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Special Issue:
Acoustic Interaction of Animal Groups:
Signaling in Noisy and Social Contexts

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Special Issue: Acoustic Interaction of Animal Groups: Signaling in Noisy and Social Contexts

Guest Editors: Joshua J. Schwartz, Todd M. Freeberg,
and Andrea Megala Simmons

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INTRODUCTION

Acoustic Interaction in Animal Groups: Signaling in Noisy and Social Contexts

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It has long been known that individuals of many species vocally communicate with one another in noisy environments and in rich contexts of social interaction. It has recently become clear that researchers interested in understanding acoustic communication in animal groups must study vocal signaling in these noisy and socially complex settings. Furthermore, recent methodological advances have made it increasingly clear that the authors can tackle these more complex questions effectively. The articles in this Special Issue stem from a Symposium held at the June 2006 meeting of the Acoustical Society of America, and illustrate some of the taxonomic and methodological diversity in studies aimed at understanding how acoustic communication functions in social grouping. This introduction to the Special Issue provides a brief overview of the articles and key ideas in this field of inquiry, and suggests some future directions to take the field to help us understand how social pressures in animal groups may influence, and be influenced by, acoustic signals.

Keywords: acoustic signals, vocal communication, eavesdropping, social interactions

Over the past few decades, research has dramatically expanded our knowledge of acoustic communication in animal groups as data have been gathered to address long-standing questions, as well as more recently articulated ones. Moreover, technical advances have improved our ability to address hypotheses that formerly would have proven extremely difficult, if not impossible, to tackle. To provide an opportunity to discuss such developments, a symposium was held at the June 2006 meeting of the Acoustical Society of America. It was impossible to include all the researchers whose work spans the huge array of topics encompassed by the purposefully broad title of our symposium. However, the symposium attracted people doing excellent science that often incorporated new perspectives and methodological approaches. The taxa discussed included insects, fish, amphibians, birds, and mammals. Most of the speakers are contributors to this special issue of the *Journal of Comparative Psychology*.

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Our own fascination with the subject of this issue goes back to the beginning of our research careers. For Schwartz, this occurred about 28 years ago when he began his doctoral research on communication in treefrogs in a flooded meadow in Panama. In addition to being impressed by the painfully loud chorus produced each evening by males in the multispecies assemblage, he and Kent Wells were immediately struck by the temporal structure of chorusing of two of the species. Males of *Hyla microcephala*, the more abundant and louder species, structured their calling into bouts lasting approximately 5 to 25 seconds. During the relatively quiescent interbout intervals, males of the second species, *H. ebraccata*, concentrated their calling (Schwartz & Wells, 1983a). Similar behavior had been reported by Littlejohn and Martin (1969) in unrelated anurans halfway around the world, and seemed to be an adaptation that enabled males of one species to reduce acoustic interference with the other species and thus improve their ability to attract potential mates. In a set of fairly straightforward experiments with both males and females, Schwartz and Wells (1983a, 1983b) obtained data consistent with this hypothesis. In response to broadcasts of recordings of heterospecific choruses and appropriately filtered noise, males of *H. ebraccata* reduced their calling rate as well as their proportion of multinote and aggressive calls. The last two changes suggested that the calls of the neighbors of test subjects were masked during chorus playbacks. Females of *H. ebraccata*, in turn, discriminated against conspecific calls that were overlapped by broadcasts of *H. microcephala* chorus recordings. Subsequent research addressed aspects of call- and note-timing in these two species on a much finer scale, as well as hypotheses that could explain the organization of *H. microcephala* choruses into bouts (reviewed in Schwartz, 2001). Addressing many of these questions required the creation of both hardware and software to monitor the calling dynamics in choruses

of calling males accurately. Of course, call-timing interactions represent just one category of the fascinating smorgasbord of acoustic interactions that occur in groups of animals. The bottom line was that Schwartz was hooked not only on studying anuran communication at the level of dyads, but especially on the challenges to frogs posed by communication in aggregations.

For Freeberg, the interest in vocal communication in social groups began with his graduate training at Indiana University in the laboratory of Meredith West and Andrew King, studying different populations of brown-headed cowbirds, *Molothrus ater*. Early studies tested the influence of social experience on the development of songs and of singing in male cowbirds, employing the traditional approach of housing young males in sound isolation chambers to control the males' social and acoustic experiences. Quite unsurprisingly, young males housed with heterospecifics developed deficient songs as assayed by female copulatory responses to song playbacks, compared to young males housed with female conspecifics (Freeberg, King, & West, 1995; West, King, & Freeberg, 1996). Thanks in part to a timely visit and methodological suggestion by the late Gilbert Gottlieb, the research moved beyond the traditional approach, however, and tested the actual courtship behavior of those young males. Quite surprisingly, the effectiveness of their songs did not necessarily predict the effectiveness of those males at courting and copulating with females. Further manipulations of the social environments of those males for an additional year pointed to the importance of social interaction with adult males to the development of courtship effectiveness (Freeberg et al., 1995; West et al., 1996). The importance of the social group to the development of vocal signals—and, perhaps more importantly, of vocal signaling—was tested in a series of studies of the social transmission of population-level variation in courtship behavior and mating preferences (reviewed in Freeberg, 2004). Furthermore, the importance of research methodologies different enough (and apparatus and housing facilities large enough) to provide for the complexity of social interactions among group members was made clear to Freeberg by this work.

In the remainder of this introduction to the Special Issue, we would like to touch on some directions for future investigation (focusing on work in anurans and in birds), and will briefly describe the articles that follow. Although some of the questions we mention have received a fair amount of attention, we suggest some novel research strategies as well as some additional questions to consider. The questions we address are relevant to taxa other than anurans and birds and, in fact, some of these are discussed in the papers that follow, as well as in contributions to the recent volume, *Animal Communication Networks* (McGregor, 2005).

In frogs, an area ripe for study is the significance, if any, of eavesdropping (sensu Peake, 2005). It is easy to imagine how eavesdropping could be significant during male-male interactions and female mate choice (see Grafe, 2005 for a detailed treatment). Males of many species attend to the calls of neighboring advertising males and may not only modify their call timing, as mentioned earlier, but also adjust the attractiveness to conspecific females of their vocal output (e.g., through elevations in call rate, call duration, or call complexity; Gerhardt & Huber, 2002; Wells, 2007). We need to know not only what are the domains in the chorus over which males are responsive in the latter manner but also whether they modify their calling in response to cues obtained

by eavesdropping on males during the final stages of female approach. At this time, a male who has detected an approaching female may, evidently to improve his chance of success, dramatically increase his calling effort to a degree that is probably only briefly sustainable. For example, in *H. versicolor*, call duration can jump to 70 pulses (about 4 times the typical average) and calling effort more than double (Schwartz, personal observations). How good are nearby males at detecting this brief change and do they quickly ratchet up their own calling effort? If so, how often are these efforts rewarded? Males also may interact agonistically by exchanging aggressive vocalizations and even by using physical combat. Do other males attend to these contests and respond differently to winners and losers? For example, might males be more likely to intrude on the territories or calling space of losers? Do females listen in as well? How might the outcome of aggressive encounters impact on their choices?

As articulated by Bee and Micheyl in this issue, we also need to know more about how both males and females acquire information from the often extremely complex acoustic scene present in the chorus (also see Gerhardt & Huber, 2002, for a review of current knowledge). What is the relative importance of spectral and temporal attributes in calls to this process? How does the spatial distribution of individuals in 3-dimensions contribute to scene analysis? Additional data are needed on the extent to which capabilities of (or constraints imposed by) the peripheral and central auditory system of males and females influence how males distribute themselves and time their calls. How might the spatial and temporal structure of the chorus influence the behavior of receptive females within it?

Without a sufficient population of males at a particular breeding area, chorusing activity may not arise (Brooke, Alford, & Schwarzkopf, 2000). Are there additional transitions in the behavior of the chorus that occur with increases in male number or density? How might acoustic phenomena that emerge from signaling in a chorus setting feedback on the individuals within these aggregations? What mechanisms are most important? For example, the bout structure of *H. microcephala* choruses may be in part linked not only to energetic limitations of males (Schwartz, Ressel, & Bevier, 1995) but also to neural processes controlling fine-scale aspects of call-timing of individual males. Indeed, patterns of both call synchrony and call alternation may be epiphenomena of such mechanisms (Greenfield, 2005), and we need to test this hypothesis in more species of chorusing organisms.

Studies of chorusing in anurans (and insects) pointed to the powerful role of the social context in influencing acoustic signaling decades before the importance of the social context was formally addressed by current interests in communication networks in birds and mammals (see McGregor, 2005). Much of the current focus of communication networks is on the functional implications of individuals attending to information in their social contexts. For example, using song playbacks, Mennill, Ratcliffe, and Boag (2002) demonstrated that female black-capped chickadees, *Poecile atricapillus*, eavesdrop on acoustic interactions between their mates and other males in the local population, and gain extrapair fertilizations based in part on how they perceive their mates to have fared in "winning" or "losing" status in those acoustic interactions (see also Otter et al., 1999 for evidence of eavesdropping in possible female assessment of males in great tits, *Parus major*; and Peake, 2005 for a review). How do the experi-

ences of individuals and the particular nature of the immediate communication network impact the way individuals respond to information they gain through eavesdropping? How do these factors impact the behavior of the individuals producing acoustic signals in these environments? Can signalers be strategic and more directional in signal production to minimize possible eavesdropping in certain contexts (e.g., McGregor, Otter, & Peake, 2000)?

Researchers have long been interested in bird song, and there is a general view that social experience must play an important role in how young birds develop their songs. However, only recently have researchers really begun to work at manipulating social contextual variables in experimental studies of song development (Beecher & Brenowitz, 2005; Marler & Slabbekoorn, 2004). Furthermore, how do the earliest vocal signaling interactions between young birds (or young animals in general) and their parents influence the vocal and nonvocal social behavioral development of those young individuals? Recent evidence in brown-headed cowbirds indicates that the social structure of cowbird groups influences the types of interaction that are possible between young and adult individuals of both sexes, and plays a role in the social preferences of young females and the song (and singing) development of young males (Freed-Brown, King, Miller, & West, 2006; Miller, Freed-Brown, White, King, & West 2006). The role that group structure plays in vocal signaling development in other avian and nonavian species is largely an open question—perhaps manipulation of social contexts may reveal more plasticity in the development of such signals than has been documented to date (for examples of the influence of social experience on primate vocal behavior and sexual behavior, see Snowden & de la Torre, 2002, and Mason, 1960, respectively). Finally, the role that vocal signaling might play in the development and maintenance of group structures is an exciting direction to take our research. For example, recent work in baboons (*Papio cynocephalus*) beautifully demonstrates how a grunt vocalization by an individual that has just acted aggressively toward another (or by the kin of such an aggressor) serves to help reconcile the social relationship between the aggressor and victim (Cheney & Seyfarth, 1997; Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007).

We are beginning to tackle many of the questions raised above, and many of the articles in this Special Issue are beginning to provide some answers. Bee and Micheyl discuss a topic of particular relevance to communication by frogs and other organisms that call in dense assemblages: the cocktail party problem. They provide a necessarily succinct yet informative historical review of the literature and cogently argue for more research by students of animal communication. Their paper also provides a lucid primer on auditory scene analysis as well as illustrative examples from work on anurans. Mechanistically, the responses of neurons at both the individual and population level will ultimately determine whether, for example, signals can be recognized and discriminated. Ronacher et al. examined the spiking patterns of auditory neurons in grasshoppers and show how these can meet the response properties required for dependable differentiation of the calls of different individuals. Furthermore, in agreement with data on other species, their analysis suggests a shift at different levels of the auditory system in the relative importance of neural coding of modulated signals based on spike timing and spike rate.

A female anuran entering a chorus to select a mate can face the problems of discriminating conspecific males from heterospecific

males and of choosing among an array of males of her own species. Often different attributes of calls facilitate these two tasks, and discerning these important acoustic cues under conditions of high ambient noise and acoustic clutter can be a challenge. Acoustic cues must also be used by females to estimate the location of males, and this information may affect their mate choice decisions. In barking treefrogs, *H. gratiiosa*, a male's distance from a female is influential, but it has not been clear which of the potential acoustic sources of distance information were most important. Murphy used a series of ingenious multispeaker phonotaxis tests to evaluate reasonable hypotheses. His results refute some of the more obvious of these and implicate a more complex mechanism. Simmons et al. have employed a technically sophisticated system (that has also been used to track echolocating bats) to study vocal interactions in choruses of the bullfrog, *Rana catesbeiana*. Two 'cubes', each housing multiple microphones, were used to record the calls of males; thus data acquisition does not depend on running microphone cables through the habitat. Signal processing, mimicking aspects of the mammalian auditory system, was used to pinpoint the location of callers and segregate vocalizations of individuals. The data reveal intriguing patterns of call timing and suggest substructuring of the chorus based on male proximity.

The ability of signalers and receivers to communicate using sound is, of course, not only a function of the ambient acoustic environment but also of the capacity of the sensory system to acquire and appropriately encode necessary information. Signal detection theory (SDT) provides an extremely powerful framework within which to examine constraints on effective communication (Wollerman & Wiley, 2002). A prediction of SDT is that under the noisy conditions of anuran and insect choruses, the task of the sensory system can be made easier by behavioral adjustments of the animals themselves, including the use of more exaggerated signals.

Males of the gray treefrog, *Hyla versicolor*, increase call duration while simultaneously reducing call rate in response to the calls of other males. Schwartz et al. present the results of experiments designed to test one explanation dealing with the selective advantage of this behavior. This 'interference risk hypothesis' is related to the problem of transmitting attractive signals to potential mates in an environment replete with calling males. However, the problem addressed is not masking per se but rather that of perceived alteration of call elements critical to call recognition by females. Greenfield and Schul discuss how receiver perceptual biases and signal production mechanisms in choruses of insects can lead to the emergence of calling alternation or calling synchrony among neighbors in a group. In some cases, the adaptive significance of these temporal patterns of calling are known and competition or cooperation between signalers may contribute to the temporal pattern that emerges. Greenfield and Schul illustrate these points using data from two species of katydids while describing models of signaling based on insect psychoacoustic parameters that can lead to such synchrony or alternation of calls.

Much of the work on choruses, and the theory that has emerged from such work, has focused on acoustically interacting individuals separated in space. Horn approaches the chorus question from the standpoint of the confines of a nest of begging nestling songbirds, and provides an overview of his experimental work on the begging interactions of nestling tree swallows, *Tachycineta bicolor*. This work has found that nestlings can alter their calling

rates and calling amplitude when begging, depending on the kind of acoustic interference they face in the nest. This work points to some of the developmental implications of this signaling, addressing the ways in which information in begging calls can influence the behavior of other nestlings and of parents. How acoustic signals can impact the movement behavior of group members is addressed in a very different context by Janik and Quick. Tracking wild bottlenose dolphins, *Tursiops truncatus*, with an array of microphones to allow for the identification of individual callers, the authors provide evidence that whistled vocal exchanges among individuals can coordinate the joining of one dolphin subgroup with another.

The vocal behavior of individuals obviously impacts the social behavior of other individuals in a group of animals. It is also becoming clear that the social behavior occurring within groups—indeed, the social structure of the group—can impact the vocal behavior of individuals in the group. Freeberg and Harvey review work indicating that differences in the number of individuals in groups of Carolina chickadees, *Poecile carolinensis*, can influence the structural complexity of individuals' calls. The impact of social groups and social relationships on the vocal signals of individuals is also demonstrated by the phenomenon of vocal convergence, in which vocal signals of individuals within a group tend to become acoustically more similar to one another over time. Tyack reviews work on vocal convergence and the social bonds that may give rise to it, and discusses some of the possible functions, and evolutionary implications, of the sharing of vocalizations.

To conclude, the articles in this Special Issue review extensive bodies of work in diverse taxa illustrating links between social groups of animals and their acoustic signals. This work is helping us to understand how acoustic signals influence behavior of members of a group and how the structures of interaction between members of a group can influence acoustic signals of individuals. Each article furthermore raises important issues that future work will need to address if we truly wish to get at the heart of how acoustic interactions socially function in animal groups.

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The Cocktail Party Problem: What Is It? How Can It Be Solved? And Why Should Animal Behaviorists Study It?

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Animals often use acoustic signals to communicate in groups or social aggregations in which multiple individuals signal within a receiver's hearing range. Consequently, receivers face challenges related to acoustic interference and auditory masking that are not unlike the human *cocktail party problem*, which refers to the problem of perceiving speech in noisy social settings. Understanding the sensory solutions to the cocktail party problem has been a goal of research on human hearing and speech communication for several decades. Despite a general interest in acoustic signaling in groups, animal behaviorists have devoted comparatively less attention toward understanding how animals solve problems equivalent to the human cocktail party problem. After illustrating how humans and nonhuman animals experience and overcome similar perceptual challenges in cocktail-party-like social environments, this article reviews previous psychophysical and physiological studies of humans and nonhuman animals to describe how the cocktail party problem can be solved. This review also outlines several basic and applied benefits that could result from studies of the cocktail party problem in the context of animal acoustic communication.

Keywords: acoustic communication, animal communication

In many animals, acoustic communication occurs in large groups or aggregations of signaling individuals (Gerhardt & Huber, 2002; Greenfield, 2005; Kroodsma & Miller, 1996; McGregor, 2005; this issue). It is important to appreciate that the sounds produced by multiple signalers in groups, as well as other biotic and abiotic sources of noise and acoustic reflections from objects in the environment, are sound pressure waves that add together to form a composite pressure waveform that impinges on a receiver's hearing organs. Thus, signaling in groups poses a number of special problems for receivers in terms of detecting and classifying signals (Brumm & Slabbekoorn, 2005; Hulse, 2002; Klump, 1996; Langemann & Klump, 2005; Wiley, 2006). These problems, and their solutions, are our concern here. For humans, solutions to these problems rest, in part, on the auditory system's ability to parse the composite acoustic waveform generated by multiple sources into perceptually coherent representations—termed *auditory objects*, *auditory images*, or *auditory streams*—that represent different sound sources in the acoustic scene (Bregman, 1990; Van Valkenburg & Kubovy, 2004; Yost, 1991).

One well-known example of a problem in human auditory scene analysis (Bregman, 1990) is the aptly named *cocktail party prob-*

lem (Cherry, 1953), which refers to the difficulty we sometimes have understanding speech in noisy social settings (reviewed in Bronkhorst, 2000; Yost, 1997). In this article, we discuss issues relating to auditory scene analysis and the cocktail party problem that have a long history in studies of human hearing and speech communication but have received less attention in the study of animal acoustic communication. The take-home messages from this article are (a) that many of the sensory solutions to the human cocktail party problem represent potentially important mechanisms underlying acoustic communication in nonhuman animals and (b) that the study of these mechanisms has important implications for our understanding of animal acoustic communication.

This article is organized around three questions. In the first section, we pose the question, What is the cocktail party problem? Here, we more explicitly outline the issues at hand and show that nonhuman animals also encounter and solve cocktail-party-like problems. In the second section, we ask, How can the cocktail party problem be solved? In this section, we draw extensively on studies of human hearing and speech perception to illustrate the diversity of mechanisms that allow humans to perceive speech in noisy social settings. We also show how many of these same auditory mechanisms operate in nonhuman animals. These studies could serve as useful heuristics to guide future research on the mechanisms of animal acoustic communication. In the third and final section we ask, Why should animal behaviorists study the cocktail party problem? Here, we raise a number of basic and applied issues to suggest the potential benefits and opportunities associated with studies of animal "cocktail parties."

The fields of study we attempt to integrate are broad; therefore, the scope of our review is necessarily broad and we make no attempt to cover any single topic in great depth. For other treatments on these topics, readers are referred to Bregman (1990, 1993, Bronkhorst (2000), Carlyon (2004), Darwin (1997), Darwin

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and Carlyon (1995), and Yost, Popper, and Fay (2007) for work in humans and to Brumm and Slabbekoorn (2005), Fay (2007), Feng and Ratnam (2000), Hulse (2002), Klump (1996, 2005), and Langemann and Klump (2005) for work in animals.

What Is the Cocktail Party Problem?

The essence of the cocktail party problem can be formulated as a deceptively simple question: "How do we recognize what one person is saying when others are speaking at the same time?" (Bronkhorst, 2000, p. 117). Finding answers to this question has been an important goal of human hearing research for several decades (see Bronkhorst, 2000, and Yost, 1997, for reviews). At the root of the cocktail party problem is the fact that the human voices present in a noisy social setting often overlap in frequency and in time and thus represent sources of direct acoustic interference and *energetic masking* that can impair the perception of speech. In addition, recent research has revealed that even those components of concurrent speech that do not overlap in frequency or time with those of the target signal can dramatically affect speech intelligibility via so-called *informational masking* (Shinn-Cunningham, Ihlefeld, Satyavarta, & Larson, 2005). The ability of concurrent speech and speechlike noise to impair speech perception is well-documented in the literature on human hearing (reviewed in Bronkhorst, 2000).

Do Animals Experience Cocktail-Party-Like Problems?

Examples of nonhuman animals that acoustically communicate in groups or large social aggregations abound in the animal behavior literature. Among the best-known examples are perhaps frog and insect choruses, the songbird dawn chorus, and flocking and colonial birds (reviewed in Hulse, 2002). For animals that acoustically communicate in such groups, the problem of perceiving acoustic signals is equivalent to the human cocktail party problem because the signals of multiple conspecifics often occur concurrently (Brumm & Slabbekoorn, 2005; Hulse, 2002; Klump, 1996). As in humans, the consequences of interference and masking for other animals include increases in signal detection thresholds and decreases in the ability to recognize and discriminate among different signal variants (Bee, 2007; Bee & Swanson, 2007; Ehret & Gerhardt, 1980; Gerhardt & Klump, 1988; Langemann, Gauger, & Klump, 1998; Lohr, Wright, & Dooling, 2003; Schwartz & Gerhardt, 1989, 1995; Wollerman, 1999; Wollerman & Wiley, 2002). Hence, humans and nonhuman animals are perhaps not so different when it comes to the problems faced when acoustically communicating in groups. For animals, we can formalize the cocktail party problem in the following question: How do animals detect and recognize conspecific signals, localize signalers, discriminate among signal types and individual signalers, and extract information from signals and signaling interactions when multiple conspecifics and heterospecifics are signaling at the same time? Note that this formalization includes the contribution of heterospecific signalers to a receiver's cocktail party problem. For many animals, the signals of heterospecifics might compound the cocktail party problem in ways that have not been considered previously in the literature on human hearing and speech communication.

Despite evidence that humans and other animals encounter problems perceiving acoustic signals in noisy groups, the cocktail party problem is not insurmountable. Personal experience tells us this is the case for humans. Field observations and playback experiments indicate that this is also the case for nonhuman animals. Consider the following examples. During their breeding seasons, frogs commonly aggregate in mixed-species choruses in which males produce loud advertisement calls (Gerhardt, 1975), and the background noise levels in a chorus can be quite high (Narins, 1982; Narins & Zelick, 1988). Nevertheless, within a chorus environment, male advertisement calls can be used by females to make adaptive mate choice decisions and by males to mediate male–male aggressive interactions (reviewed in Gerhardt & Bee, 2006; Gerhardt & Huber, 2002; Wells & Schwartz, 2006). Like frogs, songbirds communicate in noisy situations, such as the dawn chorus, and use acoustic signals for mate attraction and territory defense (Klump, 1996). The work of Hulse and others has shown that songbirds can correctly recognize the songs of a particular species and of particular individuals when these songs are digitally mixed with the songs of other species or individuals and even when they are mixed with the sounds of a dawn chorus (Benney & Braaten, 2000; Hulse, MacDougall-Shackleton, & Wisniewski, 1997; Wisniewski & Hulse, 1997). Bank swallows, cliff swallows, and king penguins are three colonial bird species for which acoustically mediated parent–offspring recognition allows parents to reunite with chicks in a large and noisy colony (Aubin & Jouventin, 1998, 2002; Beecher, 1989, 1991). Field playback tests with king penguins have revealed that chicks can detect parental calls (the signal) even when these were mixed with the calls of five other adults (the noise) at a signal-to-noise ratio of -6 dB (Aubin & Jouventin, 1998). Clearly, a diversity of animals signal in groups, and these animals both encounter and solve cocktail-party-like problems.

How Can the Cocktail Party Problem Be Solved?

The main point we wish to emphasize in this article is that effective acoustic communication will often depend heavily on the perceptual mechanisms that receivers possess for solving cocktail-party-like problems. To be sure, for many animals, both the structure of acoustic signals and the behavior of signalers represent adaptations that have evolved as a result of selection pressures associated with ameliorating cocktail-party-like problems for receivers (reviewed in Brumm & Slabbekoorn, 2005; Klump, 2005; Wiley, 2006). In this section, we focus exclusively on the receiver side of things by reviewing literature related to the perceptual processes that contribute to solving the cocktail party problem. The cocktail party problem represents a specific example of the more general task of auditory scene analysis (Bregman, 1990), which refers to the processes that form coherent and functional perceptual representations of distinct sound sources in the environment (Bregman, 1990; Hulse, 2002). In this section, we review some important topics in auditory scene analysis and describe how they relate to animal acoustic communication. We then show how several processes that function in auditory scene analysis contribute to solving the cocktail party problem in humans, and we illustrate how these same mechanisms operate in nonhuman animals.

Auditory Scene Analysis

Sequential and simultaneous integration. In his book on auditory scene analysis, Bregman (1990) proposed an important distinction between sequential integration and simultaneous integration. *Sequential integration* refers to the integration of temporally separated sounds from one sound source (e.g., syllables, words; Figure 1A) into a coherent auditory stream and the segregation of these sounds from other intervening and overlapping sounds from other sources. *Simultaneous integration* refers to the perceptual grouping of different, simultaneously occurring com-

ponents of the frequency spectrum (e.g., harmonics, speech formants; Figure 1A) into a representation of a single sound source and the segregation of these sounds from other concurrent sounds in the environment. Integration and segregation are often regarded as converse but complementary processes: When particular sound elements are integrated together, they are also segregated from other sounds (Bregman, 1990).

The acoustic signals of nonhuman animals bear two general similarities with human speech that are relevant to our discussion. First, animal acoustic signals have gross temporal structure and often comprise sequences of sounds (Figure 1B–E). Second, many

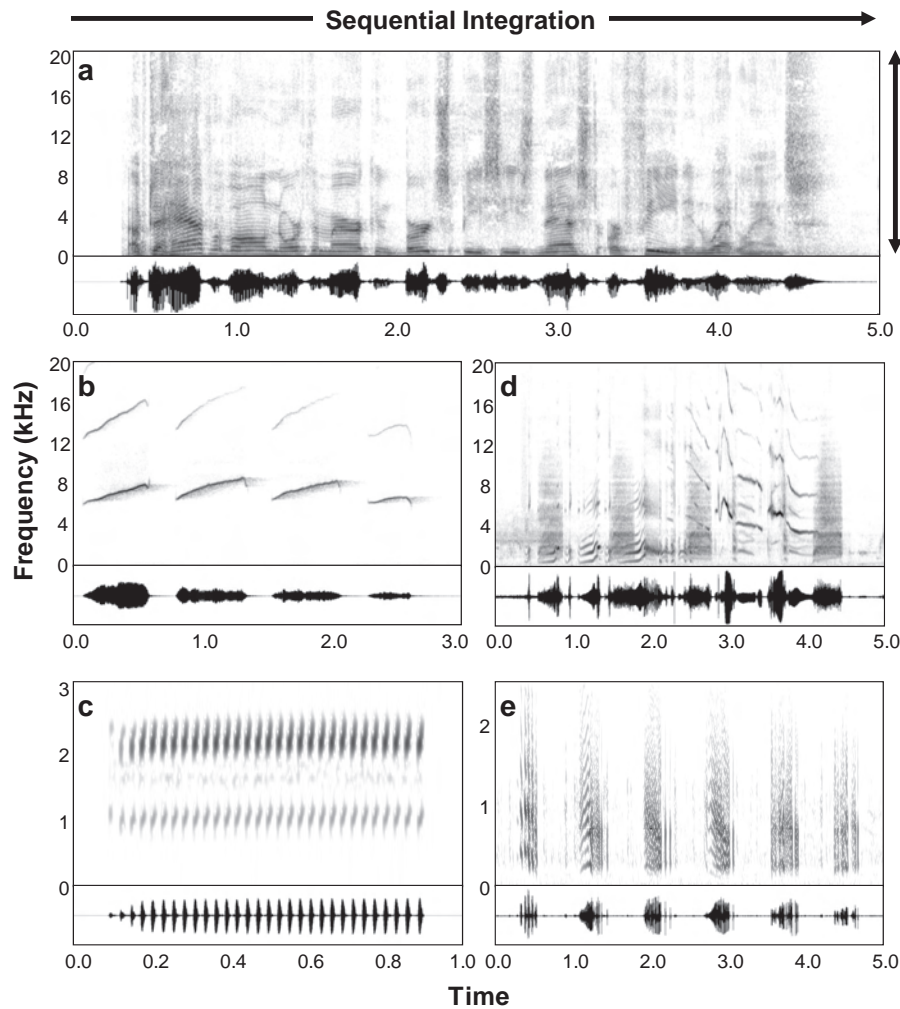


Figure 1. Spectrograms (top traces) and oscillograms (bottom traces) of animal vocalizations. (A) Human speech (“Up to half of all North American bird species nest or feed in wetlands”) spoken by President George W. Bush during an Earth Day celebration at the Laudholm Farm in Wells, Maine, on April 22, 2004 (courtesy of “The George W. Bush Public Domain Audio Archive” at <http://thebots.net/GWBushSampleArchive.htm>). (B) “Phee” calls of the common marmoset, *Callithrix jacchus* (courtesy Rama Ratnam). (C) Advertisement call of the gray treefrog, *Hyla chrysoscelis* (recorded by Mark Bee). (D) Song motif from a European starling, *Sturnus vulgaris* (courtesy Lang Elliot). (E) Portion of an advertisement call of the plains leopard frog, *Rana blairi* (recorded by Mark Bee). Note that in all cases, the vocalizations consist of sequences of sound elements (e.g., syllables and words [A], call notes [B,E], pulses [C], and song syllables [D]), many of which are comprised of simultaneous spectral components (e.g., harmonics), thus illustrating the potential necessity for sequential and simultaneous integration, as illustrated in Panel A.

animal acoustic signals are harmonic (or quasi harmonic), meaning that the frequencies of concurrent spectral components are (approximately) integer multiples of the fundamental frequency (F0) (Figure 1B–E). Hence, in the context of animal acoustic communication, receivers may often face the two basic tasks of auditory scene analysis described previously: (a) the temporally separated sounds in a sequence of signal elements produced by the same individual must be integrated over time and segregated from the overlapping, interleaved, or alternating sound sequences from other signalers, and (b) simultaneous sounds (e.g., harmonics) that originate from the same individual must be perceptually grouped together and segregated from the concurrent sounds from other signalers.

Bottom-up and top-down processing. In humans, auditory scene analysis involves both bottom-up and top-down processes (reviewed in Bregman, 1990; Carlyon, 2004; Feng & Ratnam, 2000; Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001). Bottom-up mechanisms are *stimulus driven*, meaning that they operate only or primarily on cues present in the acoustic signal itself; they are largely automatic and obligatory, meaning that they do not critically depend on attention (although this is currently a disputed issue). In contrast, top-down processes depend on a listener's prior experience and expectations and thus involve higher level cognitive processes, such as learning, memory, and attention.

Many of the bottom-up mechanisms for auditory scene analysis probably operate at relatively low levels of the auditory system and may have arisen early in the evolution of vertebrate hearing (Fay & Popper, 2000; Feng & Ratnam, 2000; Hulse, 2002; Lewis & Fay, 2004; Popper & Fay, 1997). Spectral filtering and forward suppression are examples of neural processes that may mediate important bottom-up mechanisms in auditory scene analysis. These neural processes are observed in diverse species including monkeys (Fishman, Arezzo, & Steinschneider, 2004; Fishman, Reser, Arezzo, & Steinschneider, 2001), birds (Bee & Klump, 2004, 2005), and even insects (Schul & Sheridan, 2006), and they are already present at relatively low levels of the auditory system, such as the mammalian cochlear nucleus (Pressnitzer, Micheyl, Sayles, & Winter, 2007). These facts make it very likely that bottom-up auditory scene analysis functions in vocal communication across diverse taxa.

On the other hand, top-down processes appear to operate on the output of bottom-up processes occurring at lower levels of the auditory system. The extent to which top-down processes are involved in auditory scene analysis by nonhuman animals is an interesting and important question that has not been addressed. For example, compared to fish and frogs, we might expect the operation of top-down auditory scene analysis to be more prevalent in birds and mammals, which have relatively more complex auditory systems and for which various forms of vocal learning and vocally mediated social recognition can play important roles in acoustically mediated social behaviors (Hulse, 2002). However, the generality of such a statement could be questioned given that some fish (Myrberg & Riggio, 1985) and frogs (Bee & Gerhardt, 2002) also learn to recognize individuals by voice. In what follows, it will be important to bear in mind that taxonomic differences among nonhuman animals could be reflected in potentially differ-

ent contributions of top-down versus bottom-up processes to auditory scene analysis.

Acoustic cues for sequential and simultaneous integration. Due to the physics and biomechanics of sound production, the sounds produced by a given source or individual are more likely to share particular acoustic properties in common than are the sounds produced by different sources or individuals (Bregman, 1990, 1993; Cusack & Carlyon, 2004). Auditory systems appear to evolve to exploit these cues in the analysis of acoustic scenes. As described later, sounds that share common properties are more likely to be integrated together by the auditory system (i.e., commonalities promote integration). When properties differ enough between sound elements, they probably arose from different sources (or individuals), and these elements are more likely to be assigned to different auditory objects or streams (i.e., differences promote segregation). In humans, some of the acoustic properties of sound that play important roles in auditory scene analysis include fundamental frequency (F0) and harmonic relationships among spectral components (harmonicity), temporal onsets/offsets, timbre, and patterns of amplitude modulation (reviewed in Bregman, 1990, 1993; Cusack & Carlyon, 2004; Darwin & Carlyon, 1995; Moore & Gockel, 2002). Much of what follows focuses on demonstrating how humans and other animals exploit cues related to these three acoustic properties in auditory scene analysis and in solving the cocktail party problem.

Integrating and Segregating Sequential Sounds: Auditory Streaming

In a cocktail-party-like environment, human listeners must perceptually segregate the sequences of speech sounds (e.g., syllables, words) spoken by different individuals. In other words, the auditory system must treat sounds emitted at different times by a given source as part of the same ongoing "stream," while at the same time separating those sounds from temporally adjacent sounds arising from other sources. Although these two processes involve stream integration and stream segregation, respectively, the processes that result in the formation of auditory streams are often referred to broadly as *auditory streaming* (Carlyon, 2004).

Auditory streaming can be easily demonstrated and studied in humans using stimulus sequences that consist of two tones of different frequencies, A and B, played in a repeating sequence, such as ABAB. . . or ABA–ABA–. . . (where – represents a silent gap; Figure 2A,B). The typical stimulus parameters of interest in such studies are the frequency separation (ΔF) between the A and B tones and the tone repetition time (TRT), which depends on tone duration and the intertone interval. When ΔF is relatively small (e.g., 1 semitone, or about 6%) and TRT relatively long (e.g., 5 tones/s), the percept is that of a single, coherent stream of one tone sequence that alternates in pitch (Figure 2A). In contrast, if ΔF is large (e.g., 10 semitones, or about 78%) and TRT is not too long, the percept becomes that of two separate streams corresponding to two separate sequences of A and B tones (Figure 2B). In this situation, the sensation of pitch alternation is lost, because the tones in each stream have a constant frequency and only one of the two streams can be attended at any time. These observations, which were initially reported by Miller and Heise (1950), have been confirmed and further investigated in many subsequent stud-

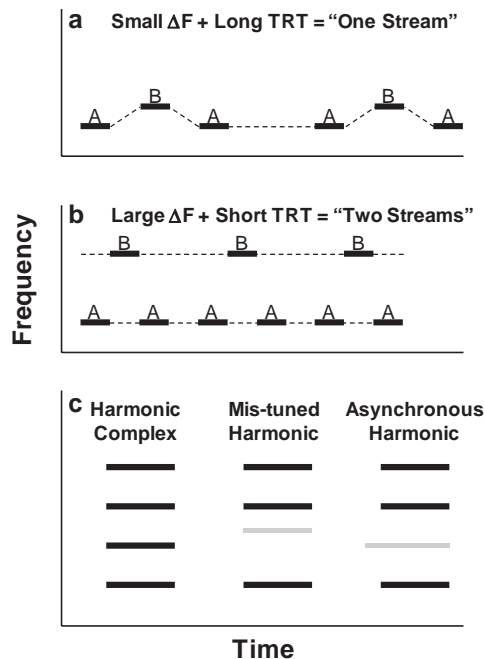


Figure 2. Schematic spectrograms illustrating experimental stimuli for investigating auditory streaming and simultaneous integration and segregation. A: An "ABA-ABA-..." tone sequence with a small difference in frequency (ΔF) between the A and B tones and a long tone repetition time (TRT); such a sequence would be perceived as a single, integrated stream of alternating tones with a galloping rhythm. B: An "ABA-ABA-..." tone sequence with a large ΔF and a short TRT; such a sequence would be perceived as two segregated streams, each with an isochronous rhythm. The dashed lines in Panels A and B indicate the percept (one vs. two streams, respectively). C: Three harmonic tone complexes showing a "normal" tone complex (left), a tone complex with a mistuned second harmonic (middle), and a tone complex with an asynchronous second harmonic that begins earlier than the other harmonics. In the later two cases, the second harmonic would likely be segregated from the rest of the integrated tone complex.

ies (reviewed in Bregman, 1990; Carlyon, 2004; Moore & Gockel, 2002).

Although highly stereotyped and simple, repeating two-tone sequences capture some essential features of the perceptual organization of more complex sound sequences. In particular, they illustrate the phenomenon of stream integration, whereby sounds are perceptually grouped or *bound* across time, yielding the percept of a coherent auditory stream that can be followed over time as a single entity. Two-tone sequences also serve to illustrate the converse phenomenon of stream segregation, whereby temporally proximal elements (e.g., the A and B tones in a sequence) are perceptually segregated, resulting in the perception of multiple streams of sounds that occur simultaneously and can be listened to selectively. In addition, with a proper choice of parameters, repeating tone sequences can be used to investigate top-down influences on the formation of auditory streams. Indeed, there is a relatively wide range of ΔF s and TRTs where the percept of one versus two streams depends on attentional factors (Carlyon, Cusack, Foxton, & Robertson, 2001; Carlyon, Plack, Fantini, & Cusack, 2003; Cusack, Deeks, Aikman, & Carlyon, 2004;

Pressnitzer & Hupe, 2006; van Noorden, 1975). However, the influence of attention is also limited; under some stimulus conditions, the percept switches back and forth between one and two streams despite the listener's efforts to maintain a percept of either integrated or segregated streams (Pressnitzer & Hupe, 2006; van Noorden, 1975).

Auditory streaming and auditory detection, discrimination, and recognition. There is often a relationship between listeners' performance in auditory perception tasks involving sound sequences and the listeners' perception of those sound sequences as either integrated or segregated streams. For example, the identification of a temporal sequence of sounds, such as a melody, is facilitated by stimulus manipulations that promote its perceptual segregation from another, temporally interleaved sequence, such as presenting the melody to different ears, in a different frequency range, or with notes differing in timbre (Bey & McAdams, 2002, 2003; Cusack & Roberts, 2000; Dowling & Fujitani, 1971; Dowling, Lung, & Herrbold, 1987; Hartmann & Johnson, 1991; Iverson, 1995; Vliegen & Oxenham, 1999). Similar findings hold for interleaved sequences of synthetic vowels generated using different F0s or simulated vocal-tract sizes (Gaudrain, Grimault, Healy, & Bera, 2007; Tsuzaki, Takeshima, Irino, & Patterson, 2007). In general, the detection or discrimination of certain target sounds among other interfering sounds is facilitated under conditions that promote the perceptual segregation of targets from interferers, especially if targets and interferers share some subset of features in common that could otherwise cause them to be confused with each other (Gockel, Carlyon, & Micheyl, 1999; Micheyl & Carlyon, 1998; Micheyl, Carlyon, Cusack, & Moore, 2005) or when they vary rapidly and unpredictably over time (Kidd, Mason, & Arbogast, 2002; Kidd, Mason, & Dai, 1995; Kidd, Mason, Deliwala, Woods, & Colburn, 1994; Micheyl, Shamma, & Oxenham, 2007). Conversely, there are some situations in which stream integration may be more advantageous than segregation. For instance, performance in the perception of the temporal order between consecutive sounds is usually higher when these sounds are perceived as part of a single stream (Bregman & Campbell, 1971; Brochard, Drake, Botte, & McAdams, 1999; Roberts, Glasberg, & Moore, 2002; Vliegen, Moore, & Oxenham, 1999).

Acoustic cues for auditory streaming. Sequences of alternating pure tones have helped to uncover some of the acoustic cues, such as ΔF and TRT, that determine whether successive sounds are likely to be integrated into a single stream or segregated into different streams (reviewed in Moore & Gockel, 2002). Recent neurophysiological studies have investigated these and other cues to discover where auditory streaming occurs in the brain (reviewed in Micheyl, Carlyon, et al., 2007). In highlighting the major role of tonotopic organization in promoting stream segregation, these neurophysiological studies are consistent with the so-called *channeling theory* of stream segregation (Beauvois & Meddis, 1996; Hartmann & Johnson, 1991). According to this theory, sounds that excite largely overlapping sets of peripheral filters (or *tonotopic channels*) tend to be heard as the same stream, whereas sounds that excite essentially nonoverlapping peripheral filters tend to be heard as different streams. Recent psychophysical studies, however, suggest that humans can even perceptually segregate sounds that excite the same peripheral channels into separate auditory streams based on difference in timbre and modulation rates (Grimault, Bacon, & Micheyl, 2002; Grimault, Micheyl, Carlyon,

Arthaud, & Collet, 2000; Vliegen et al., 1999; Vliegen & Oxenham, 1999). These findings have led to the suggestion that the auditory system takes advantage of any sufficiently salient perceptual difference between consecutive sounds to separate those sounds into different streams (Moore & Gockel, 2002).

Studies of auditory stream segregation in nonhuman animals. When sequences of repeated ABA– tone triplets are heard as a single stream, it evokes a distinctive galloping rhythm (Figure 2A); however, when the A and B tones perceptually split into two separate streams, this galloping rhythm is lost, and one hears two streams with isochronous tempi, one (A–A–A–A– . . .) three times faster than the other (–B–B– . . .; Figure 2B). Using the ABA– stimulus paradigm (Figure 2A, B) and operant conditioning techniques, MacDougall-Shackleton, Hulse, Gentner, and White (1998) took advantage of this perceived difference in rhythm between integrated and segregated streams to ask whether European starlings (*Sturnus vulgaris*) experienced stream segregation. After training starlings to discriminate between galloping and isochronous rhythms using single-frequency tone sequences, MacDougall-Shackleton et al. (1998) determined the probability that the birds would report hearing the repeating ABA– tones as a galloping sequence (one stream) or as isochronous sequences (two streams) as a function of increasing ΔF between the A and B tones. At large ΔF s, the birds more often reported hearing two streams. This result is important because it is consistent with observations in humans and provides strong evidence that at least one songbird also experiences the phenomenon of frequency-based stream segregation. Bee and Klump (2004, 2005) demonstrated neural correlates of these effects in starlings in a tonotopically organized area of the avian forebrain (field L2) that is the homologue of mammalian primary auditory cortex (for related work in macaque monkeys, see Fishman et al., 2001, 2004; Micheyl, Tian, Carlyon, & Rauschecker, 2005). Fay (1998, 2000) has reported generally similar findings on stream segregation using a classical conditioning paradigm with the goldfish (*Carassius auratus*).

Further indications that auditory streaming is experienced by nonhuman animals stems from experiments in which subjects were given a task in which performance was dependent on successful stream segregation. For example, Izumi (2001) measured the performance of Japanese macaques (*Macaca fuscata*) in the discrimination of short melodies in the absence or presence of interleaved distractor tones, which either did or did not overlap the melody in frequency. Note that this experiment is analogous to previous interleaved-melody recognition experiments in humans (Bey & McAdams, 2003; Dowling & Fujitani, 1971; Dowling et al., 1987; Vliegen & Oxenham, 1999). The results showed that the monkeys, like humans, were better at identifying the target melody when the distractor tones did not overlap spectrally with the target tones.

