likely to elicit positive unconditioned responses, while negative affect can be expected in response to calls typically produced in agonistic contexts.

Our strongest claim, though, is that conditioned affective responses play a central functional role in primate calling. Vocalizations are well-suited for this kind of learning as they are discrete and perceptually salient stimulus events that are controlled by the sender. The potential value of affective conditioning is proposed to depend on the nature of the interaction between the sender and receiver, as well as their respective positions in the social hierarchy. In the course of a social interaction involving two individuals, both the more dominant and the more subordinate animal can produce calls that elicit conditioned responses. However, the individual that is dominant in a given encounter inherently has greater control over the outcome of this interaction than does the other. As a result, the dominant animal can routinely pair its calls with other actions that elicit significant unconditioned affective responses in the subordinate. Such pairings produce conditioning, which the caller can thereafter use to elicit learned affective responses in this other animal in both affiliative and agonistic

circumstances. The subordinate individual has less opportunity to shape the outcome of an interaction, especially in the case of agonistic encounters. It is therefore proposed to rely on unconditioned effects of calling in such circumstances, while exploiting both conditioned and unconditioned responses in affiliative situations.

Acoustic Cues to Individual Identity Mediate Conditioned Affective Responses

Based on learning theory, it is expected that acoustic cues to individual identity are important mediators of conditioned effects occurring in receivers. As these responses are shaped by the history of interactions occurring between any two animals, the identity of a caller is a crucial determinant of the significance of a vocalization for a given receiver. As a result, the acoustic cues to individual identity that occur in the context of one call-type or another are more predictive of upcoming events than is the occurrence of the call in and of itself. These cues therefore come to elicit conditioned affective responses.

Principles of acoustics and vocal production suggest that various primate vocalizations afford different opportunities for carrying individually distinctive cues to caller identity. The most stable, consistent cues are proposed to be the features related to vocal-tract filtering, meaning characteristic amplification and attenuation effects produced by cavities located above the larynx. In order for such cues to appear, however, a vocalization must include broadly distributed spectral energy that reveals these effects in detail. Both low-frequency, tonal calls with rich harmonic structure and noisy vocalizations of intermediate amplitude appear to be well-suited to this function. These sounds are referred to as *sonants* and *gruffs*, respectively. In contrast, high-frequency tonal calls and high-amplitude, noisy vocalizations appear to be poorly suited to showing vocal-tract filtering effects. These sounds are referred to as *squeaks*, *shrieks*, and *screams*.

Functional Constraints Have Shaped the Acoustic Design of Vocalizations

If vocalizations function to elicit unconditioned and conditioned responses, and conditioning is mediated by cues to individual identity, it follows that the acoustic design of a primate vocal repertoire reflects the constraints imposed by these factors. In eliciting unconditioned responses, animals can be expected to produce bouts of acoustically potent vocalizations, with both repetition and variability shown in the call stream. In contrast, sounds whose primary function is to elicit conditioned responses are expected to show design features that promote conditioning and take advantage of any such learning that has already been instilled. Inclusion of discrete, salient cues to individual identity is paramount, which we propose to be provided primarily by spectral-patterning effects related to vocal-tract filtering.

SOME ISSUES OF INTEREST CONCERNING PRIMATE VOCALIZATIONS

Setting the stage for more detailed examination of both the principles and implications of our approach, a number of questions concerning primate vocalizations will now be raised. Although many different elements of such signaling have been discussed over the years, only a few integrative theories have emerged in this area. As the affect-conditioning model purports to identify some general principles of primate calling, we need first to touch on and then later return to various aspects of this behavior.

Signal Function

A fundamental part of studying communication is to determine the function of the signals being used. In work on nonhumans, this topic has spawned fruitful, but sometimes contentious and polarizing debate (see Hauser, 1996, for a recent review of these issues). One important question was outlined above—how to characterize the content or meaning of signals. A second, related question has been whether signals are inherently cooperative, involving information sharing, or are selfish in nature, primarily benefiting the sender. While a variety of frameworks and terminologies have been proposed for understanding these two issues (e.g., Hauser, 1996; Owings, 1994), important commonalities occur among the various positions. For instance, both referential and motivational approaches to signal meaning implicitly involve an informational perspective, although either need imply that signaling is inherently altruistic or even “honest” (e.g., Cheney & Seyfarth, 1990; Hinde, 1981). Efforts to distinguish between sharing and manipulation in communication have produced several convergent proposals, each emphasizing the selfish interests and active roles of both parties involved in a signaling event. For example, senders and receivers have been characterized as being “manipulators” and “mind readers” (Krebs & Dawkins, 1984) or “managers” and “assessors” (Owings, 1994; Owings and Morton, this volume), respectively.

We suggest that the diverse positions taken in these debates can be reconciled by starting from the fundamental assumption that in a well-established, species-typical communication system, signaling occurs because it has in the evolutionary past provided a net benefit to the fitness interests of the sender by influencing the immediate or later behavior of the receiver. From this perspective, it is inevitable that a number of strategies for achieving such influence will have evolved, with corresponding variety in details of signaling. For instance, a given repertoire is likely to include some calls that are primarily native in function, as well as others that are better described as engaging

cognitive systems. Depending on the circumstances, the influences that senders are able to exert may also be either beneficial or costly to receivers. To the extent that the effect of the sender's behavior is detrimental to the overall fitness of the receiver, however, natural selection will favor adaptations that decrease those costs. In this chapter, we focus primarily on the interests of the sender.

Acoustic Features of Calls and Repertoire Structure

A second important topic is why the vocal repertoires of various primates take the forms they do. A number of relevant principles have been identified in this regard, including constraints imposed by the transmission characteristics of the environment in which calls are used (e.g., Brown, Gomez, & Waser, 1995), possible relationships among acoustic gradedness, complexity of the information conveyed, and the degree to which signals in other modalities complement the acoustic event (e.g., Green & Marler, 1979; Marler, 1975), and a general relationship between the acoustics of calls and sender state (Morton, 1977, 1982). However, these and other observations, hypotheses, and principles (see for instance Fitch & Hauser, 1995) leave unaddressed many basic questions that might be asked by naïve observers of monkeys and apes. One such question is why, in some instances, calls with particular acoustic features seem to be used similarly by many primates, whereas in other cases acoustically similar calls may be used differently. Within a species, some calls seem to occur only in quite specific circumstances, while others are produced in a variety of situations. Furthermore, two acoustically dissimilar calls might be used in the same contexts, whereas other, more similar calls are used in differentiated contexts. Overall, there is no general framework that can account for the bewildering variety of acoustic form and repertoire design among primates.

Repetition and Acoustic Variability in Calling

A third, related issue concerns the use of multiple vocalizations. While calls sometimes occur singly, bouts of calling are very common. In these cases, the same call may occur a number of times. In other cases, the acoustic features of successive calls may change, either gradually or abruptly. When acoustic variation occurs, the animal may produce vocalizations that seem confined to a single identifiable call-type, jump back and forth between categories, or grade from one category to another. Complications that can arise are discussed by Green and Marler (1979), and are concretely illustrated in Green's (1975) description of the vocal repertoire of Japanese macaques (*Macaca fuscata*). However, broadly applicable principles that make sense of this overall puzzle are in short supply.

Cues to Individual Identity

A fourth question is what role is played by acoustic cues to individual identity in vocal communication processes. Evidence of either discrimination among animals or explicit recognition of individuals is available from several species (e.g., Snowdon, 1986; Rendall, Rodman, & Emond, 1996). While a critical review of the evidence does not appear to us to warrant a blanket assumption that individually distinctive acoustic cues occur in all calls of a given vocal repertoire, both discrimination and recognition of callers seem likely to occur for some calls in many, if not all species. It is not clear, however, what functional role is played by acoustic cues to individual identity, particularly among primates whose habitats allow group members to readily see one another in many of the typical contexts in which vocalizations are produced.

A common explanation for discrimination or recognition of individuals based on acoustic cues is that receivers can then respond to distress-related calling. For instance, primate mothers are proposed to be particularly attentive to distress vocalizations produced by their offspring, a claim that has been supported to varying degrees in several species. Adult primates, particularly females, are also suggested to make use of individually distinctive acoustic cues in calls in coming to the aid of related individuals or unrelated allies involved in agonistic social encounters. This proposal is consistent with the more general observation that a primate's behavior toward others is strongly shaped by kin relationships and interaction histories (see Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987; Cheney & Seyfarth, 1990). As yet, however, relatively little quantitative evidence is actually available from even the best-studied species showing that adult animals that are out of visual contact with genetically related group members consistently do respond to such distress calls in the absence of other information.

A PROPOSED ROLE OF CONDITIONING IN ANIMAL SIGNALING

Principles of Conditioning

The most basic proposal of our model is that individual primates use vocalizations to produce affective responses in conspecific receivers, thereby influencing the subsequent behavior of those animals. This claim is elaborated using concepts from learning theory concerning elicited (involuntary) responses, and changes in those responses occurring through habituation and Pavlovian (classical) conditioning. Relevant principles and data can be reviewed in any good textbook on learning (e.g., Domjan, 1993; Schwartz, 1989). The vocabulary used here is the traditional one. However, contemporary theorists emphasize that this terminology more accurately describes procedural aspects of the learning

process than its underlying mechanisms. Those mechanisms, in fact, appear to be indistinguishable from the sorts of processes implied by typical concepts from cognitive theory, particularly the notion of representation (discussed by Rescorla, 1988a, 1988b; see also Turkhan, 1989, and the commentaries therein). As the sorts of learning involved in habituation and Pavlovian conditioning are ubiquitous among animals and occur in even the simplest nervous systems, these principles appear to provide a promising starting point for eventually understanding “representation” and “processing” of information at all levels of neural organization. We believe that both the terminology and the perspective adopted here are inherently compatible with, rather than exclusive of, other learning-related or information-based formulations. Our specific hope is that by first differentiating between possible conative and cognitive roles of vocalizations, we may actually be contributing to the development of a larger framework in which these functions can be integrated.

Habituation

Habituation refers to the learned decrease in responsiveness that is typically shown by an organism when repeatedly exposed to a stimulus. The underlying process is explicitly distinguished from sensory adaptation and muscular fatigue, both of which produce response decrements but are not caused by changes in the central nervous system. In studying habituation, these alternative interpretations are therefore ruled out by showing that the decrease produced is specific to the response in question and that the behavior can immediately recover if a new stimulus is introduced. Following habituation to a particular stimulus, generalization of the effect to other, similar stimuli often occurs. Habituation is also known to involve separable short- and long-term effects on the elicited response.

Pavlovian Conditioning

Pavlovian conditioning takes place when the occurrence of a biologically significant event is reliably preceded by some other discernible stimulus. As a result of experiencing the relationship between these two events, organisms come to respond to the first, *conditioned stimulus* as if it predicts the occurrence of the more important, *unconditioned stimulus*. Through learning, then, the conditioned stimulus begins to elicit *conditioned responses* that occur before, and in the absence of the unconditioned stimulus. While these responses often resemble one or more of the *unconditioned responses* that are elicited by the unconditioned stimulus, they need not do so. Instead, these conditioned effects are best characterized as anticipatory reactions that allow the organism to respond more adaptively to the upcoming event.

Pavlovian conditioning has been demonstrated in many aspects of organismal function, and affective responses play a central role in such learning. For

instance, conditioned motivational and emotional responses have been proposed to be important in guiding an organism's instrumental, or voluntary behaviors. In one frequently used laboratory paradigm, the *conditioned-emotional-response* procedure, hungry rats are first trained to repeatedly press a lever in order to obtain food rewards. A light or tone is then presented as a conditioned stimulus, followed by an aversive electric shock. After a few such trials, lever-pressing slows or ceases whenever the fear-inducing conditioned stimulus is presented, and this suppressive effect is used as a measure of the learning that has occurred. Another common testing situation involves hungry pigeons intermittently given access to food. In this *sign-tracking* procedure, food presentations are preceded by illumination of a small, circular key. Although not required to do so, the birds typically come to quickly approach and peck the key when it is lit, treating the conditioned stimulus as if it were the unconditioned stimulus. In both of these prototypical paradigms, then, associations formed between a predictive stimulus and a biologically significant event arguably elicit affective responses in the subjects, thereby shaping their voluntary behavior.

Depending on the particular stimuli and organism involved, the number of trials required for Pavlovian conditioning to occur can range significantly. However, contemporary studies tend to emphasize learning that can be demonstrated within a few, or a few dozen trials. In general, the *associative strength* said to accrue to a conditioned stimulus is directly related to the predictive value of this event vis-à-vis the unconditioned stimulus. Therefore, the strongest conditioning occurs when an unconditioned stimulus is always preceded by the conditioned stimulus, and neither stimulus occurs otherwise. Nonetheless, even modestly predictive relationships between the two stimuli produce some learning. In general, conditioning occurs more readily when the conditioned stimulus is discrete rather than diffuse, and when it is more, rather than less, perceptually salient to the organism in question. The *context* in which learning takes place can also be a critical factor, as associative strength is normally divided among all the predictive stimuli present. As a result, more associative strength accrues to a conditioned stimulus when it is uniquely predictive than when it is partially or wholly redundant with other cues. If the stimulus has predictive value across a number of different contexts, stronger conditioning occurs. Conversely, differentiated responses can readily develop to the same conditioned stimulus if that cue predicts different outcomes when appearing in two or more distinct contexts. Thus, the significance of a conditioned stimulus can be context-dependent, producing requisitely different responses.