Auditory streaming and animal acoustic communication. Do animals that acoustically communicate in groups require the ability to perceptually integrate and segregate auditory streams? Here, we outline just two examples (out of many possible examples) for which we think auditory streaming could be at work. Consider first the case of song overlap in some songbirds (Naguib, 2005). During agonistic interactions, male songbirds can signal a high level of aggression or willingness to escalate the encounter by overlapping the songs of their opponents, whereas alternating songs indicates a relatively lower level of aggression (Dabelsteen, McGregor, Holland, Tobias, & Pedersen, 1996, 1997; Naguib, 1999). Eavesdrop-

ping males and females that listen in on such sequences of song interactions in a communication network respond differently toward males that overlap their opponents' songs and males that either were overlapped or alternated with their opponent (Naguib, Fichtel, & Todt, 1999; Naguib & Todt, 1997; Otter et al., 1999; Peake, Terry, McGregor, & Dabelsteen, 2001, 2002). For eavesdroppers, determining which song elements were produced by different males in the interaction could be a case of auditory streaming in action: song elements from each bird would presumably have to be integrated together over time and segregated from the song elements of the other bird. The question of what sorts of spectral, temporal, and spatial (including distance) cues promote auditory streaming in eavesdroppers is an important one that has not been addressed.

A second example of acoustic signaling in groups that could involve auditory streaming involves signal timing interactions in frogs. These interactions range from near synchrony to complete alternation (see Figure 3), and they play important roles in female mate choice (Gerhardt & Huber, 2002; Grafe, 2005). In some species, such as the Kuvangu running frog (*Kassina kuvangensis*), two neighboring males can even precisely interdigitate the notes of their calls (Figure 3D). Processes related to auditory streaming

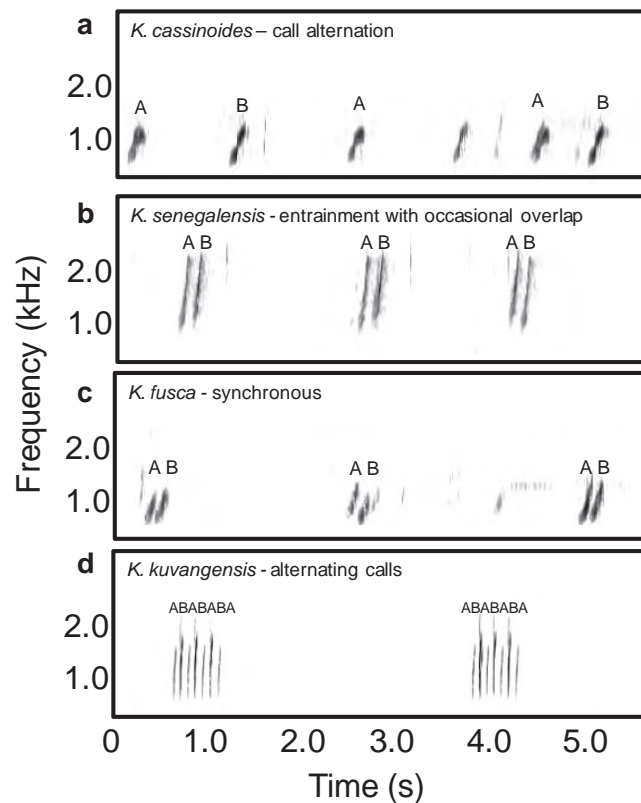


Figure 3. Spectrograms illustrating the diversity of call timing interactions in five species of frogs in the African genus *Kassina* (modified from Grafe, 2005). A: Call alternation. B: Entrainment with occasional overlap. C: Synchrony. D: Entrainment with alternating calls. In each panel, the calls of two different males are labeled as “A” and “B.” Note the general similarity between the alternating calls in Panel D and the artificial ABA– tone sequences depicted in Figure 2.

might be important in allowing females to choose one of the two signaling males. Note that the artificial ABA- and ABAB stimulus paradigms used to investigate auditory stream segregation in humans and starlings bear striking similarities to real-world problems for these particular frogs (cf. Figure 2 A, B and Figure 3). Could the cues for auditory streaming in humans and starlings identified using the ABA- paradigm also play a role in mate choice in frogs?

The important points to take from this section on the integration and segregation of sound sequences are the following: (a) diverse animal groups—for example, fish, songbirds, nonhuman primates—experience auditory streaming similar to that reported for humans using simple tone sequences; and (b) there are real-world examples of acoustic signaling interactions for which auditory streaming could be important. Thus far, however, few studies have investigated auditory streaming in the context of animal acoustic communication. One recent study of a katydid (*Neoconocephalus retusus*) suggested that spectral and temporal cues may allow them to segregate mating signals from the echolocation calls of predatory bats (Schul & Sheridan, 2006). An earlier study of the eastern gray treefrog (*Hyla versicolor*) by Schwartz and Gerhardt (1995) suggested that a common spatial origin of sound elements comprising the pulsed advertisement call could contribute to call recognition via stream integration. More recent work by Farris et al. (2002, 2005) on the túngara frog (*Physalaemus pustulosus*) and by Bee and Biemersma (in press) on Cope's gray treefrog (*Hyla chrysos-elia*), suggested, however, that female frogs may in some cases be very permissive of large spatial separations when integrating temporally distinct signal elements across time.

We believe investigating the role of auditory streaming in animal acoustic communication is important, because streaming may directly relate to mechanisms that make possible certain functional behaviors in some animals, such as eavesdropping, mate choice, and predator detection. One important goal for future studies should be to ask whether and to what extent humans and other animals exploit the same acoustic cues in the formation of auditory streams and how mechanisms for exploiting these cues function in the acoustic signaling systems of nonhuman animals.

Integrating and Segregating Simultaneous Sounds

In a cocktail-party-like environment, human listeners not only must form auditory streams of speech that can be followed through time but also must perceptually integrate the simultaneous sounds originating from one person's voice (e.g., harmonics and speech formants) and segregate these from the concurrent sounds of other talkers. Here, we focus on three acoustic cues—harmonicity, onset synchrony, and common amplitude modulation—that produce potent perceptual effects in humans and are often regarded as the most important cues for promoting the integration and segregation of concurrent sounds. There is a strong intuitive appeal to assigning important roles to spatial information and source localization in perceptually segregating concurrent sounds. Studies of humans generally suggest, however, that spatial cues are probably relatively weak cues for the perceptual integration and segregation of concurrent sounds compared to other cues, such as harmonicity or onset synchrony (e.g., Culling & Summerfield, 1995; Darwin, 2006; Hukin & Darwin, 1995). In fact, there are many examples of the influence of spatial cues being overridden by other (acoustic) cues. A dramatic example of this is provided by Deutsch's octave

illusion (Deutsch, 1974), wherein sequences of alternating tones presented simultaneously to the two ears are organized perceptually based on frequency proximity rather than by ear of presentation. We return to the role of spatial cues in our discussion of spatial release from masking (see later discussion).

Harmonicity. Humans typically hear harmonic complex tones as a single fused sound with a unitary pitch corresponding to the F0, rather than as a series of separate pure tones with different pitches (Figure 2C, left). "Mistuning" one spectral component in an otherwise harmonic complex by more than about 2%–3%, however, causes it to "pop out," so that listeners hear two simultaneous sounds: a complex tone and a separate pure tone corresponding to the mistuned harmonic (Figure 2C, middle; Darwin, Ciocca, & Sandell, 1994; Hartmann, McAdams, & Smith, 1990; Moore, Glasberg, & Peters, 1986). These two observations suggest that the auditory system takes advantage of harmonicity (i.e., common F0) for grouping together simultaneous spectral components that probably arose from the same source and for separating those components from inharmonically related components, which probably arose from a different source. Although this conclusion has been qualified by Roberts and colleagues (Roberts & Bailey, 1996a, 1996b; Roberts & Brunstrom, 1998, 2001), who have shown in a series of elegant studies that the perceptual fusion of spectral components depends on regular spectral spacing rather than harmonicity per se, most natural sounds with evenly spaced spectral components are likely to be also harmonic or quasi-harmonic.

In humans, differences in F0, and thus inharmonic relationships among spectral components, usually result in substantial improvements in the identification of concurrent speech sounds, ranging from whole sentences (Brox & Nooteboom, 1982) to isolated vowels (Culling & Darwin, 1993; de Cheveigne, McAdams, Larroche, & Rosenberg, 1995; Scheffers, 1983; Summerfield & Assmann, 1991; Zwicker, 1984). In the latter case, however, the effect is unlikely to be mediated by perceived segregation because it occurs over a range of F0 separations that are too small to evoke a percept of two separate sources (Assmann & Summerfield, 1994; Culling & Darwin, 1994). Another line of evidence for the beneficial influence of F0 differences on the perceptual segregation of concurrent sounds comes from findings that listeners can more easily identify and finely discriminate the pitch of a target harmonic complex mixed together with another complex (or *interferer*), if the two complexes have different F0s than if their F0s are similar. These benefits of differences in F0, which hold whether the target and interferer occupy the same (Beerends & Houtsma, 1986, 1989; Carlyon, 1996; Micheyl, Bernstein, & Oxenham, 2006) or distinct (Gockel, Carlyon, & Plack, 2004; Micheyl & Oxenham, 2007) spectral regions, probably contribute to why it is intuitively (and empirically) easier to follow a female speaker in the presence of a male interferer (or vice versa) than when the target and interferer are both of the same gender and thus more likely to have similar F0s. Thus, overall, many results in the human psychophysical literature indicate that differences in F0 provide powerful cues for the perceptual separation of concurrent harmonic sounds, whereas a common F0 and harmonic relationships (or common spectral spacing) among spectral components promote perceptual fusion (reviewed in Darwin & Carlyon, 1995).

Onset synchrony. Frequency components that start and end at the same time tend to be perceptually grouped together, whereas

components that start at (sufficiently) different times tend to be heard as separate sounds (Figure 2C, right; reviewed in Darwin & Carlyon, 1995). For instance, Bregman and Pinker (1978) showed that listeners tended to “hear out” the two spectral components of a two-tone complex as separate tones when they were asynchronous. More objective evidence that onset asynchronies can greatly facilitate the selective extraction of information from a target sound in the presence of another sound comes from findings that listeners can more accurately perceive (i.e., identify or discriminate) the pitch of a complex tone (target) in the presence of another complex tone (interferer), if the target tone starts later and ends earlier than the interferer. This effect has been observed when the target and interferer sounds occupied either the same spectral region (MicheyL et al., 2006) or nonoverlapping spectral regions (Gockel et al., 2004; Michéyl & Oxenham, 2007).

The influence of onset synchrony as an auditory grouping cue in speech perception was demonstrated in several elegant studies by Darwin and colleagues (Ciocca & Darwin, 1993; Darwin, 1984; Darwin & Ciocca, 1992; Darwin & Hukin, 1998; Darwin & Sutherland, 1984; Hill & Darwin, 1996; Hukin & Darwin, 1995). In particular, these authors showed that the phonemic identity of a synthetic vowel could be altered by making one of the harmonics close to a formant peak start earlier than the others. This result was interpreted as indicating that an asynchronous onset promoted the perceptual segregation of the temporally shifted component from the rest of the vowel, resulting in a shift of the perceived frequency of the formant peak closest to the perceptually removed component.

Common amplitude modulation. Sounds in the real world are often broadband and fluctuate in level, that is, they are amplitude modulated (Richards & Wiley, 1980; Singh & Theunissen, 2003). In addition, these amplitude modulations may often be correlated in time across different regions of the frequency spectrum (Klump, 1996; Nelken, Rotman, & Bar Yosef, 1999). Studies of two phenomena known as *comodulation masking release* (CMR; Hall, Haggard, & Fernandes, 1984) and *comodulation detection difference* (CDD; McFadden, 1987) indicate that the human auditory system is able to exploit correlated envelope fluctuations across the frequency spectrum (i.e., comodulation) to improve the detection of signals presented with concurrent masking noise (reviewed in Hall, Grose, & Mendoza, 1995; Langemann & Klump, 2007; Verhey, Pressnitzer, & Winter, 2003).

Two experimental paradigms have been used to investigate CMR in humans (Verhey et al., 2003). In the *band-widening paradigm* (Figure 4A), the bandwidth of a bandpass noise centered on the frequency of the target tone is varied between a narrow bandwidth (e.g., within a single auditory filter) and much wider bandwidths (e.g., spanning multiple auditory filters). At narrow bandwidths, signal detection thresholds are generally similar in the presence of comodulated and unmodulated maskers. As the bandwidth is increased beyond the critical bandwidth of the auditory filter centered on the target tone, however, signal detection thresholds become lower (i.e., signal detection is easier) in the presence of comodulated noise (Figure 4A) but remain fairly constant in unmodulated noise, even though the overall levels of the two types of maskers are the same. Hence, in the band-widening paradigm, the benefits in signal detection in comodulated noise are most pronounced when the bandwidth of the masker is sufficiently wide to span multiple auditory filters (reviewed in Verhey et al., 2003).

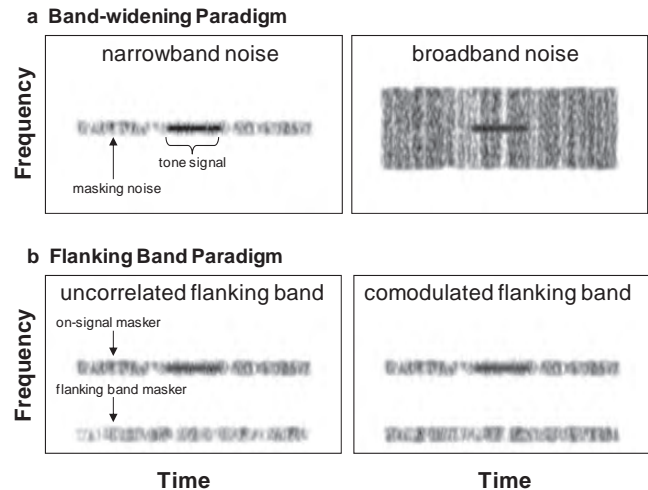


Figure 4. Schematic spectrograms illustrating experimental paradigms for investigating comodulation masking release (CMR) for detecting a short tone signal. **A:** The band-widening paradigm showing a modulated narrowband noise (left) and a modulated broadband noise (right). **B:** The flanking band paradigm showing the on-signal masker, the flanking band masker, and either the uncorrelated condition (left) or the comodulated condition (right). In the schematic examples depicted here, the magnitude of CMR would be greater in the conditions illustrated in the right panel for both paradigms.

A second approach to investigate CMR—the *flanking band paradigm* (Figure 4B)—uses a masker comprising a narrowband noise centered on the frequency of the target tone (the *on-signal band*) and one or more narrowband noises (*flanking bands*) spectrally located at frequencies remote from that of the target signal and on-signal band. Typically, flanking bands have center frequencies that fall outside of the critical bandwidth of the auditory filter centered on the target signal. In this paradigm, signal detection thresholds are typically lower when the on-signal band and the flanking bands have comodulated envelopes compared to conditions in which their envelopes fluctuate independently (reviewed in Verhey et al., 2003). Studies of CDD use a generally similar flanking band paradigm with two exceptions: (a) the target signal is a modulated narrow band of noise and not a tone, and (b) there is no on-signal masking band. In studies of CDD (reviewed in Langemann & Klump, 2007), thresholds for detecting the narrowband noise signal are lower when the flanking bands all share a common envelope that is different from that of the signal. Thresholds are higher either when the signal envelope is correlated with the comodulated flanking bands or when the signal and all flanking bands have independently fluctuating envelopes. What these studies of CMR and CDD demonstrate is that the human auditory system is sensitive to temporal correlations in amplitude fluctuation across the frequency spectrum.

One hypothesis for improved signal detection when signal envelopes fluctuate independently of a comodulated masker is that common amplitude modulations across the spectrum of the masker promote the across-channel integration of masker energy into an auditory object that is distinct from the independently fluctuating signal. Although there is evidence to support this hypothesis for CMR (Verhey et al., 2003), within-channel processes unrelated to

auditory grouping may be more important in CDD (Buschermöhle, Feudel, Klump, Bee, & Freund, 2006). Moreover, the extent to which processes related to CMR and CDD play a role in speech perception in cocktail-party-like environments is not yet clear. Early studies suggested that CMR-like processes might play a role in speech detection but probably contributed little to speech intelligibility at suprathreshold levels (Festen, 1993; Grose & Hall, 1992). More recent work, however, suggests that CMR-like processes might also contribute to speech recognition (Kwon, 2002). The debates about whether CMR and CDD share common underlying across-channel mechanisms and whether these phenomena contribute more to signal detection than signal recognition go beyond this review. The important question for our purposes is whether processes related to CMR and CDD might operate similarly in humans and nonhuman animals and contribute to acoustic signal perception in nonhuman animals.

Studies of integrating and segregating simultaneous sounds in nonhuman animals. Only a few studies have specifically addressed whether the acoustic cues that promote auditory grouping and segregation of concurrent sounds in humans also function in the acoustic communication systems of nonhuman animals. Playback studies with bullfrogs (*Rana catesbeiana*; Simmons & Bean, 2000) and cotton-top tamarins (*Saguinus oedipus*; Weiss & Hauser, 2002), for example, suggest that harmonicity could be an important cue in the perception of vocal communication signals in these species. Geissler and Ehret (2002) demonstrated in mice (*Mus musculus*) that onset synchrony between the harmonics in pup wriggling calls were important in allowing mothers to form coherent auditory objects of these vocalizations.

To our knowledge, no study of nonhuman vertebrates has directly investigated CMR or CDD in the context of how receivers perceive acoustic communication signals. Traditional psychophysical experiments, however, have revealed that at least one well-studied songbird experiences magnitudes of CMR and CDD similar to those reported for humans. Klump and Langemann (1995) used operant conditioning techniques and the band-widening paradigm to show that starlings (*S. vulgaris*) experience a mean CMR of about 11 dB in a tone detection task, which was similar to that reported in a similar study of humans (e.g., Schooneveldt & Moore, 1989). Klump and Nieder (2001) later reported neural correlates of these findings based on recordings from the starling forebrain (field L2). As in humans, starlings also experienced CMR in a flanking band paradigm (Langemann & Klump, 2001), and neural correlates of CMR using this paradigm have also been found in the responses of starling forebrain neurons (Hofer & Klump, 2003; Nieder & Klump, 2001). Starlings also experience a magnitude of CDD similar to that found in humans (Langemann & Klump, 2007), and, not surprisingly perhaps, correlates of CDD can be found in the responses of starling forebrain neurons (Bee, Buschermöhle, & Klump, 2007; Buschermöhle et al., 2006). A CDD effect similar to that observed in humans has also been reported in a recent study of the hooded crow (*Corvus corone cornix*; Jensen, 2007).

Studies of CMR in nonhuman animals have not been limited to birds. At a behavioral level, CMR has also been demonstrated in the Mongolian gerbil (*Meriones unguiculatus*; Klump, Kittel, & Wagner, 2001). Improvements in signal detection related to CMR have been demonstrated at a neurophysiological level in the auditory systems of leopard frogs (*R. pipiens*; Goense, 2004), guinea

pigs (*Cavia porcellus*; Neuert, Verhey, & Winter, 2004), and cats (*Felis catus*; Nelken et al., 1999). Together, these studies of CMR and related phenomena suggest that nonhuman vertebrates across a range of taxa possess neural mechanisms that could function to exploit common amplitude modulations across the frequency spectrum of masking noises to improve signal perception. We are aware of only one study that has investigated CMR-related effects in the context of acoustic communication in invertebrates. In that study, Ronacher and Hoffmann (2003) found little evidence for the operation of CMR-like processes in the phonotaxis response of male grasshoppers (*Chorthippus biguttulus*) to female stridulation signals. Could this represent a difference in signal-processing strategies between insects and vertebrates?

Additional studies of the roles of harmonicity and onset synchrony in the acoustic communication systems of nonhuman animals would make valuable contributions to our understanding of the extent to which these acoustic cues function in the integration and segregation of the concurrent sound elements comprising acoustic communication signals (Figure 1B–E). Future studies that quantify the modulation statistics of the natural acoustic scenes in which animals communicate (e.g., Nelken et al., 1999; Singh & Theunissen, 2003) and test the hypothesis that common amplitude modulations could be exploited to improve signal detection and recognition would also make valuable contributions to our understanding of the mechanisms of acoustic signal perception in nonhuman animals.

Spatial Release From Masking

Intuitively, it would seem that the integration and segregation of both sequential and simultaneous sounds could be as easy as assigning interleaved or concurrent sounds to the different locations in space corresponding to the positions of different sound sources. It is surprising, however, that many human psychoacoustic studies have now shown that spatial cues related to interaural time differences (ITDs) or interaural level differences (ILDs) play a relatively weak role in perceptual integration and segregation compared to other cues (e.g., Culling & Summerfield, 1995; Darwin, 2006; Hukin & Darwin, 1995). This is not to say, however, that spatial cues play no role in solving the cocktail party problem. In humans, speech intelligibility under cocktail-party-like listening conditions is improved when there is spatial separation between a source of target speech and interfering sources of speech or speechlike masking noise (Bronkhorst, 2000; Freyman, Balakrishnan, & Helfer, 2001; Hawley, Litovsky, & Culling, 2004; Shinn-Cunningham et al., 2005; Shinn-Cunningham, Schickler, Kopco, & Litovsky, 2001). For example, compared to conditions in which sources of target speech and interfering speech or noise with the spectrum and envelope modulations of speech are presented from the same frontal direction, listeners experience a 6–10 dB “release” from masking when the masker is displaced 90° lateral to the signal in speech recognition tasks (Bronkhorst, 2000). This general phenomenon is known as *spatial release from masking* or *spatial unmasking*.

Spatial release from masking of speech can result from three causes under binaural listening conditions (Bronkhorst, 2000; Shinn-Cunningham et al., 2005). First, when the masker is displaced in azimuth relative to a frontally presented signal, the head creates a sound shadow that attenuates the level of the masker at

one ear (the so-called *best ear for listening*) and results in ILDs for the masker but not the signal. Second, the displacement of the masker to one side of a frontally presented signal creates ITDs in the arrival of the masker, but not the signal, at the two ears. Finally, the locations from which the listener actually perceives the signal and masker as originating can influence the magnitude of spatial unmasking through processes thought to be related to spatial attention (Freyman et al., 2001; Shinn-Cunningham et al., 2005). For our purposes, it is important to note that the magnitudes of ITDs and ILDs vary directly with head size. Given that humans are notable for their large heads compared to most animals, should we expect nonhuman animals to experience magnitudes of spatial release from masking similar to those experienced by humans? Current evidence suggests that this is often the case.

Studies of spatial unmasking in nonhuman animals. A few studies have used traditional psychophysical techniques to investigate spatial unmasking in animals. In a study of budgerigars (*Melopsittacus undulatus*), Dent et al. (Dent, Larsen, & Dooling, 1997) reported a maximum spatial release from masking of about 10 dB when a target tone and masking noise were separated by 90°. Similar findings have also been reported for ferrets (*Mustela putorius*; Hine, Martin, & Moore, 1994). Holt and Schusterman (2007) recently reported results from a study of spatial unmasking of airborne sounds in the harbor seal (*Phoca vitulina*) and the California sea lion (*Zalophus californianus*). Depending on the frequency of the tone signal, the magnitude of spatial unmasking when an octave-band noise centered on the tone frequency was separated by 90° ranged from 8.5 to 19.0 dB and -1.3 to 11.7 dB in the harbor seal and sea lion, respectively. The magnitude of spatial release from masking in harbor seals for detecting airborne sounds was slightly larger than that previously reported in a study of underwater spatial unmasking in this species (Turnbull, 1994). Ison and Agrawal (1998) used a reflex modification technique to demonstrate spatial release from masking in the mouse (*M. musculus*) but did not report the magnitude of masking release (in dB). One particularly interesting recent study demonstrated that humans experience spatial release from masking in a task in which listeners were required to identify zebra finches (*Taeniopygia guttata*) by their individually distinct songs in the presence of an artificial zebra finch chorus (Best, Ozmeral, Gallun, Sen, & Shinn-Cunningham, 2005). It would be interesting to know how the performance of zebra finches compares to that of humans in the same task. More generally, it will be important to investigate in future studies how the performance of animals in relatively simple tone detection tasks compares with their performance in spatial unmasking tasks that require the detection and recognition of conspecific communication signals.

Two studies have used phonotaxis assays to estimate the magnitude of spatial unmasking in the context of acoustic communication in frogs. In a study by Schwartz and Gerhardt (1989) of green treefrogs (*H. cinerea*), females were required to behaviorally discriminate between attractive advertisement calls and less attractive aggressive calls separated by 180° around the perimeter of a circular test arena. In separate conditions, the positions of two broadband (0.1–10 kHz) noise sources were such so that either one noise source was located next to each signal speaker or each noise source was located 45° from each signal speaker or 90° lateral to both signal speakers and on opposite sides of the arena (180° apart). The maximum magnitude of spatial release from masking

reported in this study was about 3 dB for signal detection, but there was little evidence to suggest a spatial release from masking in call discrimination. Bee (2007) recently reported a 6–12 dB release from masking in the gray treefrog (*Hyla chrysoscelis*) when a steady-state masker with the spectrum of a natural breeding chorus was located 90° lateral to a speaker broadcasting target advertisement calls compared to a condition in which the signal and chorus-shaped noise were separated by only 7.5°. These results for gray treefrogs are similar to what might have been predicted based on neurophysiological studies of the northern leopard frog (*Rana pipiens*) in which the magnitude of spatial release from masking observed in neural signal detection thresholds was about 9 dB in the inferior colliculus (torus semicircularis), which receives binocular inputs (Lin & Feng, 2003; Ratnam & Feng, 1998). More recently, Bee (in press) has shown that spatial unmasking also improves the ability of female gray treefrogs to discriminate between conspecific and heterospecific calls.

Together, these studies of animals suggest that spatial release from masking is not at all unique to humans. The behavioral and neurophysiological studies of frogs indicate that spatial release from masking could function in the context of acoustic communication and, thus, could be one important process that allows some nonhuman animals to cope with cocktail-party-like problems. For frogs (Gerhardt & Bee, 2006; Gerhardt & Huber, 2002) and perhaps birds (Klump & Larsen, 1992; Larsen, Dooling, & Michelsen, 2006), the internal coupling of the two inner ears and the operation of pressure-difference systems probably compensate for some of the limitations on directional hearing that would otherwise result from a small head size. Ronacher and Hoffmann (2003) found little evidence for spatial release from masking in a study of the grasshopper (*C. biguttulus*). Hence, there are potentially interesting taxonomic differences in the operation of spatial release from masking in the context of acoustic communication.

It is also worth making explicit here that an approach using one or a limited number of masking noise sources in highly controlled laboratory studies of spatial unmasking does not wholly reflect the real-world listening conditions that many animals face. Nevertheless, such an approach almost certainly engages perceptual mechanisms that are important for solving cocktail-party-like problems in nature. Moreover, this approach constitutes an important and often necessary first step toward understanding the role of spatial unmasking in solving the cocktail party problem.

Why Should Animal Behaviorists Study the Cocktail Party Problem?

As the studies cited in the previous sections indicate, humans and some nonhuman animals probably face similar problems and use similar solutions when it comes to perceiving acoustic signals in noisy social environments comprised of groups of simultaneously signaling individuals. Given the interest among animal behaviorists in acoustic signaling interactions in groups, studies of auditory scene analysis and the cocktail party problem have probably received less attention than is warranted (Hulse, 2002). We believe there are excellent reasons why animal behaviorists should study the cocktail party problem.

Evolutionary Diversity in Sensory Mechanisms

Understanding the mechanistic causes of behavior has long been an important goal of animal behavior research (Tinbergen, 1963). Indeed, studies of the mechanisms of signal production and perception have a long and rich history in the study of animal communication (Bradbury & Vehrencamp, 1998). The mechanisms of auditory scene analysis, the sensory solutions to cocktail-party-like problems, and their role in animal acoustic communication represent opportunities for future research that will almost certainly yield new and important insights into the mechanisms and evolution of both hearing and acoustic communication. The sense of hearing arose early in the evolution of the vertebrates. Consequently, some of the basic processing strategies involved in auditory scene analysis may be shared (i.e., synapomorphic) between humans and other nonhuman vertebrates (Popper & Fay, 1997). However, many different taxonomic groups may have independently evolved communication systems that involve acoustic signaling in groups or large aggregations (e.g., insects and frogs and songbirds). Within the constraints imposed by the physics of sound, natural selection may have elaborated on certain basic mechanisms for auditory scene analysis in different taxonomic groups to produce a diversity of evolutionarily derived (i.e., apomorphic) sensory solutions to cocktail-party-like problems. These novel mechanisms often cannot be predicted but must be uncovered through empirical studies. Thus, one potential contribution of future research on animal cocktail parties could be the discovery of both shared and derived sensory mechanisms underlying the perception of acoustic signals in noisy social settings.

Receiver Psychology and Communication Network Theory

Arguably two of the most important conceptual advances in the recent study of animal communication are the ideas of *receiver psychology* and *communication network theory*. Our understanding of both would benefit from a better understanding of the role of auditory scene analysis in animal acoustic communication.

Receiver psychology holds that the evolution of both signal design and the behavioral strategies that signalers use depend critically on the processing strategies of a receiver's nervous system (Guilford & Dawkins, 1991; Rowe, 1999; Rowe & Skelhorn, 2004). Precisely how the physiological mechanisms underlying auditory scene analysis might have influenced the evolution of signals and signaling behaviors remains an important but still largely unexplored question. We also should not be surprised if under some conditions (e.g., extremely dense aggregations) there are evolutionary constraints on the extent to which signals and signaling strategies can be modified to improve signal perception by receivers (Bee, in press). Thus, for animals that communicate acoustically in groups, the sensory solutions to the cocktail party problem and the broader concept of auditory scene analysis deserve consideration in the context of receiver psychology (Bee, in press).

Among the most important contributions of communication network theory (McGregor, 2005) is the hypothesis that animals can gather information by eavesdropping on the signaling interactions that occur among two or more signalers (Peake, 2005). There is now considerable evidence in support of this hypothesis, especially among songbirds (reviewed in Peake, 2005). Most previous

studies of eavesdropping have emphasized the amount and adaptive value of information gathered by eavesdroppers, but eavesdropping also represents a quite interesting problem when the perceptual mechanisms that make it possible are considered. As illustrated earlier, eavesdropping in acoustic communication networks would seem to demand capabilities of auditory scene analysis (Langemann & Klump, 2005). Our understanding of the perceptual mechanisms that make possible the extraction of information in acoustic communication networks would benefit by approaching these issues from an auditory scene analysis perspective.

Anthropogenic Noise

Anthropogenic noise represents an evolutionarily recent intruder into the acoustic scenes that humans and other animals have evolved to analyze. There is increasing concern among animal behaviorists and conservation biologists that noise pollution could interfere with animal acoustic communication systems (Katti & Warren, 2004; Patricelli & Blickley, 2006; Rabin & Greene, 2002; Slabbekoorn, Yeh, & Hunt, 2007; Warren, Katti, Ermann, & Brazel, 2006). Recent experimental evidence from frogs suggests that anthropogenic noise can inhibit calling by males (Sun & Narins, 2005) and mask the perception of signals by females (Bee & Swanson, in press; see Lohr et al., 2003, for related work in birds). Some animals, such as songbirds and cetaceans, may be able to modify their signals in ways that ameliorate the effects of high anthropogenic noise levels (Fernández-Juricic et al., 2005; Foote, Osborne, & Hoelzel, 2004; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006), but this solution may not work for all animals (Bee & Swanson, in press). Moreover, as illustrated previously, animals also possess mechanisms for coping with masking noise (e.g., CMR and spatial release from masking). A better understanding of auditory scene analysis, and the general mechanisms that operate to segregate behaviorally relevant signals from noise, will be necessary to accurately assess the magnitude of the threat that anthropogenic noise poses to animal acoustic communication systems.

Applications to Humans

Behavioral and physiological studies of auditory scene analysis in a diversity of acoustically communicating animals could become relevant to translational research on auditory signal processing by humans and machines. Much of the interest in human auditory scene analysis and the cocktail party problem stems from the fact that people with hearing impairments have much greater difficulty understanding speech under noisy conditions when compared to listeners with healthy auditory systems. For example, compared to listeners with normal hearing, listeners with hearing impairments have difficulty in auditory stream segregation tasks with complex tones (e.g., Grimault, 2004; e.g., Grimault, Michéyl, Carlyon, Arthaud, & Collet, 2001) and experience less comodulation masking release (e.g., Moore, Shailer, Hall, & Schooneveldt, 1993) and less spatial release from masking (e.g., Bronkhorst, 2000; Bronkhorst & Plomp, 1992). Whereas hearing aids and cochlear implants improve speech perception in quiet settings, they typically provide their users with much less benefit in noisy,

real-world situations (Moore, Peters, & Stone, 1999; Stickney, Zeng, Litovsky, & Assmann, 2004). Basic research on both the physiological mechanisms of auditory scene analysis in a diversity of animal species and their function in animal acoustic communication systems might ultimately contribute to improvements in hearing prosthetic technology. For example, findings from studies of directional hearing in the fly *Ormia ochracea*, an acoustically orienting parasitoid of signaling crickets, have already had implications for the development of miniscule directional microphones for hearing aids (Mason, Oshinsky, & Hoy, 2001; Miles & Hoy, 2006).

In the field of computational auditory scene analysis, efforts to apply the principles of human auditory scene analysis to computer algorithms for automated speech recognition have met with some success (Cooke & Ellis, 2001; Wang & Brown, 2006). Compared to relatively quiet conditions, however, artificial speech recognition systems exhibit drastically reduced performance in noisy situations with competing speech signals (Barker, 2006; Lippmann, 1997). A better understanding of auditory scene analysis in nonhuman animals might ultimately broaden and deepen our understanding of the potential diversity of the physiological mechanisms whereby auditory scene analysis is accomplished and thereby contribute to the design of biologically inspired artificial scene analysis systems.

General Conclusions

Animals that acoustically signal in groups or large social aggregations often encounter and solve problems closely related to the human cocktail party problem. All of the mechanisms discussed previously that facilitate human speech perception in noisy social situations can also be identified as auditory processes operating in nonhuman animals. Few studies, however, have explicitly investigated these mechanisms in the context of animal acoustic communication. As Hulse (2002) recently lamented in his review of this topic, "sometimes scene analysis is so obvious it is overlooked (p. 190)." To be sure, other mechanisms that we have not touched upon may also play important roles in allowing animals to solve cocktail-party-like problems. For example, in animals with multi-modal signals, the cross-modal integration of acoustic signals with visual signals or other cues associated with the acoustic signals might improve acoustic signal perception in cocktail-party-like social environments (e.g., Ghazanfar & Logothetis, 2003; Narins, Hödl, and Grabul, 2003; Partan & Marler, 1999; Rowe, 2002). Answering questions about how animals solve cocktail-party-like problems will require that future studies adopt innovative approaches that integrate questions, methods, and hypotheses from previous psychoacoustic studies of humans with behavioral and neuroethological studies of acoustic communication in a wide diversity of animals. We also wish to stress that the use of seemingly artificial or highly contrived experimental stimuli under controlled laboratory conditions may often be the best way, and perhaps sometimes the only way, to investigate the sensory solutions to cocktail-party-like problems at deeper levels than would be possible using strictly natural stimuli presented in the animals' natural habitats. Even though approaches to studying the cocktail party problem in animals will certainly pose new challenges, the benefits of adopting the auditory scene analysis paradigm would significantly advance the study of animal acoustic communication

in much the same way that it has already contributed to our understanding of human hearing and speech communication.

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Discrimination of Acoustic Communication Signals by Grasshoppers (*Chorthippus biguttulus*): Temporal Resolution, Temporal Integration, and the Impact of Intrinsic Noise

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A characteristic feature of hearing systems is their ability to resolve both fast and subtle amplitude modulations of acoustic signals. This applies also to grasshoppers, which for mate identification rely mainly on the characteristic temporal patterns of their communication signals. Usually the signals arriving at a receiver are contaminated by various kinds of noise. In addition to extrinsic noise, intrinsic noise caused by stochastic processes within the nervous system contributes to making signal recognition a difficult task. The authors asked to what degree intrinsic noise affects temporal resolution and, particularly, the discrimination of similar acoustic signals. This study aims at exploring the neuronal basis for sexual selection, which depends on exploiting subtle differences between basically similar signals. Applying a metric, by which the similarities of spike trains can be assessed, the authors investigated how well the communication signals of different individuals of the same species could be discriminated and correctly classified based on the responses of auditory neurons. This spike train metric yields clues to the optimal temporal resolution with which spike trains should be evaluated.

Keywords: neural encoding, temporal resolution, intrinsic noise, spike distance metric, sexual selection

A prominent feature of acoustic communication signals in insects, anurans, birds, and mammals is their richness in amplitude fluctuations, and often it is the temporal structure of the signal's envelope that conveys the most relevant information (e.g., Shannon et al., 1995; Smith et al., 2002; Kroodsma & Miller, 1996; Gerhardt & Huber, 2002; Joris et al., 2004). Hence, the ability to process such temporal patterns, and, in particular, to resolve rapid amplitude changes, is crucial for the recognition and interpretation of acoustic signals. Signal recognition is, however, not only impeded by various kinds of extrinsic noise that may mask and distort the temporal pattern of signals, but also by "intrinsic noise" of the receiver: additional variability of the neuronal signals is caused by stochastic events acting on various stages of neuronal processing (e.g., Borst & Theunissen, 1999; Ronacher et al., 2004). This intrinsic noise may constrain the resolution of weak amplitude modulations and the discrimination of similar acoustic signals. To distinguish between similar signals is of particular relevance in the broad context of sexual selection and mate choice, where the task is to extract information about a signaler's quality from subtle variations of the common species-specific signal pattern—usually

a much more demanding problem than only to reject signalers belonging to different species. Here, we will relate these questions to the general problems of temporal resolution and temporal integration in sensory systems, using the example of acoustically communicating grasshoppers.

Features of the Grasshopper Communication System and Problems Related to Signal Recognition

Acoustic communication signals play a major role in the life of many grasshopper species: they serve to attract sexual partners and thus contribute directly to the mating success and the production of offspring—the basic currency in evolution. Acridid grasshoppers produce their stridulation signals by moving their hind legs in a species-specific temporal pattern against a vein on their forewings (see Figure 1). Both signal production and signal recognition by the receiver are innate behaviors and differ between species, thus constituting a major barrier against hybridization (Elsner, 1974; Gottsberger & Mayer, 2007; Stumpner & von Helversen, 1994; von Helversen & von Helversen, 1975, 1994). Behavioral experiments with song models revealed that it is mainly the temporal pattern of amplitude modulations (AM) that conveys the essential cues for signal recognition (Hennig et al., 2004; Stumpner & von Helversen, 1992, 2001; von Helversen & von Helversen, 1997, 1998).

Grasshoppers and other orthopteran insects offer important experimental advantages for studies of sensory processing: (1) they allow a rather direct connection between behavioral experiments and neurophysiological data (e.g., Machens et al., 2003; Ronacher & Krahe, 2000; cf. also Marsat & Pollack, 2006; Schildberger, 1984; Schildberger & Hörner, 1988); and (2) as in other invertebrates many neurons of these insects can be identified as individ-

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uals, on the basis of their characteristic morphology (see Figure 2), which is revealed by dye injection during intracellular recordings (e.g., Römer & Marquart, 1984; Stumpner & Ronacher, 1991). This makes possible repeated recordings from a well-defined neuron type. In addition, grasshoppers possess relatively few neurons, at least compared to vertebrate model systems for auditory processing, such as owls, gerbils, or cats. Therefore, one can hope to unravel a neuronal network that is specifically designed for the processing of AM patterns (Hennig et al., 2004).

In the context of mate finding the basic task is to recognize the acoustic signals of a potential conspecific partner, and to avoid the erroneous acceptance of signals from individuals belonging to a different species (Stumpner & von Helversen, 2001; von Helversen & von Helversen, 1994). In addition to determining species identity, it may also be important for these animals to extract from the heard signals some hints to the quality of the sender, for example indications of the sender's health and condition (see below). In theory, the decision about species identity does not seem a difficult one, since the signal patterns usually differ considerably between species (Elsner & Popov, 1978; Stumpner & von Helversen, 1994). In practice, however, several factors aggravate the problems of signal identification: (1) The acoustic signals will often be degraded on their way through the biotope by attenuation, reflections, reverberations and so forth, and masked by ambient noise and by signals produced by conspecific signalers (for reviews of various factors see, e.g., Dusenbery, 1992; Greenfield, 1994, 2005; Römer, 1998, 2001). In the following, we will subsume all these factors as *extrinsic noise*. (2) In addition to extrinsic noise, signal recognition may be impeded by *intrinsic noise* sources that result from stochastic processes within the animal's nervous system, for example, during signal transduction in the sensory neurons, during synaptic transmission and spike generation. The impact of this intrinsic noise will be the main focus of this report (see below). (3) Another factor that can impede signal recognition is *temperature*. Because grasshoppers are heterothermic animals, that is, they cannot keep their body temperature constant, changes in ambient temperature strongly influence the speed of the stridulatory movements and as a consequence the temporal pattern of their songs. For a receiver with different body temperature this may render the signals incomprehensible. How the animals cope with this "time-warp" problem of their signaling is, however, beyond the scope of this report.

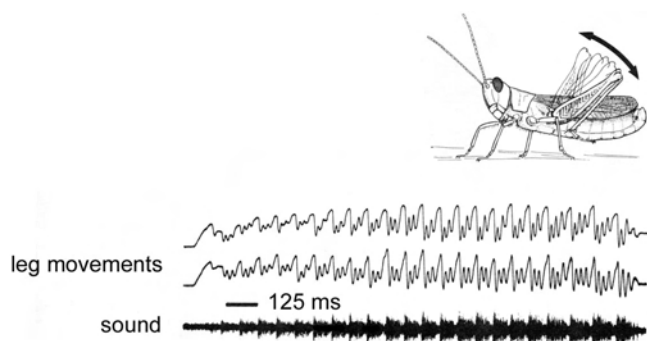


Figure 1. Stridulation of a male *Chorthippus biguttulus*. Lowest trace: sound pattern; upper traces, movements of left and right hind legs, recorded with an optoelectronic camera. Courtesy of Otto von Helversen.

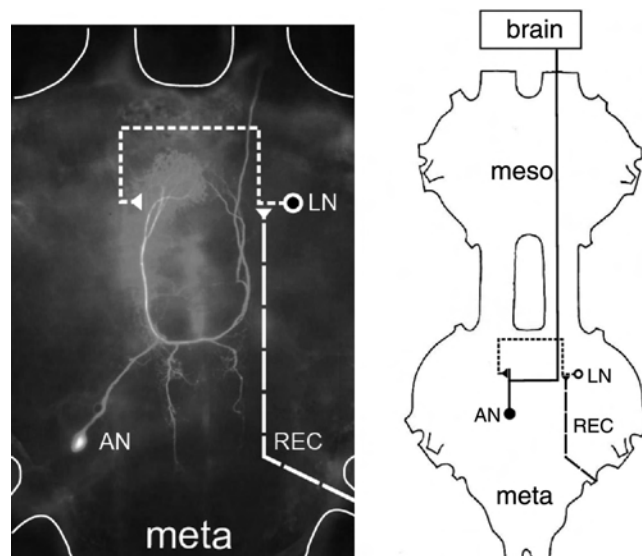


Figure 2. Sketch of the information flow in the auditory pathway of grasshoppers (right), and example of an ascending auditory neuron stained with Lucifer Yellow (left). Meta, meso indicate the third and second thoracic ganglion, respectively (the proper metathoracic ganglion is fused with the first three abdominal ganglia). REC: receptor neurons, LN: local neurons, AN: ascending neurons. For further details see text.

Intrinsic Noise May Constrain in Particular the Discrimination of Similar Signals

All information about the external world must be conveyed to the brain in the form of spike trains, that is, sequences of action potentials, provided by the sensory neurons, via higher order neurons. Both, the variations of the signals arriving at the sense organ and the additional noise generated within the nervous system contribute to the overall variability of spike trains, which is crucial for any signal recognition task (see, e.g., Borst & Theunissen, 1999; Grewe et al., 2003; Ronacher et al., 2004). Intrinsic noise becomes evident if one records from a neuron while repeatedly presenting an identical signal (see Figure 3). In the grasshopper auditory system, the variability of spike trains tends to increase from the periphery to higher-order interneurons (Figure 3; Vogel et al., 2005). It should be noted, however, that the effect of intrinsic noise depends on several factors, for example, the sound intensity (Schaeffer et al., 2005), the spike rate (Vogel et al., 2005; see also Gabbiani & Koch, 1998), and in particular the structure of the stimulus envelope. As concerns the latter, the depth and rate of change of AM is important. Very precise spiking behavior is observed in response to steep amplitude rises, in particular in receptor neurons (Machens et al., 2001; Rokem et al., 2006).