A Role for Learning Theory in Naturally Occurring Animal Behavior

Concepts related to elicited responses and learned changes in those responses are applicable to many aspects of naturally occurring animal behavior.

The potential value of such applications was noted in Hinde's (1966) integrative approach to behavior, which explicitly attempted to bring laboratory-based learning principles to bear on questions and issues in ethology. An important subsequent development was the discovery by Garcia and others (e.g., Hinde & Stevenson-Hinde, 1973) that so-called "general" learning processes like Pavlovian conditioning do not operate uniformly across the conditioned and unconditioned stimuli experienced by a given species. Instead, it was found that conditioning can proceed either quickly or slowly (or not at all), depending on the particular stimuli used. Therefore, while conditioning-related phenomena occur widely among animals, it became clear that the mechanisms involved have also been strongly shaped by the particular learning needs of each species. Classic work followed in a number of areas (e.g., Marler & Terrace, 1984; Gould, 1986; Bolles & Beecher, 1988), demonstrating inherent connections between laboratory-based learning principles and naturally occurring behavior.

Overall, though, these principles have more often been used as methodological rather than as theoretical tools in investigating ethologically relevant capabilities and behaviors. For instance, conditioning-based preparations have been routinely used to probe sensory functions, perceptual processing of communication signals, and various aspects of cognition in animals (see reviews by Cynx & Clark, in press; Stebbins & Berkley, 1990; Roitblat & von Fersen, 1992; Wassermann, 1993). Recently, some field researchers have also taken advantage of habituation effects occurring to repeated stimulus presentations in testing hypotheses about processing occurring at other levels. One technique has been to examine transfer of habituation to novel calls or callers following repeated presentation of sounds in order to better understand signal meaning (e.g., Cheney & Seyfarth, 1990). Somewhat surprisingly, then, the role that habituation may play in the many situations in which animals themselves repeatedly produce calls has not been explored.

However, some work has directly demonstrated the potential importance of conditioning processes in natural behavior (reviewed by Domjan, 1992; Domjan & Hollis, 1988). Hollis (1984), for instance, found that male blue gourami fishes (*Trichogaster trichopterus*) housed in an aquarium were more successful in defending territories when the arrival of a conspecific intruder was signaled using a discrete, salient stimulus than in the absence of this predictive event. Similarly, Hollis, Cadieux, and Colbert (1989) found that the male was more likely to show courtship behavior if the arrival of a female was signaled than if the female appeared unexpectedly. In both cases, conditioned preparatory responses in the male evidently allowed it to respond more quickly and effectively to the new situation.

Pavlovian Conditioning in Stomatopod Behavior

Work by Caldwell and his colleagues (reviewed by Caldwell, 1986) provides a potential example of the processes we propose to be important in primate

vocal signaling. Although conditioning concepts were not invoked in these studies, Caldwell's investigations of stomatopods (mantis shrimp) of the genus *Gonodactylus* demonstrate the role that Pavlovian conditioning may play in the ability of one animal to directly influence the behavior of another using individually distinctive signals. These stomatopods were shown to employ both threat displays (termed *meral spread*) and physical attack (blows delivered using a raptorial appendage) for territorial defense of crevices in preferred habitat. Further, Caldwell proposed that clumped distribution of suitable crevices and stability in territory ownership resulted in repeated, agonistic encounters among particular animals. Individual discrimination based on distinctive odor cues was demonstrated, and might also occur through visual cues presented during threat displays.

Caldwell found the meral spread to reliably precede physical attack when a resident stomatopod defended its territory against an intruder. As both the olfactory and visual cues that occur in this situation are evidently predictive of subsequent physical blows, we propose that conditioning takes place. Specifically, individually distinctive cues are paired with a biologically significant outcome, thereby potentially allowing the sender to elicit affect-like responses in the receiver during subsequent encounters between the two animals. In other words, in later interactions a sender becomes more likely to be able to use its odor cues and meral display alone to repel that particular intruder, having paired these stimuli with one or more physical blows during previous encounters.

A test of this interpretation is provided by molting-related behavior observed in these animals. During the molting stage, the stomatopod's raptorial appendage becomes ineffective as a weapon and the animal is therefore vulnerable to physical attack. During this phase, territory-holders can only use the meral display to repel intruders, and the latter become requisitely more successful in evicting residents from crevices. The key finding for our purposes is that in the days immediately preceding the molting phase, Caldwell found that residents increased the rate at which meral displays were followed by physical attack. The display was then used at elevated rates during the subsequent period of vulnerability, when it did not in fact signal impending attack. In these cases, the display was found to be more effective in fending off opponents if it had previously been paired with blows from the raptorial appendage.

Caldwell described these findings in terms of "bluffing" and "reputation." We suggest that these stomatopods are in essence conducting Pavlovian conditioning trials in which individuals pair their distinctive olfactory and visual cues with physical blows delivered to the opponent. Although Caldwell did not investigate specific pairing of odor cues with attack, it was reported that individual stomatopods in the premolting phase often pursued a fleeing opponent to deliver additional blows. As the contest had already been won in such an instance, the act of leaving the crevice served no evident immediate purpose for the resident and compromised its safety. However, such behavior arguably

provides a powerful means of promoting further learning through additional pairings of the conditioned and unconditioned stimuli experienced by the intruder.

Extending Conditioning Principles to Communication

Unconditioned Responses

Two forms of signaling in which the signal itself acts as an unconditioned stimulus will be distinguished. In the first case, the signal elicits affective responses through relatively direct effects on the sensory system of the receiver. In the acoustic modality, then, we propose that due to general properties of the mammalian auditory system, a stimulus can elicit positive or negative reactions. We expect that negative responses are particularly common and are tied to acoustic characteristics like overall amplitude and noisiness. These hypothesized effects are illustrated by crying in human infants, some forms of which are reported to be extremely aversive to human observers (e.g., Zeskind & Lester, 1978; see also Halpern, Blake, & Hillenbrand, 1986). Other acoustic dimensions of signals may also have significant unconditioned effects. For example, exaggerated pitch contours typically found in the speech of human caretakers to young infants (e.g., Fernald, 1992) have been proposed to increase, decrease, or maintain arousal levels in these receivers, depending on the particular frequency-modulation pattern involved (Papousek, Papousek, & Symmes, 1991). Corroborating evidence has been found in laboratory-based learning studies using both natural and synthetic stimuli (e.g., Kaplan & Owren, 1994; Kaplan, Goldstein, Huckleby, Owren, & Panneton Cooper, 1995), and infants have also been found to explicitly prefer listening to voices that show arousing modulation patterns (e.g., Fernald & Kuhl, 1987; Werker & McLeod, 1989).

Signals are also arguably likely to elicit unconditioned responses as a result of species-specific selective histories. In another example from human behavior, laughter has been found to elicit characteristic affective responses. When repeatedly exposed to a brief laughter recording, for instance, listeners initially demonstrate positive affect, often laughing themselves. After a few presentations, however, the sound becomes an irritant, eliciting negative affect (e.g., Provine, 1996). The rapidity of this change suggests that neither of these affective reactions results from simple sensory responses per se. Among nonhumans, species-typical signals like alarm calls are found to reliably elicit alerting or arousal responses, even in the absence of previous experience with those signals. In primates, for instance, while well-organized responses to conspecific vocalizations typically emerge later in development than do adult-like production and usage (e.g., Seyfarth & Cheney, 1997), young animals react to various species-typical sounds well before emitting those calls themselves or responding appro-

priately to them. For instance, before acquiring the differentiated response patterns shown by older offspring and adults, a very young vervet (*Cercopithecus aethiops*) hearing an alarm call typically responds by looking or running toward its mother. While other factors like visual cues may be important here as well, early emergence of affectively toned unconditioned responses (like fearful startle to alarm calls) would provide an excellent foundation for subsequently acquiring more specific response patterns.

Conditioned Responses

The occurrence of a particular signal may also be predictive of a significant upcoming event, and therefore function as a conditioned stimulus. For instance, even in species that are not capable of individual discrimination or recognition, the occurrence of “anonymous” signals that are correlated with subsequent agonism or affiliation can arguably come to elicit learned responses. A similar rationale holds if species members can discriminate or recognize one another, but use signals in which individually distinctive cues are absent. Overall, however, conditioning should accrue most quickly to the individually distinctive features of a signal. As described, these are the cues that are likely to be the most predictive aspect of the signaling event for a particular receiver. We therefore expect that these features play an important role in the signaling systems of animals that are able to discriminate or recognize other individuals and experience repeated interactions with them.

Applications to Primates

Most primates exhibit exactly this lifestyle—individuals typically live among familiar conspecifics that are encountered numerous times each day. The majority of primate groups also exhibit social hierarchies, and any animal that is dominant to another can strongly affect that individual’s everyday existence. In species like macaques and baboons, dominant individuals can routinely administer painful bites and blows to subordinates. Violent and intimidating behavior by dominant animals induces strong arousal and fear in others, and lower-ranking group members are frequently observed to avoid contact with higher-ranking ones. They cringe or move away when the dominant animals approach, often seem to avoid drawing attention to themselves, and are easily supplanted from food and water, grooming partners, or resting places. Subordinates also readily respond to both visual and vocal signals, which dominant animals can use to alter the behavior of lower-ranking group members with minimal energy expenditure. Although physical prowess and support from kin or other allies are important in maintaining social rank, energy-intensive physical contests occur much less frequently than do signals like stares, facial expressions, and calls.

We suggest that in addition to unconditioned affective responses induced by such signals, conditioned responses play an important, and perhaps primary role. These kinds of responses can be expected based on a history of interactions between the sender and receiver, or from instances in which the receiver has observed interactions between the sender and other animals. However, the significance of this sort of signal is also critically dependent on the relationship between the particular sender and receiver involved. For instance, while an individual routinely experiences interactions with higher-ranking animals in which threatening signals may be followed by pain and fear, signals produced by lower-ranking group members are not reliably predictive of such outcomes. Therefore, the individually distinctive cues that are embedded within a display or a call play a special role in determining their predictive value.

Vocalizations appear to be particularly well-suited for use as conditioned stimuli in this kind of learning process. First, they are salient, discrete events with clearly marked onsets and rapid energy fading. This form of signaling is therefore almost perfectly designed for the prototypical Pavlovian conditioning process in which a well-defined stimulus is associated with a biologically significant outcome. In fact, the same argument is applicable to short-lived visual signals like facial expressions. Laboratory-based studies suggest that as brief, discrete events, both kinds of signals should be inherently more effective as conditioned stimuli than more diffuse or longer-lived signals that have requisitely less predictive precision. Second, vocalizations are controlled by the sender and are difficult for receivers to avoid. While facial expressions are also controlled by the sender, the receiver must attend to these signals if they are to be effective. Among primates, subordinate animals often avoid visual signals given by higher-ranking group members by “studiously” looking in some other direction.

Overall, we believe that a conditioning-based framework like this one provides a useful alternative to an information-based perspective on the communication process. However, due to the proposed role of individually distinctive cues in eliciting conditioned responses in others, any constraints that species-typical production mechanisms place on the form of such cues are also likely to be very important in understanding a given signaling event. In the next section, vocal production mechanisms in primates are examined in detail.

ACOUSTIC CUES TO INDIVIDUAL IDENTITY IN PRIMATE VOCALIZATIONS

Calls produced by primates are often assumed to be individually distinctive, and there is significant empirical evidence to support this conclusion (e.g., Snowdon, 1986; Rendall et al., 1996). However, the data are also limited in

scope, and we argue in this section that not all call-types provide equivalent opportunities for discriminable individual variation to occur. For the species targeted in this chapter, we propose that a basic distinction exists between cues related to vocal-tract resonances and other characteristics of calls. While a highly detailed discussion of the acoustical and sound-production principles underlying this claim is beyond the scope of the present work, more detailed reviews of these topics are readily available (e.g., Fitch & Hauser, 1995; Owren & Linker, 1995; Schön Ybarra, 1995).

Vocal Production Processes

Call production in primates (and in mammals generally) is shaped by physical characteristics of the vocal tract. As illustrated by the schematic, midsagittal drawing of a rhesus monkey (*M. mulatta*) head shown in Figure 1, two critical components can be distinguished. The *source energy* of a typical call is derived from vibrating the *vocal folds*, which are enclosed in the larynx. This energy excites the cavities located above the larynx, which comprise the *supralaryngeal vocal tract*. These cavities shape the spectral characteristics of the source energy in accordance with its input-output relation, or *transfer function*—the effect we have referred to as vocal-tract filtering. While recent work has demonstrated both similarities (Fitch & Hauser, 1995; Owren & Linker, 1995) and important differences (Schön Ybarra, 1995) between vocal production in humans and primates, this two-component, *source-filter* perspective is applicable in both cases.

The process involved in producing a complex tonal sound is illustrated in Figure 2. This figure is based on human speech production parameters, but is applicable to primate calling as well. In the particular case shown, the vocal folds are in regular, or *periodic* vibratory motion, and by opening and closing allow puffs of air to emanate from the *glottis* (the opening between the vocal folds). The glottal airflow waveform illustrated in Figure 2(a) reflects an opening and closing rate of 100 times per sec, which corresponds to a *fundamental frequency* (F_0 or *first harmonic*) of 100 Hz in the resulting sound. Vibratory movement in the vocal folds produces signals whose frequency spectra include energy not only at the F_0 , but also at higher harmonics—spectral components occurring at integer multiples of the base rate of vibration. Figure 2(b) shows an idealized source-energy for a vowel sound. The harmonics are high in amplitude, but energy declines exponentially with increasing frequency.

The cavities and tissues of the supralaryngeal vocal tract strongly influence the glottal waveform through their resonance (amplifying) and antiresonance (damping) properties. Vocal-tract resonances, or *formants*, reinforce energy in specific frequency ranges. Figure 2(c) shows the transfer function of a relaxed human vocal tract, a “neutral” configuration whose filtering characteristics

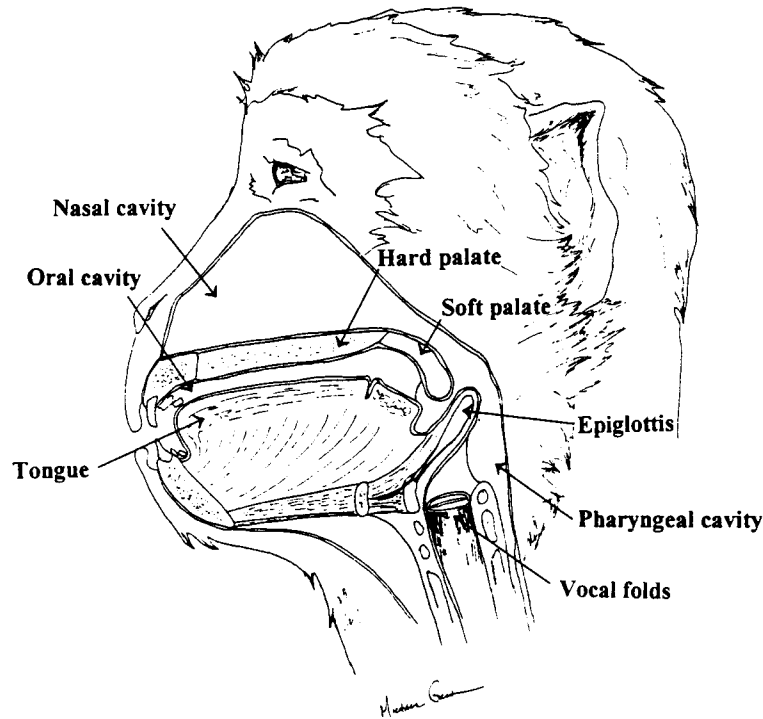


Fig. 1. A schematic, midsagittal view of a rhesus monkey vocal tract. Anatomical structures important to the basic sound-production process are labeled. Drawing by Michael Graham. After Rubin and Vatikiotis-Bateson (in press), used with permission.

closely resemble those evident in chacma baboon (*Papio cynocephalus ursinus*) grunt calls (Owren, Seyfarth, & Cheney, 1997). The characteristic frequency spectra of both vowels and these baboon grunts are marked by 4 to 5 prominent spectral peaks occurring below 5 kHz, each of which results from a vocal-tract resonance. The overall spectral pattern formed by these peaks plays a major role in determining the auditory quality of the sound. As illustrated in Figure 2(d), then, vocalization features reflect characteristics of both the source energy and vocal-tract filtering involved in the sound-production process. Important perceptual attributes like pitch, tonality, and timbre all result from the interaction of these source and filter components. Formants can also affect *noisy* sounds, whose underlying source waveforms lack periodic (cyclical) energy patterning. Such *aperiodic* source energies show a concomitant lack of orderly, patterned energy distribution in the frequency domain. Spectral patterns may nonetheless be imposed by the supralaryngeal vocal tract, as is illustrated by formant effects

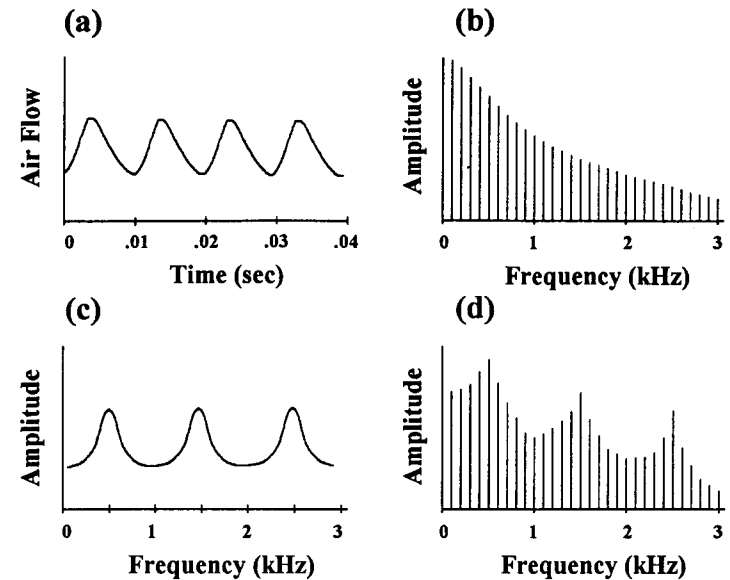


Fig. 2. An illustration of the vocal production process. (a) Periodic opening and closing of the vocal folds produces periodically varying glottal airflow. (b) The 100-Hz rate of vocal fold vibration in the glottal signal exhibits a harmonically structured spectrum with maximal energy at this fundamental frequency and its integer multiples. Energy at successive harmonics decreases exponentially. (c) A transfer function showing the resonances of a 17.5-cm vocal tract in neutral position, modeled as a straight tube closed at one end. (d) The resulting rich, tonal sound reflects both the harmonically related energy of the source and resonance characteristics of the subsequent filter. From Owren and Linker (1995), used with permission.

occurring in the spectra of whispered vowels. Humans produce these sounds using low-amplitude, broadband glottal turbulence as an energy source rather than periodic vibration.

Comparing Vocal Production in Humans and Primates

In general, only a few kinds of source energy are employed in speech production, and changes in vocal-fold vibration modes are not typically used as linguistic cues. Instead, important phonetic contrasts are produced by articulation—movements of the tongue, mandible, and lips that influence the shapes and concomitant resonance properties of the pharynx and oral cavity. These maneuvers produce differentiated filtering effects in the supralaryngeal vocal tract that shape the two source-energy types into a variety of perceptually distinctive sounds. In contrast, vocal production in primates typically reveals a wider range

of source energies and less flexible modification of the filter component. These differences are evidently traceable to disparities in both vocal tract anatomy and neural control of sound-producing structures.

Laryngeal studies by Schön Ybarra (1995) and others, for example, have shown that many primate species have a rigid "lip" on the medial extremity of each vocal fold. This lip is likely to allow a number of vocal-fold vibration patterns, evidently accounting for the occurrence of various sounds that humans cannot easily emulate. These signals include high-amplitude, noise-based sounds, virtually pure-tone sinusoids, frequency sweeps that cover multiple octaves in a fraction of a second, and source energies that combine independently produced periodic and aperiodic components. Compared to humans, however, primates have thinner tongues, larynges positioned higher in the neck, and a relative lack of flexible soft tissues in the supralaryngeal vocal tract. Thus, while many species use tonal vocalizations with rich harmonic spectra, they appear to have less opportunity to alter the formant-related spectral patterning of those sounds by modifying articulator positioning (e.g., Lieberman, 1975). In addition, whereas speech production in humans requires significant involvement of neocortical brain structures as well as circuitry in brainstem, limbic, and midbrain areas, the neocortex appears to play a negligible role in primate vocal production (see reviews in Steklis & Raleigh, 1979, and Baer, Sasaki, & Harris, 1986). Several researchers have noted that articulatory maneuvers occurring in human vocal production can make use of neural connections that are absent in primates (e.g., Deacon, 1989). Thus, while some modification of vocal-tract resonances clearly does occur among various monkeys and apes (e.g., Hauser, 1996; Owren et al., 1997), one can generally conclude that these animals produce differentiated sounds primarily through changing laryngeal source-energy characteristics.

Implications for Individually Distinctive Acoustic Cues

Based on call acoustics and production processes, several different aspects of primate vocalizations can potentially provide cues to caller identity. Nonetheless, it can also be argued that some cues are inherently more revealing than others, and that the features of greatest importance for a particular call-type depend on the sound-production processes involved. The source-filter model can therefore be used as a general framework for understanding the origins of individual variation in the acoustics of vocalizations.

Cues Related to Source Energy

Individually distinctive acoustic cues might derive from several aspects of a call's source energy. For sounds based on periodic vocal-fold vibration, for instance, mean F_0 value might be used as a caller-specific attribute. However,

we suggest that this feature is unlikely to reliably distinguish various members of a social group, especially where animals of all ages and both sexes are present and a variety of call-types are used. In humans, the length and mass of the vocal folds are known to be the primary determinants of vibration rate (Titze, 1994) and the same is likely to be true of primates. If so, however, any two callers with comparably sized vocal folds will show similar typical F_0 values. In general, such coincidences can be expected to occur regularly. Furthermore, various call-types in a repertoire often exhibit different average F_0 values or show significant frequency modulation, making vocal-fold vibration rate by itself unlikely to be a consistent source of unambiguous cues to caller identity. It has been found that F_0 measurements can play a role when vocalizations are sorted by individual caller, for example, in statistical testing of rhesus macaque coos (Rendall, Owren, & Rodman, in press) and baboon grunts (Owren et al., 1997). Predictably, however, the value of such measures decline as sample sizes are increased or other variables are entered in the classification equations used.

The detailed spectral characteristics of the source component of call production might also provide reliable cues to caller identity, as the shapes and tissue properties of an individual's vocal folds are reflected in its characteristic glottal waveform. In humans, physical characteristics of the vocal folds are known to contribute to voice quality, as is shown by aging and disease-related effects on these tissues (e.g., Baken, 1987; Titze, 1994). However, because normative speech essentially uses only two vocal-fold vibration modes, it is an excellent medium in which to reveal individual variation in vocal-fold characteristics. In primates, fine-grained, individually distinctive glottal-waveform differences are arguably less likely to be apparent due to the greater range of source energies used. Such cues are probably the most important in tonal sounds, where spectral components are arranged in a predictable, harmonically related series and idiosyncratic variation in this patterning is requisitely evident. As an example, we have observed that while very old female macaques often produce distinctive-sounding coos, the aging effects that are apparent in these sounds are much less evident in noisier vocalizations.

Noisy primate calls are in general much less likely to show individually distinctive spectral patterns due to the inherent randomness of energy distribution in these sounds. Such calls often consist of extended or pulsed energy bursts with broadband spectral energy (i.e., pure noise) or combinations of periodic and aperiodic components. Screams shown in Figure 3 illustrate some of the properties of noisy vocalizations produced by macaques and baboons. In light of both Schön Ybarra's (1995) anatomical observations and spectrographic evidence showing that noisiness in primate calls can grade in near-continuous fashion, we assume that the source energy in such calls is produced by aperiodic vocal-fold vibration. While larger-scale spectral patterning can occur in screams and other noisy calls, the energy of any particular frequency component varies randomly (or quasi-randomly) in these sorts of waveforms. Such fluctuations must tend to

mask the more fine-grained, individually distinctive spectral differences that might be occurring.

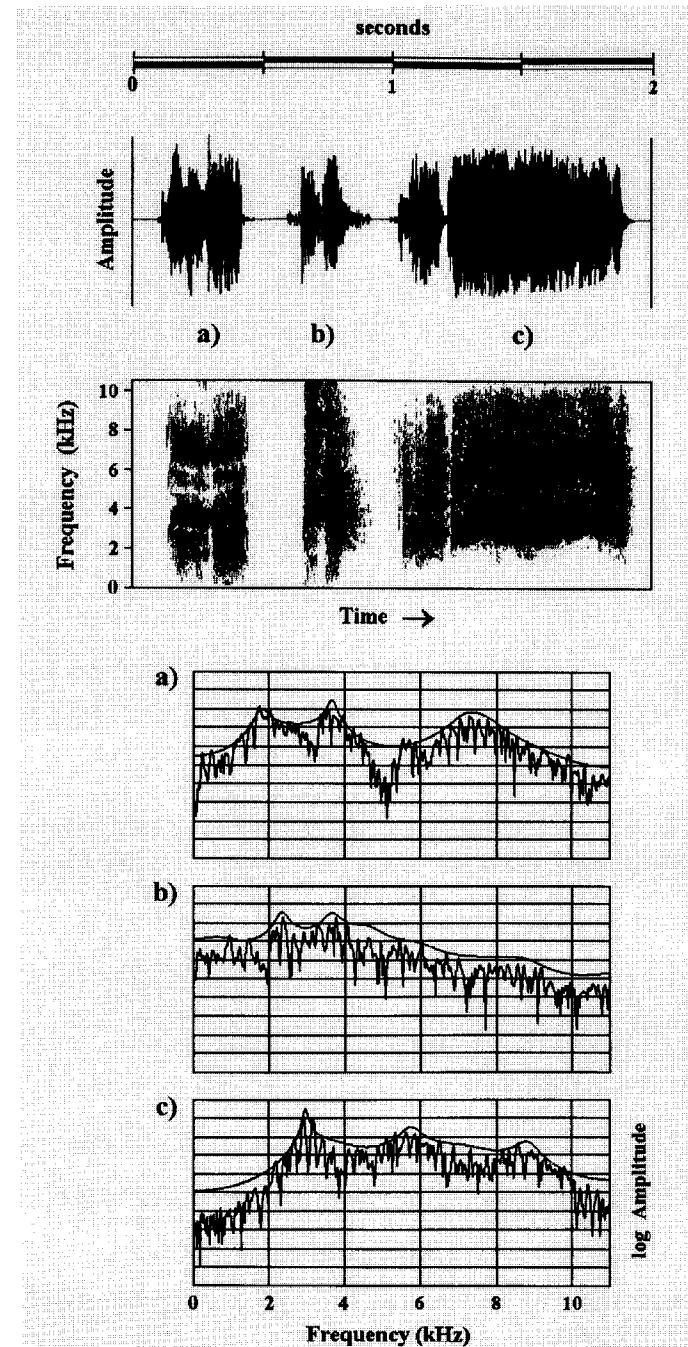
Cues Related to the Filter

While the source-energy component of primate calling is therefore not likely to provide individually distinctive voice qualities across call-types, the filter component may produce identity cues that are both consistent and broadly applicable. Subtle differences in vocal-tract cavity shapes and sizes can potentially produce individually distinctive variation in spectral patterning in a variety of call-types, so long as the sounds reveal the filtering effects involved. Examples of such formant patterns are shown for tonal and noisy calls in Figures 4 and 5, respectively.