In the next Section we will first discuss temporal integration as a means to reduce intrinsic and extrinsic noise problems, and provide some behavioral results on the size of the processing time window. Temporal integration, however, cannot be considered independently of, and must be weighted against, temporal resolution. In the following Section we therefore investigate the temporal resolution properties of neurons at different stages of the grasshoppers' auditory pathway, by determining modulation transfer functions. Finally, in the last Section, we focus on the problem of

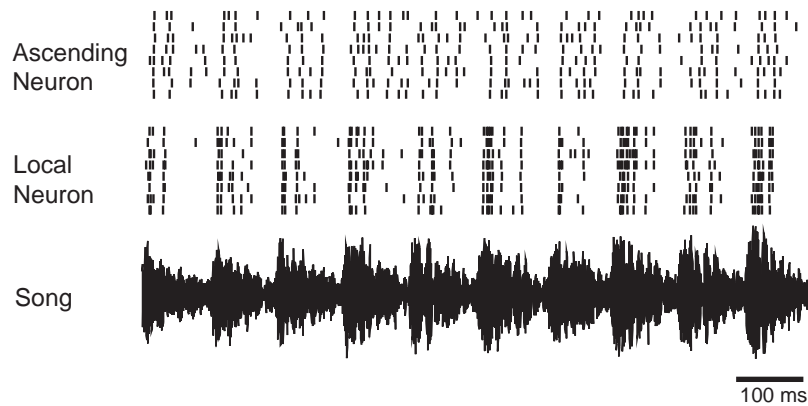


Figure 3. Spiking responses of two auditory neurons of *C. biguttulus* to a segment of the species-specific song. Spikes are shown as raster plots, that is, each spike is represented by a small vertical line. Shown are responses of a local neuron (TN1) and an ascending neuron (AN11) to eight stimulus repetitions. S. Wohlgemuth, unpublished results.

how well subtle differences between similar acoustic signals can be discriminated on the basis of spike trains—the only information a central nervous system has about the external world. To assess the discriminability of acoustic signals we apply a recently developed method to quantify the similarity of spike trains, a spike train metric (van Rossum, 2001).

Temporal Integration and the Size of the Processing Time Window

There are two principal ways to cope with signal distortions and spike train variability: temporal integration and “spatial” summation. Reliability, and hence signal recognition, can be improved by averaging neuronal responses over a longer time segment, or by averaging over the responses of many similar neuronal elements (see, e.g., Rieke et al., 1996; Shadlen & Newsome, 1998). However, considering as an example the processing of visual information, the respective major drawbacks of the two strategies become obvious: by averaging the input from many photoreceptors sensitivity is enhanced, but at the cost of reduced spatial resolution, as is evident in the rod pathway of mammals. Temporal integration, on the other hand, implies the risk of missing fast events (Warrant, 1999). Temporal integration therefore entails a particularly delicate problem in the acoustic modality, where rapid AM often convey important information. Indeed, there is an ample psychoacoustic literature devoted to the so-called integration-resolution paradox (de Boer, 1985; Green, 1985; Tougaard, 1998). This term refers to a strong discrepancy between the time constants found in different experimental paradigms. In a detection task near threshold one usually observes a trade-off between duration and intensity: the detection threshold decreases with increasing stimulus duration, up to 100 or 200 ms, and the product of threshold intensity and duration is roughly constant, indicative of energy integration (Green, 1985; Tougaard, 1998). Given the time scales of AM in acoustic communication signals, however, it is quite obvious that no auditory system could afford to sacrifice temporal resolution to such a degree (see Golisch & Herz, 2005). Indeed, in different experimental paradigms, such as double-click and gap-detection experiments, one finds much shorter time constants in

the order of a few ms (e.g., Franz & Ronacher, 2002; Joris et al., 2004; Prinz & Ronacher, 2002; Tougaard, 1996; Viemeister & Plack, 1993). As a possible solution for this integration-resolution paradox, Viemeister and Wakefield (1991) have proposed a ‘multiple-look model.’ According to this model, sensory input is initially sampled at high rate and then analyzed with different integration times depending on the task and the context of processing. To our knowledge, however, a physiological implementation of this model has not yet been demonstrated in higher vertebrates (cf. however, Alder & Rose, 1998, 2000; Edwards et al., 2002). Whether grasshoppers employ a multiple-look solution is currently unclear. However, it might be beneficial for them to analyze sounds with a range of integration times to improve information extraction from distorted or masked signals. The highly repetitive character of grasshopper songs, which consist of many stereotyped subunits (Figures 1, 3), seems to directly invite to use temporal integration as a means to alleviate the problems of signal degradation. Therefore, we asked how strongly signal recognition in these animals depends on the repetitive structure of their songs.

Behavioral Experiments to Determine Lower and Upper Bounds of the Processing Time Window

Method

Animals and test procedures. Behavioral experiments were performed on males of the grasshopper *Chorthippus biguttulus*, caught as adults or last instar larvae in the field. We took advantage of a behavior that reliably indicates whether or not an animal can identify modified signals as conspecific communication sounds. *C. biguttulus* males react very specifically to the response song of a female with a conspicuous turning movement, which is the first step of the phonotactic approach toward the female (von Helversen, 1997). This phonotactic turning response is shown with high reliability and exclusively to the female song, and is therefore an excellent indicator that a male has classified a sound as a female song signal. Tests took place in a reflection-attenuated room, by stimulating a single male with female song models of different

durations via a loudspeaker situated lateral of the animal, and recording the phonotactic turning responses of males. The standard song model consisted of 12 identical subunits and had a duration of 1,015 ms; the durations of the 5, 4, 3-subunit stimuli were 420, 335, and 250 ms, respectively. Following von Helversen and von Helversen (1997), the signal level was set at 50 dB re 2×10^{-5} Nm^{-2} (dB SPL; rms-value, which corresponded to peak levels of 64.5 dB SPL). Broadband noise (main energy between 3 and 10 kHz) could be delivered by a speaker situated 65 cm above the animal. For further details of the experimental procedure see Ronacher, Krahe, and Hennig (2000).

Results and Discussion

Using this reliable behavior as a tool we found, without continuous noise added from above, that a 250-ms signal, consisting of only three subunits, elicited a mean response rate of ~90% (median 100%; Ronacher & Krahe, 1998; see also arrow in Figure 4A). Hence, a surprisingly small segment of the female signal (the natural duration is ~1 seconds) suffices for recognition. With an even shorter signal (two subunits; corresponding to 165 ms) still one-third of the tested males (18 out of 53) responded to more than 50% of the stimulus presentations, indicating an even lower limit of the processing time window (Ronacher & Hennig, 2004). It should be emphasized that a single presentation of such shortened signals suffices to elicit the male's turning response; hence, this is a system capable of one-shot recognition, within a few hundred milliseconds!

These data indicate a *lower bound* for the signal duration that is necessary to enable recognition (for further controls see Ronacher & Krahe, 1998, and Ronacher & Hennig, 2004). To obtain an estimate for the *upper bound* of the evaluation time window (or integration time window) we performed similar tests in the presence of ambient noise. The experimental approach was analogous to measuring the integration time window in signal detection experiments (see above and Green, 1985). We tested each *C. biguttulus* male with a standard female signal consisting of 12 subunits while increasing the noise level until the phonotactic response dropped to below 50% (Figure 4A, filled symbols). We then repeated this experiment using shorter signals and measured again the noise level at which the response dropped to 50%. With the three-subunit stimulus the animals ceased to respond at somewhat lower noise levels (double arrow in Figure 4A). The long 12-subunit signal was less susceptible to noise by ~2 dB, indicating that the evaluation of a longer segment of the signal yielded a—moderate—improvement in signal detectability. This improvement, however, dropped to almost zero when a 5-subunit stimulus was compared to the long standard stimulus (Figure 4B). The regression line intersects with zero at 441 ms. In other words, an extension of the signal beyond this “critical duration” of ~450 ms does not yield any further improvement in the detection of a masked signal. Thus, temporal integration, as a means for improving signal recognition, seems to be restricted to a time window of maximally 450 ms (Ronacher et al., 2000). In summary, these experiments revealed that *C. biguttulus* males can recognize an undisturbed signal as short as 2 to 3 song subunits, but do not exploit more than five subunits for signal recognition—even in the presence of noise.

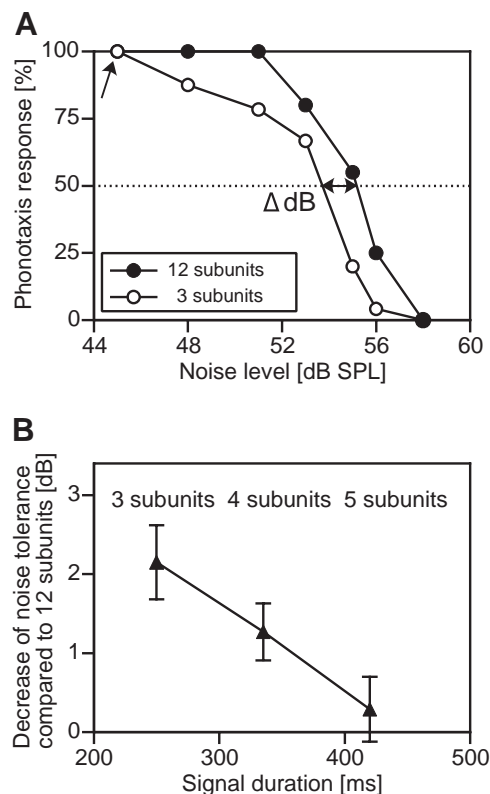


Figure 4. (A) Behavioral responses of a *C. biguttulus* male to female signals of different durations. Filled symbols: phonotactic response to a long stimulus (1015 ms; 12 subunits), open symbols: response to a short 3-subunit stimulus (250 ms). Abscissa: noise level, ordinate: phonotactic turning responses as percentage of stimulus presentations. The open symbol at 100% at low noise levels (arrowhead) indicates that even with the shortened signal this male responded to every stimulus presentation. If males do not recognize a signal as a female song the turning response does not occur, yielding 0%. Double pointed arrow indicates the shift of the 3-subunit curve to lower noise levels and the determination of the Δ dB value. Each percentage value in Figure 4A is based on between 15 and 30 stimulus presentations. (B) Δ dB values determined for different signal durations of the short signal (3 subunits, 4 subunits, and 5 subunits; always in comparison to the 12-subunit stimulus). $N = 11, 13$, and 10 males tested, for the 3-, 4-, and 5-subunit stimuli, respectively; bars indicate 95% confidence intervals. Modified from Ronacher et al., 2000.

Layout and Temporal Resolution Properties of the Auditory Pathway

As emphasized above, the ability to resolve rapid amplitude changes is crucial for signal recognition in grasshoppers. Therefore, we aimed at measuring the upper limits of temporal resolution at various stages of the auditory pathway. In brief, the layout of the auditory pathway is as follows (see Figure 2): The ears of these grasshoppers are located in the first abdominal segment, directly beneath the wing base. The axons of auditory receptor neurons (approximately 50 to 80 per ear) enter the metathoracic ganglion complex, which houses a first important stage of processing auditory information (Römer & Marquart, 1984; Stumpner & Ronacher, 1991; Stumpner & von Helversen, 2001). Because receptors exhibit rather broad tuning in only two frequency ranges

(Jacobs, Otte, & Lakes-Harlan, 1999), there is only little capacity for a fine analysis of carrier frequencies; grasshoppers probably can discriminate only between a low frequency and a high frequency range (Stumpner & von Helversen, 2001; von Helversen & von Helversen, 1997). Receptors connect to local neurons, mainly in the third thoracic ganglion (see Figure 2). A set of ca. ten to 15 local neurons receives input from the receptor neurons und transmits information to ascending neurons (ca. 15–20), which in turn project to the brain (Boyan, 1992; Marquart, 1985; Stumpner & Ronacher, 1991). The final decision whether a song signal is acceptable or not takes place within the brain circuits (Bauer & von Helversen, 1987; Ronacher, von Helversen, & von Helversen, 1986). Obviously, the set of ascending neurons represents a bottleneck in forwarding the information to those circuits.

Measuring the Temporal Resolution Capacities of Auditory Neurons by Modulation Transfer Functions (MTF)

A standard paradigm to investigate the temporal resolution of sensory systems, or their parts, is the use of modulation transfer functions (MTF; Krishna & Semple, 2000; Joris et al., 2004; Rhode & Greenberg, 1994; Viemeister & Plack, 1993). The stimuli used consist of a carrier (in our case broadband noise) that is sinusoidally amplitude modulated at different modulation frequencies (Figure 5A). Applying this MTF paradigm to neurons, there are two ways to evaluate the neuronal responses: (1) to count the spikes in a larger time window, or (2) to quantify the locking of spikes to the stimulus envelope. In the first case, this results in rate-MTF (*rMTF*), in the second in temporal-MTF (*tMTF*; see Figure 5). Obviously, these two evaluation procedures relate to the above mentioned resolution, integration paradox. On the other hand, from a different point of view, to the question of whether a nervous system encodes information by a *rate code* or a *temporal code* (e.g., Borst & Theunissen, 1999; Rieke et al., 1996). The upper limit of temporal resolution is characterized by the corner frequency, that is, the modulation frequency at which the response measure drops by a certain amount (Krishna & Semple, 2000; Rhode & Greenberg, 1994). In psychophysical experiments, the corner frequency characterizes the upper limit of AM frequencies that the system can still discriminate from an unmodulated stimulus.

Method

Animals and electrophysiology. To determine modulation transfer functions for auditory neurons we used adult locusts (*Locusta migratoria*), which were obtained from a commercial supplier. The larger locust is often used as a model system for the smaller *C. biguttulus*, by virtue of the very similar properties of the auditory pathway in both species (Stumpner, 1988; Stumpner & Ronacher, 1991; Wohlgemuth, Neuhofer, & Ronacher, 2007). The electrophysiological methods were conventional and are described in detail in Vogel et al. (2005). During the experiments the preparation was kept at a constant temperature of $30 \pm 2^\circ\text{C}$. Auditory neurons were recorded intracellularly and identified by means of dye injection (Lucifer Yellow) after completion of the physiological experiments (see Figure 2A as an example). After amplification, neural responses were digitized at a sampling rate of 20 kHz.

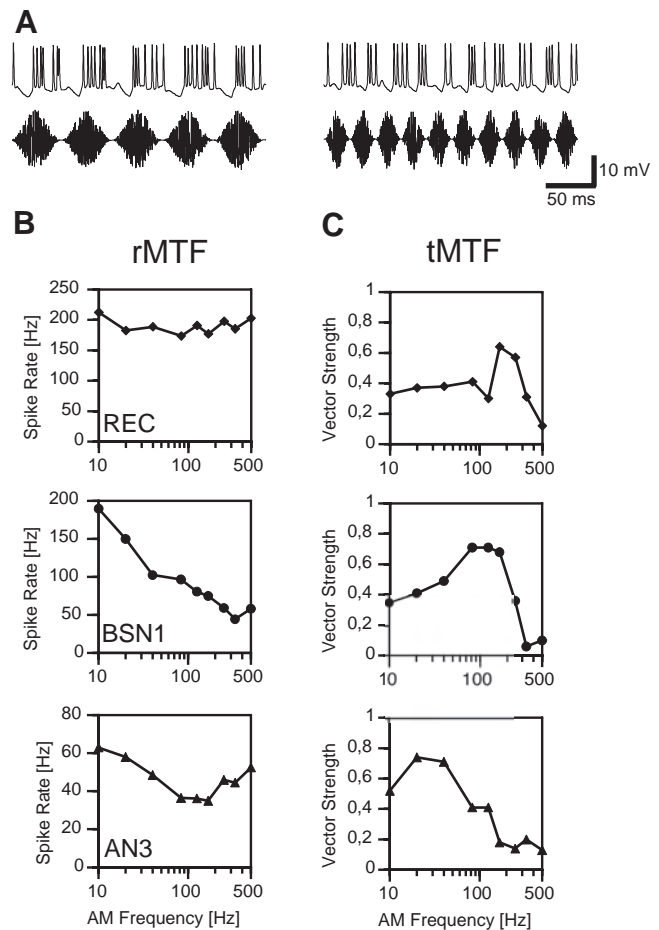


Figure 5. (A) Response of a local neuron (BSN1) to broadband noise that was sinusoidally amplitude modulated at 20 and 40 Hz (100% modulation depth); scale bars: 10 mV, 50 ms. (B, C) Modulation transfer functions (MTFs) for a receptor neuron, a local and an ascending neuron (from top to bottom). (B) rate-MTFs in which spike rates are plotted against modulation frequency; (C) temporal MTFs (based on an evaluation of vector strength; for details of the evaluation procedure see Franz, 2004, and Wohlgemuth & Ronacher, 2007).

The experimental protocols complied with the German laws governing animal care.

Acoustic stimulation. The stimuli for the modulation transfer functions consisted of a broad-band noise carrier (0.5–30 kHz) that was sinusoidally amplitude modulated at nine frequencies (10 Hz, 20 Hz, 40 Hz, 83 Hz, 125 Hz, 167 Hz, 250 Hz, 333 Hz, and 500 Hz; modulation depth 100%). To ensure that each neuron was in a well-defined adaptation state, each stimulus was preceded by a 200-ms segment of unmodulated noise, followed by a 1-s segment of constant modulation frequency and depth, and another segment of 200 ms of unmodulated noise. The stimuli were repeated four times with stimulus intervals of 300 ms. Acoustic stimuli were broadcast via one of two speakers (D-28/2, Dynaudio, Skanderborg, Denmark), situated laterally at a distance of 30 cm from the preparation. All acoustic stimuli were stored digitally and delivered by custom-made software (Labview, National Instruments), via a 100-kHz D/A-conversion (PCI-MIO-16E-1, National Instru-

ments, München, Germany), an amplifier (Mercury, 2000, Jensen, Pulheim, Germany), and an attenuator (PA5, Tucker-Davis Technologies, Gainesville, FL). Sound intensities were calibrated with a Brüel and Kjær (Nærum, Denmark) 1/2 in. microphone, positioned at the site of the preparation, a Brüel & Kjær (Nærum, Denmark) measuring amplifier (Type 2209), and are given in dB re $2 \times 10^{-5} \text{ Nm}^{-2}$ (dB SPL). The sound intensity of test stimuli was adjusted to ~ 20 dB above a neuron's threshold.

Data analysis. From the digitized recordings, the spike times were extracted by means of a voltage threshold criterion. Rate modulation transfer functions, (*rMTF*) and temporal modulation transfer functions (*tMTF*) based on vector strength were determined according to Krishna and Semple (2000). In short, for the *rMTF* (compare Figure 5B) mean spike rates were computed for the modulated part of the stimuli. For the computation of the *tMTF*, period histograms (divided into 18 bins, i.e., 20°) were obtained. From the period histograms the vector strengths (VS) were calculated according to:

$$VS = \sqrt{\left(\frac{1}{n} \sum_{i=1}^n \cos \alpha_i\right)^2 + \left(\frac{1}{n} \sum_{i=1}^n \sin \alpha_i\right)^2} \quad (1)$$

where α_i is the timing of spike i defined as the phase of the modulation waveform and n is the number of spikes. Vector strength can vary from a minimum of zero to a maximum of 1, the latter indicating a "perfect" phase locking to the stimulus envelope, that is, all spikes falling in the same bin. From the resulting *tMTF* curves, *corner frequencies* were determined following Krishna and Semple (2000) as the frequency where the curve dropped to the 90% point from the maximal vector strength value (Figure 5C).

Results and Discussion

Figure 5 shows *rMTF* curves (left) and *tMTF* curves (right) for typical neurons of the three processing levels mentioned above. Receptor neurons generally show all-pass *rMTF* curves, that is, their spike rates do not change markedly with AM frequency (Figure 5B, top). Note that it is not the carrier frequency tuning, but the frequency of the amplitude modulations, the signal's envelope, that matters in this context. A quite similar behavior is found also in some local interneurons with primary-like responses (not shown). *rMTFs* of other local neurons, however, tend to show low pass behavior, see BSN1 as an example (Figure 5B). This selectivity is increased at the next processing level, where we find low-pass, high-pass and band-stop filters (see AN3 in Figure 5B for an example of a weak band-stop filter). In their *temporal MTFs* (Figure 5C) receptor neurons usually exhibit a band pass (Figure 5C top, and Prinz & Ronacher, 2002), while among local and ascending interneurons often low-pass or bandpass filters are found. The corner frequencies, however, differ conspicuously between processing levels. Among the receptors and primary-like local neurons we found the highest corner frequencies, up to >150 Hz, indicating a precise locking of spikes to the stimulus envelope up to relatively high AM frequencies. This high temporal resolution is markedly reduced to corner frequencies mostly below 80 Hz at the next processing level, in ascending neurons (Figure 5C, see also Franz, 2004; Wohlgemuth & Ronacher, 2007). Because large differences in spike rate can influence vector strength values we

checked whether the observed differences in *tMTF* corner frequencies could have been because of spike rate differences. However, the corner frequencies did not depend significantly on mean spike rate for receptor neurons (Prinz & Ronacher, 2002), nor for auditory interneurons (Weschke & Ronacher, in press). Rather, the differences between the *tMTF* curves in Figure 5C reflect differences in the precise locking of spikes to the stimulus envelope.

Rate and temporal modulation transfer functions can provide information about the temporal limits of a sensory system. However, they do not necessarily yield an answer to the more specific question of how well different stimuli can be *discriminated*. We will pursue this question in the next section.

Discrimination of Similar Patterns in the Context of Sexual Selection

Why should grasshopper females discriminate between different conspecific songs? Apart from their basic function in assisting to avoid heterospecific pairings, grasshopper calling songs probably serve an additional function: they may be used as indicators of a potential mate's quality (Kriegbaum, 1989). Because grasshopper females invest heavily into large eggs while the males provide only "cheap" sperm, we find these animals in a situation that is typical for sexual selection (e.g., Andersson, 1994; Andersson & Simmons, 2006). Females in particular should be choosy and try to find a high quality male, or at least avoid mating with a low quality male, to optimize their investments. Exactly this has been shown for the grasshopper *C. biguttulus*: females consistently prefer the songs of certain males, indicating that the song signals yield important clues for discriminating among different conspecific males (Kriegbaum, 1989; see also Balakrishnan et al., 2001).

The central nervous system of a grasshopper must extract information about differences between song signals from the spike trains provided by auditory neurons. We tried to solve the same problem and asked how well the acoustic signals produced by different individuals of one and the same species can be *discriminated* based on the spike trains produced by single grasshopper neurons. Evidently, the repeatability of neuronal messages, which is limited by the intrinsic noisiness of spike trains, will impose constraints on the discrimination of similar signals. A prerequisite for the correct classification of two sensory stimuli is that the spike trains elicited in repeated presentations of stimulus X are sufficiently different from those caused by stimulus Y— or, in other words, spike trains of Type X exhibit higher similarity among each other than compared with spike trains of Type Y. To quantify similarities between pairs of spike trains we used a spike train metric introduced by van Rossum (2001).

Metric Similarities of Spike Trains as a Basis for Stimulus Discrimination

Method

The basic idea of van Rossum's method is to replace each spike of a pair of spike trains by a filter function (Equation 2) and then to subtract the two resulting waveforms (Figure 6A). The difference is then squared and the integral calculated, yielding a measure for the (dis)similarity of the two examined spike trains, f and g . The basic rationale is as follows: if two spike trains share many coincident

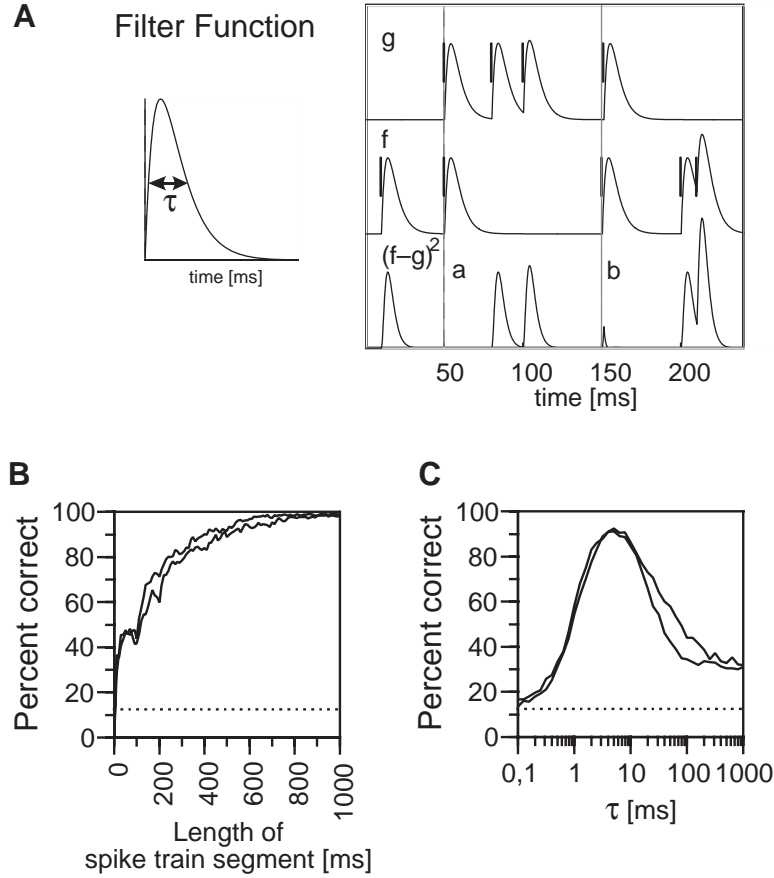


Figure 6. Classification of natural stimuli based on metric distances between spike trains. (A) Procedure to determine spike train distances (after van Rossum, 2001). To compare two spike trains, *f* and *g*, each spike (vertical line) is first replaced by a filter function. Then the two resulting functions are subtracted, and the difference is squared, to remove negative values (bottom). The integral over the resulting function is a measure for the distance between the two spike trains. The contribution of spikes that occur at the same or nearly the same time in *f*, *g* (coincident spikes) cancels out (see *a*, *b*). Two spike trains that contain many coincident spikes therefore yield a low distance value, which corresponds exactly to their common sense similarity. By varying the width of the filter function, different emphasis can be laid upon how much the timing of spikes influences the metric distances. See text for further information. (B) Classification success depends on the length of the spike train segments that are evaluated. As described in Machens et al., 2003, songs of eight individual males of *C. biguttulus* were presented and their discriminability based on spike train distances was evaluated. Data of two specimens of the local neuron TN1 of *C. biguttulus*. Note the high classification success that is possible with longer signal durations. Dotted line indicates chance level (12.5%); τ was set at 5 ms. (C) Classification success as a function of the temporal resolution parameter τ (same data as in B). (A: modified after van Rossum, 2001, and Machens et al., 2003; B,C: Wohlgemuth, unpublished results).

spikes, and are therefore similar, their contribution to the integral is cancelled out by the subtraction process (see *a*, *b* in lowest trace of Figure 6A). This results in a small value of the integral, which is indicative of a high similarity or a small distance (see van Rossum, 2001; Machens et al., 2003, for details of the procedure).

$$f(t) = t \cdot \exp(-\alpha t) \text{ for } t > 0 \quad (2)$$

$$f(t) = 0 \text{ for } t \leq 0$$

The time course of the filter function can be considered as mimicking an excitatory postsynaptic potential (EPSP) in a hypothetical downstream neuron. The width of the filter function is defined

by the temporal resolution parameter τ ($\tau \approx 2.45/\alpha$). This free parameter τ can be varied to study the influence of the temporal resolution with which spike trains are evaluated: if τ is large (>200 ms), it is mainly the difference in average firing rates that contributes to the distance, whereas for small τ values the metric distance depends on differences in spike timing. Once the distances between all spike trains of a certain neuron were computed, a cluster algorithm was applied to quantify the discrimination performance. Clustering was examined by randomly picking a spike train as a “template” for each stimulus. The remaining spike trains were classified by assigning them to that template to which they exhibited the smallest distance. This procedure was repeated

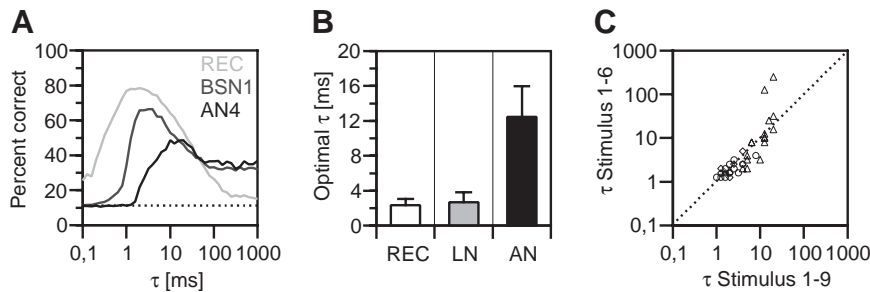


Figure 7. Discrimination of sinusoidally amplitude modulated stimuli (compare Figure 5A), based on spike train distances of neurons at different processing levels. Nine modulation frequencies between 10 Hz to 500 Hz served as stimuli (see below). (A) Percentage of correct classification as a function of temporal resolution τ for a receptor neuron (REC), a local neuron (BSN1), and an ascending neuron (AN4) (length of spike train segments evaluated: 500 ms; chance level is 11.1%). (B) Optimal temporal resolution τ (derived from the peak values of curves as in A) for neurons of the three processing levels ($N = 8, 11, 17$). Values of receptors and local neurons are not significantly different, while both are significantly different from the data of ascending neurons ($p < .001$); bars indicate 95% confidence intervals. (C) Correlation between optimal τ values measured for different stimulus sets. Stimulus set 1–9: 10, 20, 40, 83, 125, 167, 250, 333, and 500 Hz modulation frequency; Stimulus set 1–6: 10–167 Hz modulation frequency. Modified after Wohlgemuth & Ronacher, 2007.

for all possible template permutations, resulting in an average probability of correct classification (for details of the procedure see Wohlgemuth & Ronacher, 2007). Because the classification success depends on the resolution parameter τ (see Figure 6C), for each cell its optimal τ value was determined. These values ranged between 1 and 30 ms.

Results

We investigated auditory neurons of the grasshopper *C. biguttulus* and determined, with this metric, how well a set of acoustic stimuli can be classified and discriminated on the basis of the similarities of spike trains these neurons produce in response to different stimuli. Focusing on the responses of auditory receptor neurons and using a set of natural songs of eight different *C. biguttulus* males as stimuli, a surprisingly high discrimination success was found by Machens et al. (2003): ~90% of these songs were classified correctly on the basis of single spike trains from a single receptor neuron!

Using the same stimuli as Machens et al. (2003), we here extended this kind of analysis to the next stages of the auditory pathway. A similarly high classification success, as with receptor neurons, was found for a local neuron with primary-like response type (Figure 6B). Shown in Figure 6B is how the classification success develops with the length of the spike train segment evaluated. The curves exhibit a steep rise within the first 200 ms and then level off. At a spike train length of 250 ms (i.e., that is the signal duration that allows for reliable signal recognition in males, see above, Figure 4A) a discrimination level of ~80% is reached. In view of the difficult discrimination task, this high classification success based on single spike trains of a single neuron is quite remarkable.

What Determines the Optimal Time Constant for Temporal resolution?

The classification shown in Figure 6B was performed with the temporal resolution parameter τ set to 5 ms, which yielded the

optimal results for these two neurons. Figure 6C shows how the classification success depended on the resolution parameter τ . The curves are based on a spike train length of 500 ms (which corresponds to the upper limits of temporal integration derived from Figure 4B). Performance was maximal with τ between 3 and 10 ms; with larger τ , that is, reduced temporal resolution, the curves fell quickly until they reached a constant level of ~30% at $\tau > 200$ ms. We can conclude that at the input level of the auditory pathway the necessary information to reliably discriminate between the signals of different conspecifics is present, provided that the spike trains are evaluated with a high temporal resolution of $\tau \approx 5$ ms (see also Machens et al., 2003).

In this context immediately the question arises of whether the optimal time constant of approximately 5 ms reflects properties of the auditory neurons under study or whether it was imposed by the specific temporal structure of the particular set of grasshopper songs used? To answer this question we used a set of stimuli with reduced complexity, that is, the same nine stimuli with sinusoidal AM as used for the modulation transfer functions (see above and Figure 5A). We calculated spike train distances and determined the percentages of correct discrimination based on the distances between the respective spike trains. This was done for neurons of the first three levels of processing, that is, receptor neurons, local interneurons and ascending interneurons in the migratory locust (Wohlgemuth & Ronacher, 2007).

Figure 7A shows the percentages of correct classifications as a function of the temporal resolution parameter τ of the spike metric (compare Figure 6C) for representatives of the three processing levels. For this simplified stimulus ensemble, the maximal classification success of the auditory receptor neuron was around 80% (which is still high, taking into account that the stimulus set encompassed a large proportion of high modulation frequencies, see figure legend). For the auditory receptor neuron the optimal classification was achieved with a temporal resolution of 2 to 3 ms. For the local neuron the optimal τ was in the same range, but the classification success was somewhat reduced (compare Figure 7B). A marked decline in maximal classification success was

found for ascending neurons in combination with a shift of the optimal τ to values mostly above 10 ms (Figure 7A, B).

To further test for possible influences of the stimulus ensemble on τ , we compared the optimal temporal resolution for different subsets of this stimulus ensemble. A likely hypothesis was that the very small optimal τ values (<5 ms) found for auditory receptors and local neurons were influenced by the prevalence of high modulation frequencies in our stimulus set (4 stimuli above 150 Hz). We controlled for this by restricting the data evaluation to a reduced stimulus set (6 stimuli between 10 Hz and 167 Hz). The exclusion of the three highest modulation frequencies, however, had virtually no effect on the optimal τ values (Figure 7C). Thus, the small optimal τ values found for the receptor and local neurons were obviously not enforced by the large proportion of stimuli with high modulation frequencies but appear to reflect a time constant characteristic for a given neuron or processing level.

Discussion

An important property of the spike-train metric method is its focus on single spike trains. Thus, the trial-to-trial variability of neuronal responses is taken into account, which is highly relevant for the operation of nervous systems—but is ignored in many experimental paradigms, for example, by the MTF procedures introduced in Figure 5. Another advantageous feature of the spike train metric is the possibility to change the temporal resolution with which spike trains are compared, by varying the free parameter τ of the filter function used (inset in Figure 6A). Choosing a very large τ (>200 ms) implies that the timing of spikes is virtually neglected and only *spike count differences* contribute to the discrimination, whereas with a smaller τ more and more emphasis is laid on the exact *timing of spikes*. Hence, this method allows to explore the temporal resolution with which a spike train should be evaluated to obtain an optimal classification and discrimination of external stimuli, and may give clues to the encoding principles used at different stages of neuronal processing.

The data presented in Figure 7 suggest that the optimal τ of the spike train metric does reflect the properties of the investigated neurons. This leads to questions about the encoding of information within the auditory pathway. Traditionally, two coding principles are contrasted, a rate code, where the information is encoded in the average number of spikes measured over a longer time segment, and a temporal code, for which the timing of spikes contributes to the information content.

How Is Temporal Information Encoded at Different Processing Levels?

The sample curves in Figure 7A reveal three messages: first, they indicate a substantial reduction in the overall classification success at the level of ascending neurons. This impression is supported by a quantitative analysis: receptor neurons ($N = 8$) allowed for an average $78.8 \pm 4.5\%$ classification success (mean and 95% confidence intervals), whereas the mean of $N = 17$ ascending neurons was $48.9 \pm 5.2\%$ (all values for a spike train length of 500 ms). Local neurons with primary-like responses achieved similar values as receptor neurons ($81.6 \pm 3.4\%$; $N = 5$), while another local neuron, BSN1 was intermediate ($60.9 \pm 9.9\%$; $N = 6$). A similar trend to reduced classification success at higher

processing levels was observed with natural songs as stimuli (not shown).

Second, there was a clear shift of the optimal τ between local and ascending neurons (Figure 7A,B). While the optimal τ values for receptors and local neurons were very small (and not significantly different, $p = .866$), the values for ascending neurons were distinctly larger ($p < .001$; Kruskal Wallis test and Games Howell post hoc test). This indicates a reduction of temporal precision at higher levels of the auditory pathway, which is in accord with the observation of increased spike train variability in ascending neurons of the locust (Vogel et al., 2005).

A third message can be extracted from Figure 7A by comparing the classification success at the optimal τ and at $\tau = 1000$ ms. Remember that for $\tau > 200$ ms the metric procedure virtually ignores the timing of spikes, and, hence, any classification success must be based solely on spike count differences. Seen that way, the curve for the receptor neuron perfectly reflects the fact that the rMTF-curves are flat (see Figure 5B): the curve approaches chance level for large τ values. To turn the argument around, this shows that the receptor's high classification success (Figure 7A) is based almost exclusively on the timing of spikes. With the ascending neuron the picture changes: at $\tau = 1000$ ms we find a classification success around 30%, which must be attributed to spike count differences between stimuli. The best classification success obtained for this neuron, at $\tau \approx 20$ ms, was around 50%, a value to which both spike count differences and spike timing information contributed. However, the improved classification success at $\tau = 1,000$ ms for ascending neurons reveals that the relative contribution of spike timing is reduced, compared to the situation in the receptor and local neurons, and approximately equals that of spike count. Hence, this kind of data evaluation suggests a quantitative shift of coding strategy that takes place between the most peripheral and more central stages of processing, that is, a gradual change from a code based predominantly on exact spike timing toward a rate code. It also emphasizes that evaluation of spike count and spike timing information are not mutually exclusive coding principles, but might be combined with varying weights (cf. Borst & Theunissen, 1999).

General Discussion

This account focuses on the question of how auditory neurons of insects process signals whose information is contained in the temporal pattern of amplitude modulations. Signal recognition is impaired by two different types of noise, extrinsic noise that degrades the signals arriving at the receiver's ears, and intrinsic noise that introduces additional variability in the spike trains of receptor neurons as well as auditory neurons at higher processing stages. The problems caused by noisy spike trains could, in principle, be alleviated by averaging across a set of similarly reacting neurons or by temporal integration. In the auditory domain, however, temporal integration may interfere with the necessity to resolve fast amplitude modulations. The upper limits of temporal resolution (as measured by the corner frequencies of the *tMTFs*) were high for receptor neurons and a local neuron with receptor-like responses, whereas they decreased markedly in ascending neurons (Figure 5C, see also Franz, 2004; Wohlgemuth & Ronacher, 2007). Parallel to this decrease in corner frequencies, the *rMTF* curves changed from all-pass to (mostly) low-pass,

band-pass or band-stop behavior between receptors and ascending neurons (Franz, 2004).

These limits of temporal resolution can be directly related to the behavioral performance of grasshopper females in experiments that used song models in which the frequency composition of the envelopes was systematically varied. Using this approach and starting from parameters of natural songs, von Helversen and von Helversen (1998) demonstrated that a periodic envelope composed of five frequencies (10, 20, 30, 40, and 50 Hz) was sufficient to elicit a strong response of *C. biguttulus* females. However, much higher frequencies, up to 150 Hz, can cause the rejection of song models by females indicating that these frequencies are perceived by the animals. *C. biguttulus* females respond to neither natural songs nor song models if these contain tiny gaps of only 2–3 ms duration (von Helversen & von Helversen, 1997). Such gaps are characteristic for the songs of males that have lost one hind leg, and in the field females exert a very strong sexual selection against these males, which have only a 10% mating success compared to intact males (Kriegbaum, 1989). To perceive these gaps, higher envelope frequencies, up to 150 Hz, are needed (von Helversen & von Helversen, 1998). At first glance this seems to be inconsistent with the finding of a reduced temporal resolution (Figure 5C), and larger τ values (Figure 7 B), at the level of ascending neurons. However, at least in some ascending neurons a shift of the encoding scheme seems to occur by which this discrepancy is resolved. A neuron (AN4) has been described that exhibits a low corner frequency in the *tMTF*, but does nevertheless respond highly selectively to stimuli containing gaps (Ronacher & Stumpner, 1988). This selective response, which results in a band-stop filter characteristic of the *rMTF*, is caused by a preceding inhibition that is triggered by each new stimulus onset after a small gap (Franz, 2004; Franz & Ronacher, 2002). The gap detection capacity of this neuron depends, however, on the high temporal resolution of receptor neurons. This example demonstrates that a high temporal resolution capacity of neurons, while obviously essential at the level of auditory receptor neurons must not necessarily persist up to higher processing levels, a feature of the auditory pathway of grasshoppers that is shared with vertebrates.

By applying a metric that assesses the similarities between spike trains, we were able to make predictions about the limits of discriminability of similar signals. The discrimination of similar signals is a prerequisite for sexual selection processes, where the task is to assess a signaler's condition or health from often-subtle deviations from a common species-specific pattern. We found that the spike trains of receptor neurons convey surprisingly much information allowing for an excellent discrimination success, provided that the spike trains are evaluated with high temporal resolution. In other words, the information basis for female choice is already present in the responses of single neurons, if the timing of spikes is taken into account at a 5-ms scale. At this point, however, a critical remark seems in order: the high classification success found with the spike train metric paradigm describes the situation of an *ideal observer*. Experiments are under way to test to what degree the central nervous system of grasshoppers is able to exploit the information content present in the spike trains of receptor neurons. The reduced classification success found for the ascending neurons (Figure 7A) may be taken as an indication that the ultimate goal of these animals probably is not a most sophisticated discrimination of individuals but rather to find high quality

males or to reject males of inferior song quality. Interestingly, females seem to differ somewhat in their ideas of what is a good song (Balakrishnan et al., 2001).

The alpha function used in the metric paradigm can be interpreted as mimicking a postsynaptic potential in a down-stream neuron. Thus, the optimal τ values found in this kind of data evaluation would reflect the temporal resolution of the respective next processing stages.

The spike train metric thus offers the important advantage of providing information about the optimal temporal resolution with which spike trains should be evaluated and yielding clues to possible encoding principles. The shift found among ascending neurons to larger optimal τ values, that is, a reduced temporal resolution, complements the results of the MTF paradigm. It seems to be a general trend in sensory systems to shift from encoding of the stimulus pattern by the phase locking of spikes in the periphery, to a feature-extraction and feature-evaluation process at more central stages (e.g., Gabbiani et al., 1996). A loss of temporal resolution as observed here may be a necessary corollary of such a feature extraction process. Alternatively, an optimal temporal resolution of around 10 to 20 ms may reflect a compromise between the necessities to preserve information about the signal's temporal structure, and, on the other hand, to reduce noise introduced by neuronal jitter (Narayan et al., 2006; Wohlgemuth & Ronacher, 2007). This consideration fits the observation of increased spike train variability in ascending neurons of the locust (Vogel et al., 2005). The observation that at the level of ascending neurons the classification success of single neurons was clearly reduced as compared with more peripheral neurons, may be an additional indication that ascending neurons are specialized to extract different signal features, and that the information about these features is distributed among a set of neurons.

The steps of processing and extracting information performed by auditory neurons of grasshoppers appear to follow the same scheme as in vertebrates. Auditory nerve fibers of vertebrates generally exhibit all-pass rate-*MTFs*, and therefore the information about amplitude modulations must be present in the temporal placement of spikes (Alder & Rose, 2000; Joris et al., 2004; Rhode & Greenberg, 1994; Rose & Capranica, 1985). At higher stations of the auditory pathway, however, the exact phase locking of spikes tends to disappear, and a variety of rate filters, or even a filter bank for amplitude modulation frequencies is found (Joris et al., 2004; Langner, 1992).

Insects and higher vertebrates that rely on acoustic communication face similar problems of signal recognition in a noisy world. However, insects are much more limited in their neuronal hardware that is devoted to these tasks. The rather small number of auditory neurons implies that the intrinsic noise of spiking responses may become an ultimate hurdle for signal recognition and discrimination. The obvious solution for reducing the impact of intrinsic noise (to average over large numbers of similar elements) appears to be ruled out for most insects. Notwithstanding the intrinsic spike train variability, our spike metric analysis showed that a high classification performance is in principle possible even based on spike trains of single neurons (see Figure 6). This could be an indication that the communication signals of this species have been shaped by sexual selection in a way to elicit highly reliable responses in the auditory system of the female receivers.

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Assessment of Distance to Potential Mates by Female Barking Treefrogs (*Hyla gratiosa*)

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This study investigated the cues used by female barking treefrogs, *Hyla gratiosa*, to assess distances to potential mates. Eight-speaker playback experiments were used to demonstrate that distance affects female choice in complex acoustic environments and to test 3 possible cues that females might use to assess distance: (a) degradation in spectral and temporal cues of calls, (b) relative call amplitude at the female's location, and (c) the rate at which the amplitude of calls increases as a female approaches a calling male. All 3 hypotheses were refuted, suggesting that females use a more complex mechanism, such as triangulation, to assess distance. Females preferred speakers with greater source amplitudes even when they had to travel further to reach those speakers. Determination of source amplitude is possible only if females can assess independently both the distance to sound sources and the amplitude of calls at the females' location. Hence, anuran amphibians may possess greater cognitive abilities than are generally attributed to them.