In each of the tonal call-types, the F_0 is relatively low and the sound has a dense, harmonically structured spectrum that readily reveals the amplification and attenuation effects of the vocal-tract filter. In discriminant-function analyses reported by Rendall et al. (in press) for rhesus coos and by Owren et al. (1997) for baboon grunts, spectral-peak characteristics related to vocal-tract filtering were found to be more important than other acoustic measures when sounds were sorted by individual caller. For the rhesus monkeys, playback experiments showed that listening animals could readily differentiate between coos produced by relatives and other, unrelated group members (Rendall et al., 1996). However, the effect of a vocal-tract resonance only becomes apparent in a call if energy occurs in the frequency ranges affected by that formant. Therefore, as F_0 values rise and the harmonics of a tonal sound become more widely spaced, fewer details of the vocal-tract filtering are represented in the call. Individually distinctive patterning therefore disappears if the F_0 is too high. This outcome is illustrated in comparing the coos and grunts to the tonal, but high-pitched shrieks in Figure 6.

Because the vocal-tract filter is inherently better “displayed” in a vocalization if the underlying source waveform has a broadband spectrum, noisy calls

Fig. 3. Noisy screams produced by (a) an adult female baboon, (b) a juvenile rhesus monkey, and (c) an infant baboon. The figure shows waveforms (top), wideband (300-Hz) spectrograms (second from top), and corresponding spectral “slices” computed over a 512-point segment centered on each sound’s amplitude peak (bottom three panels). Each of the latter shows both fine-grained and smoothed versions of the segment’s frequency-energy structure, based on Fourier transformation (jagged envelope) and linear predictive coding (smooth envelope), respectively. (Digital sampling rates were either 20 or 22 kHz for the sounds shown in this chapter, except where otherwise noted.) In these screams, energy at any particular frequency varies semirandomly from instant to instant. However, a simple overall spectral pattern is apparent in each case—reflecting regularities in the source waveform of the call, effects of resonances, or both.



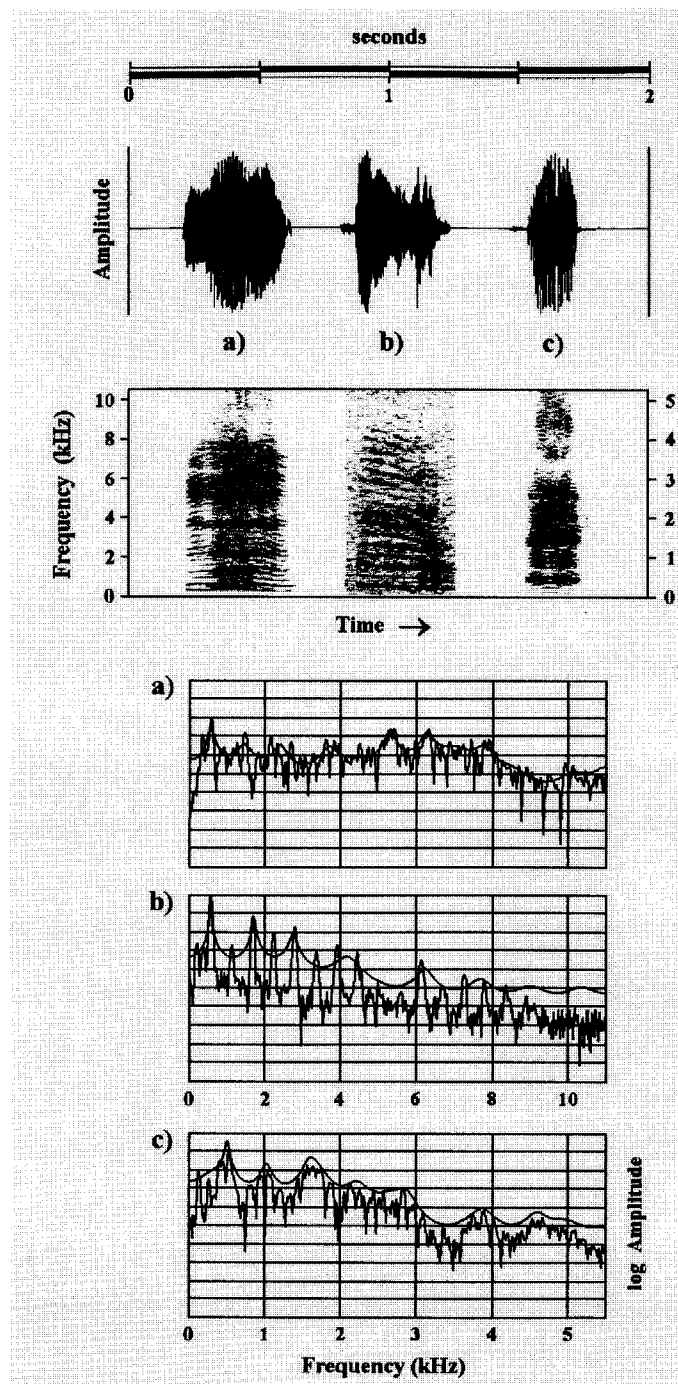
can also be a good medium for revealing filter-based cues to individual identity. Complications arise here as well, however, with call amplitude appearing to play an important role. As the spectral energy in a noisy sound is distributed more or less uniformly across the entire frequency range, the average amplitude of an individual component is typically much lower than in a tonal sound. As a result, noisy calls that are relatively quiet may not reveal formant characteristics as clearly as louder sounds. While the noisy rhesus monkey *grunts* in Figure 5, for instance, clearly show formant-related spectral peak patterns, Rendall et al. (in press) found only modest cues to individual identity in these sounds. The strongest cues were still provided by peak patterning, but results were less compelling than in Owren, Seyfarth, and Cheney's (unpublished data) earlier tests of louder pant-threats produced by rhesus and Japanese macaques (also shown in Figure 5). Fitch (1997) has provided very compelling evidence of prominent formant effects in rhesus monkey pant-threats, showing that the frequencies of resulting peaks are predictably (inversely) related to overall vocal tract length in these animals. As demonstrated by the screams shown in Figure 3, however, spectral peaks tend to disappear if the amplitude of noisy sounds becomes very high. It is not clear why this outcome occurs, or that it is caused by amplitude increases alone. Nonetheless, as discussed later, the apparent lack of differentiation in these sounds has been confirmed in both statistical analyses and playback studies (Rendall et al., in press).

Cues Related to Temporal Patterning

Temporal patterning may also provide cues to individual identity, both in single calls and when vocalizations are produced in series. Such cues would result from dynamic, rather than static aspects of acoustic energy. For instance, we noted earlier that primates may show articulation effects in their calls, but that such maneuvers do not seem to play a very important role in differentiating various call-types in a repertoire. However, as individual animals undoubtedly show minor variation in the physical characteristics and movements of their tongues, mandibles, and lips, corresponding cues to identity may be available in articulated calls. Other distinctive cues that may occur in the short-term temporal characteristics of calls include distinctive amplitude contours and F_0 patterns

→

Fig. 4. Characteristics of harmonically rich, tonal calls. Sounds in (a) and (b) are coos produced by two different adult female rhesus monkeys, while (c) shows a grunt call recorded from an adult female baboon (organized as in Figure 3). Each spectrogram is narrowband (45-Hz) and the grunt call was digitally sampled at 11 kHz. A complex, stable pattern of spectral peaks is present in these sounds, reflecting the joint source-filter characteristics of the underlying production system. As is evident in comparing peak locations in the slices to corresponding areas in the spectrograms, each call displays a fine-grained frequency-energy pattern that remains stable through the course of the sound.



(although F_0 changes are less salient to primates than to humans, as discussed below).

When vocalizations are produced in series, temporal patterning occurring over the course of one or more call bouts is arguably a rich source of individually distinctive cues. Longer-term patterning could occur, for instance, in F_0 characteristics, the arrangement of discrete energy bursts, amplitude changes over a long but continuous waveform, dynamic spectral characteristics of a harmonic-series or broadband noise, or from any combination of these elements. In each case, patterned changes in call features provide much greater opportunity for an individual to differentiate its vocal signals from others' calls than is possible using a static, unidimensional call feature. Producing multiple calls might also have a cumulative effect, for instance by allowing repeated "sampling" of one or more short-term cues. In either of these cases, however, listening animals would be slower to identify the calling individual than if cues are available in a single call, requiring at least a few seconds or more.

Evidence from Perceptual Studies

Auditory perception in primates is relatively well-understood, allowing at least an approximate evaluation of the salience of the various acoustic features we have discussed (see Stebbins & Moody, 1994, for a recent review). As a group, Old-World species are roughly similar in overall sensitivity to pure-tone stimuli across the audible frequency range (e.g., Stebbins, 1973; see also Hienz, Turkkan, & Harris, 1982; Owren, Hopp, Sinnott, & Petersen, 1988). In comparison to humans, these animals are somewhat less sensitive to frequencies below 500 Hz, significantly more sensitive to frequencies above 8000 Hz, and comparable in the intermediate range. Thus, acoustic energy in the frequency ranges represented in the various figures should be readily perceptible to macaques and baboons, as well as many other species. Psychophysical testing conducted by Sinnott and her colleagues with pure tones has shown that humans and macaques are comparable in their ability to discriminate duration changes and intensity increments (although intensity decrements were problematic; see Sinnott, Petersen, & Hopp, 1985; Sinnott, Owren, & Petersen, 1987a, 1987b). Moody (1994) found macaques to be very similar to humans in detecting amplitude

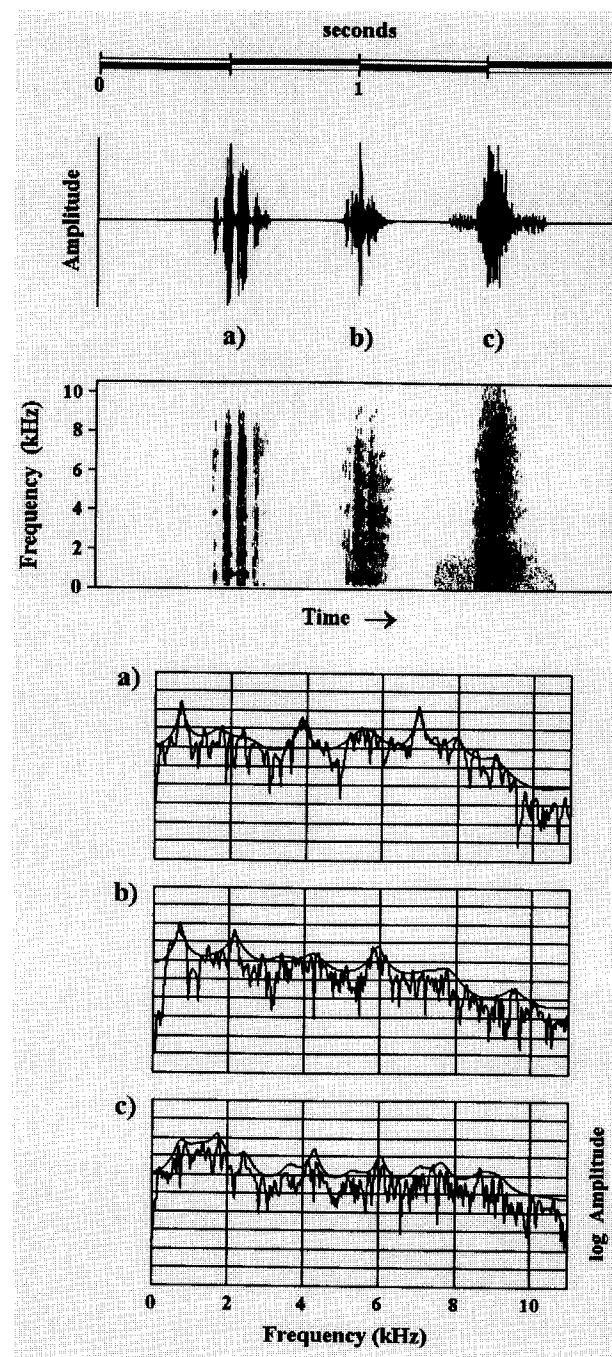


Fig. 5. Characteristics of other noisy calls in rhesus monkeys (organized as in Figure 3). These sounds are (a) a grunt, (c) a pant-threat, and (b) an intermediate version. Each call was produced by a different adult female and is shown in wideband spectrograms. The broadband energy of these sounds reveals features of the vocal-tract transfer function of the caller, but with varying fidelity and detail. The spectral peaks involved arguably reflect the effect of vocal-tract resonances, as vocal-fold vibration is unlikely to be the primary energy source in these calls.

modulation in pure tones, as well as changes in the frequency of repetitive amplitude modulations.