Keywords: mate choice, distance, triangulation, anuran amphibians, *Hyla gratiosa*

In diverse taxa, males gather in groups (e.g., leks, choruses) that females visit to choose mates (Andersson, 1994; Bradbury & Vehrencamp, 1998; Hoglund & Alatalo, 1995). The elaborate and extravagant signals produced by males serve as a basis for mate choice as well as mediating interactions between signaling males. In most taxa, especially orthopteran insects and anuran amphibians, males produce energetically expensive acoustic signals (Andersson, 1994; Bradbury & Vehrencamp, 1998; Gerhardt & Huber, 2002; Greenfield, 2002). These signals transmit information about the signaler, including size, condition, genetic quality, and motivation, and acoustic signals have been shown to be important determinants of female choice. Reliably assessing the characteristics of these signals can be a challenging task for females choosing mates from within groups of males, where the levels of background noise can be considerable (Gerhardt & Huber, 2002).

In addition to information about the signaler itself, acoustic signals can provide receivers with information about the signaler's direction and distance (Gerhardt & Huber, 2002; Naguib & Wiley, 2001). Territorial male songbirds have been shown to use rever-

beration, relative intensity of high frequencies, and overall amplitude to determine the distance to simulated intruders (Naguib & Wiley, 2001). Humans likewise use these cues in assessing the distance to sound sources in experimental settings (Naguib & Wiley, 2001; Speigle & Loomis, 1993) as well as cues associated with movement in relation to the sound sources (Ashmead, Davis, & Northington, 1995; Russell & Schneider, 2006; Speigle & Loomis, 1993).

Much less is known about the cues used to assess the distance to potential mates during mate choice. Distance to potential mates within groups of displaying males is likely to influence mate choice because of the relationship between the costs of choice (Pomiankowski, 1987) and distance. Females choosing more distant males are likely to expend more energy and be exposed to a greater risk of predation than females choosing closer males. Playback experiments with anuran amphibians and orthopteran insects suggest that distance might be an important cue in mate choice. Females generally prefer calls with greater amplitudes at the females' location, and preferences can be reversed by increasing the amplitude of the less preferred source (Gerhardt & Huber, 2002). Because signal amplitude decreases with the distance from a sound source, it is generally inferred that such preferences will result in the choice of closer over further males in natural settings, where the distances of males from choosing females will vary (Gerhardt & Huber, 2002). Indeed, females usually prefer the closer of two signals when the source amplitudes of the two signals are equal (Gerhardt & Huber, 2002; see also Castellano, Rosso, & Giacoma, 2004; Murphy & Gerhardt, 2002).

No study to date has systematically determined the cues used by females to assess distances to potential mates. In this study, I used multispeaker playback experiments to conduct such an investigation with female barking treefrogs (*Hyla gratiosa*); multispeaker arrays allowed me to examine distance assessment under complex acoustic conditions similar to those in natural choruses. For *H.*

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gratiosa, distance influences mate choice both in natural choruses and in playback experiments (Murphy & Gerhardt, 2002). In the latter, females preferred lower frequency calls over higher-frequency calls when speakers were equidistant from the release point, but this preference was reversed when the distance to the speaker broadcasting the preferred, lower frequency calls was doubled.

I tested three possible cues of distance. Signal-degradation hypothesis—As acoustic signals propagate through the environment, they are degraded spectrally and temporally, and degradation will be greater for signals that travel further (Naguib & Wiley, 2001). Females could use signal degradation to assess either relative or absolute distance to males (Naguib & Wiley, 2001). Relative-amplitude hypothesis—The amplitude of a signal, at the location of a female, will generally be greater for signals from a closer male than for signals from a more distant male. Hence, females could use the relative amplitudes of signals at their location to roughly determine the relative distance to potential mates (Naguib & Wiley, 2001). Sound-gradient hypothesis—The amplitude of a sound increases as one approaches the source of the sound, and the rate of this increase, the sound gradient, increases as one gets closer to the source (Gerhardt & Huber, 2002). Females could assess either the absolute or relative distance to a potential mate by measuring the steepness of the sound gradient (or acoustic tau, Ashmead et al., 1995; Speigel & Loomis, 1993). These three hypotheses are not mutually exclusive, and females might use more than one cue to assess distance.

Study Site and Species

This study was conducted in the Apalachicola National Forest, Leon County, FL (30° 22' N, 84°, 19' W). Details of the study site are given in Murphy (1994). The barking treefrog is a hyliid treefrog that inhabits the Coastal Plain of the Southeastern United States and breeds from March through August. At the study site, males call in choruses (leks) of up to 150 males, arriving at the pond shortly after sunset (Murphy, 1999). Choruses last for 3 to 5 hr, with individual males present for an average of 2.5 hr (Murphy, 1999). Males float on the surface of the water near the perimeter of the pond while calling, producing calls about once every second. The advertisement call consists of a short (100 to 200 ms) burst of sound with two or three spectral peaks, the fundamental and one or two upper harmonics (Murphy & Floyd, 2005; Oldham & Gerhardt, 1975).

Females arrive at the pond shortly after males, and assess the calls of at least four males from a distance (Murphy, 2004; Murphy & Gerhardt, 2002). Females move directly toward their chosen mate and do not visit males sequentially. Observations of females in natural choruses indicate that females make their final choice of a mate at a median distance of 5.6 m from their mate.

First Control Experiment

Design, Method, and Predictions

Previous playback experiments establishing an effect of distance on mate choice by female *H. gratiosa* tested females with a two-choice design (Murphy & Gerhardt, 2002). To verify that distance affects choice in more complex acoustic conditions and to

establish a difference in distance between sound sources that affects choice, I conducted a playback experiment with an array of eight speakers (see Figure 1) that mimics the spatial distribution of males and complex acoustic environment confronting a female as she chooses mates in natural groups of calling males (Murphy & Gerhardt, 2002). The two central speakers broadcast an attractive call with a fundamental frequency of 450 Hz, whereas the remaining speakers broadcast an unattractive call with a fundamental frequency of 550 Hz; in two-choice playbacks with speakers equidistant from the release cage, 16 of 17 females (94%) choose the 450 Hz call over the 550 Hz call (binomial test, $p = .0003$). All other parameters of these calls were identical and similar to the population average; these parameters are described in Burke and Murphy (2007). The distances of the two central speakers from the release point (16 m and 19 m) were chosen based on a previous eight-speaker experiment that determined the additional distance females would travel to choose a speaker broadcasting a 450-Hz call over a speaker broadcasting a 550-Hz call (Murphy, 2004).

Calls were synthesized with custom software written by Joshua Schwartz (sampling rate of 22.05 kHz, 16 bits/sample) and stored as digital files on the hard drive of a Macintosh G4 Powerbook. Eight tracks were created in the AudioDesk application (Mark of the Unicorn, Cambridge, MA), with each track corresponding to one of the eight speakers. A track consisted of 24 calls, each with a period of 1 s (call rate = 60 calls/min). The timing relationships among tracks were such that adjacent speakers (tracks) alternated calls with each other; hence, odd-numbered speakers (Speakers 1, 3, 5, and 7, in Figure 1) broadcast calls synchronously and alternated with even-numbered speakers (Speakers 2, 4, 6, and 8, in

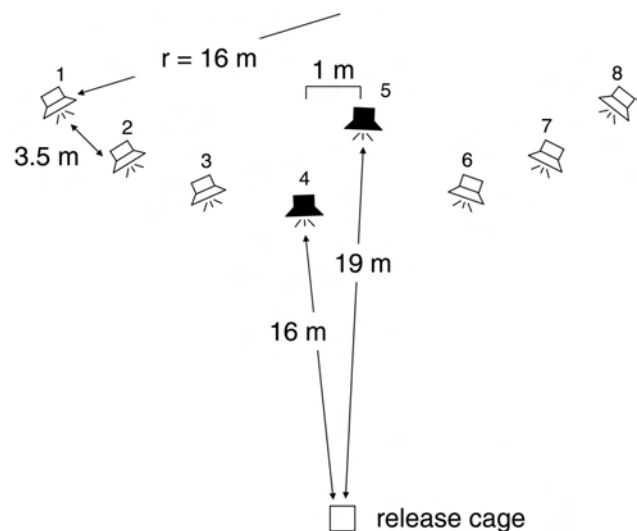


Figure 1. Playback array used to determine whether distance to potential mates affects choice by female *Hyla gratiosa* in complex acoustic environments. Speakers were set on an arc with a radius of 16 m. Speakers represented by filled icons played an attractive call with a fundamental frequency of 450 Hz; speaker represented by open icons played an unattractive call with a fundamental frequency of 550 Hz. Speakers were set upright on the ground facing the release cage; the scale of the figure exaggerates the angle between the speakers and the center line of the speaker array. Speakers are numbered to facilitate description of methods in the text.

Figure 1), which broadcast calls synchronously with each other. To prevent calls within odd- or even-numbered sets of speakers from overlapping completely, and hence making it difficult for females to localize calls, calls were offset by 0, 40, 80, or 120 ms (calls were 150 ms long). The offset was randomly determined with two constraints: (a) each channel of a four-speaker set experienced each offset an equal number of times, and (b) within each call period (i.e., 1 s), each channel was offset by a different amount. These constraints ensured that calls from all speakers experienced the same amount of overlap from other speakers in the same odd or even set. Two sequences of these offsets were created to ensure that results were not due one particular ordering pattern. The sequence used was alternated between females.

During playback, the eight tracks were routed through a MOTU 828 digital/audio converter (44.1 kHz sampling rate, Mark of the Unicorn, Cambridge, MA), amplified by a Kenwood KAC-606 stereo amplifier (Kenwood, USA, Long Beach, CA), and broadcast from ARS Edge Sequel speakers. The root mean square (*RMS*) SPL (SPL, re: 20 μ Pa, "fast" response, "C" weighting) of calls broadcast from each speaker was set to 85 dB at 1 m, similar to the average of males in natural choruses (Murphy & Floyd, 2005). Because SPL meters underestimate the SPL of short calls (<500 ms, Murphy & Floyd, 2005; Prestwich, Brugger, & Topping, 1989), reference 450-Hz and 550-Hz signals were created; each had the same harmonic structure as their respective calls but had durations of 1 s. The *RMS* pressure of the reference signal and its respective call were equalized digitally within the software, and the reference signals were used to set the SPL of each speaker using a RadioShack SPL meter (Model 33-4050; ANSI Type II; RadioShack Corporation, Fort Worth, TX) set on the ground and pointed directly at the speaker.

Females were collected in amplexus from two small breeding ponds and transported to an outdoor playback arena located approximately 1.75 km from the breeding ponds. The arena spanned an unpaved sand road, with vegetation intervening the lanes of the road. The vegetation was trimmed periodically to permit observation of females during playbacks. All speakers were visible to females from the release point, but the speakers were partially obscured at some spots in the arena due to the topography of the arena. Females choosing mates in natural choruses approach calling males over similar terrain, as males tend to call from the periphery of ponds (Murphy & Gerhard, 2002). Playbacks were conducted between 2300 and 0230 hr.

At the arena, the female was separated from her mate and placed in an acoustically transparent, hardware-cloth release cage. After 30 s of playback, the cage was opened remotely to release the female. The female was observed with an infrared video camera and auxiliary infrared light, and she was scored as making a choice if she either passed within 10 cm of a speaker or circled it. In natural choruses, this behavior almost always results in mating. If the female did not leave the cage after 10 min or if she hopped out of the playback arena, a "no response" was scored. To avoid any side biases, the 16-m speaker was Speaker 4 in roughly half of the trials and Speaker 5 in the other half (see Figure 1); alternation of speakers was done between nights, rather than between females, because of the considerable amount of time it took to set up the playback arena and set SPLs each night. Each female was tested

only once. All playback experiments presented in this paper used these same methods except where noted.

If females prefer closer over more distant males and exhibit such preferences in complex acoustic environments, then a significant majority of the females should choose the 16-m speaker.

Results and Discussion

Of the 20 females tested, 17 females (85%) chose the 16-m speaker broadcasting a 450-Hz call; two females (10%) chose the 19-m speaker broadcasting the 450-Hz call, and one female (5%) chose one of the speakers broadcasting the 550-Hz call. This result represents a significant preference for the 16-m speaker over the other seven speakers (binomial test, expected value = 1/8, $p < .0001$) and over the 19-m speaker (binomial test, expected value = 1/2, $p = .0004$).

From this test, I conclude that, under complex acoustic conditions, females prefer closer males over more distant males when females must travel an additional 3 m (19% of 16 m) to reach a more distant male that produces equally attractive calls.

Test of Signal-Degradation Hypothesis

Design, Method, and Predictions

To test this hypothesis, females were presented with a choice of speakers broadcasting calls with the same amount of signal degradation but set at different distances from approaching females. The eight-speaker array used was the same as that used in the first control experiment, except that the two central speakers (Speakers 4 and 5) were placed at 15 m and 18 m, respectively, from the release point. The 15-m speaker broadcast 450-Hz calls recorded at a distance of 4 m from the speaker, and the 18-m speaker broadcast the same calls recorded 1 m from the speaker. Therefore, at the release point, calls from the two speakers had the same apparent signal degradation, with respect to spectral and temporal features, equivalent to that of calls broadcast from 19 m.

To record the calls from each speaker, the speaker was set at 19 m from the release point, and the *RMS* SPL of the calls was set to 85 dB at 1 m. The *RMS* SPL was then measured at 4 m from the speaker, and 24 repetitions of the call were recorded at 4 m from the speaker (15 m from the release cage). The *RMS* SPL of the calls at 1 m from the speaker was then set to be the same as it was at 4 m, and 24 repetitions of the call were recorded at 1 m from the speaker (18 m from the release point). Using the same *RMS* SPL of calls for both recordings ensured that the amplitude of the calls in the two recordings was the same relative to that of the background noise. Separate 1-m and 4-m recordings were made for both Speakers 4 and 5.

Calls were recorded with a Sennheiser ME 66 "shotgun" microphone and a K6 powering module (Sennheiser Electronic Corporation, CT) placed approximately at the height of a female's head. The signal from the microphone was passed through the MOTU 828 A/D converter (44.1 kHz sampling rate) and recorded to a digital file using the Raven sound analysis program. Recordings were filtered below 200 Hz and above 3 kHz to remove background noise outside the frequency range of the call (e.g., calls of insects). The four sequences of calls, one for each combination of speaker and distance, were used to construct four playback files. For

example, when Speaker 4 was set at 15 m from the release point, that speaker played the calls recorded at 4 m from that speaker, and Speaker 5, which was placed at 18 m from the release point, played the calls recorded at 1 m from that speaker. I alternated which speaker was set at which distance between nights. The remaining six speakers broadcast 550-Hz calls. The source amplitudes of the two speakers broadcasting 450-Hz calls were equalized to 85 dB RMS SPL at 1 m; hence, the amplitude of the 15-m speaker was higher at the release point than that of the 18-m speaker.

To determine whether calls recorded at 4 m were significantly degraded relative to calls recorded at 1 m, nonparametric analyses of variances (ANOVAs) were conducted. Parametric repeated-measures and one-way ANOVAs were not valid because the normality assumption of these tests was not met and transformations failed to normalize residuals. To determine whether calls degraded temporally with distance, and to assess whether degradation differed between the two speakers, the duration of calls were compared between the four speaker (4 or 5) and distance (1 m or 4 m) combinations with a Kruskal–Wallis Test; significant differences in duration among speaker–distance combinations would be indicative of temporal degradation (e.g., reverberation). To determine whether calls were spectrally degraded, the amplitude of each of the five harmonics relative to the fundamental was compared across the four speaker–distance combinations using a Kruskal–Wallis test. Because five tests were conducted (one for each harmonic), the sequential Bonferroni technique was used to maintain comparison-wide α rates at .05 (Rice, 1989); the adjusted α level (α_{SB}) was set to .01 ($= .05/5$). When significant overall effects were detected with a Kruskal–Wallis test, post hoc pairwise comparisons between treatments were conducted by comparing individual medians with Mann–Whitney tests. Alpha levels were

adjusted with the sequential Bonferroni technique. The statistical significance of results was the same whether α_{SB} was set to control error rates less conservatively across the five comparisons (i.e., the five harmonics, $\alpha_{SB} = .01$) or more conservatively to control error rates across all 30 post hoc tests ($= 5 \text{ harmonics} \times 6 \text{ post hoc tests per harmonic}$; $\alpha_{SB} = .05/30 = .0017$); the more conservative α_{SB} was used to interpret the results of post hoc comparisons.

If females use spectral or temporal degradation of calls to assess distance, then the proportion of females choosing each speaker should be the same.

Results and Discussion

The durations of calls recorded at 1 m (Speaker 4: $Mdn = 150.1$, interquartile range [IQR] = 149.7 to 150.5; Speaker 5: $Mdn = 149.9$, IQR = 149.6 to 150.1) and at 4 m (Speaker 4: $Mdn = 150.2$, IQR = 149.7 to 150.5; Speaker 5: $Mdn = 149.9$, IQR = 149.7 to 150.4) did not differ among the four speaker–distance combinations, Kruskal–Wallis test, $\chi^2(3, N = 96) = 2.64$, $p = .45$, indicating that temporal degradation of calls did not occur over a distance of 3 m. However, the amplitudes of the harmonics, relative to the fundamental, were altered significantly over that same distance (overall Kruskal–Wallis tests, all $ps < .0001$, $\alpha_{SB} = .01$). The relative amplitudes of the second, third, and fourth harmonics were 0.2 to 0.7 dB greater at 4 m than at 1 m, whereas the relative amplitudes of the fifth and sixth harmonics were about 1.9 and 4.8 dB lower, respectively, at 4 m than at 1 m (Figure 2; post hoc Mann–Whitney tests, all $ps < .0001$, $\alpha_{SB} = .0017$). There were no differences between the two speakers in the relative amplitudes of the harmonics at either 1 m (post hoc Mann–Whitney tests, all $ps \geq$

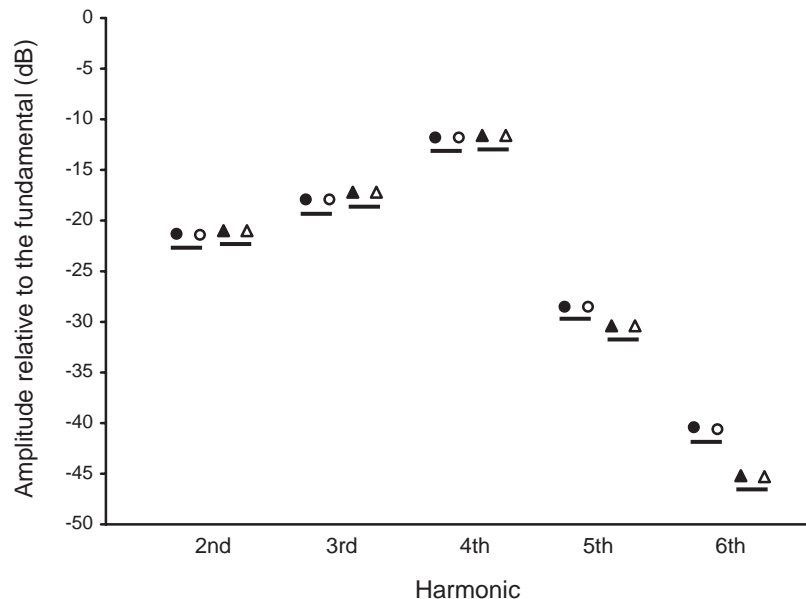


Figure 2. Median amplitudes, relative to the fundamental, of the second through sixth harmonics of the 450-Hz call recorded from Speaker 4 (circles) and Speaker 5 (triangles) at 1 m (filled symbols) and 4 m (open symbols) from the respective speakers. Lines represent medians that did not differ significantly in post hoc comparisons of the four speaker–distance combinations for a harmonic (see text for statistical tests). Interquartile ranges are not shown because most were too small to be easily seen in the figure.

.11) or 4 m (Figure 2; post hoc Mann–Whitney tests, all p s \geq .013; α_{SB} = .0017). Hence, calls degraded spectrally over 3 m, but the amount of degradation was similar for the two speakers over that distance.

Twelve (86%) of the 14 females tested chose the 15-m speaker; the remaining two (14%) chose the 18-m speaker, a significant preference for the 15-m speaker over the other seven speakers (binomial test, expected value = 1/8, p < .0001) and over the 18-m speaker (binomial test, expected value = 1/2, p = .003).

The preference of females for the 15-m speaker over the 18-m speaker argues against the hypothesis that females use spectral and temporal degradation of calls to assess the distance to potential. Because I did not record calls at the release point or at other points between the release point and the speakers, the possibility remains that the amount of signal degradation differed between the Speakers 4 and 5 at these distances. The results of the playback experiment suggest that any difference between speakers in the amount of degradation between the 15-m position and the release point was not great or that, even if it was, females do not use signal degradation. If signal degradation over this distance were significantly greater for one speaker (4 or 5) than the other, then that speaker would appear further away, and females, if they use degradation to assess distance, should preferentially chose the other speaker. This preference would in turn result in a relatively even distribution of choices between the 15-m and 18-m speakers because these speaker positions were alternated between Speakers 4 and 5. The results of the playback experiment do not support these predictions. Half (N = 7) of the females chose Speaker 4, and the other half chose Speaker 5 (binomial test, p = 1.0), and females exhibited a strong preference for the 15-m speaker. Thus, it appears that females do not use signal degradation to assess distance to potential mates.

Test of Relative-Amplitude and Sound-Gradient Hypotheses

Design, Method, and Predictions

These two hypotheses were tested simultaneously using the same playback arena and methods as in the first control experiment, except that the sound gradient of the 16-m speaker was manipulated such that both the amplitude of calls at each distance from the speaker and the rate of increase in amplitude along the approach paths to the speaker (the sound gradient) were the same for the 16-m and 19-m speakers. As females approached the speakers, an assistant attenuated the amplitude of calls incrementally as females passed arcs of string centered on the 16-m speaker and set at 9, 6, 4.25, 3, 2, and 1 m, respectively, from the 16-m speaker. The *RMS SPL* of calls broadcast from the 19-m speaker was set to 85 dB at 1m and that for calls from the 16-m speaker was set to either 82 dB when Speaker 4 was the 16-m speaker or to 82.5 dB at 1m when Speaker 5 was the 16-m speaker. The difference in the initial attenuation between Speakers 4 and 5 was necessary to compensate for the acoustics of the playback arena. The initial attenuation resulted in *RMS SPL*s for the calls from the 16-m and 19-m speakers being close to 60 dB at the release point (see Figure 3). Subsequent attenuation of the 16-m speaker was accomplished by creating six additional tracks in the AudioDesk application with attenuations of -1.0, -2.0, -3.2, -4.7, -7.3, and -10.1 dB relative to the other tracks, corresponding to arcs at 9, 6, 4.25, 3, 2, and 1 m, respectively. When a female crossed each successive arc, my assistant rapidly (almost always within 1 s) switched tracks to the new attenuation. If the rare case when a problem was encountered in switching tracks, the trial was discarded.

To check whether these procedures produced identical amplitudes and sound gradients, the *RMS SPL* of calls from each speaker

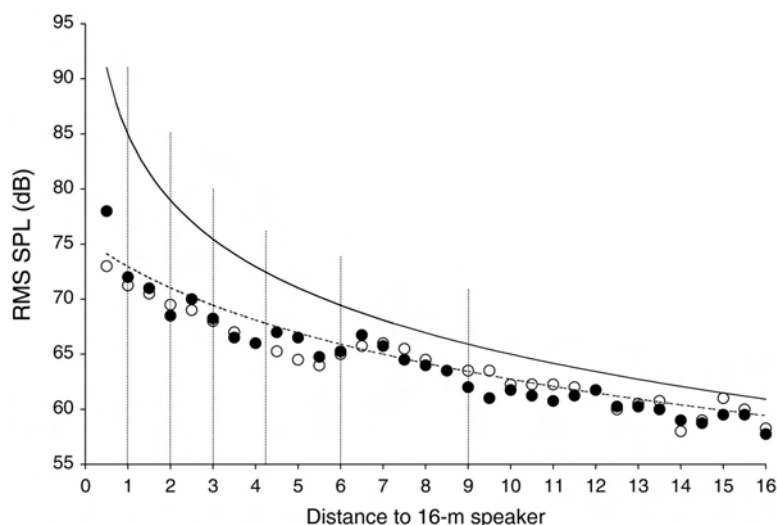


Figure 3. Root mean-square SPL (*RMS SPL*) of calls from the 16-m speaker (solid circles) and 19-m speaker (open circles) in the playback in which the sound gradient of the 16-m speaker was manipulated to match that of the 19-m speaker. The release cage was set at the 16-m point on the graph. The exponential curves represent the theoretical SPLs, based on spherical spreading, of the 16-m speaker (solid line) and 19-m speakers (dashed line) in the absence of manipulation. Vertical dotted lines represent the distances from the 16-m speaker at which the amplitude of calls from that speaker was attenuated as the female approached the two speakers.

was measured every 0.5 m along a line connecting that speaker with the release point, beginning at the release point and ending 15.5 m from the release point. These data are shown in Figure 3 for the set-up with Speaker 4 as the 16-m speaker. There was no significant difference between the 16-m and 19-m speakers in either *RMS SPL* or increase in *SPL* (dB per 0.5 m) when either Speaker 4 or Speaker 5 was the 16-m speaker (Wilcoxon signed-ranks test, $N_{SPL} = 32$; $N_{increase\ in\ SPL} = 31$, all p s $\geq .48$). Because the 16-m and 19-m speakers did not differ with respect to either amplitude along the approach path or sound gradient, this experimental design allowed me to test simultaneously both the relative-amplitude and sound-gradient hypotheses.

If females use either the amplitude of calls at their location or the sound gradient to determine distance to potential mates, then an equal proportion of females should choose the 16-m and 19-m speakers.

Results and Discussion

Of the 14 females tested, 11 females (79%) chose the 19-m speaker broadcasting the 450-Hz call; 2 females (14%) chose the 16-m speaker broadcasting the 450-Hz call, and 1 female (7%) chose one of the speakers broadcasting the 550-Hz call. This result represents a significant preference for the 19-m speaker over the other seven speakers (binomial test, expected value = 1/8, $p < .0001$) and over the 16-m speaker (binomial test, expected value = 1/2, $p = .023$).

These results do not support either the relative-amplitude or the sound-gradient hypothesis, and females unexpectedly chose the more distant speaker over the closer speaker. One possible explanation for this result is that females discriminated against the manipulated sound gradient of the 16-m speaker. To test this hypothesis, I conducted a second control experiment.

Second Control Experiment

Design, Method, and Predictions

In the previous playback, the 16-m speaker had a manipulated sound gradient, with a source *RMS SPL* at 1m of 72 dB, whereas the 19-m speaker had a normal sound gradient with a source *RMS SPL* of 82 dB (source *SPL*s calculated from logarithmic regression equations fitted to measured *SPL*s). In the second control experiment, the combinations of source amplitudes and sound gradients were reversed. Both speakers were sat at 16 m from the release point, with the source *RMS SPL* of one speaker set to 72 dB at 1 m and of the other set to 90 dB at 1 m. The sound gradient of the speaker with the greater source amplitude was manipulated in the same manner as in the previous experiment; the sound gradient of the speaker with the lower source amplitude remained unmanipulated (see Figure 4). The six speakers broadcasting 550 Hz calls were not included because the *RMS SPL* of calls from these speakers would be greater (58 to 60 dB) at the release point than calls from the speaker with the lower source amplitude and normal sound gradient (estimated to be roughly 48 dB). Choice by females of speakers broadcasting 550 Hz calls would greatly complicate interpretation of the results.

If the preference in the previous experiment for the speaker with the greater source amplitude were due to discrimination against the manipulated sound gradient, then females in the present experi-

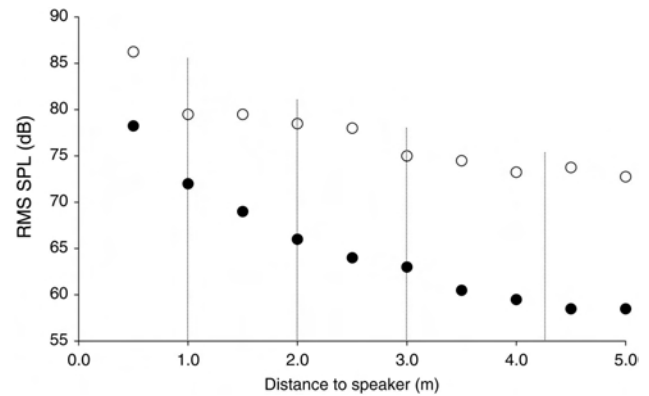


Figure 4. Root mean square *SPL* (*RMS SPL*) of calls in the second control experiment, in which one speaker had a manipulated sound gradient and a greater source amplitude (open circles) and the other had a normal sound gradient and a lower source amplitude (solid circles). Data are shown only up to 5 m from the speakers because the sound meter used did not permit accurate readings of *SPL* below about 57 dB. Vertical dotted lines represent the distances from the speaker at which the amplitude of calls from the speaker with the manipulated sound gradient was attenuated as the female approached the two speakers.

ment should prefer the speaker with the normal sound gradient. Furthermore, the proportion of the females choosing the speaker with the greater source amplitude should be less in this experiment than in the previous experiment. Finally, if females use sound gradients to assess distance to potential mates, then they should choose the speaker with the unmanipulated sound gradient because its sound gradient was steeper than that of the speaker with the manipulated gradient (see Figure 4).

Results and Discussion

All 10 of the females tested chose the speaker with the manipulated sound gradient (binomial test, $p = .002$), and the proportion of females choosing this speaker, which had the greater source amplitude, was not significantly different from the proportion of females choosing the speaker with the greater source amplitude and the normal sound gradient in the previous experiment (Fisher's exact test, $p = .31$). Thus, it appears that a manipulated sound gradient does not affect choice by females. In the previous experiment, therefore, the preference of females for the speaker with the greater source amplitude was not due to discrimination by females against a manipulated sound gradient. The preference in the present experiment for the speaker with the shallower sound gradient also argues against the sound-gradient hypothesis. The combined results of this, and the previous, experiment argue strongly against the relative-amplitude and sound-gradient hypotheses. Furthermore, the results of this experiment provide additional evidence against the signal-degradation hypothesis because females preferentially chose the more distant speaker, which had the greater temporal and spectral degradation.

Source Amplitude Experiment

Design and Method

To explore further the effect of source amplitude on female choice, females were presented with two speakers separated by

1 m, both broadcasting 450-Hz calls and set at 16 m from the release point. To allow comparisons with the second control experiment, the other six speakers broadcasting 550-Hz calls were not included. The *RMS SPL* at 1 m for one of the speakers was set to 85 dB; the sound gradient of calls broadcast from this speaker was not manipulated. For the second speaker, the amplitude of calls was initially set to 87 dB *RMS SPL* at 1 m, and its sound gradient was manipulated in the same manner as in the experiment to test the relative-amplitude and sound-gradient hypotheses. As a result of this manipulation, the *RMS SPL* of calls broadcast from the speaker with the manipulated gradient was greater at the release point than that of calls broadcast from the speaker with the unmanipulated gradient, and remained 1 to 2.25 dB greater until about 6 m from the speakers (see Figure 5). Between 6 m and 4.5 m from the speakers, the *RMS SPL*s of calls from the two speakers were equivalent, and closer than 4.5 m, the *RMS SPL* of calls from the speaker with the unmanipulated sound gradient was greater than the *RMS SPL* of calls from the other speaker. As a result of the manipulation, the source amplitude of the speaker with the manipulated sound gradient, as calculated from a logarithmic regression equation fitted to measured *SPL*s, was 79 dB, as compared to 85 dB for the speaker with the unmanipulated sound gradient.

Results and Discussion

Twelve (92%) of the 13 females tested chose the speaker with the greater source amplitude and the unmanipulated sound gradient; the other female (8%) chose the speaker with the lower source amplitude and the manipulated sound gradient (binomial test, $p = .003$). The proportion of females choosing the speaker with the greater source amplitude did not differ between this experiment and the second control experiment (Fisher's exact test, $p = .57$).

In this experiment, females chose the speaker with the greater source amplitude, even though the *RMS SPL* of calls from that speaker remained less than, or equal to, the *RMS SPL* of calls from the other speaker until females were within less than 4.5 m from the speakers. In natural choruses, 57% of females have already made their final choice of mate by the time they have approached this close to their eventual mate (based on data in Murphy & Gerhardt, 2002).

The results of this experiment, along with those from the second control experiment and the test of the relative-amplitude and sound-gradient hypotheses, strongly suggest that females base their choice of mates on source amplitude. In all three playback series, females chose the speaker with the greater source amplitude. In the test of the relative-amplitude and sound-gradient hypotheses, females chose the speaker with the greater source amplitude, even though they had to travel an additional 3 m beyond the other speaker broadcasting the attractive 450-Hz call, a difference in distance that, in the first control experiment, was enough to result in a strong preference for the closer of two speakers broadcasting that call. Furthermore, the present experiment argues against the relative-amplitude hypothesis because the amplitude of calls from the preferred speaker was less than, or equal to, that of calls from the other speaker for most of the distance over which females assess potential mates.

General Discussion

The present study experimentally demonstrated that distance to potential mates affects female choice in *H. gratiola* under the complex acoustic conditions that confront females as they choose mates in groups of males. These results support and extend observations of a distance effect in natural choruses and previous two-speaker playback experiments demonstrating an effect of

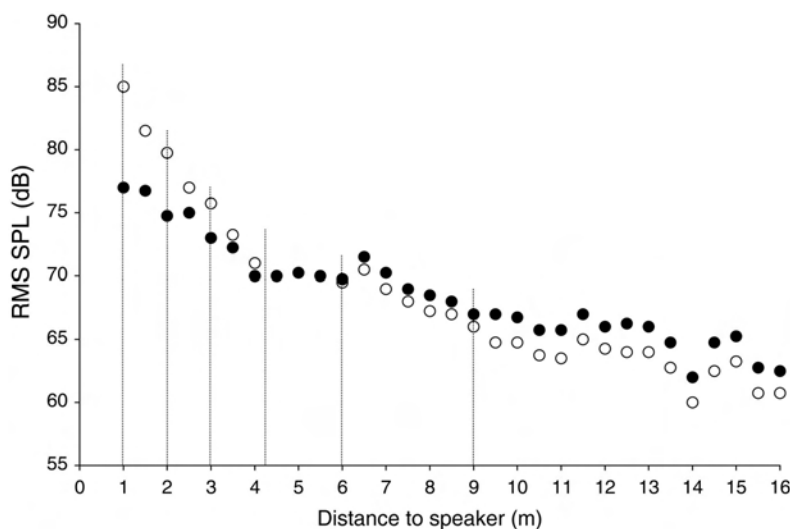


Figure 5. Root mean square *SPL* (*RMS SPL*) for calls from the speaker with the sound gradient (closed circles) manipulated such that the *RMS SPL* of calls from this speaker, relative to those the speaker with a normal sound gradient (open circles), were greater at the release point but lower close to the speaker. The release cage was set at the 16-m point on the graph. Vertical dotted lines represent the distances from the speaker at which the amplitude of calls from the speaker with the manipulated sound gradient was attenuated as the female approached the two speakers.

distance on choice (Murphy & Gerhardt, 2002). The present study did not explore the benefits females might obtain from choosing closer males, but by doing so, females may reduce energy expenditure or predation risk. Energy savings may not be very substantial: A female choosing a mate 16 m from the start of her mate choice process would only save 16% ($= 3/19$) of the energy she would expend reaching a male at a distance of 19 m. This savings is unlikely to represent a substantial portion of a female's daily or annual energy budget. However, reducing predation risk by 16% may be important given that female *H. gratiosa* are known to suffer predation in natural choruses (Murphy & Gerhardt, 2002).

The results of playback experiments ruled out three mechanisms females might use to assess distance to potential mates: (a) degradation of spectral and temporal aspects of calls, (b) the relative amplitude of calls at the female's location, and (c) differences in the sound gradient of calls from males at different distances from the choosing female. These results are somewhat surprising given previous research. The degradation of signal properties is used by humans and by songbirds in territorial interactions to assess distance to sound sources (Naguib & Wiley, 2001). Female bladder grasshoppers, *Bullacris membracioides*, show increased response to advertisement calls recorded close to males relative to those recorded at some distance, even when all calls have the same source amplitude (Couldridge & van Staaden, 2006). These results suggest that females of this species might use such cues to choose closer males over more distant ones. Preferences by female anuran amphibians and orthopteran insects for the louder of two equidistant speakers are common (Gerhardt & Huber, 2002), results that are consistent with the hypothesis that females of these species use relative signal amplitude at their location to assess distance. Indeed, preferences for louder signals are often interpreted as a preference for closer males (Gerhardt & Huber, 2002). Finally, there is evidence that humans can use the sound gradient to assess absolute and relative distances to sound sources (Loomis, Klatzky, Philbeck, & Golledge, 1998).

What cues then might females *H. gratiosa* use? One possibility is triangulation (or absolute motion parallax, Loomis et al., 1998;

Speigle & Loomis, 1993). As a female approaches and moves through a chorus of calling males, the angle between the female and a closer male will change more rapidly than that between the female and a more distant male (see Figure 6), much the same as objects close to the road appear to move past a moving car faster than more distant objects. A female could triangulate on a male by comparing angles between herself and the male discontinuously (e.g., before and after a movement) or continuously, as the rate of change in angle (i.e., angular velocity). Either mechanism would allow females to assess either relative or absolute distances to calling males.

Studies of sound localization in orthopteran insects and anuran insects demonstrate that they can fairly accurately measure the angle between themselves and sound sources (Gerhardt & Huber, 2002). A study of sound localization by female *H. gratiosa* indicated that females of this species can discriminate between sound sources separated by at little as 15° (Klump & Gerhardt, 1989). However, this study likely underestimated the ability of females to localize sound sources because the accuracy of localization was measured only for the initial jump females made after listening briefly to advertisement calls and females were not allowed to update directional information as they would when moving in natural choruses (Gerhardt & Huber, 2002). This limitation applies to similar studies with other species (Gerhardt & Huber, 2002). Studies of humans have shown that the accuracy of perception of distance to sound sources is improved when subjects move toward sound targets than when they remain stationary (Ashmead et al., 1995; Speigle & Loomis, 1993), although the designs of both of these experiments greatly reduced the likelihood that subjects could use triangulation. Hunting barn owls have been shown to triangulate on prey (Konishi, 1973).

The possibility that females may use acoustic triangulation to assess distance to potential mates has not, to my knowledge, been investigated in nonhumans. In fact, experiments that attempt to determine which acoustic cues are used to assess distance are often designed to explicitly exclude this cue. For example, in studies of distance estimation in songbirds, playback is typically halted as

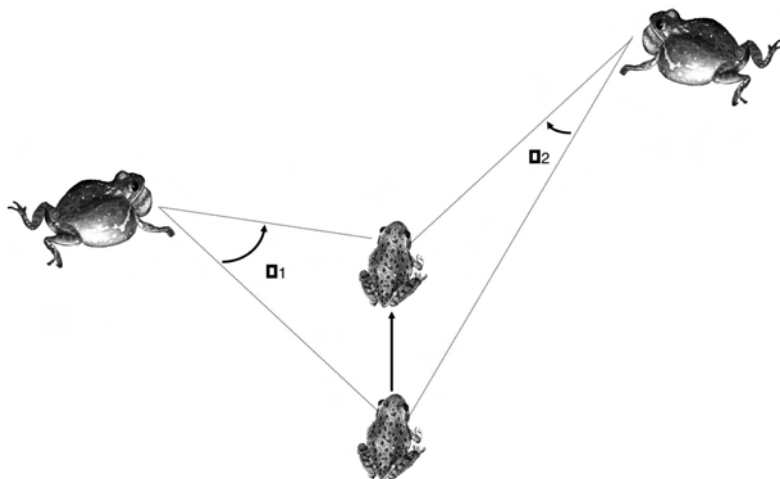


Figure 6. Change in the angle (θ) between a female and potential mates as she moves through a chorus. The angle between the female and the closer male (θ_1) changes faster than that between the female and the more distant male (θ_2).

soon as test birds leave perches to approach speakers (e.g., Nelson, 2002; Nelson & Stoddard, 1998). This approach is necessary to isolate cues other than triangulation, but triangulation may also be used by these species.

The triangulation hypothesis predicts that females should preferentially choose speakers whose angle relative to the female changes more rapidly than other sound sources broadcasting identical calls. I attempted to test this hypothesis with *H. gratiosa* using playback experiments, but it proved too difficult logistically to maintain precise angles between females and speakers when females were free to move in any direction. Such experiments would be feasible with species that could be tethered (e.g., orthopteran insects).

One unexpected result of the present study was the preference for greater source amplitude in all three experiments in which speakers differed in source amplitude. A preference for greater source amplitude has also been reported by Castellano et al. (2004) for green toads, *Bufo viridis*. In two-choice playback experiments, females preferred speakers with source amplitudes 6 dB greater than alternatives when the further speaker was twice as far as the closer speaker, even though the amplitude of calls at the release point was the same both speakers. Hence, females of both *B. viridis* and *H. gratiosa* will travel additional distance to reach speakers with greater source amplitudes. In contrast, Arak (1988) studying natterjack toads, *B. calamita*, and Bishop, Jennions, and Passmore (1995) and Grafe (1997) studying painted reed frogs, *Hyperolius marmoratus*, did not find preferences for speakers with greater source amplitudes. This lack of a preference may have been due to the shorter distances to speakers used by these three studies compared to those in Castellano et al. and the present study. Shorter distances to speakers may not allow females to accurately assess distance cues (Castellano et al., 2004). Indeed, Castellano et al. found a stronger preference for the speaker with the greater source amplitude when speakers were further from the release point (5 m vs. 10 m), than when speakers were closer (1 m vs. 2 m). This interpretation is compromised, however, by the fact that Castellano et al. found significant preferences for speakers with greater source amplitudes in tests in which speakers were at similar distances (i.e., 1 m vs. 2 m) to those used by Arak; Bishop et al.; and Grafe. Another possibility is that these three studies used linear arrays with the release point set between speakers, whereas Castellano et al. and the present study used arrays in which the release point was placed in front of the speakers. In such triangular arrays, females may be better able to assess distance because movement toward one speaker does not necessitate movement away from the other speaker, as it does in linear arrays. This effect of speaker arrangement would be especially important if females use triangulation to assess distance. Playback experiments with other species using both linear and triangular arrays are needed to assess whether choice for greater source amplitude in *B. viridis* and *H. gratiosa* represent exceptions or the norm.

For females to choose males who produce calls with greater source amplitude, females must assess independently and simultaneously two cues (Castellano et al., 2004): the distance to potential mates, and the relative amplitude of signals at their (the females') location. Assessment of the latter might entail simply comparing the relative amplitudes of received signals. Use of relative amplitudes might be a sufficiently accurate measure of source amplitude but will likely be subject to some error due to

environmentally induced fluctuations in call amplitude. Accuracy might be improved if females sample the sound gradient (Gerhardt & Huber, 2002) and use that information to predict source amplitude. The experiments in the present study cannot distinguish between these mechanisms.

Assessment of source amplitude has also been demonstrated for eastern towhees, *Pipilo erythrophthalmus* (Nelson, 2000). These songbirds estimate the source amplitude of calls used in territorial interaction from several spectral and temporal features that are correlated with source amplitude. They then compare this estimated source amplitude with the amplitude perceived at their own location to determine distance to the sound source.

The results of the present study of *H. gratiosa* and those of Castellano et al. (2004) on *B. viridis* suggest that anuran amphibians may possess greater cognitive abilities than are generally attributed to them. The results of experiments reported here refute three simpler mechanisms by which female *H. gratiosa* might assess distance to potential mates and suggest a much more complex mechanism of distance assessment, triangulation. The finding that females from two species from different families (Hylidae and Bufonidae) base their choice of mates on source amplitude, and must therefore combine information about both distance to potential mates and the relative amplitude of calls, further suggests more complex cognitive processing. Furthermore, female anuran amphibians incorporate a substantial number of call characteristics into their mate-choice decision (Gerhardt & Huber, 2002), and combine preferences for traits in apparently complex manners (Burke & Murphy, 2007). Additional studies that test for complex cognitive processes, rather than assuming simple processes, are likely to produce intriguing results and a greater understanding of the cognitive abilities of anuran amphibians.

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Analyzing Acoustic Interactions in Natural Bullfrog (*Rana catesbeiana*) Choruses

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Analysis of acoustic interactions between animals in active choruses is complex because of the large numbers of individuals present, their high calling rates, and the considerable numbers of vocalizations that either overlap or show close temporal alternation. The authors describe a methodology for recording chorus activity in bullfrogs (*Rana catesbeiana*) using multiple, closely spaced acoustic sensors that provide simultaneous estimates of sound direction and sound characteristics. This method provides estimates of location of individual callers, even under conditions of call overlap. This is a useful technique for understanding the complexity of the acoustic scene faced by animals vocalizing in groups.