Less evidence is available concerning processing of resonance-related spectral peaks, but Sommers, Moody, and Prosen (1992) have provided telling data. They tested spectral resolution capabilities in Japanese macaques and humans using synthetic stimuli in which a harmonic series was shaped so as to mimic the effect of a formant occurring either at 500 or 1400 Hz. The monkeys and humans performed almost identically in this task, demonstrating comparable sensitivity to small changes in the spectral peak locations in the two sounds. This outcome is consistent with earlier studies showing that both yellow baboons (Hienz & Brady, 1988) and Japanese macaques (Sinnott, 1989) can be trained to discriminate English-language vowels based on formant characteristics. In contrast, macaques have been found to be much less sensitive than humans when detecting frequency changes in pure-tone stimuli. Again testing at 500 and 1400 Hz, Sommers et al. (1992) found that while human participants were significantly more sensitive to pure-tone frequency shifts than to spectral peak changes, their monkey subjects showed the opposite outcome. Overall, macaques are approximately 6 to 10 times less sensitive than humans to frequency changes in tones, whether shifts occur as discrete steps (Prosen, Moody, Sommers, & Stebbins, 1990; Sinnott et al., 1985; 1987a; Sinnott & Brown, 1993) or continuously modulated sweeps (e.g., Moody, May, Cole, & Stebbins, 1986).

While it is inherently difficult to extrapolate from sensitivity measurements obtained in the laboratory to species-typical communication processes, a notable pattern has emerged. Under controlled conditions, primates and humans have been found to be essentially equivalent when detecting pure-tone energy in intermediate frequency ranges, variation in the temporal and intensity characteristics of these simple stimuli, and changes in formant-related spectral features of harmonically rich tonal sounds. In contrast, F_0 variation has been found to be significantly less salient to monkeys than to humans. Taken together, these psychophysical studies indicate that spectral and temporal patterns in species-typical calls are inherently more likely to be perceptually important to primates than are simple F_0 changes.

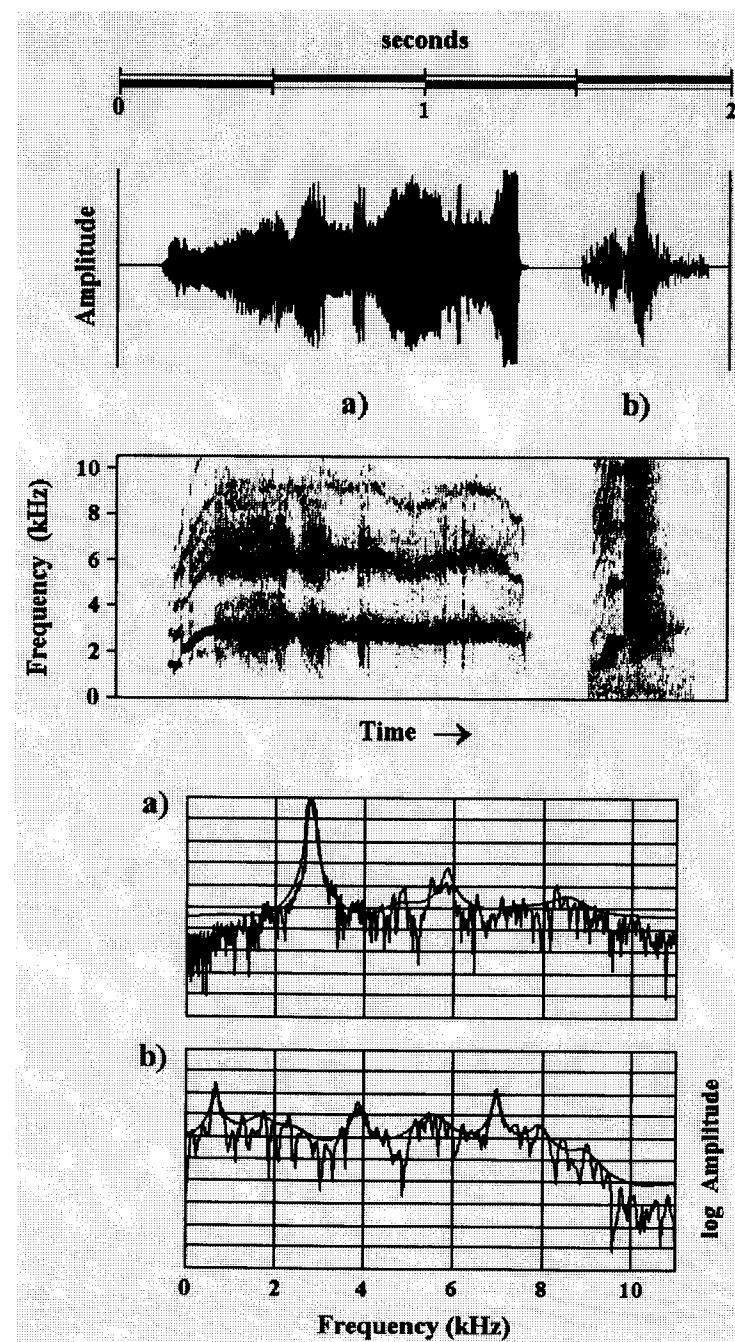


Fig. 6. Characteristics of high-pitched, tonal shrieks (organized as in Figure 3). The first, longer call (a) was produced by a juvenile rhesus monkey, exhibiting both a very high fundamental frequency and a requisitely simple, harmonically structured frequency spectrum. A juvenile baboon gave the second, shorter call (b), which illustrates the grading that can routinely occur among sound types in these and other species. Here, a noise overlay is added to the initial high-pitched tonal output approximately halfway through the call. Both components are extremely noxious-sounding when produced at high amplitudes, and neither provides salient cues to potentially distinctive aspects of the calling animal's vocal-tract transfer function. Spectrograms are wideband.

Conclusions about Individually Distinctive Cues in Vocalizations

Overall, we suggest that in species like macaques and baboons, the best opportunity to convey discrete, salient cues to individual identity occurs through vocal-tract filtering effects displayed in low-pitched tonal calls with dense harmonic structures and in broadband, noisy sounds of intermediate (or lower) amplitude. This claim is supported by the results of various studies in which acoustic analysis has been used to sort vocalizations by individual caller, and by data from laboratory studies of primate auditory perception. The results of the playback studies cited so far are also consistent with this conclusion, but some potentially contradictory data from field experiments involving screams will be considered later.

High-pitched tonal calls and high-amplitude noisy sounds do not readily reveal vocal-tract filtering effects, but might be individually distinctive through distinctive temporal-patterning cues. The perceptual data that are available concerning sensitivity to intensity and duration changes in simple acoustic stimuli are consistent with this suggestion, although tests of more complex, temporally patterned stimulus sequences are needed. F_0 changes, which are very common among various call-types, appear to be much less salient to primate receivers than to humans hearing the same sounds. Taking into account both production-related factors and this perceptual constraint, primates are unlikely to make use of simple F_0 contrasts as cues to individual identity and arguably must use exaggerated F_0 jumps or modulations if such changes are to be perceptually important to others.

AN AFFECT-CONDITIONING MODEL OF PRIMATE VOCAL SIGNALING

Integrating the arguments we have presented so far, the reasoning underlying the affect-conditioning model is as follows. We assume that communication signals are most fundamentally a means by which organisms influence the immediate or future behavior of others, and that in a given situation, senders use vocalizations whose influences provide the greatest net benefit to themselves. Important influences can be produced by eliciting unconditioned and conditioned affective responses in receivers, effects to which the principles of habituation and Pavlovian conditioning apply. However, the potential benefit of producing a call that primarily elicits either unconditioned or conditioned responses depends on the relationship between the sender and receiver. A caller that typically has little opportunity to control the outcome of its interactions

with the receiver derives the greatest benefit from producing vocalizations that elicit unconditioned responses. In contrast, a caller that is able to control the outcomes of its interactions with the receiver is likely to benefit most from first inducing conditioned affective responses to its calls by pairing these sounds with unconditioned stimuli delivered directly to the receiver, then later taking advantage of the conditioning that has accrued by using the same calls as conditioned stimuli. Vocalizations are well-suited to either kind of function, as they are discrete, salient, controlled by the sender, and difficult for the receiver to avoid.

Calls can produce unconditioned affective effects both through their relatively generic effects on the auditory system or by tapping into more specific, evolved sensitivities in the species in question. Characteristics like high overall amplitude, noxious spectral qualities, abrupt transitions, high F_0 , and pronounced F_0 modulation exemplify features that are likely to elicit unconditioned responses. We refer to these calls collectively as squeaks, shrieks, and screams. Such sounds are likely to be used repetitively or in bouts in order to maximize the unconditioned responses being elicited. As receivers inevitably habituate to repeated stimuli, the sender also varies the acoustic features of the sound stream. Conditioned affective responses occurring to vocalizations are specifically mediated by acoustic cues to the caller's identity. However, the primate vocal-production and auditory-perception systems shape the forms that such calls can take, depending on the particular call-type involved. Individually distinctive vocal-tract filtering effects can provide immediate and clearly perceptible cues to caller identity, both in low-pitched tonal vocalizations with dense harmonic structures and intermediate-amplitude, noisy sounds with broadband energy. These are the calls we have referred to as resonants and gruffs. Repetitive call production is not inherently as useful for such sounds as for calls whose function is to elicit unconditioned responses. High-pitched tonal calls and high-amplitude noisy sounds do not readily reveal vocal-tract filtering effects, but may provide identity cues through distinctive temporal patterning.

To illustrate the implications of these proposals, we now describe four scenarios in which two animals interact and one of them calls. In each scenario, the interests of the sender are evaluated based both on its relationship to the receiver and on the general function proposed for calling in that circumstance. In a given situation, the caller is either subordinate or dominant to the receiver, and the interaction is either agonistic or affiliative in nature. We then return to the general issues concerning primate vocal signaling that were raised earlier. The various topics are revisited in reverse order, and a variety of implications of the affect-conditioning model are considered. A number of predictions are also presented, both to flesh out the scope of the approach we are proposing and to make the model as specific and testable as possible.

Four Scenarios Illustrating the Use of Unconditioned and Conditioned Effects

Subordinate Caller in an Agonistic Interaction

The first scenario is the simplest. In this situation, an animal vocalizes during an agonistic encounter with a more dominant group member and calls function to discourage impending or ongoing aggression. Being subordinate, the caller's most effective tactic is to produce noxious-sounding vocalizations in a loud, repetitive fashion, eliciting aversive unconditioned responses in the dominant animal. High-amplitude, grating calls like shrieks and screams are best-suited to this purpose, and the deterrent effect of the subordinate's calling is proportional to the magnitude and noxiousness of the acoustic energy involved. Variation in the acoustic features of the vocalization series also occurs, in order to alleviate habituation in the unconditioned responses experienced by the receiver. The subordinate animal has relatively little opportunity to effect or take advantage of conditioning in the dominant individual, as it cannot exert much control in this kind of encounter. Therefore, the caller's best available vocal option is to use sheer magnitude and raw features of acoustic signals for inducing aversive unconditioned responses in opponents, even though this option is energetically expensive.

Dominant Caller in an Agonistic Interaction

In the second scenario, an animal vocalizes during an agonistic encounter with a subordinate individual. The function of calling is to elicit an affective response, such as fear, that makes the receiver more likely to depart or show submissive behavior. Here, the caller could arguably take advantage of both unconditioned and conditioned effects. For instance, high-amplitude, noxious sounds could be used to induce fear in the receiver as an unconditioned response. However, conditioning can be effected by producing "threat" vocalizations that include salient, discrete cues to individual identity and then engaging in violent behavior that traumatizes the subordinate. After a small number of such encounters, the dominant individual can effectively influence the behavior of the other animal by using its energetically inexpensive threat calls to elicit conditioned affective responses. The acoustic features of the calls reflect the need to embed the individually distinctive cues in a signal whose unconditioned effects add to, or are at least compatible with, the desired affective response. Such calls should therefore be from the sonant and gruff class.

Dominant Caller in an Affiliative Interaction

The third scenario is one in which an animal interacts affiliatively with a subordinate. Here, for example, calls might be produced as the dominant animal

roaches and sits with the other, possibly grooming it or being groomed itself. The approach or proximity of a dominant group member evidently induces anxiety in a subordinate individual, the calls used should encourage the receiver to participate in the interaction by decreasing its fearfulness or inducing positive affective responses. The calling animal has at least some control over the course of the interaction, and can therefore make use of conditioned effects.

The dominant animal should again promote conditioning by using calls that include salient, discrete cues to individual identity in energy that has compatible unconditioned effects and (usually) following those vocalizations with affiliative behaviors that lead to positive affective states in the receiver. These calls will therefore be from the sonant and gruff class, but should be clearly differentiated from the calls used to elicit conditioned fear or other negative affective responses.