Keywords: bullfrog, chorus, advertisement call, auditory scene, microphone array

During their breeding season, male anurans of many species form aggregations or choruses, in which they vocally advertise their presence, possession of a territory, and willingness to mate. These choruses can be quite dense, both spatially and acoustically. This density imposes significant perceptual demands on the chorus residents. Males need to regulate the timing of their own calls to minimize interference or masking by the calls of neighbors and to facilitate efficient broadcasting of their calls to recipient females. Field recordings and playback experiments have identified particular strategies males adopt to solve this task, with synchrony of calls or alternation of calls between neighbors being the most common (reviews: Gerhardt & Huber, 2002; Wells & Schwartz, 2007). An individual male within a chorus can also acquire important information about the identity and location of other chorus members by listening to their calls (Boatright-Horowitz, Horowitz, & Simmons, 2000; Davis, 1987). Analysis of interactions between chorusing males suggests that males space themselves within choruses and respond to each other by means of certain behavioral “rules” (Boatright-Horowitz et al., 2000; Greenfield & Rand, 2000).

During their spring/summer breeding season, male bullfrogs (*Rana catesbeiana*) form nightly choruses in ponds or lakes and broadcast

advertisement calls, both to attract females for mating and to advertise their presence to rival males. The structure of these choruses is typically quite stable, with individual male frogs occupying essentially the same locations over periods of days, weeks, or even months (Boatright-Horowitz et al., 2000; Howard, 1978; Ryan, 1980). The possession of stable, well-defended territories and the prolonged breeding season facilitates familiarity among neighboring males. To a large extent, interactions between males are acoustically mediated. Each male produces advertisement calls periodically, but there are considerable between-male differences in both temporal and spectral properties of these calls, including differences in call rate, fundamental frequency and note duration (Bee & Gerhardt, 2001; Bee, 2004; Simmons, 2004). Within an active chorus, however, it is not always possible to distinguish calls of individuals by spectral or temporal properties alone, because calls of multiple bullfrogs can occur simultaneously or with significant overlap in time. Moreover, successive notes from the calls of the same individual vary in envelope modulation (Suggs & Simmons, 2005), which produces additional spectral cues that may be difficult to segregate from those in notes of neighboring males. An alternative or supplemental means of individual identification is to identify the sources of calls using information about the relative spatial locations of males in the chorus. Some individuals are located in close proximity while others are spaced further apart, so that any given male receives an assortment of calls from other males in different directions and at different distances (Boatright-Horowitz et al., 2000). The use of both kinds of information (acoustic cues and spatial location) can provide the means of reliably distinguishing individual callers, and then describing their acoustic interactions with other callers. Our understanding of the structure and dynamics of frog choruses has been limited, however, by technical aspects involved in first recording, and then sorting and identifying calls of individual males in a dense, noisy chorus in such a manner that all of the relevant information can be obtained.

Much of our knowledge of vocal interactions between chorusing male frogs is based on responses to sound playbacks by individual focal males (often separated from other chorusing males), or on recordings of natural vocal interactions between small groups (two through five) of callers within a larger chorus (e.g., Arak, 1983;

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Brush & Narins, 1989; Klump & Gerhardt, 1992; Rosen & Lemon, 1974; Schwartz, 1987, 1993). Much of this work relies on the use of single microphones for localizing and identifying calling males. While multichannel recording and call monitoring systems have been described (Brush & Narins, 1989; Grafe, 1996; Schwartz, Buchanan, & Gerhardt, 2002), they have not as yet been widely adopted, even though such techniques offer the ability to analyze choruses over large spatial and temporal scales. Grafe (1997) monitored chorusing behavior of male painted reed frogs (*Hyperolius marmoratus*) during female phonotaxis, using an array of four widely spaced microphones. Locations of calling males were derived by triangulation based on arrival time differences of vocalizations at pairs of microphones. The focus of this study was on female preferences and not on chorusing dynamics, so vocal interactions between calling males were not analyzed in detail. The array used by Grafe (1997) is similar to those developed for analyses of songbird vocal behavior (McGregor et al., 1997; Merrill, Burt, Fristrup, & Vehrencamp, 2006). While these techniques are promising, recordings and interpretations of vocal interactions within dense, natural choruses, taken as a whole and over long chorusing times remain relatively rare, both for anurans and for other chorusing animals (D'Spain & Batchelor, 2006; Greenfield & Snedden, 2003).

In this paper, we describe a technique developed for acoustic surveying that we adapted for the task of identifying individual male bullfrogs in a large active chorus. Our technique is based on audio recordings obtained using a pair of cube-shaped acoustic sensors, each containing multiple closely spaced microphones, placed in two separate locations around the chorusing site. Data recorded by the sensors are subsequently processed by a computational model of the peripheral auditory system (Mountain, et al., 2007) that provides acoustic analysis of recorded sounds, as well

as estimates of sound source direction around each cube. Because information about the acoustic characteristics of bullfrog vocalizations and about the location of individual callers can be derived from the same records, this is a promising methodology to fully characterize acoustic interactions in noisy environments.

Method

Acoustic recordings were made between 2200 and 2400 hours during the months of June and July, 2005 and 2006, at a pond on private property in a heavily wooded location in central Massachusetts (Figure 1A). The pond is approximately 40 m long and 15 m wide at its widest point, and is surrounded by heavy vegetation. It supports a population of both bullfrogs and green frogs (*Rana clamitans*). At this site, some males are found close to the margins of the pond, while others are located in clumps of vegetation at some distance from the shore. On any given chorusing night, between 8 and 12 bullfrogs are actively vocalizing. Animals were not captured for visual inspection or morphological measurements, and thus were not disturbed or handled during sound recordings.

Sensor Array

Vocalizations of male bullfrogs were recorded using two acoustic sensors (cubes) designed and constructed by the Department of Electrical and Computer Engineering at Boston University as part of a Defense Advanced Research Projects Agency (DARPA) Acoustic Microsensors Program. The concept guiding this methodology is to use several widely spaced complete sensor arrays, each consisting of multiple closely spaced microphones, rather than a single array consisting of several widely spaced single

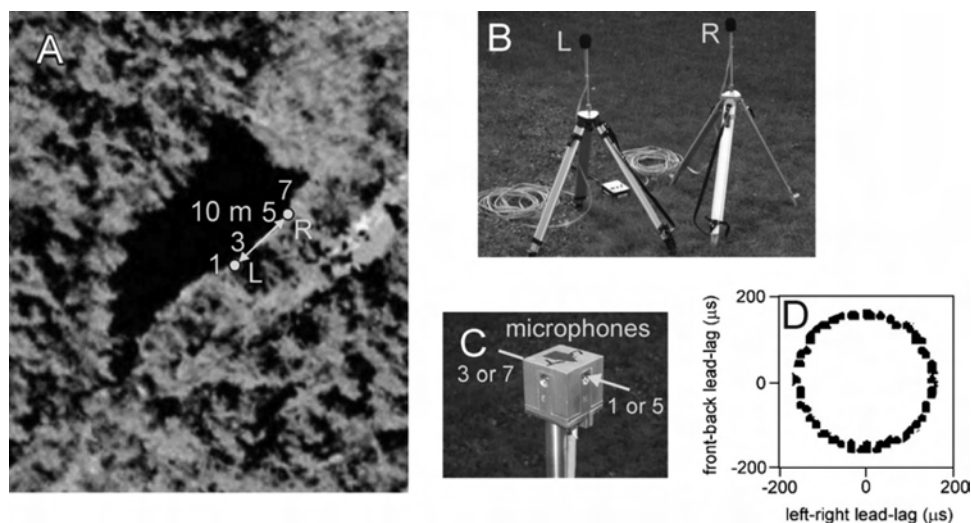


Figure 1. A. Google Earth satellite photograph of the study site (north is to top). Because the pond is located entirely on one side of the array axis, only channels 1 and 3 were used from the left (L) cube, while channels 5 and 7 were used from the right (R) cube. B. Photograph of the two acoustic sensors (cubes) on top of the survey tripods. Each sensor is covered by a black foam windscreen. C. Photograph showing one of the four-microphone sensors (cubes). D. Plot showing reconstruction of the circular movement of a loudspeaker moved to different locations around one of the four-microphone arrays to illustrate fidelity of localization by arrival-time differences (lead-lag in μ s). The test signal was a frequency sweep from 200 Hz to 1,000 Hz.

microphones (Grafe, 1997; McGregor et al., 1997; Merrill et al., 2006). Because the multiple microphones in each sensor array are close together (separated by 3.3 cm in our case), each one receives a nearly identical version of the propagating sound displaced only in time according to the spatial separation between the microphones. Thus, the signals at these microphones are highly correlated because they have undergone virtually identical scattering, reverberation, and filtering by the environment. This simplifies the time-to-angle (azimuth) transformation used to localize the source of the sound. Use of single microphones placed far apart (e.g., 16 m in Grafe, 1997; 75 m in Merrill et al., 2006) allows recording of larger time differences between pairs of microphones to achieve potentially greater accuracy in azimuth; however, the signals arriving at pairs of widely spaced microphones can be decorrelated by multipath effects and environmental filtering that would be different at each microphone. Even over short distances, decorrelation can be severe in areas of heavy vegetation. This would lead to inaccurate localization, thus offsetting the benefits of this approach.

In our application, we used two acoustic sensors (cubes) separated by 10 m (array axis shown in Figures 1A, 3A) placed on one side of the pond. The 10-m separation was chosen because this was the length of an area around the pond that was relatively clear of heavy vegetation. In principle, any separation can be chosen, but there are some constraints. If the sensors are too far apart, then some frogs will be picked up by only one cube, making triangulation difficult. If the sensors are too close together, then some frogs may be missed by both cubes. The sensors were each mounted on top of a vertical aluminum rod that was itself held in a position about 0.6 m above the ground by an adjustable survey tripod (Figure 1B). Each sensor consisted of a 3.3-cm aluminum cube with four sensitive, calibrated, omni-directional electret condenser microphones (Knowles Model FG3329, Itasca, IL), one placed in each of its four vertical faces (Figure 1C), and covered by a black foam windscreen. Over the 200–2,000 Hz frequency range contained in bullfrog advertisement calls (Bee & Gerhardt, 2001; Wiewandt, 1969), the frequency response of these microphones is flat within ± 2 dB. The accuracy of localization in azimuth of each sensor was calibrated by tracking the direction of a known sound source (a frequency modulated sweep from 200 Hz to 1,000 Hz) moving at a fixed distance of 3 m in a circular direction 360° around the center of the cube. The estimates of direction made by each sensor match well the circular track of the sound source (Figure 1D), with deviations from this circular track of approximately 10° . The sensors can locate sound sources in 360° of azimuth; however, because the pond and the frogs were located entirely on one side of the array axis (Figure 1A; it was not feasible to place the cubes in the center of the pond), only two of the four microphones in each sensor provided useful data. In the left-most cube (L in Figure 1A), the two microphones and their recorded signals were designated as channels 1 (to the left) and 3 (to the right). In the other cube, located on the right (R in Figure 1A), channel 7 is the right-most microphone and channel 5 is the left-most microphone. These four microphones were aligned with respect to each other on the array axis by mounting a green laser pointer on top of each sensor and rotating that sensor until the green spot pointed at the other sensor 10 m away.

Data Analysis

Signals picked up by the two active microphones in each sensor were carried by multiconductor shielded coaxial cables to a custom-built power supply and preamplifier (gain $10\times$) and recorded on four channels of a Sony SIR-1000W wideband digital instrumentation recorder (Sony Manufacturing Systems, Lake Forest, CA). The simultaneous sampling rate for the recordings was 48 kHz per channel. Binary files containing the four channels of data [two from the 13 (left) cube and two from the 57 (right) cube] were subsequently downloaded into a Pentium-3 PC using Sony PCScan programs supplied with the Sony recorder (Sony Manufacturing Systems, Lake Forest, CA). These files were broken into 10-s long consecutive segments using custom-written MATLAB routines. They were then analyzed by a binaural computational model of the auditory system implemented in Matlab (Mathworks, Natick MA) and available online at the Boston University EarLab website (Mountain et al., 2007) for estimates of sound location.

The EarLab model incorporates 32 channels of partly overlapping bandpass filter channels (sixth order Butterworth) with center frequencies spaced at logarithmic intervals from 60 Hz to 5,000 Hz. The audio signal is thus segmented into these frequency bands, to facilitate identification of a signal in the appropriate frequency band for bullfrog advertisement calls, and a threshold value is set for each band so as to avoid triggering on background noise. The model then makes a running estimate of arrival time differences (range $-180\ \mu\text{s}$ to $+180\ \mu\text{s}$; Figures 2, 3A) at each frequency band between microphone pairs in overlapping (50% overlap) 100-ms bins; this degree of overlap was used because it allowed smooth interpolation between separate samples. For a single bullfrog call note with a duration of 500 ms, at least five time estimates are made at each sensor. These time estimates are then pooled across all filter frequencies by generating a histogram (bin width $10\ \mu\text{s}$) of time differences at these different frequencies, with the final estimate determined to be at the peak of the histogram. The model then plots peaks in successive histograms to give the running history of time differences across the entire 10-s long data segment (top plots in Figure 2). Consequently, for each 10-s segment analyzed, the resulting dataset consists of a series of up to 250 separate time difference estimates between the pairs of microphones in each sensor. The intrinsic timing accuracy of each cube is based on the sampling rate of the data used in the processing programs, which was 100 kHz (achieved by upsampling the recorded files). At the sampling interval of $10\ \mu\text{s}$ used for processing, out of a total intermicrophone time separation of $180\ \mu\text{s}$ at 90° (Figure 3A), this yields an angular accuracy of about 6° assuming a good signal-to-noise ratio for recording. Under noisy conditions, accuracy could be worse. Calibration of the cubes with test signals in the frequency range of bullfrog calls confirmed that the cubes plus the processing software could reliably locate sound sources in angle bins of 10° .

Direction and distance information are obtained by comparing the time difference estimates for a given sound source at each sensor by a process of vector triangulation. That is, the model displays a running vector emanating from each sensor to each sound source. The point of intersection of these vectors gives an estimate of the location of the source (Figure 3B). To correlate the direction estimates derived from the sensors with actual locations of the calling bullfrogs, one observer visually censused the pond

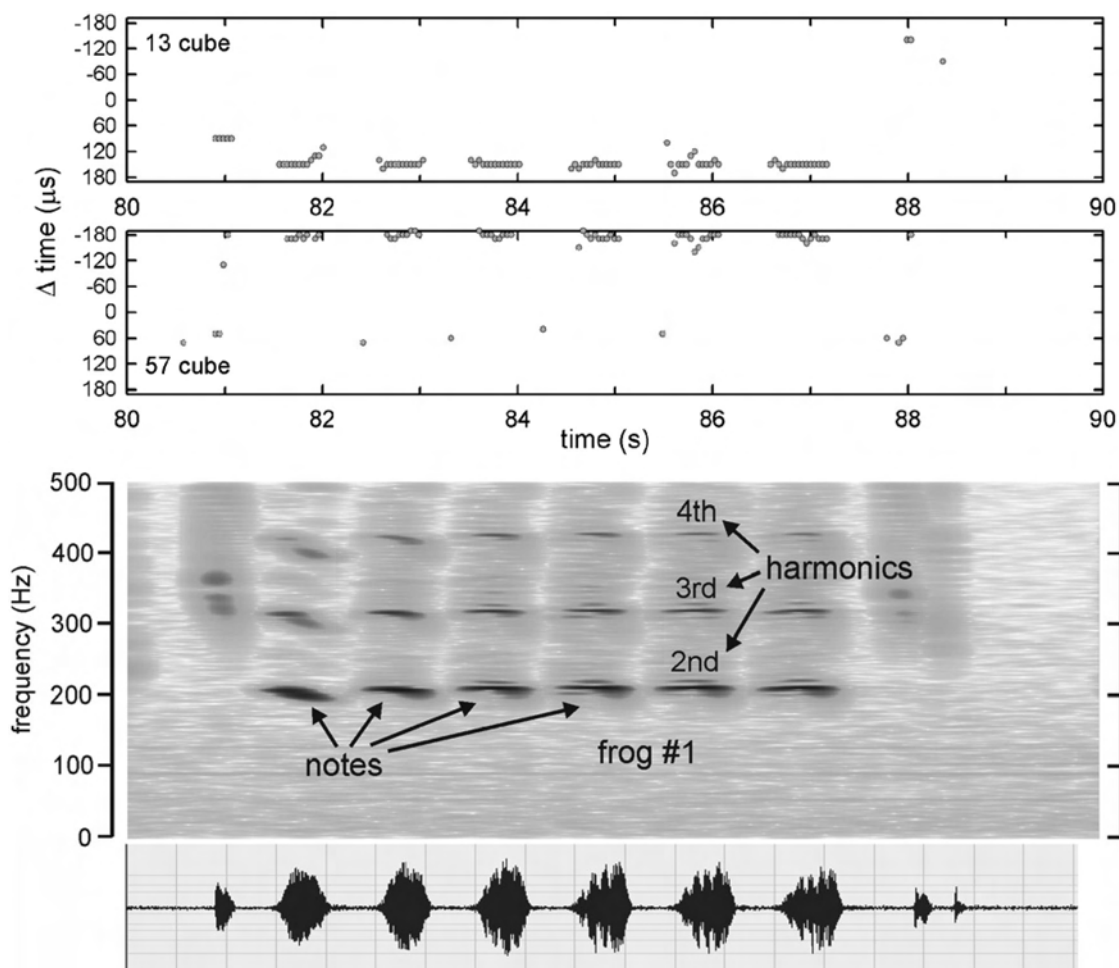


Figure 2. Six note call of single bullfrog (frog #1; see Figure 3). Top: Plots showing time differences (y axes, Δ time in μ s) over 10 sec of recording (x axes) for arrival of sounds at the left (13) cube and at the right (57) cube separately. Each data point (gray circle) represents the output of the auditory model for a 100-ms segment of the sound waveform. Middle: Spectrogram showing the position of the second, third, and fourth harmonics (arrows) in each of the six notes. Bottom: Sound pressure waveform recorded at channel 3 of the left cube. The two waveforms preceding and following the notes of frog #1 are calls of the green frog (*R. clamitans*).

during recordings and marked the location of each animal on a scaled map.

To determine the spectral content of each recorded sound, the four-channel binary files were further separated into two stereo .wav files, one for channels 1 and 3 from the left sensor and the other for channels 5 and 7 from the right sensor. General acoustic characteristics of the calls (duration, duty-cycle, harmonic frequencies, onset time) were analyzed with custom-written MATLAB routines and then displayed as spectrograms and sound pressure waveforms using Adobe Audition v 1.5 (Adobe Systems, San Jose CA).

Results

To illustrate the usefulness of the recording method, data presented here are drawn from 8,000 s of continual chorus recording from one night (070906). On this particular night, 12 male bullfrogs were vocalizing. Visual and audio analysis of

calling patterns within this chorus revealed that males often overlapped or synchronized their calling with other males. Approximately 640 s of the total recording time (about 8% of the total) consisted of an individual male vocalizing alone, so that none of the individual notes in his advertisement call overlapped or alternated with those from another male (see Figure 2). This kind of acoustic pattern could be easily analyzed by ear, or by single-microphone recordings from individual focal males. On the other hand, a considerably larger proportion (about 38%) of the total chorus time, approximately 3,000 s on the sample night, consisted of multiple (2–5) frogs calling together, with both overlap and alternation of individual notes in their advertisement calls (Figures 4 and 6). It is this kind of calling pattern that is difficult to analyze by ear or by recordings from individual focal males, and where knowledge of location becomes valuable for segregating the acoustic contribution from each individual.

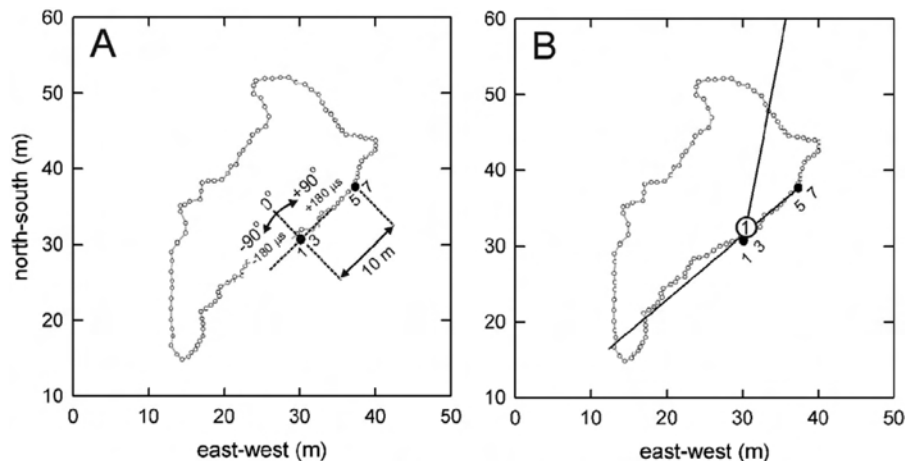


Figure 3. (A) Map of pond showing locations of the two sensors (13, 57; solid dots) and coordinates for direction derived from time differences at the left (13) cube. Each cube provides a time estimate between $-180 \mu\text{s}$ and $+180 \mu\text{s}$ (corresponding to angles between -90° to the left and $+90^\circ$ to the right). A sound source located directly at a particular sensor would have an angle of 0° . (B) Estimated location of frog #1 (circled number) from the angle of intersection of the individual vectors (solid lines) from the two cubes.

An example of the output of the model for one animal (frog #1) calling alone (total time interval 10 s) is shown in Figure 2. This recording was taken under conditions of minimal background noise (good signal-to-noise ratio). Time difference estimates (Δ time in μs) derived from each cube separately are shown in the top two plots; the spectrogram is shown in the middle blot, and the sound pressure waveform recorded at microphone #3 is shown in the bottom plot. As indicated in the time waveform, this bullfrog's advertisement call consists of six individual notes (croaks), with durations varying from 542 (first note) to 631 (last note) ms. The spectrogram shows that each note consists of a series of harmonics ranging up to around 400 Hz (for clarity, upper harmonics are omitted) with a dominant second harmonic frequency of 210 Hz for each note. Both the time waveform and the spectrogram together provide frequency and amplitude information. Direction of the sound source (bullfrog) with respect to the two cubes can be derived from the top two plots. Each of these plots gives the time difference estimates for consecutive, overlapping 100 ms segments in each note, as well as for any background sounds present that exceed the thresholded value. The plot for the 13 (left) cube shows estimates of arrival times for each note at around $+150 \mu\text{s}$, which calculates to a direction of about 55° to the right of this sensor. Conversely, the plot for the 57 (right) cube shows estimates of arrival times at about $-175 \mu\text{s}$, which calculates to a direction of about 85° to the left of this sensor. The plot for the 57 cube also shows the presence of other sounds at about $+100 \mu\text{s}$ occurring both before and after this series of notes. We acoustically identified these sounds as the call of the green frog. Figure 3B shows the triangulated location (circled) of frog #1, based on the intersection of the direction vectors from the two cubes, on a map of the pond. This particular animal is located on the near side of the pond, to the immediate right of the 13 cube.

A 20 s segment of vocal activity from three bullfrogs is shown in Figure 4. This segment was chosen for display because it represents a very common calling pattern in the chorus on this particular recording night. The sound pressure waveforms and

spectrogram show that one frog calls individually, and his calls are followed by calls of two animals whose individual notes alternate. These latter two frogs were the most frequent callers on the sample night, with this pattern of note-by-note alternation occurring often (280 occurrences total in 8,000 s of recording). The time difference plot for the 13 cube (top plot) indicates that these three frogs (labeled frog #6, frog #7, and frog #8; labels were given to individuals in the order in which they are localized in the data analysis) are located in different directions with respect to this cube. The cube gives an estimate of direction of about $-175 \mu\text{s}$ for frog #6, about $-120 \mu\text{s}$ for frog #7, and about $+110 \mu\text{s}$ for frog #8. The time difference estimates from the 57 cube indicate that these bullfrogs are all located to the far left of this sensor (at about $-175 \mu\text{s}$), but that the three individuals cannot be separated from this cube alone. That is, use of the microphones in this cube alone (and, by extension, use of one microphone at this particular location) cannot separate the calls of these two animals but provide a general location direction. By the use of triangulation, however, estimates of location can be made for these three animals, as shown in Figure 5. Frogs #7 and #8 are separated by about 15 m, indicating that farther neighbors do engage in call alternation.

Figure 5 also shows the triangulated locations of the other animals we identified in the chorus. Each of these triangulations was made on the basis of multiple location estimates over the entire 8,000 s of recording, combined with analysis of the spectrograms of the calls to ensure that closely spaced individuals were in fact different frogs and not the same frog moving in location over the course of the recordings. Animals are not evenly or uniformly spaced around the pond but more often are found in clusters. Because of the angular accuracy of the cubes ($6\text{--}10^\circ$ for strong signals), we cannot, particularly for animals located at some distance from the cubes, specify the exact width of each animal's territory.

Figure 6 shows an example of a complex calling bout in which five frogs participated, and which took place against high levels of background wind noise (as indicated by the time domain wave-

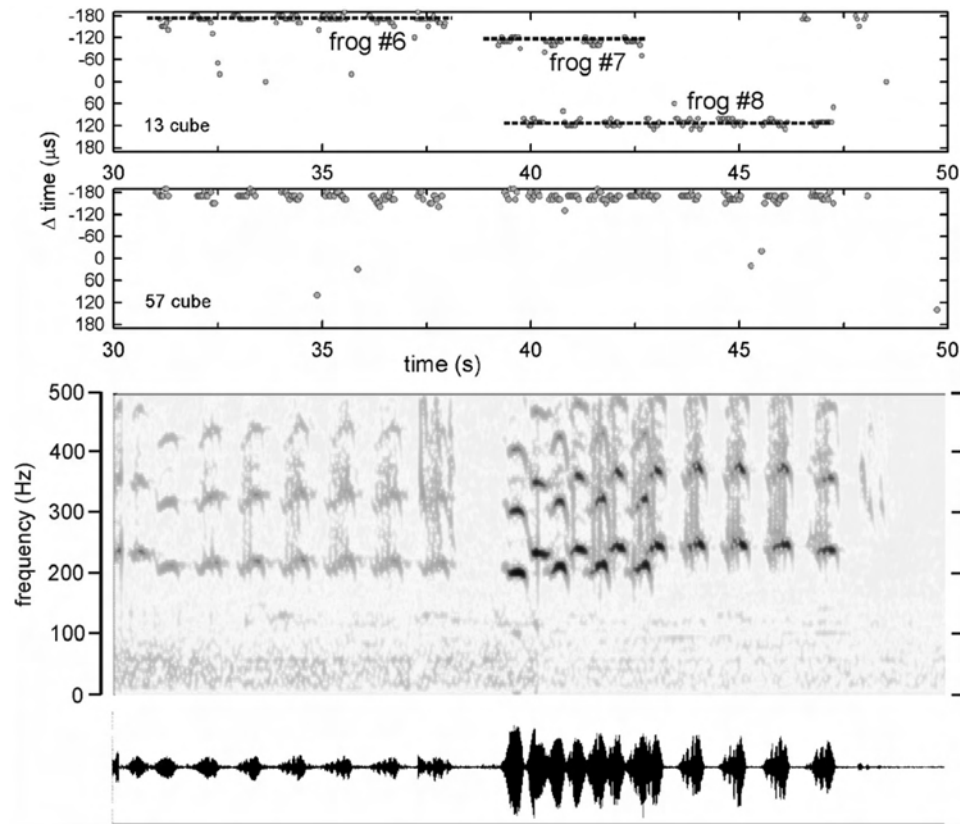


Figure 4. Plots showing time differences (Δ time in μ s) from the two cubes (top two plots), spectrogram (middle plot), and sound pressure waveform (bottom) for a 20-s segment in which three bullfrogs are calling. Two of these animals (labeled as frog #7 and frog #8) call in note-by-note alternation. All three animals can be distinguished both by location with respect to the 13 cube (dashed lines for each identified individual in the top plot). The animals cannot be clearly separated by the 57 cube alone. The spectrograms show that the individual notes of these three bullfrogs differ in second harmonic frequency. The initial note in the spectrogram display (at about 30 s) is from a different individual, not identified further in this figure.

form). This example was chosen because it shows both the usefulness and the limitations of the sensor array in identifying and localizing individuals in a noisy chorus, particularly when the males are close together and when their calls overlap, and when the signal-to-noise ratios of recordings may have been degraded. Notes from the individual animals cannot be easily separated in amplitude from the time domain waveform or in harmonic frequencies from the spectrogram, and it is not clear from either of these displays how many animals are vocalizing. The output of the model (triangulated locations in Figure 5) suggests that three of the frogs (frog #9, frog #10, and frog #11) are located very close together on the opposite side of the pond from the array. Frog #9 and frog #10 call in synchrony with almost complete note overlap, with frog #11 calling in partial overlap with these two. These particular animals were among the most inactive callers in the chorus, but when they did vocalize, they did so in this pattern of synchronous calling (about 40 occurrences in 8,000 s of recording).

For the data in Figure 6, the time difference plots from each cube give slightly different information showing that the output from both cubes together is needed to separate the individuals. The

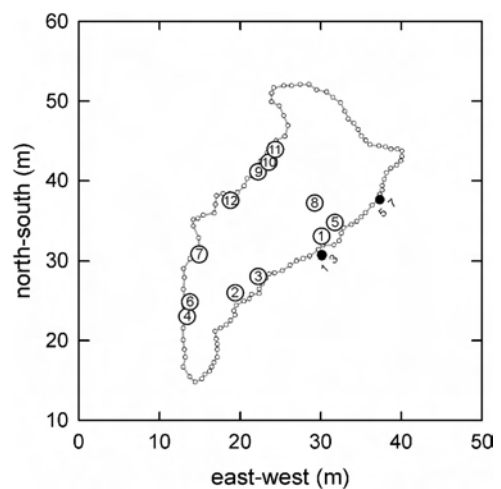


Figure 5. Map of the pond showing locations of 12 calling bullfrogs (numbered circles) based on intersections of the vectors derived from time differences at the left (13) and right (57) cubes. Multiple estimates were made to determine the locations of each frog.

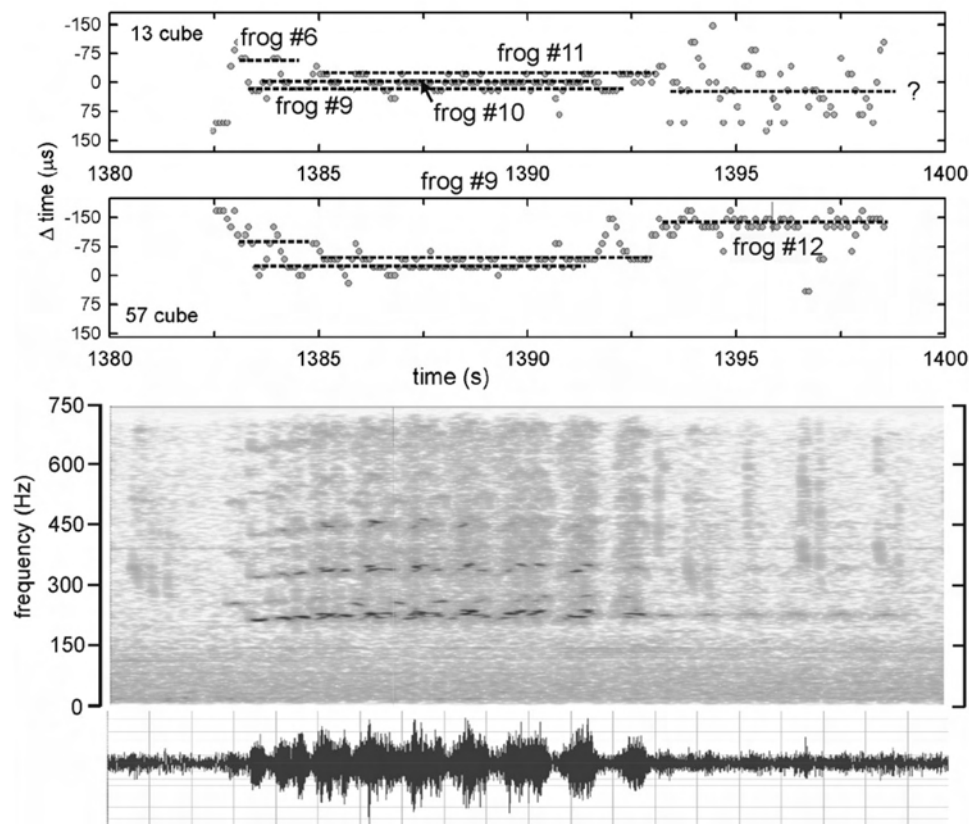


Figure 6. Plots showing time differences from the two cubes (top two plots), spectrogram (middle plot), and sound pressure waveforms (bottom) for a 20-s segment in which multiple bullfrogs are calling. In the time difference plots, clusters of circles (estimates of location) for the individual bullfrogs are joined by dashed lines for clarity. Because of the overlap of notes in the calls of these individuals and the considerable background noise present during recordings, there are fewer estimates than for the data in Figures 2 and 4. The smaller number of estimates increases the error of localization. In this example, the location of frog #12 cannot be reliably derived from the output of the 13 cube, while the location of frog #11 cannot be derived from the output of the 57 cube.

plot from the 13 cube suggests that calls of four frogs (frogs #6, #9, #10, #11) can be separated by location. But, because of the overlap of sound sources (both bullfrog call notes and extraneous background noise that exceeded the thresholded value) from different locations occurring within the same time window used for deriving location estimates, fewer discrete data points (gray circles) are available in the model output, and there are fewer estimates for each call note and more scatter in the data. The plot from the 57 cube also identifies frogs #6, #9, and #10, but cannot separate out frog #11. This plot also indicates the presence of yet another individual, here designated as frog #12, located to the far left of this cube. There is no consistent estimate of location for frog #12 in the plot from the 13 cube, however, because of the wide scatter in the estimates (shown by the dashed line and question mark) due to weak recorded signals. Because only the vector direction from the 57 cube is known, a triangulated location for this bullfrog cannot be made from this particular segment of recording. This example shows that sensor array must make multiple estimates in order to accurately triangulate a location. Presumably, however, each individual frog must itself make multiple listening estimates in order to localize its rivals. In fact, estimates of direction from

other segments of the recording produce an estimate for location of frog #12 to the left of frog #9 (see Figure 5).

Discussion

The goal of our project was to adapt an acoustic recording array using multiple closely spaced microphones to facilitate identification of individual bullfrogs in an active chorus on the basis of both their spatial location and the acoustic characteristics of their calls. Advantages of our system include the small size and portability of the sensors and the ease in setting up the array. A large amount of data can be recorded from the multiple microphones in each sensor simultaneously, thus providing excellent temporal synchrony between events on each channel. The use of the sensors permits recording and analysis of all vocalizations of all animals in the chorus, even those where vocalizations overlap in time, because they facilitate separation of overlapping calls in terms of both directions and distances. Moreover, when combined with subsequent acoustic processing, the sensor array can distinguish frogs by the spectral characteristics of their calls as well. The difficulty of segregating calls from individual males (see Figure 6) without the

location information provided by the sensor array shows the importance of having this information for accurate description of the chorus. These data allow the parsing of complex acoustic interactions between individuals, which may play a vital role in chorus dynamics.

We note that our array technique is not necessarily superior to other array techniques (Grafe, 1997; McGregor et al., 1997; Merrill et al., 2006). However, the small distance between the microphones in our sensors mitigates problems of decorrelation at widely separated microphones caused by environmental transmission effects. In our experience, such decorrelation is underestimated as a difficulty in field recordings. An ideal set-up would include several multiple-microphone sensors placed at multiple locations around the calling site, although the computational demands of such a system would be a serious disadvantage. Even with the two sensors we used here, the computational load required to retrieve and process the data, both in terms of spatial location and in terms of spectral analysis of sounds, is considerable. Another disadvantage of our system lies in its accuracy for estimating locations. Because of the shape of the calibration curve (Figure 1D), small errors in time difference estimates could translate into larger errors in direction at increasing distances from the array. As the data in Figure 6 show, there can be considerable scatter in these estimates, particularly under realistic conditions of overlapping calls. Localization accuracy would presumably have been improved if all four microphones in each sensor were active. The array could also be tailored specifically to the frog species of interest; for example, increasing the microphone spacing to the first harmonic frequency of the advertisement call (100 Hz or 30 cm in the case of the bullfrog) might improve localization accuracy. Another limitation of our study is the spatial constraints we experienced in placement of the sensors. We chose the configuration in Figure 1A because of difficulties in placing the sensors in the middle of the pond, the limited amount of cleared space around the margins of the pond, and because visual observations indicated the presence of male bullfrogs closer to and to the right of the 57 (right) cube. These particular bullfrogs did not, however, vocalize during our recording sessions. Because most of the vocalizing animals were located far to the left of the 57 cube, the microphones in that sensor provided very similar estimates of location for some animals (see Figure 4). These animals could be distinguished, however, by the spectral characteristics of their calls, showing the importance of spectral information, and by the information from the 13 cube, showing the importance of multiple sensors. These examples also show that errors in pinpointing the actual location of the calling bullfrogs could arise from suboptimal placement of the two sensors. Some prior knowledge of chorus structure could facilitate proper placement of the sensors; however, movements of individual males from one calling site to another may occur between recording nights and thus complicate positioning.

Some of the details of our acoustic analyses confirm other reports on bullfrog advertisement calling, showing that the recording array is appropriate for identification of these vocalizations. This is important because these previous data, although collected during active choruses (Bee & Gerhardt, 2001; Bee, 2004; Simmons, 2004; Suggs & Simmons, 2005; Wiewandt, 1969), are based on recordings from focal animals, where presumably the individual notes chosen for analysis did not occur in overlap with the notes of other frogs. Consistent with the work of Bee (Bee & Gerhardt,

2001; Bee, 2004), we observed individual differences in the second harmonic frequencies in the notes (in particular, first notes) of calls of individual bullfrogs. These individual differences aid in separating the calls of closely spaced males. Analysis of acoustic interactions between males at another bullfrog chorus site suggested that bullfrogs call preferentially in response to far, as opposed to near, neighbors (Boatright-Horowitz et al., 2000). Because of the difficulty in separating overlapping notes from analog tape recordings, those data were based only on analysis of calling patterns where no note overlap occurred. The data reported here, which include analysis of overlapping notes, show that two of the most active callers alternated individual notes with farther neighbors (see Figure 4), while closely spaced males called in synchrony with their close neighbors (see Figure 6). This suggests that males may adopt different calling strategies depending on intermale spacing. Further work using the sensor array will more closely examine these patterns of interactions, and will examine their stability over multiple recording nights.

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Interference Risk and the Function of Dynamic Shifts in Calling in the Gray Treefrog (*Hyla versicolor*)

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Male gray treefrogs call to attract females under challenging acoustic conditions. At higher chorus densities, there is considerable background noise and a good chance that a male's calls will often be overlapped by calls of other individuals. Call overlap may reduce the probability of mating because females prefer calls with internal pulse structure that is not obscured. With increases in acoustic stimulation, males lengthen call duration while simultaneously reducing call rate such that "pulse effort" changes little. In our study, we tested the "interference risk hypothesis." This proposes that males change call duration so that, on average, there will be a sufficient number of pulses and interpulse intervals clear of acoustic interference per call to attract a female. However, female choice experiments employing call alternatives of different durations, rates, intensity levels, and degrees of call overlap refuted this hypothesis. Our results leave open the possibilities that the dynamic shift in the two components of pulse effort are related to the problem of call detection in a noisy environment or are responses by males to the perceived threat of competition for females.

Keywords: frog, acoustic, communication, interference

Hyla versicolor is a relatively common treefrog in the north-eastern and central United States. In evenings in the late spring and early summer males call at or near wetland venues from trees, bushes, shorelines, and the water surface. Although advertising males may be diffusely distributed, in some areas that evidently possess a suite of appropriate habitat characteristics, aggregations can be quite dense (e.g., 100 + males per hectare) and generate high levels of background noise. The advertisement call consists of a series of individual pulses, the structure, number, and timing of which have been shown to be critically important in eliciting positive phonotaxis (i.e., movement to a sound source) from gravid females (Gerhardt, 2001). Such receptive females are typically found at breeding aggregations at considerably lower densities than are advertising males. Accordingly, males at choruses usually face extremely high levels of competition for potential mates. This is not an exceptional situation for many species of treefrogs (Gerhardt & Huber, 2002), and the calling behavior of males responds to the dynamic changes in the acoustic environment in ways that may help males maintain their relative attractiveness (Wells & Schwartz, 2006).

In *H. versicolor*, males respond to calls of neighboring males by appending pulses to their calls. An extensive experimental data set has demonstrated that females find longer calls (i.e., those with more pulses) a more potent stimulus for phonotaxis than shorter calls (see Figure 15 in Gerhardt, 2001). This preference can, in some larval environments, confer a genetic benefit on the offspring of females choosing males using longer calls (Welch, 2003; Welch, Semlitsch, & Gerhardt, 1998). Intriguingly, when males lengthen calls they simultaneously reduce the rate at which the calls are delivered such that the average long-term rate at which pulses are produced (pulse effort) remains about the same (Schwartz, Buchanan, & Gerhardt, 2002; Wells & Taigen, 1986). A question that remains unresolved is why male gray treefrogs shift the two components of pulse effort (call rate and pulses per call) in opposite directions in response to acoustic changes that accompany changes in chorus size.

Wells and Taigen (1986) speculated that at equal pulse efforts, producing longer calls could utilize more glycogen (relative to lipid) than producing shorter calls and so confer a degree of honesty on the signaling pattern. Their observations that males giving longer calls ceased calling sooner in the evening were consistent with the hypothesis. However, Grafe's (1997) measurements of respiratory quotients in calling males were inconsistent with the hypothesis. The Wells and Taigen hypothesis that, at equal pulse efforts, longer calls should be more attractive to female gray treefrogs than shorter calls was subsequently confirmed in two-stimulus choice tests performed in an acoustic chamber (Gerhardt, Dyson, & Tanner, 1996; Klump & Gerhardt, 1987; Schwartz, Buchanan, & Gerhardt, 2001). However, in eight-speaker choice tests conducted at the edge of a pond there was little discrimination against all but the shortest call alternative (a six-pulse call), and choice tests with calling males in an artificial pond indicated that call duration accounted for less than 10% of the variance in male "mating success" (Schwartz et al., 2002).

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Moreover, during experimental manipulations of choruses in the enclosed pond, males changed their call durations but maintained their relative rank in a hierarchy based on call duration. Thus in smaller choruses, males gave shorter calls than they were capable of giving and so sacrificed a higher position in the hierarchy. This behavior seems inconsistent with the notion that adjustments by males in their call duration and rate are directly associated with the inherent attractiveness of calls and threat of being out competed by other males.

Based on the above findings, Schwartz et al. (2001, 2002) proposed that shifts in call duration and rate were tied to the problem posed for communication by environments replete with potential sources of acoustic interference and thus increased risk of call overlap among neighboring males. Some other solutions to the problem of call overlap do not appear to be utilized by gray treefrogs. Although a pair of males may alternate their calls, with increases in chorus size and density the chance that such a strategy is entirely successful declines (Schwartz et al., 2002). Moreover, selective timing of signals (Brush & Narins, 1989; Greenfield & Rand, 2000; Schwartz, 1993; Snedden, Greenfield, & Jang, 1998) whereby males shift their call-timing in response to their closest neighbors while allowing their calls to overlap those of more distant callers and thus less potent sources of acoustic interference, appears to be absent. In fact, males of *H. versicolor* were more likely to overlap the calls of closest neighbors than those of more distant individuals (Schwartz et al., 2002). Finally, work in progress in our laboratory indicates that females seem incapable of significant temporal induction (Warren, 1999), a process that could enable their brains to "reconstruct" segments of calls that were masked or otherwise acoustically degraded by overlapping calls.

The "interference risk hypothesis" (IRH) posits that males of *H. versicolor* change their calling in a way that significantly improves the chances that within individual calls there will be a sufficient number of call pulses and interpulse intervals clear of interference to attract a female (see Figure 8 in Schwartz et al., 2001). Essential to the argument is that overlapped calls are less attractive than nonoverlapped calls and very short calls are particularly unattractive relative to longer calls. Both of these requirements are met. In addition to the significant bias against only the shortest calls in the pond-based choice test (Schwartz et al., 2001), in two-stimulus choice tests, the strength of the female bias against short calls increased dramatically for the shortest calls (Gerhardt, Tanner, Corrigan, & Walton, 2000). Female gray treefrogs also exhibit strong discrimination against advertisement calls that are overlapped by the calls of other males relative to nonoverlapped calls in arena-based choice tests (Marshall, Schwartz, & Gerhardt, 2006; Schwartz, 1987; Schwartz & Marshall, 2006). Moreover, choice experiments with calling males in the artificial pond demonstrated that males with fewer overlapped call pulses had a significantly greater chance of attracting a female than other males (Schwartz et al., 2001). The degradation of important fine-temporal attributes of the call (pulse shape, pulse duration, interpulse interval) accompanying overlap likely accounts for much of the observed bias (Marshall et al., 2006; Schwartz & Gerhardt, 1995; Schwartz & Marshall, 2006).

In a preliminary test of the IRH, Schwartz et al. (2001) examined levels of call overlap in the enclosed artificial pond. In support of the hypothesis, in pairwise comparisons of males in the same choruses who had nearly equivalent (within about 10%; \bar{x} =

4.6%) pulse efforts but very different call durations ($> 25\%$; \bar{x} = 57.1%), the male producing longer calls had a greater total number of nonoverlapped pulses in his calls (beyond a six pulse putative attractiveness threshold) than the male producing shorter calls significantly more often (19:7; $p = .029$, two-tailed binomial test). The goal of the present study was to determine whether patterns of female discrimination are consistent with expectations of the IRH using a set of choice stimuli and acoustic background environments specifically designed to rigorously test the hypothesis.

Method

During evenings in May and June of 2005, we obtained amplexed females of *H. versicolor* at a pond in the Blue Mountain Reservation in Peekskill, New York. The females were separated from their mates, returned to our laboratory, and held until testing (usually the next day) in plastic containers in a refrigerator (1 to 2°C) to postpone oviposition. We returned each group of frogs to the pond within a day of completing our tests with them. We conducted phonotaxis experiments within a temperature-controlled ($\sim 20^\circ\text{C}$) chamber floored with waterproof low-pile carpet and walled with echo-attenuating acoustic foam at the Pleasantville, New York campus of Pace University (chamber inner dimensions: 255 cm long \times 225 cm wide \times 195 cm high, Ultimate Walk-Ins, Inc., Monsey, NY, USA foam: Silent Source TFW-4). The "choice arena" was illuminated using infrared LEDs (part #1165OP, Marlin P. Jones & Assoc. Inc., part #11665OP) and the movements of the females monitored from outside the chamber with a closed circuit video security system (item #49-2511, #49-2513; Radio Shack, Fort Worth, TX, USA). During each test, females were held briefly in and then released (via an externally controlled pulley) from an acoustically transparent cage on the floor of the arena.

We used a Commodore Amiga 600 computer (Commodore Business Machines; West Chester, PA, USA) running Future-Sound software (Applied Visions, Cambridge, MA, USA), a Realistic SA-10 amplifier (RadioShack, Fort Worth, TX, USA) and RCA PRO-X33AV speakers (AudioVox Electronics Corp., Hauppauge, NY, USA) to broadcast synthetic stimulus calls (synthesized using custom software written by Schwartz; eight-bits per sample; 20 kHz, low-pass filtered at ~ 6 kHz) that were modeled after the natural calls of *H. versicolor* (Schwartz, unpublished software). We adjusted sound amplitudes with a calibrated Gen Rad, 1982 Precision Sound Level meter (IET Labs; Westbury, NY, USA; flat weighting, fast RMS response). These adjustments were made using broadcasts of calls identical in form and duration (i.e., 18-pulse calls without overlapped sections) from both speakers so that we could be sure that the amplitude of the pulsed sections of our test stimuli would have equal Sound Pressure Levels (SPLs). SPL for calls was 85 dB SPL (re 20 μPa) unless otherwise indicated (relative attenuation values are given below). In all tests, we equalized the pulse efforts of the call alternatives offered from two speakers. Stimulus calls were broadcast in alternating fashion from speakers on the floor at opposite sides of the arena (1 m from the central release point) and each subject was exposed to the call stimuli for 60 s prior to lifting of the release cage. Females displayed discrimination by moving to within 10 cm of one of the speakers within 10 min or less.

In some tests, using a second Amiga 600 and Realistic SA-10 amplifier, we simultaneously broadcast (Realistic Minimus 0.3 speaker) either calls or filtered noise from an elevation 63 cm above the release point. This elevated arrangement was chosen so that test females would orient to the floor speakers. The SPL was adjusted at the release point to 83 dB (flat weighting, fast RMS response). The software used to broadcast the sounds was written by the senior author and was designed so that one could specify the amount of broadcast time that would be occupied by calls and intervening silent intercall intervals. The duration of each call (or noise burst) and subsequent interval were individually chosen using a random number routine (a different starting "seed" was used to begin each playback; Knuth's algorithm, see pp. 212–213 in Press, Flannery, Teukolsky, & Vetterling, 1988) with the restriction that either (a) both durations fell within those of calls 12 to 24 pulses long (inclusive durations: 575 ms to 1,175 ms) yielding a long-term sequence in which calls (or noise) filled 50% of the broadcast time or (b) calls were 12 to 24 pulses long and intervals half as long yielding a long-term sequence in which calls filled ~ 67% of the broadcast time. Therefore, these broadcasts simulated the calling activity of other neighboring individuals in a chorus that, on average, would overlap either 50% or ~ 67% of the pulses broadcast from the floor speakers. In the tests of Schwartz et al. (2002) within an artificial pond, these levels of overlap are similar to those that occurred in choruses of four and eight males, respectively. Because the temporal relationship between the calls from the floor and ceiling speakers was not static, the amount and timing of the overlap between the background calls and call alternatives varied as would be expected in a natural chorus (Schwartz et al., 2002).

Experiment 1

In these tests, females were presented with call alternatives of either (a) 12 pulses and 24 pulses or (b) 6 pulses and 12 pulses. The shorter call was presented at twice the rate of the longer call so that the stimulus alternatives had identical pulse efforts (e.g., 240 pulses per min for stimulus pair "a"). Each of the longer pulsed calls was timed to fall midway between two shorter pulsed calls so that there was no acoustic interference between these call alternatives. In tests with the 12-pulse and 24-pulse calls, randomly timed calls from above the arena occupied 50% of the broadcast time. Therefore, as indicated previously, by chance, equal proportions of the pulses in the 12-pulse and 24-pulse calls were eventually overlapped. However, unobscured segments of the long call were, on average, twice the length of those of the short call. Based on previous data (e.g., Klump & Gerhardt, 1987; Schwartz et al., 2001), we predicted that females would discriminate in favor of the long calls. To determine the strength of this preference, the relative intensity of the 24-pulse call was to be lowered (in 3 dB steps) until the preference was abolished.

We also ran two tests without the overlapping calls to obtain results to which the results of the aforementioned tests could be compared. In one of these tests, we used 12- and 24-pulse calls. In the second test, we broadcast 6- and 12-pulse calls. Again, we determined the relative intensity difference that abolished the preference for the longer call in each of these tests. Because females have previously shown very strong discrimination in choice tests against extremely short calls (e.g., 6-pulses long), we

anticipated that the intensity difference that abolished the preference should be greater in the second test than the first (see Gerhardt et al., 2000). The IRH predicts that when the interfering chorus was broadcast, the strength of the preference against the 12-pulse call when offered against the 24-pulse call should be comparable to the strength of the preference against the 6-pulse call in the second test without the interfering chorus.

Experiment 2

In this and subsequent experiments we made modifications to the acoustic background and or the call alternatives to increase our confidence in the generality of the results we had obtained with Experiment 1. Our results were such that we did not need to run additional tests to determine preference strength as described above. In Experiment 2, we offered females a choice between 12- and 24-pulse calls and doubled the ratio of calls relative to silent intercall intervals from above the arena. Accordingly, on average, ~ 67% of the pulses of the short and long call alternatives would be overlapped. We expected that this would more heavily skew any female bias for the 24-pulse call.

Experiment 3

In Experiment 3, we again offered females a choice between 12- and 24-pulse calls. However, rather than broadcast calls from above, we used bursts of filtered noise and silent interburst intervals following protocol "a" above (50% noise:50% silent). The noise was computer-generated white noise that had been digitally filtered to resemble the spectrum of a chorus of gray treefrogs (spectral peaks at 1100 and 2200 Hz; 10 dB bandwidth ~ 750 Hz for each).

Experiment 4

In Experiment 4, we gave females a choice between long and short calls both without background calls as well as with background calls with the two calls:silent ratios (i.e., 50:50, 67:33). However, in the three tests we conducted, the call alternatives were 20-pulse calls and 10-pulse calls (pulse effort of each alternative = 200 pulses per min).

Experiment 5

One test of Experiment 5 was run without and one test with background calls broadcast from above the arena (50% calls:50% silent). However, in these two tests, we offered females alternatives with a less extreme difference in call pulse number (18-pulse calls vs. 24-pulse calls). To equalize the pulse efforts of the call alternatives (240 pulses per min), the call period of the 24-pulse call was set to 6 s and the call period of the short call to 4.5 s. Therefore, the relative timing of the long and short call shifted during the course of playback and the calls often overlapped to varying degrees. These tests, then, not only provided for a more conservative test of the IRH (because any long-call preferences should be less pronounced) but also offered a dynamic pattern of call timing between the call alternatives. Both of these characteristics of the tests simulated situations that females in actual choruses would be expected to frequently encounter (Schwartz et al., 2002).

Experiment 6

In a final test, we gave females a choice between 12-pulse calls and 24-pulse calls (pulse effort = 240 pulses per min). However, rather than create a dynamic pattern of call overlap using call broadcasts from above the arena, we incorporated the call overlap within the individual call alternatives. The pulses of the first 50% of each call were interleaved with pulses of either a 12-pulse call (for the 24-pulse alternative) or a 6-pulse call (for the 12-pulse alternative). This was the least conservative test of the IRH (which predicts a strong preference for the 24-pulse call) because the alternatives are always overlapped and overlap occurs in the section of the call most likely to negatively influence female attraction (Gerhardt & Schul, 1999; Schwartz & Marshall, 2006).

Results

Experiments 1 to 3

Without background calls, females exhibited significant discrimination in favor of the 24-pulse call relative to a 12-pulse call (see Table 1). However discrimination was absent when the 24-pulse call was attenuated by 3 dB. When we offered females a choice between a 6-pulse and a 12-pulse call, females discriminated in favor of the longer call until the intensity of the longer call was lowered by 6 dB.

In contrast to the predictions of the IRH, with the background calls broadcast from above, females either failed to discriminate in favor of the longer call (calls:silent = 50:50) or discriminated in favor of the shorter call (Experiment 2, calls:silent = 67:33). Females did not discriminate when we broadcast noise bursts from above (Experiment 3, noise:silent = 50:50). Rather, as with the overlapping call broadcasts, there was a response bias favoring the 12-pulse call alternative.

Experiments 4 to 6

In Experiment 4, in which we offered females a choice between 10-pulse and 20-pulse calls, subjects failed to significantly discriminate with or without background calls (see Table 2). Signif-

Table 1

Choice Results of Females in Experiments 1 to 3

Overlap	Relative amplitude ^a	Females' choices (Short Call:Long Call)	<i>p</i>
12 pulse versus 24 pulse			
No	0	9:21	.043
No	3	17:13	<i>ns</i>
Calls (50:50)	0	19:11	<i>ns</i>
Calls (67:33)	0	21:9	.043
Noise (50:50)	0	21:11	<i>ns</i>
6 pulse versus 12 pulse			
No	0	5:15	.041
No	3	9:21	.043
No	6	17:13	<i>ns</i>

Note. The *p* values are for a two-tailed binomial test. Overlap = whether the alternatives were offered without (no) or with broadcasts of background calls (calls:silent ratio) or noise bursts (noise:silent ratio); amplitude = attenuation of the longer call alternative; *ns* = not significant.

^aGiven in dB.

Table 2

Choice Results of Females in Experiments 4 to 6

Overlap	Females' choices (Short Call:Long Call)	<i>p</i>
10 pulse versus 20 pulse ^a		
No	11:19	<i>ns</i>
Calls (50:50)	12:18	<i>ns</i>
Calls (67:33)	12:18	<i>ns</i>
18 pulse versus 24 pulse ^a		
No	18:12	<i>ns</i>
Calls (50:50)	15:15	<i>ns</i>
12-pulse versus 24-pulse ^a		
Fixed	18:12	<i>ns</i>

Note. The *p* values are for a two-tailed binomial test. Call alternatives were presented at equal intensity. Overlap = whether the alternatives were offered without (no) or with broadcasts of calls (calls:silent ratio) or incorporated a fixed overlapped section; *ns* = not significant.

^aCall alternatives: 10-pulse versus 20-pulse call (Experiment 4); 18-pulse versus 24-pulse call (Experiment 5); 12-pulse versus 24-pulse call (Experiment 6).

icant discrimination was also absent in Experiment 5 (18-pulse vs. 24-pulse calls with and without background calls) and Experiment 6 (12-pulse vs. 24-pulse calls each with fixed 50% overlap).

DISCUSSION

We had hypothesized that by lengthening calls under more competitive and thus noisier conditions, males could maintain the relative attractiveness of their advertisement signals. Specifically, males would add pulses to calls to compensate for the increased probability that critical fine-temporal information would be obscured by the vocalizations of others. Without such adjustments in vocal behavior, acoustic overlap could result in the perception by females of individual calls lacking a sufficient number of attractive elements to elicit phonotaxis.

To test the IRH, we offered females call alternatives of different duration with and without broadcasting sources of acoustic interference. In most tests, the interference was in the form of bouts of calling or filtered noise alternating with blocks of silence to produce a pattern of stimulus overlap comparable to that occurring in a natural chorus. Previous results had demonstrated that discrimination against a shorter call alternative is accentuated when call alternatives are selected from the short end of the distribution of male call durations (Gerhardt et al., 2000). Therefore, we predicted that we would observe an increased bias against the shorter call alternatives in the presence of acoustic interference. To obtain data on bias strength for comparison, we tested females with shorter call alternatives in the absence of acoustic interference. Selective attenuation of the preferred stimulus alternatives was used to gauge the strength of discrimination.

Our results constitute a solid refutation of the IRH. Under no circumstances did we observe an increase in preference strength or significant bias for a longer call alternative in the presence of acoustic interference. We are extremely confident in this finding because we employed a range of call alternatives under conditions of interference: 24-pulse versus 12-pulse calls, 20-pulse versus 10-pulse calls, and 24-pulse versus 18-pulse calls. Moreover, in our tests we used two types of acoustic background that had

different average probabilities of overlapping with the call alternatives (calls:silent ratios of 50:50, 67:33, noise:silent ratio of 50:50) as well as 24- and 12-pulse calls with a fixed and overlapping timing relationship. According to the IRH, interfering backgrounds with a more extreme (67:33) ratio of calling to quiet intervals should have elicited a stronger bias in favor of longer calls than either the 50:50 backgrounds or the choice tests using call alternatives half as long without an acoustic background. This did not happen. Most surprisingly, females actually showed an increased likelihood of approaching the source of the shorter call alternative when calls were subjected to the possibility of overlap. This unexpected result was even statistically significant using 24-versus 12-pulse call alternatives with background calls presented in a calls:silent ratio of 67:33. A potential criticism is that most of these tests, although they may resemble the situation in the wild, are too conservative because over the relatively brief time windows during which different females may have compared call alternatives, we do not know the actual pattern of overlap with the background calls or noise—although we can calculate confidence intervals for particular time intervals (or for the number (n) of call broadcasts from a floor speaker; CI around the mean expected overlap of 50% in Experiment 1, $T_{\text{est}} = \pm (\sqrt{1/24}) \times (Z/\sqrt{n})$, assuming independence of call overlap proportions)). For this reason, in particular, we conducted Experiment 6 in which half of each call alternative was always overlapped. Again, the results refuted the IRH.

Our data also confirm that the female preference for long calls is quite weak (and stimulus specific) when choice alternatives are of equal pulse effort. In the case of 24-pulse versus 12-pulse calls, the female preference for the longer call was eliminated when it was attenuated by just 3 dB. Consistent with our qualitative expectation based on earlier work (Gerhardt et al., 2000), when offered 12-pulse versus 6-pulse calls it was necessary to attenuate the longer call to a greater degree (6 dB) to eliminate significant discrimination by females. Gerhardt et al. found a mean preference strength of 2 dB for a 27-pulse call paired against an 18-pulse call but a mean preference strength of 7 dB for a 12-pulse call paired against an 8-pulse call (unequal call effort stimuli). In the tests using the other pairs of call alternatives (24-pulse vs. 18-pulse calls, 20-pulse vs. 10-pulse calls), females failed to discriminate. Using alternative stimuli with nearly equal pulse efforts, Klump and Gerhardt (1987) also found that females discriminated in favor of longer calls under some circumstances (24-pulse vs. 12-pulse calls) but not others (18-pulse vs. 12-pulse calls). In the latter case, the relative timing of the call alternatives shifted and so there were periods of overlap and alternation as was the case with our test using 24-pulse and 18-pulse calls. In contrast, Schwartz et al. (2001) found a significant preference for 18-pulse as opposed to 12-pulse calls using a static timing relationship with partial overlap among call alternatives. It therefore seems that choice results with females in such tests are idiosyncratic, depending on the pulse disparity among call alternatives, the nature and stability of call timing as well as the presence of background calls or noise.

Our study leaves unresolved the question of why males shift call duration and call rate in opposite directions as their acoustic environment changes. It is possible that using longer calls facilitates call detection under conditions of especially high ambient noise (Brumm & Slabbekoorn, 2005). Our playback test using filtered noise did not explicitly test this hypothesis because our

noise background was structured into relatively brief on and off periods and was presented at a background intensity that was insufficient to mask the call alternatives. The viability of this idea depends on the integration time of the female's auditory system because the vulnerability of calls to masking is mediated, in part, by the time period over which the female auditory system sums sound energy (Brumm & Slabbekoorn, 2005). Tests underway may provide a behavioral estimate of the maximum integration time for female gray treefrogs as well as assess the susceptibility of calls of different duration to masking.

Another hypothesis proposes that call duration and rate are adjusted by males in response to the perceived threat of competition for females (Wells & Taigen, 1986). Although the preference for longer calls under conditions of equal pulse effort are conditional and, even then, relatively weak, it may be that on average males' chances of attracting a mate are improved by dynamically modulating call rate and pulse number. The tendency for males to maintain their rank among neighbors for call duration seems, on its face, to be inconsistent with the male competition hypothesis. However, the threat of enhanced vocal competition by high ranked males may explain this behavior. According to this scenario, if a male who is not top-ranked fails to drop pulses from his calls in response to a decline in chorus size (or background noise), other, formerly higher ranking males, detect this and shift back to giving calls longer than the "cheater." Thus a cheater might gain only a momentary and insignificant, advantage. A test of whether such a constraint operates is planned.

Finally, shifts in call duration and call rate may have communicative significance in male-male communication. Perhaps there is an agonistic message conveyed in advertisement calls that increases with duration. According to this hypothesis, addition of pulses to calls represents a graded response that may ultimately transition to aggressive calls. Although males of *H. versicolor* append pulses to their calls in response to broadcasts of individual calls simulating an individual neighbor, re-examination of data from an earlier study (Schwartz, 1987) indicated that there was only a small effect of stimulus intensity or stimulus duration on response duration. However, the effect of stimulus duration on aggressive call responses was not explicitly tested. Accordingly, considerable work remains before one of most intriguing aspects of the communication system of this fascinating anuran is understood.

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Mechanisms and Evolution of Synchronous Chorusing: Emergent Properties and Adaptive Functions in *Neoconocephalus* katydids (Orthoptera: Tettigoniidae)

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Synchronous interactions arise in various animal species that rhythmically broadcast acoustic, vibratory, and visual signals. These interactions are characterized by a coincidence in both rate and phase of the rhythms of neighboring signalers. Theory predicts several ways in which synchronized rhythms may specifically benefit the interacting signalers. However, synchrony may also arise as an emergent property, a default phenomenon that is neither preferred by conspecific receivers evaluating the signals nor advantageous to the signalers themselves. Here, we examine several well-studied cases of acoustic synchrony in *Neoconocephalus* katydids (Orthoptera: Tettigoniidae), a New World genus wherein males broadcast loud advertisement songs. We report that call synchrony found in *N. spiza* and *N. nebrascensis* results from two rather different mechanisms of rhythm adjustment. Moreover, synchrony in the former species appears to represent an incidental byproduct of signal competition between evenly matched males, whereas in the latter species synchrony functions as a specific adaptation in which cooperating males ensure that critical call features can be perceived by females. We discuss the separate evolutionary trajectories that may have led to similar outcomes, synchronous chorusing by advertising males, in these closely related species.

Keywords: acoustic communication, mate choice, sexual selection, signal interactions, species recognition

Chorusing displays of acoustically signaling insects and their counterparts among bioluminescent species are acknowledged to include some of the “great spectacles of the living world” (Wilson, 1975, p. 331). In some species such as the periodical cicadas (*Magicicada* spp.) of North America, these acoustic interactions are most noteworthy for the number of participants and the collective sound intensity broadcast. However in other cases, the temporal precision of the interactions represents the salient feature. Here, neighboring signalers adjust the relative phases and rates of their signaling rhythms and thereby display various forms of synchrony or alternation of song (Greenfield, 2005). Synchronous interactions, in particular, have attracted the attention of human observers, as the timing in these phenomena may attain a very high level of precision. Moreover, this choreography appeals to a general human fascination with pattern and order in the natural world, an interest attested to by several scholarly and popular books published recently on synchrony and related events (Pikovsky,

Rosenblum, & Kurths, 2002; Strogatz, 2003). Notably, associations have been made between synchronous mechanisms in the nervous system and the origin of music in humans (Bispham, 2006).

In the present paper we analyze the mechanisms and evolution of synchrony of male song rhythms in acoustic insects and focus specifically on *Neoconocephalus* katydids (Orthoptera: Tettigoniidae), a New World genus of approximately 25 species (Walker & Greenfield, 1983). Synchronous chorusing appears in several *Neoconocephalus* species (Greenfield, 1990), and detailed, experimental studies have been made of two, *N. spiza* (Greenfield & Roizen, 1993) and *N. nebrascensis* (Meixner, 1976; Meixner & Shaw, 1986). More important, these two species adjust signal rhythms with dissimilar mechanisms, but both display the same collective interaction: Neighboring males sing in phase, and they do so with enough precision that a human observer may have difficulty recognizing that more than one singer is present. Synchrony in these two species, however, has probably arisen under the influence of somewhat different selection pressures. Thus, *Neoconocephalus* is a model in which to investigate how separate evolutionary trajectories, involving the assembly of different neuromuscular elements may ultimately yield similar interactive behavior. These possibilities also remind us that communal phenomena, including interactions among acoustic animals, may reflect selection acting at multiple levels as well as feedback loops between these levels.

The Players

Male *Neoconocephalus* katydids attract females with loud (85 – 90 dB SPL at 1 m; 0 dB = 20 μ Pa), incessant calling songs that

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they broadcast while at stationary perches in their habitat, typically grassland or forest edges (Greenfield, 1990). Songs are produced by stridulating the forewings at 14 to 250 cycles of movement per second, the specific rate depending on species and temperature (see Walker, 1975). In most species, stridulation yields broad-band sound whose energy is concentrated between 7 and 16 kHz (Deily, 2006; Deily & Schul, 2006; Schul & Patterson, 2003). The genus may be roughly divided into those species whose songs are continuous “whines” or “buzzes” and those that are rhythmically repeated notes, onomatopoeically termed “chirps” or interrupted buzzes. This latter, discontinuous manner of singing has evolved independently on at least two occasions within *Neoconocephalus* (Greenfield, 1990). Several species of chirpers and interrupted buzzers, including *N. spiza* in Central America and *N. nebrascensis* in North America, synchronize their calling rhythms with varying degrees of precision (Greenfield & Shaw, 1983; Figure 1).

N. spiza males broadcast 20 to 70 ms sparrow-like chirps (hence the specific epithet), which represent the sound generated by 3 to 10 consecutive cycles of wing movement (3–10 sound pulses), at 1.8 to 5.0 chirps per second. Solo individuals often sing at a slow and irregular chirp rate, but they may accelerate their rhythms and attain greater regularity when neighboring males sing in the vicinity. Under these conditions of higher local density, singing males adjust the phase of their chirp rhythms, and two or more neighbors may synchronize for 10 to 20 s, and occasionally longer. This interaction is an imperfect synchrony, though, as a given individual will often drop out of the chorus for one or two chirp cycles and then reenter in phase (see Figure 2). In addition, a male normally “leads” his neighbor’s chirp by up to 50 ms, only to have this offset reversed on the next chirp cycle when he is just as likely to “follow” the neighbor by a comparable interval. Recordings show that chirp rates during bouts of synchrony vary less than 15% (coefficient of variation; c.v.), both within and between individuals.

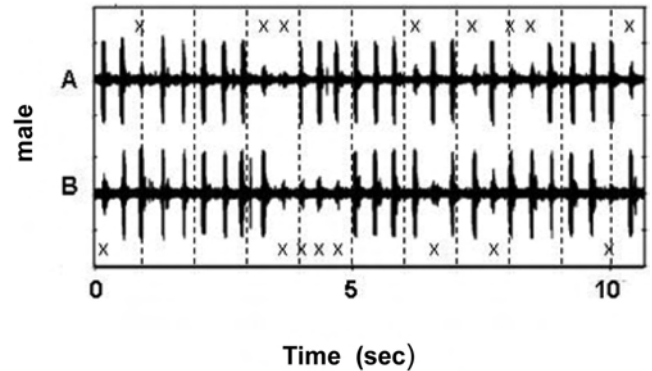


Figure 2. Oscillogram depicting recording of two *N. spiza* males (A and B) calling in imperfect synchrony. Xs indicate call cycles where one male, either A or B, dropped out of the chorus temporarily (figure modified from Greenfield, 2005).

N. nebrascensis song is generated by the same basic stridulatory movements as in *N. spiza*, but the structure of its notes and the nature of synchrony between interacting individuals are somewhat different. Male *N. nebrascensis* produce relatively long (1000–1200 ms) interrupted buzzes, “verses” representing 160 to 180 consecutive cycles of wing movement, that are regularly separated by 800 to 1000 ms silent intervals. This rhythm remains rather consistent (c.v. < 3%) in both solitary and interacting singers (Meixner, 1976). When *N. nebrascensis* males sing in the presence of neighbors, they, like *N. spiza*, adjust their rhythms and synchronize, but here the interaction is a more precise affair in which the participants do not repeatedly drop out and reenter during a chorusing bout. In the field, these bouts may last for several hours during the evening. Leader–follower relationships also occur in *N. nebrascensis* synchrony, but they generally reflect differences in buzz length and buzz rate between the singers: When a male

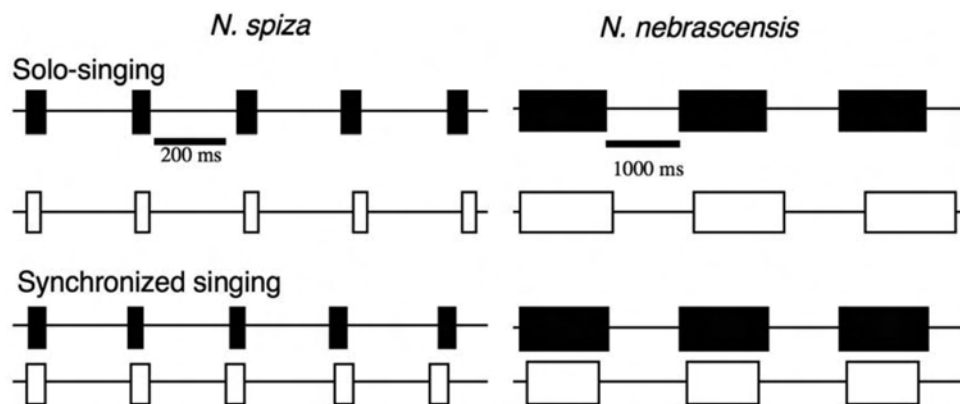


Figure 1. Scheme of temporal interactions between the songs of two males of *N. spiza* (left) and *N. nebrascensis* (right) during solo singing (top) and synchronized singing (bottom). The top two traces indicate the hypothetical call pattern of two males calling alone. The calls depicted in the top (filled) traces have faster solo call rates than the other calls (open traces). The bottom two traces (synchronized singing) represent typical call patterns if the two males call at the same time. In *N. spiza*, the two males alternate the leader position, whereas in *N. nebrascensis* the male with the faster call rate usually becomes the leader for the duration of the calling bout, while the other male follows and usually shortens his call duration. Note the different time scales for *N. spiza* and *N. nebrascensis*.

produces a shorter buzz than his neighbor or sings at a slower solo buzz rate, he typically follows the onset of the neighbor's longer buzz and also ends before the neighbor. However, at long inter-neighbor distances (> 7 m), followers may end their buzzes after the leading neighbor, and at close distances (< 2 m) they may shorten their chirps further. When males have equivalent buzz lengths and rates, a male who initiates singing at the beginning of a chorusing bout may become its leader. As in the relative constancy of song rhythm and the regularity of synchrony, leader-follower roles seldom waver within pairs of *N. nebrascensis* males.

Playback experiments testing the broadcast of male song stimuli to female *N. spiza* and *N. nebrascensis* in laboratory sound rooms provide information on response and preference that can ultimately help resolve the function of synchronous chorusing. In both species, females must hear a discontinuous song, that is, chirps or interrupted buzzes, before orienting toward the stimulus. In *N. spiza* females orient toward the longer of two synthetic chirps presented at different azimuthal directions, but this preference declines markedly when chirp length exceeds 150 ms, and orientation disappears completely for chirps ≥ 300 ms in length. Rhythmic information within chirps is relatively unimportant, as females will orient to "pulse-less chirps": artificial notes that are an appropriate length, sufficiently intense, and include sound energy within the requisite 7 to 16 kHz frequency range (Greenfield, 1993). That is, the fine temporal structure generated by regular cycles of wing movement is apparently unnecessary. On the other hand, female *N. spiza* are strongly influenced by the temporal sequence of chirps broadcast from spatially separated sources. As has been found in various acoustic animals, *N. spiza* females orient toward the first of two or more chirps when the first leads the other(s) by a brief time interval, 0 to 50 ms (Greenfield & Roizen, 1993). This influence of leading chirps, akin to the psychoacoustic precedence effects described in birds and mammals (Litovsky et al., 1999; Zurek, 1987), is strong enough to override several aspects of sound energy and power: Females still choose a leading male song even when its chirps are 50% shorter or 4 to 5 dB SPL lower in amplitude (Snedden & Greenfield, 1998). These preferences are likely to have selected for phase adjustments in chirp rhythm by *N. spiza* males, adjustments that ultimately create the synchronous chorusing observed in this species.

Unlike in *N. spiza*, the temporal sequence of songs has little influence on female selectivity in *N. nebrascensis* (see Figure 3). Females show a weak preference for the leader of two overlapping calls; however the advantage gained by the leader can likely be overridden by a 0.5 to 1.5 dB amplitude advantage of the follower (data not shown). This weak preference has therefore little if any relevance for mate choice. However, when the follower is delayed to the extent that the two calls alternate, rendering sound continuous, female *N. nebrascensis* cease orienting to either call (see Figure 3). This is likely caused by the minimum amplitude modulation required to recognize the verse pattern: In single speaker presentations, females require the quiet interval between the buzzes to be attenuated by more than 18 dB (relative to the buzzes) for the call to be attractive (Deily, 2006). The peripheral directionality is seemingly not sufficient to generate such a modulation depth. Like *N. spiza*, female *N. nebrascensis* do not have to perceive any rhythmic information from pulse structure within buzzes.

Rhythm Generation and Adjustment

Synchrony of song is basically a rhythmic phenomenon, and any progress in understanding how it is accomplished, and why the males bother to create it, demands a thorough analysis of the rhythms underlying song. We deem a fundamental analysis necessary before examining the mechanisms responsible for adjustments to rhythm that occur during synchronous chorusing. Calling songs in male *Neoconocephalus* katydids entail at least two central rhythm generators, one controlling the rate of wing cycles and the resulting sound pulses and a second controlling the rate at which groups of pulses, whether they are chirps, interrupted buzzes, and so forth, are produced. These two rhythms are at least partly distinct, judging from thermal studies in other Orthoptera that indicate different influences of temperature on pulse and chirp rates (Walker, 1962). Moreover, in solo *N. spiza* singers, repetition rates of chirps tend to be considerably more variable than those of pulses. That is, chirp rhythm is not determined by a simple division of pulse rhythm by a fixed value representing the number of pulses per chirp plus the length of the silent, interchirp interval.

Various neurophysiological investigations in orthopteran insects demonstrate that the repetition rate of sound pulses, driven by cycles of wing movement, is controlled by a central rhythm generator (e.g., Hedwig, 2000). The evidence for central control of chirp rate, however, is less direct. Although chirp rhythm is generally more regular in individuals who are interacting acoustically with neighbors, solo singers are nonetheless capable of maintaining this rhythm. In addition, a solo singer will often skip producing one or two chirps but then produce his next one almost exactly two or three chirp cycles later, and chirp rhythm is maintained in deafened males (see Buck, Buck, Hanson, et al., 1981; Greenfield, 2005; Shaw, 1968; Walker, 1969). These several findings imply that chirp rhythm is not dependent on regular exogenous stimuli, and that a male does not have to hear his own song or even sing—indications of reafference—to maintain this rhythm.

Given that chirp rhythm in *Neoconocephalus* song appears to be under endogenous control, one means of describing it is a "sawtooth oscillator model" that represents periodic fluctuations of the central generator and associated peripheral events. In this model the hypothetical oscillator ascends steadily until it attains a "trigger level," at which point the production of a chirp is released. However, the actual onset of the chirp does not occur until after an "effector delay," comprised of both neural and motor elements, has elapsed following release. This delay would represent the time required for transmission of a neural message from the central generator to the motor unit (muscles controlling forewing stridulation) plus the time for activation of that unit (Greenfield, 1994a, 1994b; Figure 4). Playback experiments designed to examine rhythm adjustment have revealed that effector delays in various species of Orthoptera range from 50 to 200 ms (Greenfield, Tourtellot, & Snedden, 1997). Once attaining the trigger level, the oscillator then descends relatively quickly to a "basal level" and immediately begins the ascent of the next cycle. We subscribe to the sawtooth oscillator model because of its simplicity and consistency with available data.

Our next step in understanding synchronous interaction is to examine how an oscillator, as modeled above, may respond when perturbed by an external acoustic stimulus such as a neighboring male's song or a loudspeaker broadcast. This examination is done

most directly by presenting a solitary, calling male with single stimulus chirps broadcast by a loudspeaker at random points in time. In *N. spiza* these presentations generally elicit a simple delay in phase that affects one and only one chirp cycle, following which the chirp rhythm returns to its previous rate of chirp repetition, the endogenous or free-running rate (Figure 5a,b). Thus, when a stimulus chirp is presented d ms following a focal male's chirp, he delays his next chirp by an interval slightly shorter than d , but

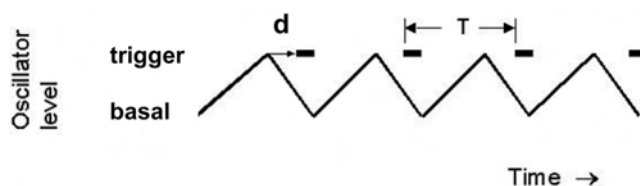
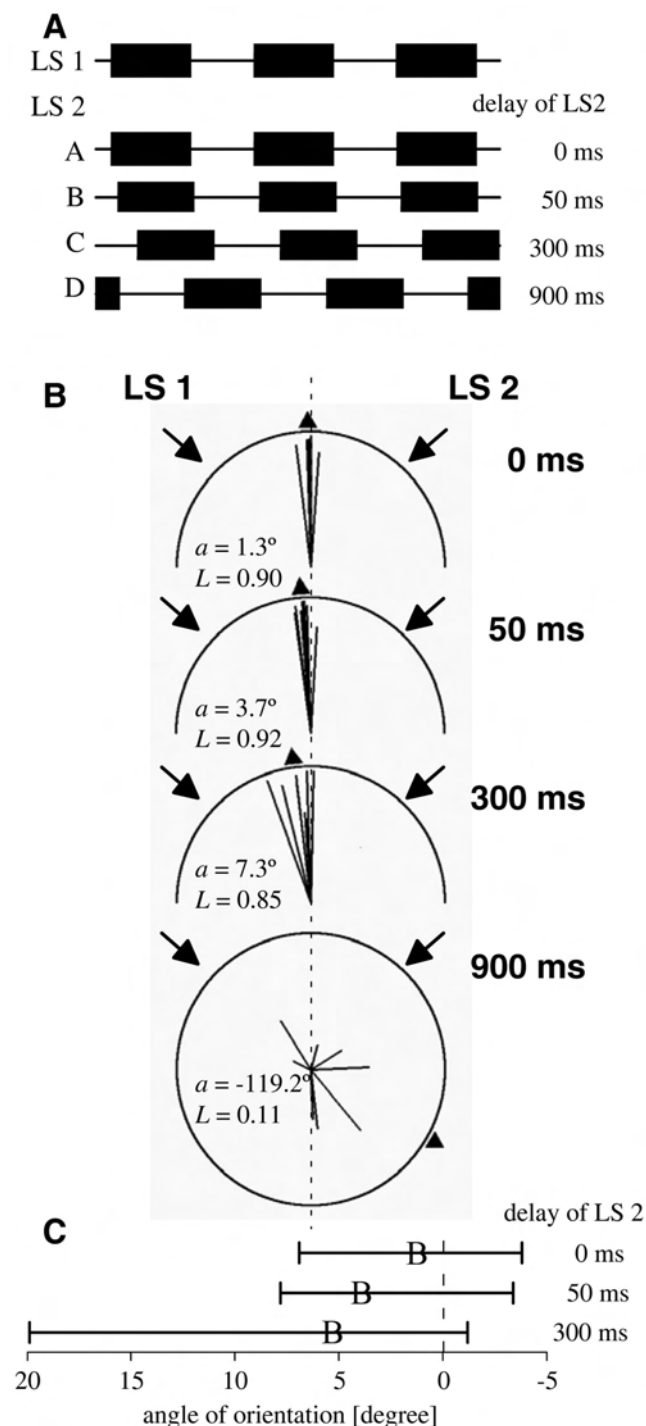


Figure 4. Sawtooth oscillator model for central control of chirp rhythm. The central oscillator (sawtooth line) ascends periodically from its basal level to a peak level, at which point the production of a chirp (thick, horizontal line segment) is triggered. T represents the period of the oscillator and the chirps, and d represents the effector delay that elapses between central triggering and chirp onset (figure modified from Greenfield, 2005).

subsequent chirp cycles immediately resume lengths equivalent to those observed prior to the stimulus chirp. However, when the stimulus chirp is presented just prior to a male's anticipated chirp, that is, d is nearly as long as the mean chirp period, that chirp occurs as anticipated but the subsequent chirp cycle is slightly shortened. As above, the chirp cycle after the modified one is again of normal length. Viewed from the perspective of the sawtooth oscillator model, these adjustments suggest that the oscillator responds to a stimulus chirp by descending immediately to its basal level but then resumes normal behavior. These general responses, first studied in the rhythms of bioluminescent signals in *Pteroptyx* fireflies (Buck, Buck, Case, & Hanson, 1981; Hanson, Case, Buck, & Buck, 1971), have been termed "phase delay," although there is a small portion of the cycle when their effect is actually an advance of phase.

Further playback experiments with stimulus chirps of various lengths have allowed fine tuning of the phase delay model. As stimuli are lengthened, *N. spiza* males lengthen their phase delays commensurately (Greenfield & Roizen, 1993; Figure 5b). This relationship suggests that the oscillator responds by descending to the basal level and remaining inhibited at this level until the end of

Figure 3. Responses of female *N. nebrascensis* in the presence of two male songs. The song at LS 2 (right) was delayed relative to song at LS 1 (left). **A:** The temporal relationship of the two songs. **B:** Vector diagrams of the circular orientation of females. Each line in the circular plots represents the vector characterizing the responses of one female to the stimulus situation; the triangle indicates the direction of the mean population vector. Direction (a) and length (L) of the population vector are given each diagram; 0° denotes the midline between the speakers, located at 52° (leader) and -52° (follower). Loudspeaker positions are indicated by the arrows. **C:** Orientation angles (median and range, $n = 8$) of individual females in response to the situations with delays of 0, 50, and 300 ms. Median angles during the 50 and 300 ms situation differed significantly from the median angle during the 0 ms situation (Nonparametric paired sample testing with angles (Zar, 1984); 50 ms: $R^* = 1.50$, $p < .01$; 150 ms: $R^* = 1.32$, $p < .02$). For delays of 50 and 300 ms, females show a weak orientation toward the leading loudspeaker, relative to their orientation with perfectly synchronous calls (0-ms delay). At a delay of 900 ms (= alternating calls), females showed no responses to either stimulus, as indicated by their random orientation and short vector lengths. Orientation was tested on a locomotion compensator (see Schul, von Helversen, & Weber, 1998, for methods).

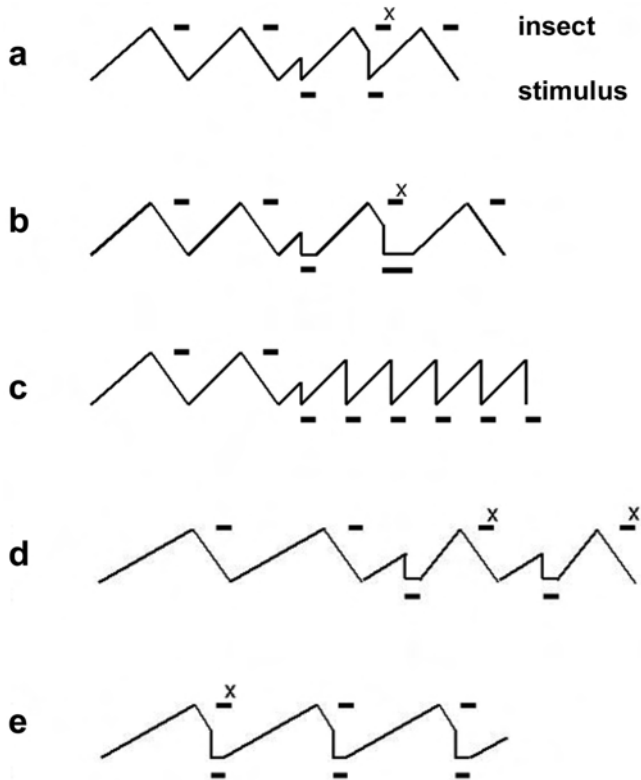


Figure 5. Inhibitory-resetting model for phase-delay adjustment of central chirp oscillator. Upper trace of horizontal line segments represents insect's chirps and lower trace represents stimuli with which insect is interacting. a) Oscillator is reset by first stimulus, and insect chirp (X) is roughly synchronized with second stimulus. b) Oscillator incorporates tonic inhibition in which it is held at its basal level for the duration of the stimulus. Thus, lengthier stimuli influence greater lengthening of the insect's chirp period (as at X). c) Oscillator is repeatedly reset to its basal level by a rapidly repeated stimulus, which causes insect to stop singing after its second chirp. d) Insect alternates with a stimulus that is repeated at a rate slower than the insect's free-running chirp rhythm; steeper ascents of the oscillator reflect rapid rebounds from inhibition that occur after stimuli perceived by the insect late during its chirp cycle. e) Insect exhibits imperfect synchrony with a stimulus that is repeated at a rate approximately equal to the insect's free-running chirp rhythm (figure modified from Greenfield, 2005).

the stimulus, at which point its phase is reset. Hence, this specific mechanism has been termed *inhibitory resetting*. An examination of responses to stimulus chirps can also reveal the length of the effector delay as well as the descent and ascent of the oscillator. For stimulus chirps presented shortly before a male's anticipated chirp, the effector delay is represented by the maximum interval observed between the onset of the stimulus and the onset of the male's chirp at its anticipated time: This chirp is produced because it had already been triggered by the central oscillator (Figure 5a, b, c), whereas a stimulus presented only slightly earlier would have delayed the male's chirp until after a lengthened concurrent chirp period. In *N. spiza* this inference indicates that the effector delay is approximately 50 ms. Stimulus chirps presented after this inferred triggering point of the central oscillator cause a shortening of the subsequent chirp cycle (phase advance; Figure 5a), but as the

stimulus is delayed further the male makes a sudden transition to lengthening of the concurrent cycle (phase delay). We infer that this transition reflects the point at which the oscillator has descended to its basal level and begun the ascent portion of the next chirp cycle. In *N. spiza* this transition point occurs just after the time of chirp onset; that is, the oscillator descent is slightly longer in duration than the effector delay.