Subordinate Caller in an Affiliative Interaction

In the fourth and final scenario, an animal calls to a dominant group member in an affiliative context, for instance when approaching to groom that individual. Although it is subordinate in this situation, the caller has some control and leverage—it can provide stimulation that evidently constitutes a strongly positive event for the other animal. The subordinate individual's interests are therefore analogous to those of a dominant animal that is acting affiliatively. Specifically, the subordinate benefits by associating individually distinctive cues in its calls with the pleasant outcome experienced by the other animal, and thereby promoting positive affective conditioning to those features. The caller gains some ability to use vocalizations to elicit a positive conditioned response in the dominant individual on other occasions, for instance making it more likely to participate in an affiliative interaction or less likely to be aggressive. These vocalizations will be from the sonant and gruff class, and should have unconditioned effects that are compatible with the positive conditioned affect that is elicited.

Cues to Individual Identity

A variety of predictions concerning cues to individual identity can be derived from the affect-conditioning model, beginning simply by restating its assumptions and testable hypotheses. For instance, individually distinctive cues in calls labeled as sonants and gruffs are predicted to derive primarily from differentiated spectral timing in these sounds. Squeaks, shrieks, and screams, in contrast, are proposed to be readily identifiable based on the static features of individual calls. The acoustic features of calls may be identifiable, but we suspect that cues are more likely to emerge from temporal patterning occurring over a series of calls. As

resonance frequencies and spacing are inversely related to vocal tract length (e.g., Fitch, 1997), calls of younger, smaller animals can be expected to show both higher and more widely spaced formants than the calls of older, larger individuals. As vocalizations of young animals also show higher F_0 s, sonant and gruff calls in these individuals are predicted to be significantly less individually distinctive than comparable sounds produced by more mature conspecifics. In fact, very young primates may be unable to produce calls with salient spectral patterning cues, and hence might not be expected to use true sonants or gruffs. Evidence of all these predicted effects should be found in each important testing domain—acoustic analysis of calls, perceptual testing conducted in laboratory settings, and playback trials examining functional responses.

Cues to Individual Identity in Screams

As some of the evidence that is available from playback studies with screams may be inconsistent with our predictions, several relevant experiments will be reviewed. In primates, the best evidence of individual discrimination and recognition based on vocal cues has arguably been provided by Cheney and Seyfarth (1980). In their studies of wild vervet monkeys, these investigators used a hidden speaker to play screams of juveniles to their mothers and other adult females. A bout of calls was presented on each trial, averaging approximately 7 sec in length. When several females sitting together heard the screams, the caller's mother was the animal most likely to look in the direction of the speaker. In addition, the other females were found to be more likely to look at this mother than to look toward the source of the calls. Gouzoules, Gouzoules, and Marler (1986) have also tested the distinctiveness of screams, but did so by playing back single calls to free-ranging rhesus monkeys. An earlier study had distinguished 5 acoustic variants of screams, and two of these subtypes were tested (Gouzoules, Gouzoules, & Marler, 1984). For *noisy* screams, an example of which is shown in Figure 3, Gouzoules et al. (1986) reported that adult females were quicker to look, and looked longer when hearing calls of related rather than unrelated juveniles. No differences were found for arched screams.

Based on the acoustic features of these rhesus screams, we would not expect that the identity of the caller would be clearly revealed by a single exemplar of either type. Little spectral energy patterning is evident in noisy screams, for instance, while arched screams are piercing calls with very high F_0 s. Consistent with this point of view, Rendall et al. (in press) found no evidence of kin-based discrimination when they played back noisy screams produced by adult females to other adults in the same rhesus groups that had been tested by Gouzoules et al. However, the response latencies and durations reported for the experimental groups in the two studies were actually almost identical. In both cases, responses were clearly slower and shorter than was the case when Rendall et al. (1996) tested adult females in these groups using coo calls. The difference

between typical responses to the coos of female kin and nonkin was quite dramatic and also quite unlike response patterns reported in the two studies testing rhesus screams (see Rendall et al., in press, and Rendall, 1996, for further discussion).

The discrepancies among the various outcomes of these tests of vervets and macaques may have resulted from differences in the durations of the playback stimuli used. Gouzoules et al. (1984) presented individual screams because subjects that heard scream bouts in pilot trials approached or even charged the speaker. In other words, the most compelling evidence of individually distinctive acoustic cueing occurred when scream bouts were played—first in Cheney and Seyfarth's tests of vervets and later in Gouzoules et al.'s preliminary tests. When Rendall and his colleagues presented either single coos or single screams (by design, the methodologies were as similar as possible in the two cases), evidence of kin-based discrimination emerged only for coo calls. Results were different when screams were tested, showing no evidence of discrimination but matching the latencies and durations reported for a comparable condition in Gouzoules et al.'s (1986) experiment.

We interpret these outcomes as showing that cues to individual identity are present in individual coos, but are more likely to emerge over the course of a bout of screams than in the features of single calls. This proposed difference is supported by acoustic measurements and statistical classification results described by Rendall et al. (in press). In this work, coos were readily sorted by caller based both on acoustic measures related to vocal-tract filtering effects and other features. However, across calls, formant-related cues were primary, showing the least intraindividual variability and allowing the most accurate statistical classification. Screams, in contrast, were more homogeneous, did not show distinctive spectral patterning, and could not be successfully classified by caller.

Repetition and Acoustic Variability in Calling

Unconditioned and Conditioned Effects

A number of implications can be drawn from the proposal that the balance of power in a social relationship determines whether a caller should attempt to elicit unconditioned or conditioned affective responses. For instance, the argument that a subordinate individual under attack should elicit aversive unconditioned responses in the receiver is a general one, applicable to any situation in which an individual with little direct power over another individual attempts to influence that animal's behavior. By extrapolation, younger individuals and subordinate animals of all ages can be predicted to rely primarily on unconditioned effects of calling. A prototypical example is a young animal being weaned,

who calls while unsuccessfully seeking caretaking behavior from its mother. Such sounds are predicted to act as unconditioned stimuli and should therefore be drawn from the squeak, shriek, and scream class, occur repetitively, and show significant acoustic variation. Anecdotally at least, when frustrated young animals call to their mothers or other caretakers, their vocalizations often occur in long bouts and are marked by features like exaggerated F_0 modulations and “melodramatic” plaintiveness. The calls are often also noxiously noisy or screechy, and are produced in seemingly endless streams that can be very annoying to human listeners.

Vocalizations that capitalize on conditioned effects should not be used in this fashion. For these calls, repetitive use might increase the immediate response, but simultaneously decrease the long-term value of the calls as predictive stimuli. Therefore, another implication of the model is that sonants and gruffs are less likely to be produced in long bouts than are squeaks, shrieks, and screams. However, animals producing sonant- and gruff-like calls may in fact be using them primarily to elicit unconditioned responses, or both kinds of responses. As noted, younger animals are expected to have less opportunity to produce calls with rich harmonic spectra and prominent filtering effects, and may therefore rely on repetition and variation. If so, features that are arguably related to unconditioned responses should be more prominent. If older, larger individuals use sonant-like calls in this way, otherwise individually distinctive spectral features should be made less prominent, for instance through increases in F_0 .

Positive versus Negative Affect

While we consider positive affective responding to be an important component of the model, we also expect that primates do not have equivalent opportunities to elicit positive and negative affective responses in others. For instance, a dominant animal can induce negative affective states in another individual very quickly and effectively through directed actions like biting, hitting, kicking, scratching, chasing, or lunging. Multiple conditioning trials can occur in a given interaction, as the caller can repeatedly pair its vocalizations with these traumatic unconditioned stimuli. The situation is rather different for a dominant individual attempting to induce positive affective states. Such responses might be effected by grooming a subordinate, allowing it to groom, or simply tolerating its presence. However, each of these outcomes is rather diffuse and the dominant animal is inherently less able to control the subordinate's responses in such circumstances. A subordinate behaving in an affiliative fashion faces similar constraints. It might groom a dominant animal or allow this individual access to an infant, but cannot induce positive affective states in this individual in the direct, controlled manner afforded by using noxious sounds as negative unconditioned stimuli.

Using Calls as Conditioned Stimuli for Other Vocalizations

An additional tactic that a subordinate may use is to condition another animal by using its own calls as the unconditioned stimulus. For example, we have proposed that screams are aversive to receivers and can be used to shape their behavior. By predictably pairing calls from the sonant and gruff class with these biologically significant events, subordinate senders may be able to produce some conditioned effects in receivers. This tactic could be used both by adults facing attack from higher-ranking group members and by young animals seeking attention from caretakers. Bouts of vocalizations being used in this fashion are predicted to consist of some calls carrying prominent cues to individual identity interspersed with other vocalizations eliciting unconditioned effects. In other words, while both kinds of calls should appear, the vocalization sequences observed should reflect the differentiated roles being played by each type of call.

Discrete and Graded Signaling

Marler and others (reviewed by Green & Marler, 1979) have suggested that a distinction can be drawn between discrete and graded call-types, or discrete and graded vocal repertoires. A discrete call-type is one in which variation in acoustic features is clearly bounded, creating a category of sounds that is readily distinguished from other calls in the repertoire. A graded call-type, in contrast, is one whose acoustic features vary substantially, such that continuous gradation along one or more acoustic dimensions can bridge between this sound and other call categories. An entire vocal repertoire, then, might be labeled as being discrete or graded depending on whether the call-types involved are predominantly of one kind or the other. A general relationship has been noted between discreteness and gradedness and the degree to which the vocal signals in question are complemented by information that is simultaneously available in other modalities. Discrete repertoires (or call-types) are proposed to be of greatest value when vocalizations are used in the absence of other information, primarily when senders and receivers cannot see one another. Graded repertoires (or call-types) are more likely to involve sounds used at close quarters, where vocalizations are supplemented by other kinds of signals. Graded repertoires or vocalizations have also been suggested to encode more information than do their discrete counterparts, for instance through allowing acoustic variability to be partitioned into meaningful subcategories (e.g., Marler, 1975; Hauser, 1996). However, as the functional significance of acoustic variation also depends on perceptual processing in the species in question, it is often difficult to classify a call-type or a vocal repertoire unambiguously.

The affect-conditioning approach provides a different perspective. In this framework, acoustic variability is linked to minimizing habituation of elicited responding in receivers. Call-types in the squeak, shriek, and scream class are

therefore predicted to always be subject to acoustic grading. Analogously, grading should routinely occur in sounds used by very young animals that cannot readily produce true sonant and gruff calls. In normative calling, different versions of similar calls may also be found, where one variant is used primarily to elicit unconditioned responses alone and another includes cues to individual identity and is used as a conditioned stimulus. Grading that occurs among call variants or separable call-types may reflect shifting or mixed tactics by a sender that is responding to the complexities of an unfolding interaction. From this viewpoint, no clear distinctions can be expected between discrete and graded vocal repertoires. Instead, all repertoires should show graded call-types, as the opportunity to elicit unconditioned responses using vocalizations can be expected in every primate species.

However, the general relationship between the discreteness or gradedness of signals and habitat characteristics can also be reinterpreted, by taking into account probable influences of vegetation density on the effectiveness of the vocalizations that function as unconditioned stimuli. When sender and receiver are separated by dense vegetation, sound energy traveling between them is subject to significant attenuation and degradation. While subordinates that are being physically tormented by dominant animals can still use noxious screams to good effect, calls that might have been used to elicit unconditioned responses in animals farther away in other sorts of interactions are arguably much less effective. In addition, senders are less likely to be able to approach or closely follow a given receiver at will in heavily vegetated habitats than in open environment. The effectiveness of conditioned responses, in contrast, should not be greatly affected by the relative density of vegetation. Conditioning trials can be conducted opportunistically whenever two animals are in close proximity, thereafter allowing senders to elicit responses based on learning rather than the sound energy per se. Salient cues to individual identity must be preserved in the calls used as conditioned stimuli, however, if this strategy is to be effective, thereby favoring greater stereotypy in these signals.

Overall, we suggest that the repertoires traditionally considered to be discrete are ones in which environmental constraints decrease the sender's ability to elicit unconditioned responses in receivers—except when the animals are close together. Under these circumstances, then, both habituation effects and the corresponding strategy of producing acoustically variable calls are significantly less important. Repertoires traditionally considered to be graded are ones in which callers can routinely elicit both conditioned and unconditioned effects. Calls used during physical attack or by young animals that are close to their mothers should not differ between repertoires otherwise considered to be either discrete or graded. The distinction should instead apply mainly to calls in the sonant and gruff class. In these cases, discrete call-types or repertoires are predicted to occur when acoustic variability cannot be used to elicit unconditioned responses in addition to conditioned effects based on individually distinct

tive spectral-patterning cues in sonants and gruffs. Graded call-types, in contrast, will occur when conditioned effects can be supplemented by unconditioned effects, or when sonant and gruff calls are modified so as to decrease cues to individual identity and increase their value as unconditioned stimuli. It is predicted that grading is much more likely to occur in acoustic dimensions related to unconditioned rather than conditioned effects.