Responses of *N. spiza* males to series of stimulus chirps repeated at different rhythms are consistent with the inhibitory resetting mechanism, and they help us to understand how synchrony between neighboring males is attained in natural choruses (Figure 5c, d, e). In general, a solitary *N. spiza* male will synchronize for up to 20 s with stimulus chirps presented at a repetition rate similar to his previous solo rate. As the stimulus is repeated at increasingly higher rates, however, the male sings less and less regularly. He may produce a chirp only every two or three stimulus cycles, each chirp produced in approximate synchrony with the stimulus, and stop singing entirely in response to much faster stimulus rates; for example, stimulus rates faster than twice his solo rate (Figure 5c). On the other hand, a male will typically alternate, that is, sing 180° out-of-phase, with stimulus chirps repeated at a rate slower than his solo rate (Figure 5d; alternation is facilitated by faster rebounds from inhibition after stimuli occurring late during a male's chirp cycle, a relationship depicted by steeper ascents of the oscillator).

Using the proposed inhibitory-resetting mechanism as a guide, observed responses to single and repeated stimulus chirps as well as the imperfect nature of synchronous chorusing in *N. spiza* indicate that synchrony in this species is a "default phenomenon" (Greenfield, 1994a). When two or more neighboring males, who can sustain comparable chirp rates in solo, interact acoustically, their mutual influences lead to only minor phase delays or phase advances after the initial chirp cycle of a chorusing bout. These phase adjustments remain minor because the chirps produced by a focal male's neighbors will necessarily occur very close in time to his own chirps. Thus, an approximate synchrony arises in which more or less random leader-follower relationships occur (Figure 5e). The synchrony is broken occasionally when stochastic variation in free-running chirp rhythms causes one male to slow or another to accelerate. As a consequence of these fluctuations in rhythm, one male may skip a chirp and reenter the chorus in synchrony on the next cycle. However, when neighboring males are unevenly matched and one can sustain a much faster rate than another, regular synchrony does not appear because the faster male produces most of the chirps, at his free-running rhythm, while the other(s) are repeatedly inhibited and reset before triggering their chirps. These rough predictions have been confirmed via Monte Carlo simulations of two or more rhythmic signalers that are regulated by an inhibitory-resetting mechanism: Imperfect synchrony emerges by default when simulated signalers have similar endogenous rhythms and stochastic variation is small (Greenfield et al., 1997).

In *N. nebrascensis*, responses to the playback of single isolated stimulus buzzes and series of repeated buzzes indicate that the mechanisms responsible for rhythm adjustment, and ultimately synchrony, are different from and more complex than in *N. spiza*. In common with *N. spiza*, male *N. nebrascensis* lengthen their concurrent buzz period in response to a stimulus buzz that begins after the onset of their own buzz and extends into the interbuzz interval afterward (Meixner, 1976; Meixner & Shaw, 1986). Sim-

ilarly, they will shorten their concurrent buzz period in response to a stimulus buzz that begins before their own buzz and ends during it. However, these phase delays and advances involve lengthening and shortening, respectively, of both the interbuzz interval and the subsequent buzz. However, it is responses to series of rhythmically repeated buzzes that provide the clue that rhythm adjustment in *N. nebrascensis* is quite different and that an inhibitory-resetting mechanism cannot account for it. Male *N. nebrascensis* will synchronize with stimulus buzz rhythms that are as much as 17% slower or 50% faster than their solo buzz rhythms (Meixner, 1976). As above, rhythm matching entails the lengthening or shortening of buzzes. Moreover, *N. nebrascensis* do not exhibit a lengthy poststimulus interval during which they fail to initiate buzzes, a response that characterizes acoustic interactions in *N. spiza*. These findings imply that *N. nebrascensis* synchrony does not arise as a simple default property and that the males adjust their actual rhythm in addition to its phase. Here, neighboring males may achieve a coupling of their oscillators via small mutual adjustments to both phase and buzz length that are repeatedly made until the several rhythms match in both rate and alignment of buzzes. And once synchrony is attained, should a male start to accelerate or to fall behind a neighbor, these small adjustments allow the males to regain synchrony quickly. This general mechanism of oscillator coupling may also underlie the nearly perfect synchrony found in some *Mecopoda* katydids of Southeast Asia (Nityananda & Balakrishnan, 2007; also see Hartbauer, Kratzer, Sterer, & Römer, 2005; Sismondo, 1990), *Oecanthus* tree crickets of North America (Walker, 1969), and the synchronous flashing of some *Pteroptix* spp. fireflies (Ermentrout, 1991).

Effects and Functions

Female responses to male song in both *N. spiza* and *N. nebrascensis* allow us to interpret rhythm adjustments and synchronous chorusing in an adaptive context. In *N. spiza*, the strong attraction of orienting females toward leading chirps indicates that males are subject to intense selection pressure to avoid producing chirps that follow neighbors' chirps (Greenfield & Roizen, 1993). The inhibitory-resetting mechanism that males adhere to while interacting with neighbors can increase this avoidance in two ways. First, a male who adjusts his chirps by inhibitory resetting will not call during a 200 to 300 ms interval that begins approximately 50 ms after the onset of a neighbor's chirp. The 50-ms postonset interval during which calling may yet occur is an inevitable consequence of the limitations of nervous systems, as chirps produced at this time had already been triggered prior to the neighbor and cannot be suppressed. Second, when a male hears a neighbor's chirp d ms after his last chirp, he lengthens his concurrent chirp period by a duration slightly less than d ms. Thus, his subsequent chirp is likely to occur just before the neighbor's next chirp, given that the two males have similar free-running chirp rates. The Monte Carlo simulation that had been developed to model synchrony was also adapted to analyze this prediction by comparing the chirps produced by two simulated males, one adhering to inhibitory resetting and one calling with identical characteristics save that he disregarded his neighbors; that is, he called as if deaf. These simulations show that inhibitory resetters produce up to 25% more leading calls than disregarders and do not suffer from broadcasting markedly fewer calls in the process, features that

would make them more attractive to females whose orientation is influenced by a precedence effect.

The interpretation presented above argues that synchrony in *N. spiza* is a byproduct that emerges from acoustic perception. We can only speculate on the origin of the perceptual mechanism that causes female attraction toward leading calls: Possibly, it represents part of a general mechanism of orientation that improves localization of sound sources and occurs in some form throughout the clade (see Römer, Hedwig, & Ott, 2002; cf. Greenfield, 2002); for example, the weak preference for leading calls observed in *N. nebrascensis* (see Figure 3). However, given that this perceptual bias does occur, mechanisms of rhythm adjustment that reduce production of following calls by males are selected for in certain species, which in turn yields collective synchrony when neighbors happen to be evenly matched. In this situation females do not specifically prefer synchronous chorusing over other temporal arrangements, and males do not specifically benefit from broadcasting in phase with their neighbors. Rather, synchrony is merely an emergent property. Further observations of *N. spiza* largely support this view. Females do not hesitate to orient toward either of two (or more) alternated chirps provided their onsets are staggered by at least 50 to 70 ms (Snedden & Greenfield, 1998). Moreover, no evidence from the field indicates that synchronizing males, as opposed to those who alternate or call in some haphazard manner; tend to avoid phonotactic predators or parasitoids. In fact, phonotactic parasitoids (dipterans) have not been reared from *N. spiza* males, and insectivorous bats are not observed foraging within the tall grass microhabitat where *N. spiza* males sing.

Being an emergent property, however, would not preclude synchrony from influencing the basic mechanisms that generate it (see Greenfield, 2005). For example, in *N. spiza* synchronous chorusing presents a situation in which relatively small differences between solo male chirp rates become magnified owing to the effects of inhibitory resetting on slower singers. Because chirp rate is a measure of acoustic power and may be preferred by females as an indication of a male's physical prowess, his acquisition of energy during immature development, and so forth, once a rudimentary form of male phase adjustment and collective synchrony emerge, selection may favor stronger precedence effects in females. We predict this evolutionary response because when males begin to exhibit inhibitory resetting and synchrony, females who orient toward leading calls may receive a tangible benefit in the sexual selection arena from this perceptual bias: Females are now automatically attracted toward males who call faster, a discrimination that may otherwise be perceptually difficult if not impossible. In turn, selection on male phase adjustment may be further strengthened. Thus, feedback loops between collective behavior and its individual elements may have led to the exaggerated levels of perceptual bias, signal interaction mechanisms, and synchronous chorusing that we observe in some species.

In *N. nebrascensis* both female responses and mechanisms of male signal adjustment suggest that synchronous chorusing is not merely an emergent property but represents a specific function. Because females must hear a strongly attenuated interval between a male's buzzes before orienting toward him (see Figure 3), mechanisms by which males synchronize with their neighbors would be favored. To sing with any other temporal arrangement would be spiteful, behavior that we normally do not expect. Consequently, *N. nebrascensis* males either accelerate or deceler-

ate their buzz rate depending on their rhythm relative to neighbors. When the focal male is slower, he advances his phase slightly and may sustain a faster rate by shortening his buzzes (Meixner & Shaw, 1986; cf. Walker, 1969). If the focal male is faster, he delays his phase and lengthens his buzzes slightly, which is generally accompanied by a lengthening of his buzz period. This latter response is fundamentally different from that seen in *N. spiza*,

where a faster male does not decelerate his chirp rate to match a slower neighbor, and a male whose chirp rate is faster than a rhythmic stimulus alternates with the stimulus, a consequence of inhibitory resetting, rather than aligning with its phase.

Evolutionary Trajectories

How do we explain such marked differences among signal interactions within the same genus, particularly where the several species share fundamental features of acoustic signaling and perception? We emphasize that males in both *N. spiza* and *N. nebrascensis* produce a rhythmic calling song in which each repeated note is comprised of multiple pulses, sound produced by a cycle of wing movement, and both species make phase adjustments to their rhythms in response to acoustic stimuli. From the perspective of perception, females in both species exhibit a psychoacoustic precedence effect in which they orient preferentially toward leading calls, albeit rather weakly in *N. nebrascensis*. Nonetheless, synchrony in *N. spiza* appears to be the byproduct of signal competition when neighboring males happen to be evenly matched and can chirp at comparable rates, whereas *N. nebrascensis* synchrony may be a cooperative event that does not depend on these special circumstances and that specifically benefits the participants.

Further consideration of information available on these two species suggests that a clue might be found in the requirement that *N. nebrascensis* females have for hearing a strongly attenuated silent interval separating consecutive male buzzes. However, we point out that *N. spiza* females must also hear distinct chirps separated by silent intervals, which implies that a complete explanation must rely on additional factors. Such factors may reside in the very different duty cycles (= note length/note period) in *N. spiza* and *N. nebrascensis* song and the process of chance. Because the duty cycle in *N. spiza* is normally quite low, approximately 10%, specific mechanisms for maintaining requisite silent intervals are probably unnecessary: Interchirp silent intervals of sufficient length and attenuation will nearly always occur regardless of the temporal arrangement between neighboring males' chirps and local population density. However in *N. nebrascensis*, a duty cycle of approximately 60% renders regular synchrony mandatory, as continuous sound would otherwise result. Thus, selection may

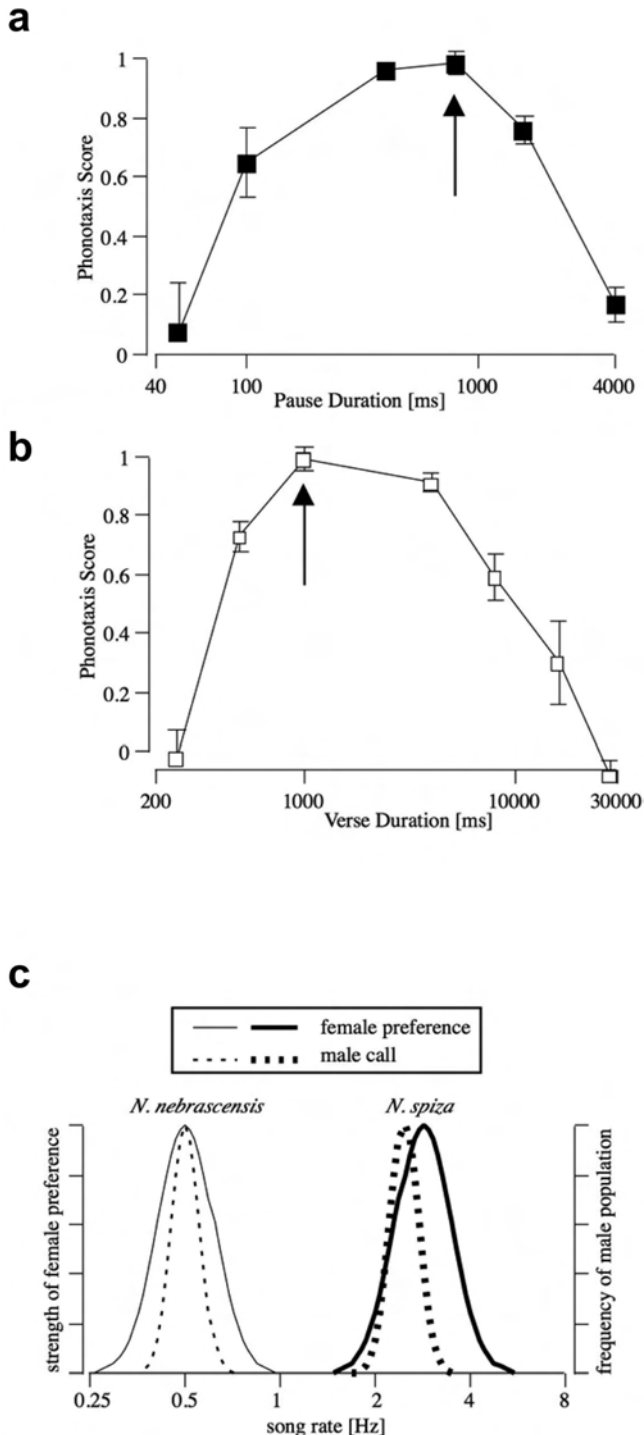


Figure 6. Selectivity of female *N. nebrascensis* for temporal parameters of the male call. Female responses toward synthetic male calls were measured on a locomotion compensator and are expressed as a phonotaxis score (mean \pm SEM, $n = 10$; see Schul et al., 1998 for methods). a) The duration of the verses was held at 1000 ms while the duration of the silent interval between verses varied. b) The verse duration was varied while the duration of the silent interval was held at 800 ms. The mean call and interval duration of this population (measured at 25°C) were 1000 ms and 800 ms, respectively, and are indicated by vertical arrows in a) and b). The results indicate stabilizing selection for both call parameters (data from Deily, 2006). c) Schematic representation of male song rates (dotted lines) and female preference for this parameter (solid lines) in *N. spiza* (thicker lines at right) and *N. nebrascensis* (thinner lines at left). In *N. nebrascensis*, female preference and male trait have the same mean value; in *N. spiza*, female preference is shifted toward faster calls relative to the male trait (data from Greenfield & Roizen, 1993), thus exerting directional selection on male song rate.

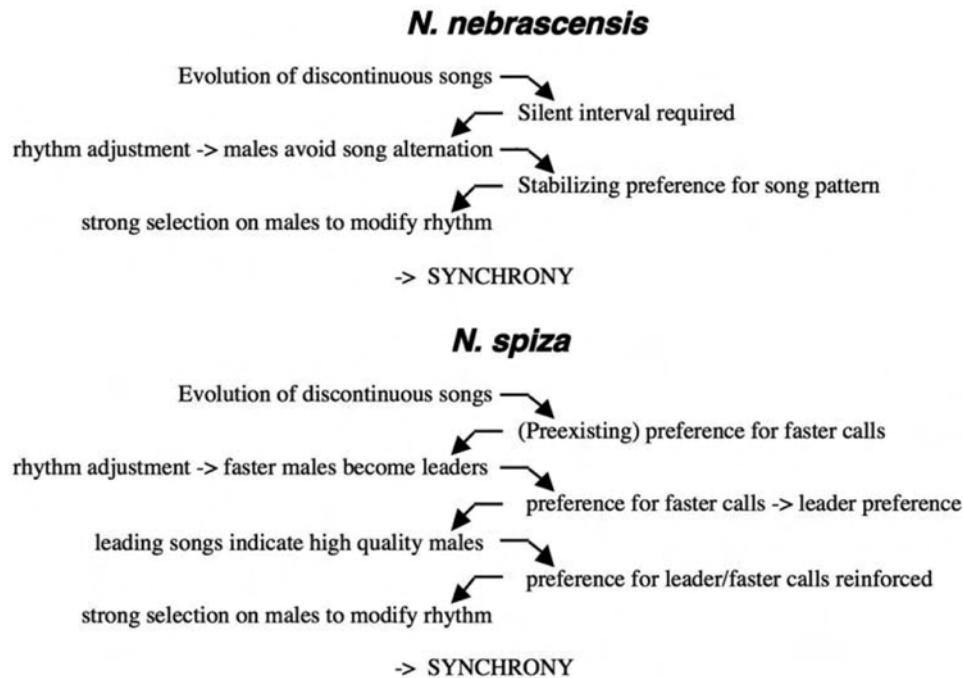


Figure 7. Proposed evolutionary trajectories leading to synchronous calling in *N. nebrascensis* and *N. spiza*.

have favored specific modifications of fundamental mechanisms of phase adjustment that preserve the matching of neighbors' rhythms; for example, modifications of the pulse generator that lengthen or shorten interrupted buzzes. Although a weak precedence effect evidently does occur, the relatively long duty cycle combined with the premium associated with synchrony preclude directional selection for faster buzz rates (Figure 6; note that females do not prefer buzz lengths or interbuzz intervals shorter than the mean values). In the absence of such directional selection of fast singers, the "runaway process" envisioned above (see Figure 7) does not appear, and the precedence effect does not become sufficiently exaggerated to favor selection of inhibitory-resetting or similar mechanisms of competitive signal interaction.

From the results summarized here, it should be clear that our understanding of the neural and behavioral mechanisms controlling signaling, perception, and signal interaction in *Neoconocephalus* remains incomplete. Based on certain components for which key information is available, however, we have been able to present a model explaining how a complex signal interaction, synchrony, may evolve independently along very different trajectories with convergent endpoints. At the same time, we also show how the fundamental mechanisms controlling signaling may evolve distinctive features owing to the very nature of signals in different species. These several examples hint at the rich field awaiting students of the evolutionary process through investigations of chorusing interactions in acoustic animals.

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Acoustic Interactions in Broods of Nestling Birds (*Tachycineta bicolor*)

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Studies of acoustic interactions in animal groups, such as chorusing insects, anurans, and birds, have been invaluable in showing how cooperation and competition shape signal structure and use. The begging calls of nestling birds are ideal for such studies, because they function both as a cooperative signals of the brood's needs and as competitive signals for parental allocation within the brood. Nonetheless, studies of acoustic interactions among nestlings are rare. Here we review our work on acoustic interactions in nestling tree swallows (*Tachycineta bicolor*), especially how calls are used in competition for parental feedings. Nestlings attracted parental attention and responded to acoustic interference mainly by increasing call output. However, nestlings also gave more similar calls when they called together and decreased their call bandwidth when exposed to elevated noise. We suggest that these competitive uses of calls might intensify the cooperative brood signal, affecting both parental provisioning and vocal development. Given their tremendous variation across species, begging calls offer promising opportunities for developmental and comparative studies of acoustic signaling.

Keywords: begging, acoustic interactions, acoustic signaling, vocal development, ambient noise

Studies of acoustically signaling groups of animals have been instrumental in showing how cooperation and competition shape the structure and use of signals (Gerhardt & Huber, 2002; Greenfield, 2002; Todt & Naguib, 2000). Studies of birds, for example, have shown how group breeders signal cooperatively by using intricately coordinated joint songs (e.g., Hale, 2006) and how territorial songbirds interact competitively through the timing and patterning of their song exchanges (e.g., Naguib, 2005). Despite extensive research on such vocal interactions, one of the most widespread and striking examples of acoustic signaling in groups, begging by nestling birds, has received very little attention.

Nestling birds beg for food from their parents with loud calls, accompanied by a visual display that includes stretching upward, waving wings, and gaping. In contrast to more extensively studied

group vocalizations, begging calls combine cooperative and competitive functions, offering a unique opportunity to see how both affect acoustic signaling. Specifically, begging calls function both as a joint signal of the brood's hunger, which parents use to regulate their overall provisioning rate, and as individual, competitive signals, which parents use to decide which nestling to feed on a given visit (Horn & Leonard, 2002, 2005). Detailed studies of acoustic interactions among nestlings are needed to clarify how these two contrasting functions are reconciled in the structure and use of calls.

Such studies would be useful and interesting for several reasons. First, an understanding of how nestlings interact acoustically would help clarify competitive interactions among nest mates, which have been studied extensively but are still poorly understood (as discussed in Royle, Hartley, & Parker, 2004). Second, in many species, nestling calls develop into important adult signals such as contact calls and advertising song (reviewed in Sharp & Hatchwell, 2006), and acoustic interactions among nestlings might affect this development. Finally, across species, begging call structure varies tremendously (Popp & Ficken, 1991), and an understanding of how call structure relates to acoustic interactions might help to explain this variation.

In this article, we review our work on acoustic signaling within broods of our main study species, the tree swallow (*Tachycineta bicolor*). First, we briefly review evidence that parents regulate provisioning rate based on calling by the brood as a whole. Because this function has been widely studied (Hinde & Kilner, 2007), we focus most of our review on the more controversial role of calling in competition for parental food distribution within the brood. We then show how acoustic interference among competing nest mates might affect call structure and use and suggest how those changes, in turn, affect the brood level signal. Finally, we briefly suggest how further studies of acoustic interactions among nestlings might relate to vocal development and interspecific variation in call structure.

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Study Species

The tree swallow (*T. bicolor*) is a common North American passerine. Like the great tit (*Parus major*) and pied flycatcher (*Ficedula hypoleuca*) of Europe, the tree swallow has become a model organism for field ornithology (Jones, 2003), largely because it nests readily in artificial nest boxes. Nest boxes not only facilitate studies of breeding biology but, for our purposes, also provide experimental chambers in which a nestling's acoustic environment is easily recorded and manipulated in both field and lab. A nestling placed in a warmed nest box in the lab experiences very similar conditions to a nestling in the field and can usually be stimulated to beg when a recorded adult provisioning (contact) call is played back (Leonard, Fernandez, & Brown, 1997).

The breeding cycle of tree swallows is typical of most temperate passerines (Robertson, Stutchbury, & Cohen, 1992). Young hatch naked and completely reliant on parents for food and warmth. Parents arrive at the nest with food about every 10 min throughout the day, feeding one nestling on each trip with a bolus of insects they have collected in flight near the nest. The female parent broods the nestlings regularly until they can thermoregulate, when nestlings are 7–10 days old. Typically, young leave the nest about 21 days after hatch, following the parents for about a week thereafter before feeding independently (Robertson et al., 1992).

Growth during the nestling period is accompanied by dramatic changes in the structure of nestling begging calls, from unmodulated, brief, high whistles that appear shortly after hatching to highly variable, frequency modulated and sometimes harmonically structured calls in the second week after hatching (see Figure 1; Leonard & Horn, 2006; Robertson et al., 1992). By Day 15, these calls, now usually given in pairs or triplets, have a complex pattern of frequency modulation that is stereotyped within the individual and, to some extent, distinctive between broods (Leonard, Horn, Brown, & Fernandez, 1997). After fledging, these same calls are used to beg and to maintain contact with the parents, and eventually they become the contact calls of adults (Brown & Brown,

1995). Adult contact calls are used in a broad range of contexts, including provisioning young, coordinating nest visits between members of the pair (Leonard, Fernandez, & Brown, 1997), copulation (in females), and as one of several call types that make up male song (Sharman, Robertson, & Ratcliffe, 1994). The origin of the approximately 12 other adult vocalizations (Robertson et al., 1992) is unknown; presumably they first appear after fledging.

Signaling by the Brood

Our review of the cooperative and competitive influences on calling begins with a brief review of how calling is a joint signal of brood hunger. The main evidence that calling is a joint signal of need is that, in a wide range of species, begging by the brood increases when parents provisioning rate decreases, and parents deliver more food to the brood in response (Budden & Wright, 2001; Wright & Leonard, 2002).

In tree swallows, calling by the brood encodes information on hunger. Specifically, the duration of calling by the brood at each parental visit increases the longer the parent has been away from the nest and when food availability is low (Hussell, 1988; Leonard & Horn, 1996; Leonard et al., 2000; Thomas & Shutler, 2001). In turn, parent tree swallows use this variation in calling to regulate how often they return to the nest with food. Specifically, parents deliver food more frequently when nestlings call longer at each parental visit (Hussell, 1988) and when nestlings give more intense visual begging displays (Leonard & Horn, 1996), which correlate with higher calling rates (Leonard & Horn, 2001a). Also, playback of begging calls increases parental visitation rates, relative to control playbacks of background sounds (Leech, 1996). Thus, as in many other species, begging calls in tree swallows form a joint signal of the need of the brood as a whole that signals to the parents how often to provision the brood. It is unclear whether nestlings coordinate their calls to achieve this function, although this possibility is indirectly addressed by our work on how calling affects food allocation within the brood, which is discussed next.

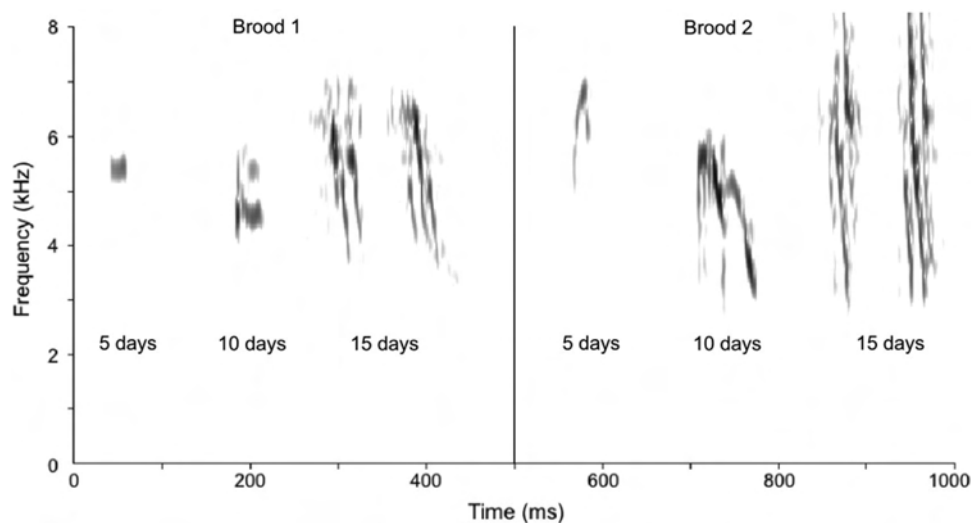


Figure 1. Spectrograms (bandwidth 761 Hz; resolution 1 ms, 23 Hz) of tree swallow nestlings from two different broods (left and right sides of graph), with one call from each of three ages (5, 10, and 15 days posthatch; Day 15 call has two notes).

Signaling by Individuals Within the Brood

In contrast to their function as a joint signal of brood need, the function of begging calls as individual signals affecting which nestlings are fed has rarely been demonstrated (Forbes, 2007). Such evidence is, of course, key to understanding the effect of competitive interactions on begging calls. Three pieces of evidence support this function in tree swallows: (a) the calls of individual nestlings vary with individual need, so a parent could use them to gauge each nestling's needs and direct feedings accordingly; (b) nestlings use calls in situations in which calling is a particularly effective way to attract the parent's attention; and (c) calls affect parental feeding decisions.

The first of these points, that a nestling's calls advertise its hunger, has been shown in several species (e.g., Kilner, Noble, & Davies, 1999; Price & Ydenberg, 1995; Sacchi, Saino, & Galeotti, 2002). In tree swallows, for example, calling rate and length increase with nestling hunger throughout the nestling period, and amplitude and frequency range also increase with hunger in older nestlings (Leonard & Horn 2001a, 2006). The second two points, however, have rarely been demonstrated, so we explain the evidence in more detail.

Are Calls Used to Attract Parental Feedings?

If calls are used to attract parental feedings, one would expect nestlings to call more when their ability to catch the parent's attention is compromised, for example, when their visual display is obscured or when other nestlings are closer to optimal feeding locations within the nest. The first of these situations has been created experimentally by dimming illumination within nest boxes (Heeb, Schwander, & Faoro, 2006). Such experiments have not examined the effect of lighting on calling but do show that this manipulation is a promising approach.

In our work, we took the second approach, manipulating the position of nestlings within the nest. Parents preferentially feed nestlings near the entry hole at the front of the nest box (Leonard & Horn, 1996; Whittingham, Dunn, & Clotfelter, 2003), so we used Plexiglas partitions to prevent nestlings from approaching this optimal feeding location (Leonard, Horn, & Parks, 2003). In experimental nests, two nestlings were confined to the back of the nest; in control nests, nestlings were free to move to the front of the nest, toward the parent. We predicted that nestlings that were prevented from approaching the parent would call more to compensate for their poor position in the nest.

Indeed, confined nestlings called at nearly double the rates of unconfined nestlings. Moreover, among the control, unconfined nestlings, those that remained in the back of their nests called more than those that chose to move forward toward the parent. Thus calls were indeed used in ways that might help to draw the parent's attention toward nestlings that are farther away. Calling rate and hunger, as measured by the time since the parent's previous visit, were not correlated in this experiment (Leonard, Horn, & Parks, 2003), despite their strong correlation in our other work (e.g., Leonard & Horn, 2001a, 2006). Thus, in certain contexts, the use of calls to signal hunger might be superseded by their use in attracting the parent's attention, highlighting the competitive, as opposed to cooperative, dimension of calling.

Do Parents Use Calls to Allocate Feedings Within the Brood?

Of course, the most fundamental requirement for calls to be used competitively to affect food allocation is that parents actually use nestling calls to select which nestling to feed. In the experiment just described, parents did indeed preferentially feed nestlings that called more, and partial correlations showed that this preference was independent of their strong preference for nestlings that had more intense visual begging displays (Leonard, Horn, & Parks, 2003). Similar correlational evidence exists in a few other species (Kilner et al., 1999; Price & Ydenberg, 1995; Sacchi et al., 2002). A more direct approach, however, would test for a preference with no cues other than the vocal signal.

We conducted such an experiment by placing small speakers on either side of a nest box, next to a nestling that we had thoroughly satiated by hand feeding so that it would not move or call during the experimental trial (Leonard & Horn, 2001b). When a parent arrived at the nest, we played the calls of a deprived versus a fed nestling and video recorded which nestling the parent attempted to feed. Parents preferentially directed feeding attempts to calls played back at higher rates (Leonard & Horn, 2001b), showing that, in the absence of visual cues, parents did use calls to deliver feedings to particular nestlings. Similar results, using similar paradigms, have been reported in two other species (Kilner, 2002; R. Brandt, personal communication, August 2000). In contrast, muting red-winged blackbird (*Agelaius phoeniceus*) nestlings did not reduce parental feedings to those nestlings (Glassey & Forbes, 2002), but this may be because parents switched to visual cues when acoustic cues were not available. Indeed, although the influence of visual cues on parental feedings is well established (albeit mainly from correlational rather than experimental studies), the interaction between visual and acoustic cues is virtually unexplored and deserves more study (Kilner, 2002).

How Do Nestlings Overcome Acoustic Interference From Nest Mates?

Having shown that calls function to influence food allocation within the brood, we now consider how competition for parental feedings shapes call structure and use. The most obvious form this competition might take is acoustic interference among nest mate calls, so we would expect calling by individual nestlings to show features that circumvent this masking. To identify these features, we have used two approaches that have yielded different, but complementary, results. The first and most obvious was to expose nestlings to calling nest mates and see how the nestlings changed their calls.

How Do Nestlings Respond to Interference From Nest Mate Calls?

Following from studies of call interference in better studied systems, that is, chorusing insects, anurans, and adult songbirds, we could think of three main ways that nestlings might call to reduce interference. Specifically, nestlings might alternate calls, give individually distinctive calls, or simply increase the output, that is, the rate, length, or amplitude, of their calls. To test these alternatives, we deprived nestlings of food for an hour and then

stimulated them to beg either alone or with another nestling undergoing the same treatment behind an opaque partition (Leonard & Horn, 2001c). We performed the test at two ages (Days 7–8 and Day 13) and tried all combinations of the largest and smallest nestling from each brood.

We found no significant relationships in the timing of nest mates' calls as measured by their phase relationships analyzed with circular statistics (Klump & Gerhardt, 1992). Nestlings did, however, increase their call rate in response to calling nest mates by nearly 50% (see also Leonard & Horn, 1998). Otherwise, we found no consistent changes in call amplitude, length, frequency, or bandwidth, although one marginally nonsignificant effect ($p = .06$) suggested that small nestlings may have increased the amplitude of their calls by 3 dB when they were calling with a larger nestling.

The most surprising result, however, was the thorough contradiction of our prediction that nestlings would increase the distinctiveness of their calls to overcome masking. When nestlings called together, the structure of their calls, as measured by cross-correlation, did not diverge but instead converged; that is, nestling calls were more similar when nestlings called together than when they called alone (Leonard & Horn, 2001c). Whether this convergence is a response to competition per se is uncertain. As nestling tree swallows age, their calls become more similar to those of brood mates and less similar to those of other broods, partly, perhaps, to facilitate parent–offspring recognition after fledging (Leonard, Horn, et al., 1997). Thus perhaps the increase in call rate in response to nest mates coincidentally yielded more calls that matched the brood's typical call structure.

Certainly the nestlings' responses to competing calls—increasing call rate and call similarity—would seem to increase rather than decrease acoustic interference. These acoustic interactions appear to be competitive scrambles to capture the parent's attention and perhaps to mask competing signals rather than more intricate exchanges that would reduce interference overall. That said, tests in other contexts or at other ages might well yield more sophisticated forms of interaction. For example, shortly before fledging, nestlings do appear to alternate their calls (personal observation), as experimentally shown in the closely related bank swallow (*Riparia riparia*; Beecher & Beecher, 1983) and in starlings (*Sturnus vulgaris*; Chaiken, 1990; see also Muller & Smith, 1978; Price & Ydenberg, 1995). Further work, for example, studies that use playbacks of calls, would be worthwhile.

How Do Nestlings Respond to Interference From Ambient Noise?

An alternative approach to studying how nestlings effectively transmit their calls despite noise from nest mates is to present nestlings with sound that can mask their calls but is neutral in content, such as white noise. Given that nest mates are the main source of acoustic interference within the nest, whatever calling strategies nestlings use in elevated noise presumably evolved partly to cope with noise from nest mates. Thus this approach uses neutral noise as a surrogate for noisy nestlings. A caveat to this approach, of course, is that nestlings might actually respond differently to such noise than to noise from nest mates, so the results should be interpreted cautiously. In particular, noise from ambient sources such as wind and running water has more energy in low

frequencies than nestling noise, so one strategy for circumventing noise, raising call frequency (see later discussion), might be ineffective for dealing with nestmate calls.

Recently, we conducted several experiments testing how nestlings change their calls in the presence of 65 dB (sound pressure level [SPL]) white noise that is synthesized to cover the frequencies from 0 to 22 kHz, that is, encompassing the frequency range of nestling calls (approximately 2–10 kHz). We predicted that nestlings might show some of the same adjustments documented in other acoustic signalers exposed to elevated noise. Specifically, nestlings might simply increase call amplitude so that it remains high relative to the noise amplitude, a widespread strategy known as the *Lombard effect* (Brumm & Slabbekoorn, 2005). They might also increase call redundancy through an increase in call length or rate (Brumm & Slabbekoorn, 2005). Finally, they might change the frequency structure of calls. They might increase the lowest frequency of calls, which raises the calls above the low frequencies that predominate in most ambient environmental noise (Slabbekoorn & Peet, 2003) albeit not necessarily the higher frequency noise that comes from nest mates. Alternatively, however, they might decrease call bandwidth, which concentrates signal energy into a narrow frequency so that the call is easier to detect in any broadband noise (Lohr, Wright, & Dooling, 2003), including noise from nest mates. These vocal adjustments are usually studied as responses to abiotic and heterospecific noise; but because they are responses to acoustic interference per se, they might well apply to the acoustic interference from nest mates that interests us here.

Our experiments showed some of these responses, but the particular response varied depending on the time scale of the noise exposure. During 1 or 2 hours of exposure in the lab or field, nestlings did not change the length or frequency of their calls but did elevate call amplitude by approximately 10 dB (SPL; Leonard & Horn, 2005, 2007b). Thus, as in virtually every acoustic signaler tested to date (Brumm & Slabbekoorn, 2005), nestlings simply increased their call amplitude in response to elevated ambient noise. We tested whether this amplitude increase improved reception by parents by presenting parent tree swallows in the field with the same choice between different call rates as we used in the choice tests described previously, except that white noise was played at 60 dB (SPL) within the nest box and the sets of calls that parents had to choose between were played at either low (55 dB) or high (65 dB) SPLs. As in the earlier choice tests, parents preferentially directed feedings toward higher call rates but only when the calls were played back at the higher levels. Thus, noise interfered with parents' responses to calls, and raising call amplitude was an effective strategy for overcoming that interference.

These experiments tested nestlings' responses to short periods of elevated noise, simulating the short-term elevations in noise levels that might occur, for example, when the whole brood is hungry and thus calling loudly. If noise persisted for longer periods, however, as in a nest with a particularly large brood, nestlings might respond differently. In particular, even if begging is energetically cheap, as in tree swallows (Leech & Leonard, 1996; Leonard, Horn, & Porter, 2003), delivering louder calls at a higher rate might be marginally more expensive or riskier in attracting predators (Leech & Leonard, 1997) than calling more quietly. Thus nestlings might use a different strategy to respond to noise levels that are sustained over days rather than the hour or less used in the experiments described previously.

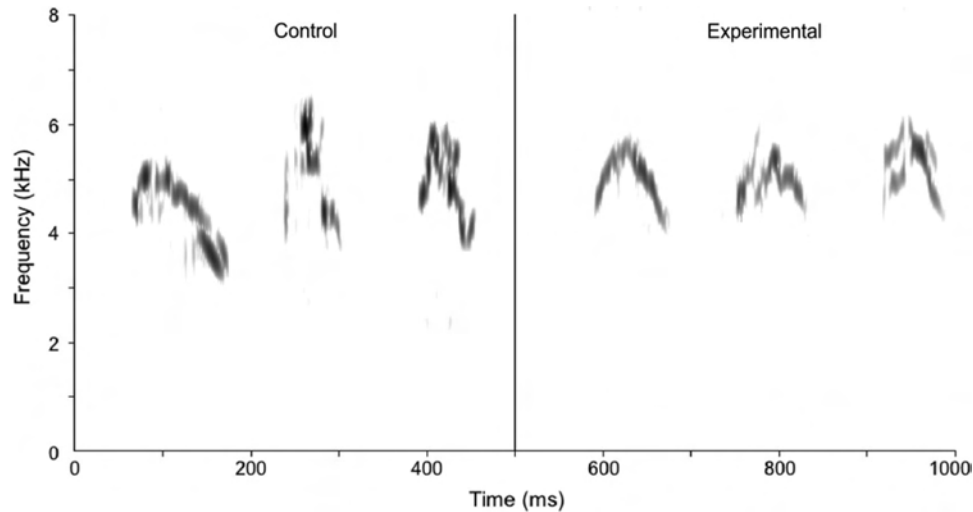


Figure 2. Spectrograms (bandwidth 761 Hz; resolution 1 ms, 23 Hz) of calls of nestlings after 48 h of ambient noise playback at 55 dB (sound pressure level [SPL]; control, left three calls) or 65 dB (SPL; experimental, right three calls). Each call is from one of the three broods whose changes in call bandwidth were the closest to the median for that treatment.

To test the responses of nestlings to noise over longer time periods, we played back white noise at nests in the field for 48 hours and compared several call characteristics at the end of the noise exposure (Leonard & Horn, 2007b). Out of call length, amplitude, emphasized frequency, and frequency range, the only call variable that showed a significant effect was call frequency range, which decreased in experimental relative to control nestlings (see Figure 2). Call structure changes quite rapidly during the nestling period (Leonard & Horn, 2006), so even this difference sustained over just 2 days might have a more persistent effect on call development. Indeed, we have since extended the experiment by playing white noise from Day 3 to Day 15 of the nestling period (Leonard & Horn, 2007a). Nestlings at nests with elevated ambient noise again produced calls of narrower bandwidth, and the difference persisted through the nestling period to at least 2 days after the noise was turned off, consistent with a more permanent, developmental change in call structure. Neither experiment showed any detectable effect of elevated noise on parental feeding rates or nestling growth.

These results are consistent with our expectation that nestlings might use more efficient strategies than simply increasing call amplitude to deal with noise over the long term. Higher minimum frequencies and narrower frequency ranges are both call features that have been cited as adaptive responses to elevated noise (see earlier discussion). Thus nestlings might adaptively shift the frequency structure of their calls to deal with noise, which is perhaps a cheaper strategy than sustaining the high call amplitudes they showed in the short-term lab experiment. Alternatively, the shift in frequency could be a nonadaptive by-product of disrupted auditory feedback, although previous studies of auditory feedback have applied much more intense sound levels or deafening with variable results (e.g., Heaton & Brauth, 1999; Watanabe, Eda-Fujiwara, & Kimura, 2007).

Whether the frequency changes we observed were adaptive adjustments to noise or not, the results do show that ambient noise

at the nest can affect call structure and perhaps call development. In turn, given that nest mates are the predominant source of acoustic interference in the nest, the results suggest that acoustic interactions might affect not only call output (rate and amplitude) on the short term but also, over a developmental time scale, the frequency structure of nestling calls.

Summary and Conclusions

We have shown that calling by nestling birds is both a group signal, which influences parental feeding rate, and a collection of individual signals, which influence food allocation within the brood. Here we summarize how these two contrasting functions of calling might account for the structure and use of begging calls.

The competitive function of calling has been our main focus. Our experiments show that nestlings increase call rate when nest mates call and increase call amplitude when ambient noise levels increase. These results suggest that the main effect of the competitive use of calls on call structure is an increase in overall call output. It may also affect the frequency patterning within calls; nest mates that call together tend to converge on a shared call structure, and nestlings exposed to moderate levels of elevated noise give calls with narrower bandwidths.

These results also have implications for the cooperative function of calling. Most obviously, nestlings' increase in call output in response to acoustic interference presumably intensifies the signal of the brood as a whole, more than it would if nestlings avoided interference, for example, by alternating calls. Thus, although nestlings' responses to interference appear inefficient, they might be compensated at the brood level by increased provisioning rates to the brood (Royle et al., 2004). Indeed, what seem to be escalations between nest mates may actually be cooperative efforts to amplify the signal of the brood as a whole (Forbes, 2007; Wilson & Clark, 2002; see also Bell, 2007; Mathevon & Charrier, 2003).

Our finding that calls became more similar when nestlings called together fits well with this possibility.

Clearly, the results suggest an interplay between signaling by and within the brood that might have important effects on how calls regulate provisioning. In this respect they contribute to the increasing evidence from a wide range of signaling systems that competitive interactions within groups can benefit individuals by increasing the signal output of the group as a whole (Bell, 2007). For example, the competitive interactions within choruses of frogs and toads create a collective signal that attracts females more effectively than lone males (Wells & Schwartz, 2006).

Nestling calling is unique among the systems studied to date, however, in that the interplay between competition and cooperation may affect signal development. For example, convergence in call structure during acoustic interactions among nest mates might account for how calls become more similar within but more distinctive between broods in many species, including tree swallows (Leonard, Horn, et al., 1997). Similarly, changes in the frequency range of calls in response to ambient noise might partly account for interbrood variation in call structure. Especially given that nestling calls often develop into adult vocalizations (Sharp & Hatchwell, 2006), the effect of acoustic interactions on call development deserves more study.

How cooperative and competitive acoustic interactions among nestlings relate to signal design is likely to vary widely among species. Nestling calls display an enormous range of variation across species, from abrupt, broadband calls to long whistles (Popp & Ficken, 1991). Even within species, nestling calls can be diverse in structure and function (Sharp & Hatchwell, 2006), such as the whistles and whines given between and during feedings, respectively, by nestling white-browed scrubwrens (*Sericornis frontalis*; Maurer, Magrath, Leonard, Horn, & Donnelly, 2003).

This variation, especially between species, might relate partly to variation in nest structure or resource competition within the nest (see discussions in Horn & Leonard, 2002, 2005), but ultimately they are bound to affect, and be affected by, acoustic interactions among nest mates. For example, several studies suggest that the calls of cavity nesting species, such as woodpeckers, have more abrupt onsets and offsets and broader frequency ranges than the calls of open nesting species (Horn & Leonard, 2002). If so, then cavity species might tend to compete via strategic timing of calls, compared to open nesting species that might tend to vary the frequency structure of their calls.