Acoustic Features of Calls and Repertoire Structure

Functional Differentiation of Calls

As illustrated by a number of the preceding points, the functional distinction proposed between calls eliciting unconditioned and conditioned responses has implications for both the broad structure of a vocal repertoire and more detailed patterns of acoustic variation within each of the two broad call classes we have described. In contrast to other approaches, the affect-conditioning model does not necessarily segregate calls according to the social contexts in which they are produced, or on the basis of their acoustic features alone. Again, starting from the assumption that the fundamental function of vocalizations is to influence the behavior of others, we instead suggest that within the two call classes, natural selection pressures drive an ongoing process of acoustic differentiation. In other words, from relatively simple beginning stages, vocalizations of both general types are likely to diversify through continual emergence of acoustic variants that increase the ability of callers to elicit affective responses. Within the general constraints imposed by the differentiated functions of the two call classes, the process of differentiation can be expected to differ among species, in accordance with the much more specific constraints imposed by species-typical social organization, ecology, and habitat.

Motivation-Structural Rules

The affect-conditioning model also provides an alternative to Morton's (1977, 1982) proposed "motivation-structural" rules for linking internal motivational states of senders to the acoustic characteristics of their signals. Most importantly, Morton suggested that animals use harsh, low-frequency vocalizations with concomitant broadband spectra when in a hostile, aggressive state, and tonal, high-frequency sounds when frightened, appeasing, or affiliative. Distinct motivational states were proposed to be reflected in acoustic grading between these endpoints, for instance producing combinations like upward-moving noisy sounds or downward-moving tonal sounds. These patterns were linked to an overall relationship between a caller's body size and the pitch of its vocalizations. As larger animals are generally more threatening to others, an

aggressive individual was described as seeking to make itself seem bigger by producing low-frequency vocalizations. Conversely, an affiliative or submissive animal emulates the higher-frequency sounds of smaller individuals.

These rules have been found to be consistent with some, but not all of the available data (see Hauser, 1996, for a recent review). While Hauser (1993) reported the predicted relationship between pitch and evident motivational state to hold in a variety of primate species, exceptions to the rules are also readily found. Owren, Dieter, Seyfarth, and Cheney (1992), for instance, noted that group-housed rhesus macaques produced noisy, broadband grunts in *play* and *infant* contexts that can both be described as affiliative situations involving contact-seeking. When a familiar human observer approached the large outdoor cage in which the group was housed, these animals also produced grunts, but with no indication of affiliative intent. In similarly housed Japanese macaques, tonal coos were recorded in each of these contexts. Furthermore, each of the two species could produce both coos and grunts, and sometimes used these very different-sounding calls interchangeably.

The motivation-structural rules are similar to the affect-conditioning model in emphasizing effects of signals on receivers, and in some cases the two approaches make similar predictions. However, the affect-conditioning perspective differentiates more specifically between unconditioned and conditioned effects, and suggests that the acoustic features of vocalizations reflect the calling strategy being employed rather than the caller's motivational states per se. For instance, according to the motivation-structural rules, an animal producing first high-pitched tonal sounds and noisy broadband screams in an agonistic situation is showing motivational states of fearful submission and aggression, respectively. A priori predictions about the calls that will be produced can be made only to the extent that the caller's internal states can be anticipated. The affect-conditioning model proposes that the animal is taking advantage of calls that have unconditioned effects on the receiver, and that calling should therefore show repetitive, but varying acoustic form. Vocalizations are predicted not to exhibit individually distinctive cues in spectral-patterning aspects of individual calls, unless such calls are being used in an identifiable conditioning process.

Motivation-structural rules predict that a dominant individual in an agonistic circumstance should give low-pitched, harsh calls, which is consistent with the affect-conditioning model. The latter, however, proposes that cues to individual identity play a primary functional role when primates call in this circumstance and that formant-based cuing is therefore more important than the tonality or noisiness of the sound. The occurrence of either tonal or noise-based threat calls may therefore evolve, depending on the particular species and vocal repertoire involved. In an affiliative circumstance, a subordinate animal can be expected to be fearful and therefore to produce high-frequency tonal calls according to the motivation-structural rules. In the affect-conditioning model, the form of the calls will depend on the degree of control the subordinate has

over the other animal's subsequent affective state. Finally, the motivation-structural rules appear to make no clear prediction concerning a dominant animal in an affiliative situation, the affect-conditioning model predicts the occurrence of calls with cues to individual identity that are used to elicit conditioned effects.

Correlations between Calls and Behavior

In suggesting that vocalizations are most fundamentally related to influencing the behavior of a receiver, we have also shifted the emphasis away from functional explanations that propose that senders provide information about their internal states or upcoming behavior. Consistent with this approach, studies that have explicitly examined correlations between signals and subsequent sender behavior have shown that the relationship is typically more probabilistic than precise (e.g., Hauser, 1996). We predict instead that a stronger relationship should be found between the occurrence of signals of one form or another and the receiver's subsequent behavior. While natural selection will favor receivers that can resist influences that are detrimental to their overall fitness, the sender's control of signaling event inherently makes this role primary in an ongoing process of differentiation and innovation in the vocal repertoire. Therefore, the ability of senders to influence receivers should be at the leading edge of this process.

Signal Function: Evolution of Vocalizations

As discussed early in this chapter, we believe that the evolutionary origins of communication lie in conation-like rather than cognition-like functions, with the requisite caveat that the processes involved are fundamentally intertwined. An implication of the affect-conditioning framework is that the simplest and most ancient "communication" function would have been to influence the behavior of a receiver by producing an unconditioned stimulus that elicited an unconditioned response. The emergence of signals specialized for use as conditioned stimuli must have occurred later, but would have been an early development in the evolution of vocal repertoires. This bifurcation of function may have been particularly important in that it arguably laid the foundation for more sophisticated cognitive processing, particularly in receivers. While the learning process that takes place in Pavlovian conditioning procedure is basic and ubiquitous, it is nonetheless complex in that the association involved reflects predictive power and a relationship between two stimuli. As argued by Rescorla (1988a, 1988b), Pavlovian conditioning does not occur because stimuli are merely paired, with connections thereby being "stamped in." Instead, the underlying associations are inherently indistinguishable from simple cognitive structures and have identifiable representational properties. From this point of view,

a satisfactory framework of either conditioning or cognition will be one that unifies the two disciplines, rather than separating them.

Continuing our evolutionary scenario, then, we suggest that the emergence of using calls as conditioned stimuli was an important factor in the evolution of cognition, in that selective pressure was created that then favored increasing powers of inference in receivers. While senders serve their own interests by signaling, receivers probably benefit by behaving as the sender desires in some circumstances, but not others. Whereas it is of benefit to senders to produce conditioned affect in receivers, such responses also constitute a form of knowledge—a representation of the signal, the sender, and past interactions. In cognitive terms, conditioned affective responses thereby encode information concerning the characteristics and behavior of other group members. Naturally, the receiver's best interests are served by making use of such information and being able to respond as flexibly as possible to the particular circumstances of each interaction. Selection pressure acting on receivers, then, may have contributed to the emergence of more sophisticated processing capabilities that built on the representational capacity inherent to affective responses. We suggest that this sort of information processing would be added to existing components, allowing modulation of the behavioral effects of activity occurring at affective levels.

CONCLUSIONS

A general theme of this chapter has been that the study of animal communication should not be restricted to information-based approaches. This suggestion is not new, having been anticipated by a variety of important empirical and theoretical developments, and similar recommendations from others. One important component, for instance, has been work highlighting the inherent difficulty of separating information potentially encoded in signals from inferences derived by receivers through active evaluation of both the signal and the context of signal emission (e.g., Smith, 1977; Marler et al., 1992; Leger, 1993). Another component has been proposals for how to enlarge the domain of study to include the role played by motivational and emotional processes in both sender and receiver (see Owings, 1994; Owings & Morton, this volume). The affect-conditioning model is inherently closer to the latter, emphasizing a conative rather than a cognitive perspective. We suggest that many primate calls do not involve "meaning," in the normal sense of this word, and that neither referential nor motivational information is necessarily encoded in such signals.

We also believe that many of the available data concerning primate vocal behavior are consistent with the spirit of our approach. This intuition is based on the evident functional importance of vocalizations in "coordinating" interindividual relationships and social behavior in primates, a theme that has emerged

again and again in various forms over the history of acoustic primatology. Our specific contribution lies mainly in suggesting that conditioning-related constructs can be applied to understanding how such coordination might occur. In our view, this sort of function is probably more fundamental for the broad sweep of primate calls than representation of either external or internal designata, and has been largely unaddressed by information-based interpretations. Furthermore, only in a few cases has the purported information content or designata of primate vocalizations been specified, and the cognitive mechanisms implicitly thought to process such information are left as hypothetical constructs. Overall, while it can indisputably be useful to view communication processes in informational terms, the general inability to describe either signal content or the processing mechanisms involved points up the pressing need for additional approaches.

The approach we have outlined is meant to be compatible with findings like those of Bauers and de Waal (1991), who reported that female stumptailed macaques (*M. arctoides*) were more likely to engage in affiliative approach and contact after directing coo calls to one another. Similarly, Silk, Seyfarth, and Cheney (1996) found that in chacma baboons, adult females routinely produced grunt vocalizations when reestablishing affiliative contact with a subordinate animal that had recently been an opponent in an aggressive interaction. In fact, females were virtually never found to engage in nonaggressive interactions with former opponents during the postconflict period unless they grunted during their approach. Both in this case and in interactions that were not preceded by aggressive interactions (Cheney, Seyfarth, & Silk, 1996), grunts played a critical role in facilitating affiliative social encounters. Like Bauers and de Waal (1991), we see calls like these as "social tools" and suggest that over time, natural selection has favored those individual primates that were the most effective in using these tools to influence others. The predictable and observable outcome is that every species now exhibits a "toolbox" full of vocalizations.

The affect-conditioning model may be found to be broadly applicable—in accordance with the ubiquity of phenomena like elicited responses, habituation, and Pavlovian conditioning. Applied on a case-by-case basis, the principles we have proposed could be useful in understanding a variety of communication systems, from the simplest to the most complex. This flirtation with hyperbole is borne out by a growing recognition that even in human speech—the most complex communication system of all—individual variability plays a central and necessary role in normative, linguistic processes (e.g., Johnson & Mullenix, 1997). Pisoni and Lively (1995), for instance, review compelling evidence that voice characteristics of individual human talkers play an important role in "abstract" phonemic representations. While long thought to be a barrier to the speech-decoding process, individual variability has been discovered to be informative to listeners making linguistic judgments. After more than 40 years of largely unsuccessful effort to eliminate or dramatically reduce such effects in the acoustic descriptions of speech sounds (Miller, 1989), researchers in speech

perception, word recognition, and computerized speech recognition have independently concluded that individual characteristics should instead be explicitly included in speech representations (Johnson, 1995). For both humans and primates, then, we therefore suggest that examining the simpler, fundamental components of a communication system is a necessary prerequisite for understanding the principles that govern its more complex functions.

ACKNOWLEDGMENTS

The authors benefited significantly from discussions with, and helpful manuscript comments from Jo-Anne Bachorowski, Dorothy Cheney, Tecumseh Fitch, Allen Neuringer, Don Owings, Peter Rodman, Robert Seyfarth, and Nicholas Thompson. Thanks go to Michael Graham for donating the drawing of a rhesus monkey head shown in Figure 1, to Robert Seyfarth and Dorothy Cheney, who recorded the baboon calls used here, and to Don Owings for pointing out the work of R. Caldwell and colleagues. Chapter preparation was partially supported by awards from the Dean's Development Fund at Reed College to M.J.O. and the NSERC of Canada to D. R.

REFERENCES

- Baer, T., Sasaki, C., & Harris, K. S. (1986). *Laryngeal function in phonation and respiration*. Boston, MA: College-Hill Press.
- Baken, R. J. (1987). *The clinical measurement of speech and voice*. Boston, MA: College-Hill Press.
- Bauers, K. A., & de Waal, F. B. M. (1991). "Coo" vocalizations in stump-tailed macaques: A controlled functional analysis. *Behaviour*, *119*, 143–160.
- Bolles, R. C., & Beecher, M. D. (1988). *Evolution and learning*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Brown, C. H., Gomez, R., & Waser, P. M. (1995). Old World monkey vocalizations: Adaptation to the local habitat? *Animal Behaviour*, *50*, 945–961.
- Caldwell, R. (1986). The deceptive use of reputation by stomatopods. In R. W. Mitchell & N. S. Thompson (Eds.), *Deception: Perspectives on human and nonhuman deceit* (pp. 129–145). New York: State University of New York Press.
- Cheney, D. L., & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, *28*, 362–367.
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago, IL: University of Chicago Press.
- Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour*, *50*, 249–257.
- Cynx, J., & Clark, S. J. (in press). The laboratory use of conditional and natural responses in the study of avian perception. In S. L. Hopp, M. J. Owren, & C. S. Evans (Eds.), *Animal acoustic communication: Sound analysis and research methods*. Heidelberg: Springer-Verlag.

- Deacon, T. (1989). The neural circuitry underlying primate calls and human language. *Human Evolution*, *4*, 367–401.
- Domjan, M. (1992). Adult learning and mate choice: Possibilities and experimental evidence. *American Zoologist*, *32*, 48–61.
- Domjan, M. (1993). *Domjan and Burkhardt's: The principles of learning and behavior*, (3rd ed.). Pacific Grove, CA: Brooks/Cole.
- Domjan, M., & Hollis, K. L. (1988). Reproductive behavior: A potential model system for adaptive specializations in learning. In R. C. Bolles & M. D. Beecher (Eds.), *Evolution and learning* (pp. 213–327). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Fernald, A. (1992). Human maternal vocalizations to infants as biologically relevant signals: An evolutionary perspective. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 391–428). New York: Oxford University Press.
- Fernald, A., & Kuhl, P. (1987). Acoustic determinants of infant preference for motherese speech. *Infant Behavior and Development*, *10*, 279–293.
- Fitch, W. T. (1994). *Vocal tract length perception and the evolution of language*. Unpublished doctoral dissertation, Brown University, Providence, RI.
- Fitch, W. T. (1997). Vocal tract length and formant frequency dispersion correlate with body size in rhesus monkeys. *Journal of the Acoustical Society of America*.
- Fitch, W. T., & Hauser, M. D. (1995). Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on 'honest' advertisement. *American Journal of Primatology*, *37*, 191–219.
- Gould, J. L. (1986). The biology of learning. *Annual Review of Psychology*, *37*, 163–192.
- Gouzoules, H., Gouzoules, S., & Ashley, J. (1995). Representational signaling in non-human primates vocal communication. In E. Zimmermann, J. Newman, & U. Jürgens (Eds.), *Current topics in primate vocal communication* (pp. 235–252). New York: Plenum Press.
- Gouzoules, H., Gouzoules, S., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: Representational signaling in the recruitment of agonistic aid. *Animal Behaviour*, *32*, 182–193.
- Gouzoules, H., Gouzoules, S., & Marler, P. (1986). Vocal communication: A vehicle for the study of social relationships. In R. G. Rawlins & M. J. Kessler (Eds.), *The Cayo Santiago macaques: History, behavior, and biology* (pp. 111–129). Albany: State University of New York Press.
- Green, S. (1975). Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study. In L. A. Rosenblum (Ed.), *Primate behavior, Vol. 4* (pp. 1–102). New York: Academic Press.
- Green, S., & Marler, P. (1979). The analysis of animal communication. In P. Marler & J. G. Vandenbergh (Eds.), *Handbook of behavioral neurobiology, Vol. 3: Social behavior and communication* (pp. 73–158). New York: Plenum Press.
- Halpern, D. L., Blake, R., & Hillenbrand, J. (1986). Psychoacoustics of a chilling sound. *Perception & Psychophysics*, *39*, 77–80.
- Hauser, M. D. (1992). Articulatory and social factors influence the acoustic structure of rhesus monkey vocalizations: A learned mode of production? *Journal of the Acoustical Society of America*, *91*, 2175–2179.
- Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: Effects of phylogeny, body weight and social context. *American Naturalist*, *142*, 538–542.
- Hauser, M. D. (1996). *The evolution of communication*. Cambridge, MA: MIT Press.
- Hauser, M. D., Evans, C. S., & Marler, P. (1993). The role of articulation in the production of rhesus monkey, *Macaca mulatta*, vocalizations. *Animal Behaviour*, *45*, 423–433.
- Hienz, R. D., & Brady, J. V. (1988). The acquisition of vowel discriminations by nonhuman primates. *Journal of the Acoustical Society of America*, *84*, 186–194.
- Hienz, R. D., Turkkan, J. S., & Harris, A. H. (1982). Pure tone thresholds in the yellow baboon (*Papio cynocephalus*). *Hearing Research*, *8*, 71–75.

- Hinde, R. A. (1966). *Animal behaviour: A synthesis of ethology and comparative psychology*. New York: McGraw-Hill.
- Hinde, R. A. (1981). Animal signals: Ethological and games-theory approaches are not incompatible. *Animal Behaviour*, *29*, 535–542.
- Hollis, K. L. (1984). The biological function of Pavlovian conditioning: The best defense is a good offense. *Journal of Experimental Psychology: Animal Learning and Behavior*, *10*, 413–425.
- Hollis, K. L., Cadioux, E. L., & Colbert, M. M. (1989). The biological function of Pavlovian conditioning: A mechanism for mating success in the blue gourami (*Trichogaster trichopterus*). *Journal of Comparative Psychology*, *103*, 115–121.
- Johnson, K. (1995). Talker variability in vowel perception. *Journal of the Acoustical Society of America*, *98*, 2949–2950.
- Johnson, K., & Mullenix, J. W. (Eds.). (1997). *Talker variability in speech processing*. San Diego: Academic Press.
- Kaplan, P. S., Goldstein, M. H., Huckleby, E. R., Owren, M. J., & Panneton Cooper, R. (1995). Dishabituation of visual attention in infant- versus adult-directed speech: Effects of frequency modulation and spectral composition. *Infant Behavior and Development*, *18*, 209–223.
- Kaplan, P. S., & Owren, M. J. (1994). Dishabituation of infant visual attention in 4-month-olds by infant-directed frequency-modulated sweeps. *Infant Behavior and Development*, *17*, 347–358.
- Krebs, J. R., & Dawkins, R. (1984). Animal signals: Mind-reading and manipulation. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (2nd ed., pp. 380–402). Sunderland, MA: Sinauer Associates.
- Leger, D. W. (1993). Contextual sources of information and responses to animal communication signals. *Psychological Bulletin*, *113*, 295–304.
- Lieberman, P. (1975). *On the origins of language: An introduction to the evolution of human speech*. New York: Macmillan Publishing.
- Marler, P. (1975). On the origin of speech from animal sounds. In J. F. Kavanaugh & J. E. Cutting (Eds.), *The role of speech in language* (pp. 11–37). Cambridge, MA: MIT Press.
- Marler, P., Evans, C. S., & Hauser, M. D. (1992). Animal signals: Motivational, referential, or both? In H. Papoušek, U. Jürgens, & M. Papoušek (Eds.), *Nonverbal vocal communication: Comparative and developmental approaches* (pp. 66–86). New York: Cambridge University Press.
- Marler, P., & Terrace, H. (1984). *The biology of learning*. Berlin: Springer-Verlag.
- Mason, W. A. (1979). Wanting and knowing: A biological perspective on maternal deprivation. In E. Thoman, (Ed.), *Origins of the infant's social responsiveness* (pp. 225–249). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Miller, J. D. (1989). Auditory-perceptual interpretation of the vowel. *Journal of the Acoustical Society of America*, *85*, 2114–2134.
- Moody, D. B., May, B. J., Cole, D. M., & Stebbins, W. C. (1986). The role of frequency modulation in the perception of complex stimuli by primates. *Experimental Biology*, *45*, 219–232.
- Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, *111*, 855–869.
- Morton, E. S. (1982). Grading, discreteness, redundancy, and motivation-structural rules. In D. E. Kroodsma & E. H. Miller (Eds.), *Acoustic communication in birds* (pp. 183–212). New York: Academic Press.
- Owings, D. H. (1994). How monkeys feel about the world: A review of "How monkeys see the world." *Language & Communication*, *14*, 15–30.
- Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology*, *26*, 389–406.
- Owren, M. J., Hopp, S. L., Sinnott, J. M., & Petersen, M. R. (1988). Absolute auditory thresholds in three Old World monkey species (*Cercopithecus aethiops*, *C. neglectus*, *Macaca fuscata*) and humans. *Journal of Comparative Psychology*, *102*, 99–107.

- Owren, M. J., & Linker, C. D. (1995). Some analysis techniques that may be useful to acoustic primatologists. In E. Zimmermann, J. Newman, & U. Jürgens (Eds.), *Current topics in primate vocal communication* (pp. 1–27). New York: Plenum Press.
- Owren, M. J., Seyfarth, R. M., & Cheney, D. L. (1997). The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*): Implications for production processes. *Journal of the Acoustical Society of America*, *101*, 2951–2963.
- Papoušek, M., Papoušek, H., & Symmes, D. (1991). The meanings and melodies in motherese in tone and stress languages. *Infant Behavior and Development*, *14*, 415–440.
- Pisoni, D. B., & Lively, S. E. (1995). Variability and invariance in speech perception: A new look at some old problems in perceptual learning. In W. Strange (Ed.), *Speech perception and linguistic experience* (pp. 433–459). New York: York Press.
- Prosen, C. A., Moody, D. B., Sommers, M. S., & Stebbins, W. C. (1990). Frequency discrimination in the monkey. *Journal of the Acoustical Society of America*, *88*, 2152–2158.
- Provine, R. R. (1996). Laughter. *American Scientist*, *84*, 38–45.
- Rendall, D. (1996). *Social communication and vocal recognition in free-ranging rhesus monkeys (Macaca mulatta)*. Unpublished doctoral dissertation, University of California, Davis.
- Rendall, D., Owren, M. J., & Rodman, P. S. (in press). Rhesus monkey vocalizations: Individuality, vocal recognition, and the determinants of acoustic design. *Journal of the Acoustical Society of America*.
- Rendall, D., Rodman, P. S., & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, *51*, 1007–1015.
- Rescorla, R. A. (1988a). Behavioral studies of Pavlovian conditioning. *Annual Review of Neuroscience*, *11*, 329–352.
- Rescorla, R. A. (1988b). Pavlovian conditioning: It's not what you think it is. *American Psychologist*, *43*, 151–160.
- Roitblat, H. L., & von Fersen, L. (1992). Comparative cognition: Representations and processes in learning and memory. *Annual Review of Psychology*, *43*, 671–710.
- Rubin, P., & Vatikiotis-Bateson, E. (in press). Measuring and modeling speech production. In S.L. Hopp, M.J. Owren & C.S. Evans (Eds.) *Animal acoustic communication: sound analysis and research methods*. Heidelberg: Springer-Verlag.
- Schön Ybarra, M. (1995). A comparative approach to the nonhuman primate vocal tract: Implications for sound production. In E. Zimmermann, J. D. Newman, & U. Jürgens (Eds.), *Current topics in primate vocal communication* (pp. 185–198). New York: Plenum Press.
- Schwartz, B. (1989). *Psychology of learning and behavior* (3rd ed.). New York: W. W. Norton & Company.
- Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development*, (pp 249–273). New York: Cambridge University Press.
- Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (1996). The form and function of post-conflict interactions between female baboons. *Animal Behaviour*, *52*, 259–268.
- Sinnott, J. M. (1989). Detection and discrimination of synthetic English vowels by Old World monkeys (*Cercopithecus*, *Macaca*) and humans. *Journal of the Acoustical Society of America*, *86*, 557–565.
- Sinnott, J. M., & Brown, C. H. (1993). Effects of varying signal and noise levels on pure-tone frequency discrimination in humans and monkeys. *Journal of the Acoustical Society of America*, *93*, 1535–1540.
- Sinnott, J. M., Owren, M. J., & Petersen, M. R. (1987a). Auditory frequency discrimination in primates: Species differences (*Cercopithecus*, *Macaca*, *Homo*) and humans. *Journal of Comparative Psychology*, *101*, 126–131.

- Sinnott, J. M., Owren, M. J., & Petersen, M. R. (1987b). Auditory duration discrimination in Old World monkeys (*Macaca, Cercopithecus*) and humans. *Journal of the Acoustical Society of America*, 82, 465–470.
- Sinnott, J. M., Petersen, M. R., & Hopp, S. L. (1985). Frequency and intensity discrimination in humans and monkeys. *Journal of the Acoustical Society of America*, 78, 1977–1985.
- Smith, W. J. (1977). *The behavior of communicating*. Cambridge, MA: Harvard University Press.
- Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (1987). *Primate societies*. Chicago: University of Chicago Press.
- Snowdon, C. T. (1986). Vocal communication. In G. Mitchell & J. Erwin (Eds.), *Comparative primate biology, Volume 2A: Behavior, conservation, and ecology* (pp. 495–530). New York: Liss.
- Sommers, M. S., Moody, D. B., & Prosen, C. A. (1992). Formant frequency discrimination by Japanese macaques (*Macaca fuscata*). *Journal of the Acoustical Society of America*, 91, 3499–3510.
- Stebbins, W. C. (1973). Hearing of Old World monkeys (Cercopithecinae). *American Journal of Physical Anthropology*, 38, 357–364.
- Stebbins, W. C., & Berkley, M. A. (Eds.). (1990). *Comparative perception, Vol. II: Complex signals*. New York: John Wiley & Sons.
- Stebbins, W. C., & Moody, D. B. (1994). How monkeys hear the world: Auditory perception in nonhuman primates. In R. R. Fay & A. N. Popper (Eds.), *Comparative hearing: Mammals*. Berlin: Springer-Verlag.
- Steklis, H. D., & Raleigh, M. J. (Eds.). (1979). *Neurobiology of social communication in primates: An evolutionary perspective*. New York: Academic Press.
- Titze, I. R. (1994). *Principles of voice production*. Englewood Cliffs, NJ: Prentice-Hall.
- Todt, D., Goedeke, P., & Symmes, D. (Eds.). (1988). *Primate vocal communication*. Berlin: Springer-Verlag.
- Turkhan, J. S. (1989). Pavlovian conditioning: The new hegemony. *Behavioral and Brain Sciences*, 12, 121–179.
- Wassermann, E. A. (1993). Comparative cognition: Beginning the second century of the study of animals intelligence. *Psychological Bulletin*, 113, 211–228.
- Werker, J., & McLeod, P. (1989). Infant preference for both male and female infant-directed talk: A developmental study of attentional and affective responsiveness. *Canadian Journal of Psychology*, 43, 230–246.
- Zeskind, P. S., & Lester, B. (1978). Acoustic features and auditory perception of the cries of newborns with prenatal and perinatal complications. *Child Development*, 49, 580–589.
- Zimmermann, E., Newman, J., & Jürgens, Ü. (Eds.). (1995). *Current topics in primate vocal communication*. New York: Plenum Press.