Detailed studies of nestling calls are so few that such specific predictions are probably premature. Nonetheless, the few existing descriptions of acoustic interactions among nestlings suggest they are indeed more diverse than implied by the relatively simple interactions we report here for tree swallows. For example, unlike tree swallows, barn owl (*Tyto alba*) chicks engage in complex vocal interactions that appear to determine which chick will get the next feeding from the parent (Roulin, 2002). Similarly, individual field sparrow (*Spizella pusilla*) nestlings call at different frequencies when calling with nest mates, perhaps to avoid overlap in call frequency (Popp & Ficken, 1991)—a response we predicted but did not observe in tree swallows.

Like the better understood choruses of male birds, anurans, and insects, begging nestlings illustrate how cooperation and competition affect acoustic signaling. Moreover, nestling calls have a developmental dimension not found in the more thoroughly stud-

ied systems. Given their tremendous variation across species, begging calls clearly offer promising opportunities for developmental and comparative studies of acoustic signaling.

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Whistle Rates of Wild Bottlenose Dolphins (*Tursiops truncatus*): Influences of Group Size and Behavior

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In large social groups acoustic communication signals are prone to signal masking by conspecific sounds. Bottlenose dolphins (*Tursiops truncatus*) use highly distinctive signature whistles that counter masking effects. However, they can be found in very large groups where masking by conspecific sounds may become unavoidable. In this study we used passive acoustic localization to investigate how whistle rates of wild bottlenose dolphins change in relation to group size and behavioral context. We found that individual whistle rates decreased when group sizes got larger. Dolphins displayed higher whistle rates in contexts when group members were more dispersed as in socializing and in nonpolarized movement than during coordinated surface travel. Using acoustic localization showed that many whistles were produced by groups nearby and not by our focal group. Thus, previous studies based on single hydrophone recordings may have been overestimating whistle rates. Our results show that although bottlenose dolphins whistle more in social situations they also decrease vocal output in large groups where the potential for signal masking by other dolphin whistles increases.

Keywords: call rates, masking, passive acoustic localization, whistles, *Tursiops truncatus*

Animals use acoustics actively in many different ways, including echolocation, prey manipulation, and communication. Generally, acoustic communication displays can be split into two classes, long and elaborate song displays often used by males to attract females and defend territories, and nonsong vocalizations that are addressing only one or a small group of receivers and are more interactive. Marine mammals use both these types of acoustic communication signals. Phocids as well as baleen whales produce song during the breeding season that may either be used in male–male competition and/or as reproductive advertisement displays to attract females (Tyack, 1999). Singing males usually defend underwater territories (Bartsh, Johnston, & Siniff, 1992) or seek spatial distance to other singers (Frankel, Clark, Herman, & Gabriele, 1995), which decreases masking of their sounds by other singing males.

Nonsong vocalizations are often brief and dependent on social stimuli, such that their function is relevant to an immediate social context. One example here is calls that help to maintain contact.

These are used by mothers and offspring in many animal species, including pinnipeds (Collins et al., 2005) and pigs (Illmann, Schrader, Spinka, & Sustr, 2002) or by social groups, such as in elephants (McComb, Moss, Sayialel, & Baker, 2000), monkeys (Ramos-Fernández, 2005), bats (Boughman & Wilkinson, 1998) or birds (Hopp, Jablonski, & Brown, 2001). Similarly, food calls, alarm calls, or calls to mediate social interactions belong to this class. Here, masking of one's signals by those from conspecifics can create a major problem as group sizes get larger. This is an even bigger problem in the marine environment where sounds travel much further than in air (Janik, 2005). Offshore dolphin groups can consist of hundreds of animals, so the development of specific adaptations to counter the masking effects of conspecific vocalizations may be expected.

One such adaptation is the signature whistle of bottlenose dolphins. Each animal has its own individually distinctive whistle that it uses whenever it is isolated from its group members (Janik & Slater, 1998; Sayigh, Esch, Wells, & Janik, 2007). Signature whistle development is influenced by vocal learning (Tyack & Sayigh, 1997) and listening dolphins use the frequency modulation pattern, a component invented by the signature whistle owner, to identify the caller (Janik, Sayigh, & Wells, 2006). The use of vocal learning allows dolphins to develop signature whistles that are more distinctive than identification signals in other species (Janik, 2005). This makes them more recognizable in high background noise.

However, signature whistles contribute only between 39% and 52% of whistles heard from wild dolphins (Cook, Sayigh, Blum, & Wells, 2004; Watwood, Owen, Tyack, & Wells, 2005). The remaining 50% are made up of other whistles, the function of which is largely unknown. Thus, other mechanisms to reduce the effects of masking by conspecifics must be in place.

In this study we investigate the whistling behavior of wild bottlenose dolphins to see how it relates to group size and behav-

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ioral context. If dolphins try to avoid masking they may limit their vocal output when group size increases. Such an investigation needs to consider behavioral contexts because different contexts also require different amounts of communication.

Studying whistle usage in the wild is difficult because dolphins are agile and whistles cannot easily be allocated to individuals. Most studies describe whistling behavior of whole groups (dos Santos, Caporin, Onofre Moreira, Ferreira, & Bento Coelho, 1990; Herzing, 1997; Jones & Sayigh, 2002; Scarpachi, Bigger, Corkeron, & Nugegoda, 2000; Smolker, Mann, & Smuts, 1993). However, this might be problematic because dolphin whistles have been shown to travel large distances (Janik, 2000) and as such it is not clear if the observed group is producing the recorded sounds. Assigning calls to individuals or contexts based on this method then becomes problematic. Thus, data on individual whistling behavior are sparse and novel techniques are needed to relate whistling to behavioral context.

In this study we used passive acoustic localization to ascribe sounds to groups of different sizes to investigate the effects of group size on whistle rates. We also describe how whistle rates vary in different behavioral contexts. The localization method allows whistles to be accurately assigned to a direction that can then be correlated with surface behavior observations (e.g., Janik, Van Parijs, & Thompson, 2000). This also allowed us to assess the validity of interpretation of whistle use in previous studies.

Method

Data Collection

This study was conducted off the northeast coast of Scotland between Arbroath and Fife Ness from July to September in 2003 and 2004. The subject animals were individuals of a bottlenose dolphin population numbering approximately 130 individuals (Wilson, Hammond, & Thompson, 1999) and known to travel large distances around the northeast Scotland coast from the Moray Firth to St Andrews Bay (Wilson, Reid, Grellier, Thompson, & Hammond, 2004). Focal follows (Altmann, 1974), employing concurrent acoustic recordings on a four element distributed array and nonacoustic, behavioral sampling with 2 min summaries, as well as standard photo-identification techniques were undertaken from a small boat when sea state was Beaufort 3 or less and weather was dry. We used two observers for our behavioral sampling. One observed the focal group and the other one reported position and group sizes of other groups within 300 m of the boat using 2-min point sampling. In our behavioral sampling on the focal group we collected data on behavioral patterns (Column 2 of Table 1) continuously and data on group size, distance from the boat, and swimming direction using 2-min point sampling. For this study, groups were defined as two or more dolphins in which each individual was within 10 m of at least one other member of the group.

The distributed array consisted of three HTI-94-SSQ hydrophones and one HTI-96-MIN hydrophone (High Tech, Inc., Gulfport, MS) all with a frequency response of 2 Hz to 30 kHz \pm 1 dB, attached to tensioned 2m pieces of chain with waterproof tape. The four elements were then distributed around the boat in a box array to allow passive acoustic localization. Hydrophones were positioned at 2m depth and were placed between 160cm and 280cm

Table 1

Definitions of Behavioral Activities Assigned to Focal and Other Groups During Behavioral Sampling

Behavior type	Definition
Surface travel	Animals all moving in the same direction, not creating white water in their wake
Nonpolarized movement	Animals exhibiting nondirectional movements with all surfacings facing different directions
Socializing	Animals interacting with each other in close proximity; including rubbing together, rolling over, showing bellies, fins and heads out
Jumping/body slaps	Animals leave water to exhibit aerial behavior, often causing splashing

Note. All events are mutually exclusive.

apart. Recordings were made onto a Fostex D824 multitrack digital recorder (Fostex, Tokyo, Japan) during 2003 and an Alesis adat HD24 multitrack digital recorder (Alesis, Cumberland, RI) during 2004 (sampling frequency 48 kHz, 24 bit for the Fostex, 32 bit for the Alesis). Spoken tracks of the two observers, one detailing the surface behavior of the animals in the focal group and one the positions and behavior of nonfocal groups were also recorded on the multitrack recorder. These observations included descriptions of group composition and size, distance and direction of groups from the boat (based on a standard clock face with the bow being 12 o'clock) and group activity (see Table 1). A behavior pattern was assigned to a group when at least 50% of the group was engaged in it. The classification of behavior was standardized between the observers during an initial training phase to reduce any chance of misinterpretation of behavioral activity. Dorsal fin photo-identification of the focal and its associates was completed using a Canon Digital D30 SLR camera (Canon, Tokyo, Japan) with a Sigma 100 to 300 mm APO lens (Sigma Corp., Bandai, Fukushima, Japan).

Data Analysis

The acoustic recordings were catalogued using Cool Edit Pro LE (Syntrillium, Phoenix, AZ) using a spectrogram display (Hanning window, FFT 512) and the start and end time of each vocalization event was transcribed into a spreadsheet. Instances of engine noise were also catalogued and graded. Engine Noise Level 1 referred to times when dolphin signals from our focal group would be masked, this occurred whenever the engine exceeded 2000 rpm. Engine Noise 2 referred to times when dolphin signals could be reliably seen through the background noise, this was at times when the engine was running at below 2000 rpm or was switched off. Each 2-min period in a follow was categorized as belonging to a behavioral state by using definitions shown in Table 1.

We discarded any 2-min sections containing any amount of Level 1 noise from the analysis. Similarly, any sections in which behavioral observations were incomplete, the focal animals were lost or the focal animals were more than 60m away from the boat were also discarded. We chose 60m based on the calibration results for our localization system indicating that signals were received

and could be localized at this distance (Quick, Rendell, & Janik, in press).

Whistle localization to individual was conducted using the TOADY localization program (Quick et al., in press). Toady uses the method of cross-correlation of time of arrival differences between hydrophone pairs to determine signal source, a method possible when delays are preserved on a multitrack recorder. Each whistle was localized in turn and the caller position noted if localization was successful. If whistles could not be successfully localized the reason was recorded. Reasons for nonlocalization ranged from low signal-to-noise ratio, to overlap with other signals, to caller position localized to the engine location. Once all whistles were localized, each caller position was compared to focal group position and activity at the same time of the whistle event. For each follow, the average whistle rate per 2-min section was determined for localized whistles only and also for all whistles, (localized, not localized, and localized to other groups), recorded in the sections. All whistle rates reported here are per individual, which was achieved by dividing the rate by the median group size for each analyzed section. We found that the percentages of nonlocalized whistles were variable throughout the follows, and showed no correlation with group size (Spearman's Rank correlation: $r = .016$, $p = .937$). Furthermore, no behavioral context was correlated to a specific group size (Spearman Rank Correlation: surface travel $p = .557$, nonpolarized movement $p = .084$, socializing $p = .313$), (see Table 2).

A general linear model (GLM) was used to analyze the variation in whistle rates across behavior types. The numbers of localized whistles in each follow for each behavior category was taken as the quasi-Poisson distributed response variable. Behavior type was modeled as the categorical predictor variable and could take one of three values: surface travel, socializing, or nonpolarized movement. The numbers of whistles during socializing and nonpolarized movement were modeled against the number for surface travel. The logarithm of average group size was modeled as a linear predictor variable and the logarithm of duration (total number of usable minutes in each follow) was added as an offset. The offset was used to specify the relationship between whistle number and duration since an increase in whistle number explained by the animals having a longer duration in some follows in which to whistle. Initially a model including each follow number as a categorical variable to account for using multiple sections from individual follows was run. This showed that only one follow (Follow 5) showed follow number to be a significant factor in determining whistle rate, due to one section of nonpolarized movement having a significantly larger whistle rate than all the other data (see Table 2). However, with greater than 20 follows at least one such event is expected by chance. The final model was therefore run excluding follow number. Data were grouped by behavior for each follow resulting in 41 different data points for the model. No interaction terms were considered due to small sample size. Model fitting was completed in R software (The

Table 2

Summary of Whistle Rates per 2 Minutes for Localized and Total Number of Whistles for Each of the Four Behavior Types

Follow number	Group size	Surface travel			Nonpolarized movement			Socializing		
		Rate/2 mins (localized)	Rate/2 mins (total)	No. of sections	Rate/2 mins (localized)	Rate/2 mins (total)	No. of sections	Rate/2 mins (localized)	Rate/2 mins (total)	No. of sections
1	20+	3.25	9.88	8	5.33	13.0	6	5.0	9	2
2	10-15	1.25	1.50	4						
3	2	0.00	0	1						
4	2	0.00	0	1						
5	10-15	0.75	2.75	4	39.00	39.0	1			
6	15-20	0.67	5.67	3	7.20	33.8	5			
7	10-15	0.09	0.45	11				0.0	13	1
8	2	0.00	0.36	14						
9	20+	0.00	0.14	14						
10	40+	0.77	1.85	13	4.00	10.5	2			
11	40+	0.00	0	6						
12	15	0.00	1	2	2.00	6.0	1			
13	10-15	0.17	0.33	6	3.00	10.0	1			
14	8-10	0.00	0	4						
15	8-10				5.00	44.0	1	9.5	33	2
16	30+							1.0	12	1
17	30+	1.00	10.50	2	10.00	29.0	2			
18	12-15	0.00	1.20	5	0.00	11.5	2			
19	3	0.00	0	2						
20	12-15	0.00	1	1						
21	12-15	0.00	10.00	1	4.00	15.0	2			
22	6	0.00	0.50	2						
23	30-40				4.00	22.0	1	1.0	11	3
24	15-20	0.00	0	1	5.33	22.0	3			
25	15	0.00	0	8						
26	10-15	0.00	0	6	0.00		1			
<i>M</i>		0.35	2.05		6.84	19.68		3.3	13	
<i>SE</i>		0.07	0.32		1.90	2.53		1.32	3.28	

R-Foundation for Statistical Computing, Vienna, Austria). We recognize that sections of different behavior types from one follow may not be independent. To affect our results, this would have to result in dolphins changing whistle rates in the same behavioral category depending on what behavior they engaged in previously. Unfortunately we do not have sufficient sections to address this question. However, the risk of such a bias in our data set is small because all but five of the 2-min sections analyzed were separated by at least one 2-min section not included in the analysis.

Results

In total 29 follows were considered. Three follows were discarded due to being incomplete either through missing observations or equipment failure, leaving 26 follows from 13 separate days, totaling 13 hr and 52 min of recordings and 1,783 whistles for analysis. Of a possible 332 two-min sections, 161 were of sufficient quality for further analysis. These sections were distributed throughout the 26 follows in different numbers (see Table 2). Of the 1,783 whistles identified, 954 (54%) were in these usable sections. The percentage of the total whistles in usable sections varied between follows from 0 to 100%. For 4 of the follows, no whistles were identified at any time during the whole follow. For 1 follow all identified whistles were in discarded sections. Of the whistles in usable sections, not all could be localized. In total, of the whistles in usable sections, 321 (34%) could be localized and 633 (66%) could not. This was variable between follows (mean percentage of localized whistles was 25%, range 0–100%).

In 20 out of the 26 follows used, other dolphin groups were observed within 100 m of the focal group. Figure 1 shows that whistle rates ascribed to dolphins will be incorrect if localization is not used. Several whistles were localized to dolphins outside of the focal group. All observations we have for this analysis were from cases in which other dolphins were within 100 m of our focal

group. We expected fewer whistles to be localized successfully if they came from groups further away because the signal to noise ratio is lower in distant whistles. Thus, the contribution of whistles from dolphins outside of our focal group is almost certainly higher than shown in Figure 1.

For all but 3 of the 161 usable sections, the focal group was engaged in one of four behavior types, surface travel, nonpolarized movement, socializing, or jumping/body slaps (see Table 1). For the remaining 3 sections, all animals were submerged for the entirety of the 2 min. Although many other behavior types were observed during the follows, many such as feeding or tail slapping were one-off events exhibited by only one individual, or occurred in sections that had to be excluded before further analysis. Additionally, only 2 sections contained jumping/body slaps, so at this stage this behavior was removed from the analysis due to small sample size.

The whistle rate for each of the four behavior types for localized whistles per 2-min section was variable across follows (see Table 2). In total, 14 of the follows consisted of usable sections of two or more of the behavior types. Twenty-three of the follows contained sections of surface travel, 13 contained sections of nonpolarized movement, and 5 contained sections of socializing. There were marked differences in the mean whistle rates across all follows for the three behavior types (Table 2, Figure 2), with surface travel exhibiting the lowest rate and nonpolarized movement the highest.

The results of the general linear model are shown in Table 3. There were significant differences in whistle rates across behavior types. The whistle rate during nonpolarized movement was significantly different to that during surface travel ($p < .001$), showing dolphins produce significantly higher whistle rates during nonpolarized movement. Similarly, significantly higher rates were observed during socializing ($p < .01$) than during surface travel.

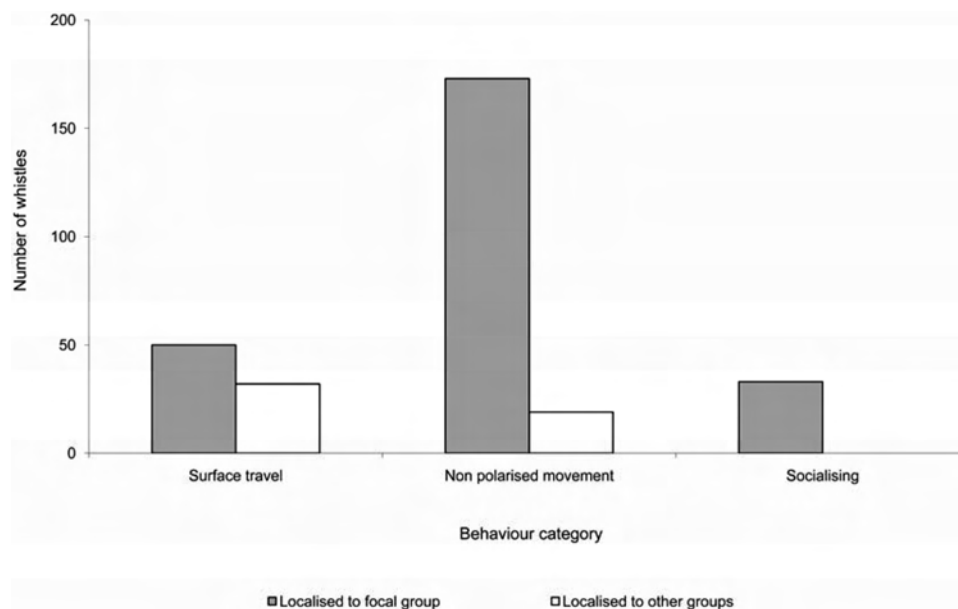


Figure 1. Number of whistles during different behavioral patterns that were localized to the focal and to other groups.

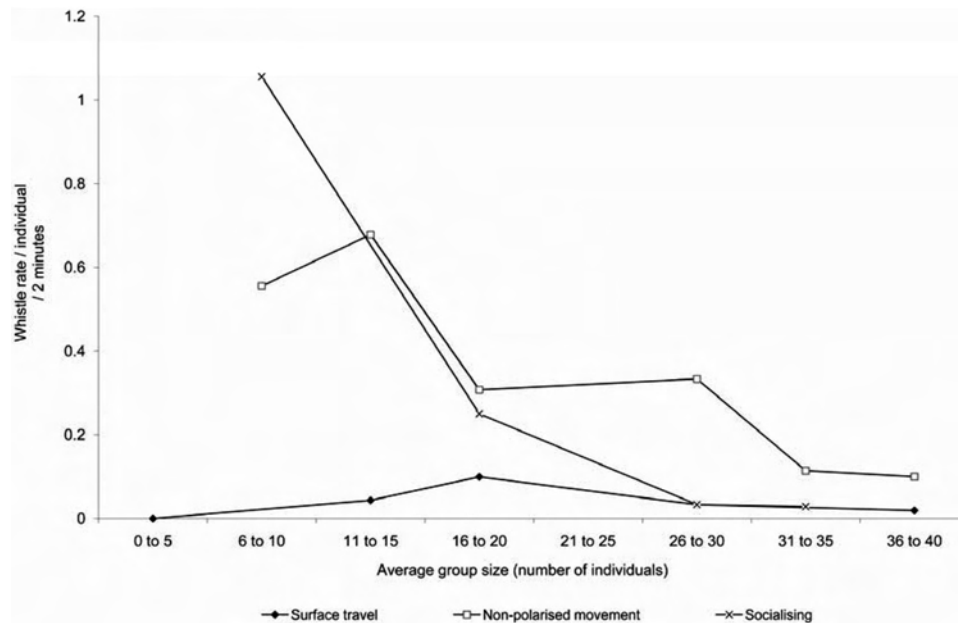


Figure 2. Individual whistle rates for each behavior type in relation to group size. Note that not all group sizes were found to perform all behavior patterns.

Group size did not have a significant effect on whistle rate in the GLM ($p = .793$). Because whistle rate was considered for the whole group in the model, this means that individual dolphins whistled less when group size increased (see Figure 2). For follows in which group size did not change and surface travel and either nonpolarized movement or socializing were seen within the follow, the whistle rate was higher during nonpolarized movement or socializing than during surface travel, confirming that individuals are producing more whistles during these activities. However, whistle rate decreased with increasing group size (see Table 3). Whistle rates for small traveling groups was almost zero. The whistle rate per individual is highest with group size categories up to 20 animals, when group sizes are bigger than this, the whistle rate per individual declines. Interactions between group size and behavior could not be tested with our data set due to a relatively small sample size in some categories.

Discussion

Whistle rates were affected by behavior patterns and group size. Previous studies have shown that whistle rates generally increase as

group sizes get larger (*Tursiops*: Cook et al., 2004; Jones & Sayigh, 2002; *Sousa*: Van Parijs, Smith & Corkeron, 2002). This is the case for group sizes of up to about 10 animals. In our study, we also encountered larger groups. We found that individual whistle rates decreased in groups of more than 15 individuals. This finding suggests that there is an upper limit of how many whistles can transmit information successfully at any one time. As whistle number increases potential masking by other whistles increases as well. It appears that dolphins try to avoid such masking as group sizes get larger. However, why would an individual decrease its whistle rates for the benefit of others? We think that this decrease is a by-product of individuals reacting to different noise conditions rather than an altruistic strategy. Despite decreased whistle rates, the noise caused by whistles is still high in large groups. Thus, it may be more economical for an individual to limit its vocal output to signals of high priority (e.g., group cohesion for a mother and calf) and use other signaling modalities to transmit information to animals nearby or wait for quieter conditions for other vocalizations.

We also found that whistle rates of wild bottlenose dolphins are dependent on the behavior type exhibited by the individuals within a

Table 3
Estimates and p Values From the General Linear Model for Comparisons of Whistle Rates Between Surface Travel and All Other Behaviors

	Estimate	SE	T value	Pr(> t)
Intercept	-1.8483	1.2085	-1.529	.13466
Behavior SOC	2.2319	0.7039	3.171	.00305*
Behavior NP	2.6674	0.5702	4.678	.00004*
I(log(Av.grp.size))	0.1106	0.4186	0.264	.79310

Note. SOC = socializing; NP = nonpolarized movement.

* $p < .05$.

group. Surface travel consistently showed the lowest whistle rate of all the behavior types both between follows and averaged across follows. Whistle rates during nonpolarized movement and socializing were significantly higher than the rates during surface travel. An increase in group size did not produce a significant linear effect on whistle rate across behavior patterns. Some individuals are therefore whistling at a higher rate during nonpolarized movement and socializing compared to when they are engaged in surface travel.

A direct comparison of whistle rates across studies is often difficult due to differences in methods, sample sizes, site characteristics, or dolphin behavior. For example, the only behavior we observed in groups of less than five dolphins was surface travel, although at other sites dolphins display all their behavior patterns in such small groups (Cook et al., 2004; Jones & Sayigh, 2002). This is an interesting finding in itself and suggests that the social structure at our site might be different. Our surface travel whistle rates in small group sizes of less than five animals are almost zero. This is similar to studies in Sarasota Bay, Florida, and Wilmington, North Carolina (Cook et al., 2004; Jones & Sayigh, 2002). Jones and Sayigh, however, found one site on the North Carolina coast off Southport in which bottlenose dolphins tended to have higher whistling rates overall. This was also reflected in a higher whistling rate during travel of one whistle per dolphin per minute. Buckstaff (2004) found that dolphins can double their whistling rates when additional boats approach. This was not a problem in our study because boat traffic was low but could explain higher rates at other sites.

In our study, whistle rates during socializing in groups of 6 to 10 animals was 0.53 whistles per minute per dolphin, for nonpolarized movement it was 0.27. Dolphins in Sarasota only whistled half as often in similar group sizes during these behavior patterns (Jones & Sayigh, 2002). In Wilmington, whistle rates during milling were the same as in Sarasota, but for socializing they were 0.7 to 1.1 whistles per minute per dolphin depending on the exact site. In Southport, nonpolarized movement whistling rates of 0.5 whistles per minute per dolphin were much higher than at all other sites including Scotland (Jones & Sayigh, 2002). The whistling rate during socializing, however, was similar to the one found in Scotland. Most data in Jones and Sayigh came from groups of less than 10 animals. Therefore, there is no comparison for the rates we reported from larger group sizes.

It appears that there is no simple explanation as to when dolphins whistle more or less at any particular site. There are many possible reasons for this. We would like to add a methodological one here. As demonstrated in our study, whistle rates can be overestimated if other dolphins are in the vicinity of the focal group. In our study, the distance between the focal and other groups never exceeded 100 m. However, dolphin whistles can travel long distances underwater (Janik, 2000). We suspect that incorrectly assigning whistles to the focal group is a more general problem that is also affected by dolphins much further away from a focal group. This is a significant problem if studies are conducted without using localization techniques.

In a relative comparison, our study supports similar findings from other studies of wild bottlenose dolphins that have also shown increased whistling rates during times of social behavior (Cook et al., 2004; Jones & Sayigh, 2002) and nonpolarized movement (Cook et al., 2004) when compared with surface travel. Increased whistle rates during nonpolarized movement may be due

to animals remaining in contact at a time when individuals are more random in their movements and are easily lost within the group, or they may be part of a transitional state preceding a behavioral change. Nonpolarized movement is commonly referred to as *milling* (Cook et al., 2004; Jones & Sayigh, 2002). This term is often used to refer to behavior during times when animals are not engaged in a defined behavioral context such as socializing or travel and as such its function is not completely clear. It is also likely that the behavior pattern termed *nonpolarized movement* here would have been classed as foraging in other studies because erratic movements or rushing behavior at the surface are often interpreted as foraging (Jones & Sayigh, 2002; Van Parijs & Corkeron, 2001). In this study, nonpolarized movement was the second most observed behavior after surface travel, but whether it is merely a less obvious form of what is often considered socializing is unclear. The main reason for only testing differences between surface travel and all other behavior types in this study was to discount subjective observer bias when splitting nonpolarized movement and socializing. At other field sites where animals are visible even when submerged, behavioral categories may be easier to define.

Increased whistle rates during socializing may be due to animals communicating information to social associates or using calls to maintain contact. According to our definition animals were socializing when they were within very close proximity, often rubbing body parts and touching (see definition in Table 1). Rates may be dependent on social bonds between the individuals present or may be a consequence of increased arousal due to contact with individuals and not be dependent on social relationships. Cook et al. (2004) showed higher signature whistle rates during socializing and suggest that this may function to maintain contact as other group members get more dispersed while individuals are engaged in socializing.

A similar pattern in the differences of call rates in other species that exhibit fission-fusion living has been shown. Spider monkeys emit a whinny call, thought to be used for maintaining contact, at an increased rate when another subgroup is within hearing range (Ramos-Fernández, 2005). In chimpanzees (*Pan troglodytes*), the rate of production of the pant hoot vocalization has been shown to be dependent on male rank and context. High ranking males exhibited a higher pant hoot call rate than low ranking males and pant hoot rate was highest before and after traveling behavior (Mitani & Nishida, 1993) suggesting the calls may help to maintain contact between conspecifics. In addition, males hooted significantly more often when their allies and associates were not in their immediate vicinity than when they were accompanying them (Mitani & Nishida, 1993). Generally, call rates appear to increase when animals are more dispersed. In dolphins, call rates decrease again if groups become larger, which counters masking effects. Such effects are more pronounced in dolphins most likely because sound travels further underwater than in terrestrial environments.

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Group Size and Social Interactions Are Associated With Calling Behavior in Carolina Chickadees (*Poecile carolinensis*)

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The complexity of a social group may influence the vocal behavior of group members. Recent evidence in Carolina chickadees, *Poecile carolinensis*, indicated that one component of social complexity, group size, influenced the complexity of the “chick-a-dee” call, a vocalization functioning in social cohesion. Individuals in larger social groups used calls with greater information than did individuals in smaller social groups. Here, the authors review this earlier work, and describe a recent study indicating that social interactions between females and males within female-male pairs of chickadees were associated with rates of chick-a-dee call production in the males. Together, these studies suggest that the nature and complexity of social interactions among members of chickadee social groups influence chick-a-dee calling behavior.

Keywords: social complexity, social interaction, chick-a-dee call, information, Carolina chickadee

Variation in the vocal signals of avian species can be influenced by sexual selection and by characteristics of the physical habitat (reviews in Catchpole & Slater, 1995; Kroodsma & Miller, 1982, 1996). It has become apparent that characteristics of the social group of which an individual is part can influence the vocal signals it uses (Catchpole & Slater, 1995; McGregor, 2005). This “social selection” pressure is an exciting hypothesis on which to frame tests of variation in vocal communication systems for at least two main reasons. First, within avian genera (or within species), different species (or populations) can vary substantially in patterns of social organization, thus providing for strong comparative tests. Second, recent hypotheses argue that, as the social complexity of a group increases, there is a need for individuals to have increased cognitive processing abilities (e.g., the Machiavellian Intelligence Hypothesis: Byrne & Whiten, 1988; Shettleworth, 1998). One extension of the Machiavellian Intelligence Hypothesis is that increased social complexity within animal groups demands greater communicative complexity—individuals in larger and more complex groups need to be able to produce a greater diversity of messages. Several studies have obtained comparative evidence

indicating that more complex social groups tend to have greater vocal complexity (e.g., Blumstein & Armitage, 1997; McComb & Semple, 2005). Recent experimental support for this idea has emerged in Carolina chickadees, *Poecile carolinensis* (Freeberg, 2006; described in more detail below), an avian species with a large vocal repertoire and complex social organization (Ekman, 1989; Mostrom, Curry, & Lohr, 2002).

One of the most commonly used vocalizations in the repertoire of chickadees is the “chick-a-dee” call. The chick-a-dee call of the avian genus *Poecile* is produced in a variety of social contexts related to group cohesion, as individuals move through their territories and may be out of visual contact with one another for periods of time (Ficken, Ficken, & Witkin, 1978; Hailman, 1989; Smith, 1991; Smith, 1972). The most extensive work on chick-a-dee call structure has been conducted with black-capped chickadees, *P. atricapillus*. The call in this species comprises four distinct note types (arbitrarily defined as A, B, C, and D notes) that may be produced a varied number of times within any given call and that follow a general A-B-C-D rule of note ordering (Charrier, Bloomfield, & Sturdy, 2004; Hailman, Ficken, & Ficken, 1985, 1987). The chick-a-dee call in Carolina chickadees, *P. carolinensis*, the focal species of the current studies, is structurally similar to that of black-capped chickadees, but appears to have a greater number of distinct note types (Bloomfield, Phillmore, Weisman, & Sturdy, 2005). The different note types can be present or absent in any given call and, if present, can occur more than once, following general rules of note ordering (Figure 1; Bloomfield et al., 2005; Lucas & Freeberg, 2007).

It has been suggested that chick-a-dee calls differing in note composition could convey different messages to receivers (Hailman & Ficken, 1986; Hailman et al., 1985). Studies are providing increasing evidence to support this suggestion. For example, in a study of captive black-capped chickadees, Templeton, Greene, and Davis (2005) found that when individuals detected smaller, quicker, and therefore more threatening avian predators, they called more and their calls had a greater number of D notes,

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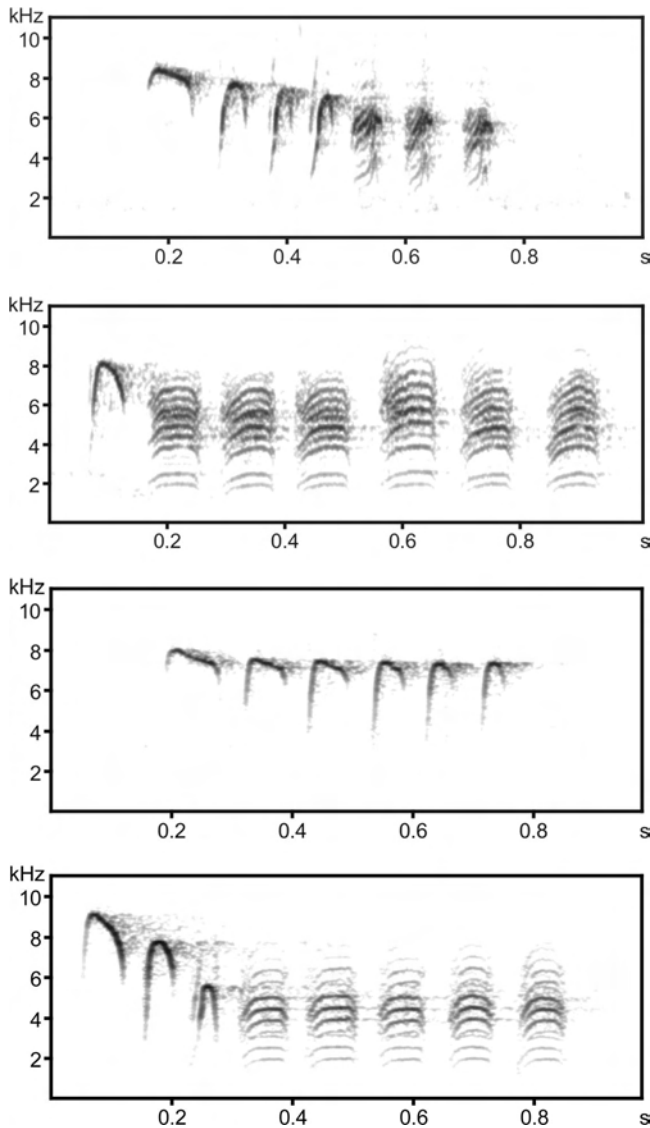


Figure 1. Sound spectrograms of chick-a-dee calls of Carolina chickadees, illustrating some of the diversity in note composition. In each panel, the Y-axis measures frequency (0–11 kHz) and the X-axis measures time (0–roughly 1 sec). Sound spectrograms were generated using Avisoft SASLab Pro with an FFT length of 512, frame 75%, and Blackman window.

compared to when individuals detected larger, less agile, and therefore less threatening avian predators. In addition, playbacks of chick-a-dee calls differing in numbers of D notes produced mobbing-like behavior in receivers that was predictive of predator size. Thus, calls differing in note composition may provide information about urgency or immediacy of threat (see also Baker & Becker, 2002). Further support for the notion that calls with different note composition may convey different messages has been obtained in Mexican chickadees, *P. sclateri* (Ficken, Hailman, & Hailman, 1994) and in Carolina chickadees, *P. carolinensis* (Freeberg & Lucas, 2002). These findings increasingly support the arguments of Hailman et al. (1985), that the structural rules

governing the way chick-a-dee calls are produced result in a call system that can transmit a very large amount of information (see also Lucas & Freeberg, 2007; Sturdy, Bloomfield, Charrier, & Lee, 2007).

Is this large amount of information in the chick-a-dee call somehow related to the fact that chickadees (and related species) have a complex social organization? Many of these species form overwintering flocks, often of unrelated individuals, that are fairly stable (Ekman, 1989). Flocks persist for months, and flock members jointly defend their territory from other flocks. Perhaps this social complexity has generated a need for greater vocal complexity, and part of that vocal complexity is packaged into the chick-a-dee call. Here, we provide two lines of evidence to suggest this may be the case.

The remainder of this article is broken into three parts. First, we briefly review the Freeberg (2006) study mentioned above. That study indicated that individuals in larger groups used more diverse calling behavior than individuals in smaller groups. However, the Freeberg study did not provide information on the nature of social interactions in the groups that were tested. We next describe a recent study conducted with 14 female-male pairs in captive laboratory settings that began to address social interactions. In this study, we asked whether close spatial associations between the female and male of a pair, which provide a context for close-proximity interactions between those two individuals, were associated with rates of calling in the males of these pairs. If so, it would suggest that not only call structure, but also call use, may be influenced by the nature of interactions among chickadees in stable social groups. The final part of the article briefly raises some questions that we need to answer in chickadees, as well as in other species, to determine the ways in which social interactions within stable social groups may developmentally and evolutionarily constrain the structure and complexity of vocal signals of group members.

Group Size Influences Vocal Complexity: A Review

Freeberg (2006) addressed the question of a relationship between group size and chick-a-dee call complexity in two studies. The first study was conducted with nonmanipulated groups of chickadees in field settings in the winter and early spring of 2003. The second study took an experimental approach, in which a number of individuals were manipulated in captive groups of chickadees tested from Fall 2004 through Spring 2005. Both studies are described briefly here; see Freeberg (2006) for more detail.

In the first study, chickadees (*Poecile carolinensis*) were recorded at 30 different sites. Each recording site was at least 400 m from the next closest site. This distance helped ensure that birds from different sites were from different flocks. Recording involved approaching a group of chickadees to roughly 10–20 m to obtain high-quality calls, but also to avoid disrupting normal behavior patterns. At the time of recording, Freeberg noted the total number of individuals observable within a 10 m × 10 m recording space. Sites were classified into “small groups” (19 sites) if most of the calls from the site were recorded when only one or two birds were in that recording space; and “large groups” (11 sites) if most of the calls from the site were recorded when three or more birds were in that recording space.

Over 4100 calls were obtained ($M = 138.4$ calls/site; range = 58 – 272). Notes of calls were classified according to the nine note categories published for the species by Bloomfield et al. (2005). Freeberg analyzed the note compositions of all the calls for each site using the UNCERT program (written by E.D. Hailman and J. P. Hailman; Hailman et al., 1985). UNCERT generated uncertainty measures (bits of information) for the set of calls for each site. Here we report data on first-order uncertainty (U_1), which is calculated as $U_1 = -\sum [P_{ij} \log_2 (P_{j|i})]$, where P_{ij} is the probability of the i and j note occurring in the ij sequence, and $P_{j|i}$ is the conditional probability of the j unit occurring given that the i unit has occurred. U_1 therefore assesses the uncertainty in these calls due to the transitional probabilities between ordered pairs of notes. Maximum first-order uncertainty would occur in a call system in which all note types were equally likely to follow one another. (In the case of a call system with eight units, such as the chick-a-dee call of Carolina chickadees, maximum uncertainty would be 3.0 bits of information. Typically U_1 in nonhuman animal vocal signals is much lower than the maximum possible uncertainty, as the presence of one unit is often highly predictive of the next unit in a signal.) Greater uncertainty represents greater diversity of note compositions and of *potential* messages in calls being produced by the birds.

Calls obtained from birds at the “large group” sites had greater uncertainty (greater complexity) than calls obtained from birds at the “small group” sites. See Figure 2a; mean \pm SD of 0.81 ± 0.20 bits for “large group” calls and 0.62 ± 0.17 bits for “small group” calls; $F(1, 28) = 7.15$, $p = .012$. These uncertainty measures were not correlated with the number of calls obtained at each site (Spearman rank-order correlation, $N = 30$, $r_s = .121$, $p = .526$). Calls recorded in “large groups” did not differ from calls recorded in “small groups” in terms of the number of calls recorded, $F(1, 28) = 0.252$, $p = .620$, or the average number of notes per call, $F(1, 28) = 0.088$, $p = .769$.

The first study suggested that when birds interact in larger groups, they tend to use chick-a-dee calls with greater diversity of note compositions, compared to birds producing calls by themselves or when they are interacting closely with only one other individual. The findings of this first study suggest a potential relationship between group size and call complexity, but no causal inference could be made. In the second study, conducted in outdoor aviaries, Freeberg (2006) manipulated group size to determine its effect on the complexity of calls used by individuals interacting in these groups.

Typical Carolina chickadee flock sizes are roughly 3 – 5 birds (range 2 – 8; reviewed in Mostrom et al., 2002). Freeberg established groups that spanned these flock sizes in two large aviaries (6 m \times 9 m \times 3.5 m). Groups of size 2, 4, and 6 were generated at different times from late fall of 2004 through early spring of 2005. Each group was made up of chickadees captured from the same site and closely in time on the same day. Due to the stability and territoriality of chickadee flocks, this capture method helps ensure that each group comprised individuals from the same flock (Mostrom et al., 2002). Sex of individuals was balanced as much as possible within each group, to mimic the 1:1 ratio of females and males in natural flocks (Mostrom et al., 2002). Sex was determined based on wing chord measurements: birds with wing chords ≤ 60 mm were classified as females, and birds with wing chords ≥ 62 mm were classified as males (based on Thirakhuat,

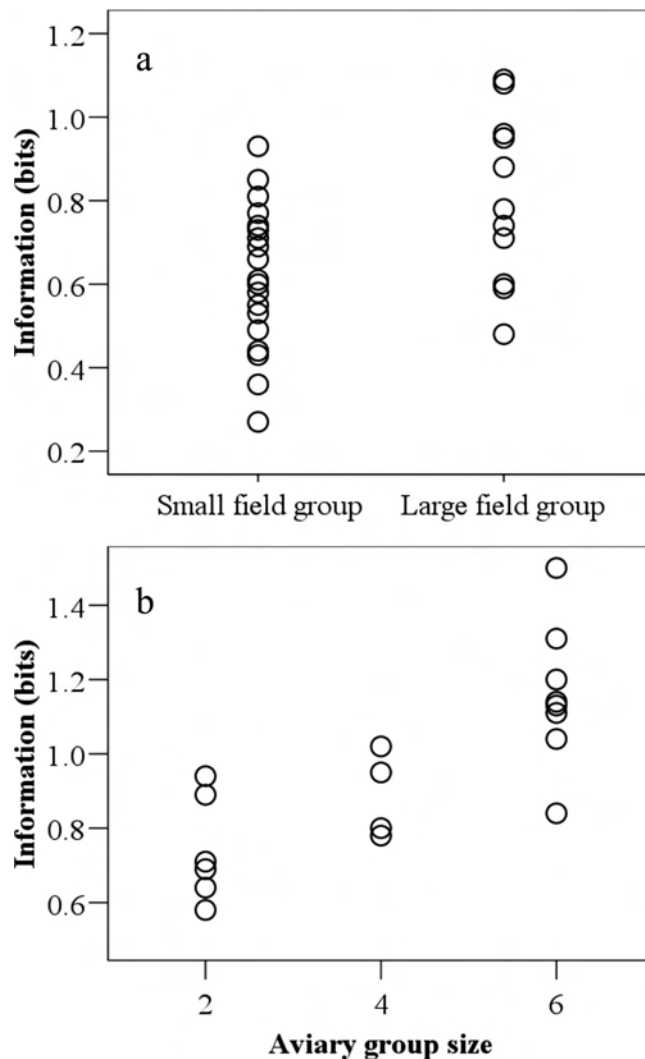


Figure 2. Information in chick-a-dee calls of birds of different group sizes; redrawn from Freeberg (2006). A. Each circle represents the uncertainty value of calls produced at a single site, with sites classified as either “small groups” or “large groups.” B. Each circle represents the uncertainty value for the calls of each individual in the three different group sizes. The measure of complexity here is First-Order Uncertainty, which represents the uncertainty associated with transition probabilities between consecutive pairs of notes in a call. As this measure of uncertainty increases, calls have greater diversity of note pairings. Some birds in the aviary study did not produce enough calls to be included in the analysis, thus were not plotted.

1985). Birds were uniquely color-banded to permit individual identification in the aviaries. After being placed into the aviaries, birds in the different groups were given roughly 3 weeks to acclimate to their new setting and social context, and then were recorded.

Over 1300 calls were obtained ($M = 73.4$ calls/individual; range = 10 – 248). As described above, notes of calls of each individual were classified according to the note categories of Bloomfield et al. (2005). The note compositions of the call set for each individual were analyzed using UNCERT, such that each individual had its own uncertainty measure that went into the

statistical analyses. As in the field study reviewed above, group size had a significant effect on call complexity. In the aviaries, individuals placed into larger groups were using calls with greater uncertainty than birds placed into smaller groups. See Figure 2b; mean \pm SD of 1.16 ± 0.19 bits for calls of birds of group size 6, 0.89 ± 0.12 bits for calls of birds of group size 4, and 0.74 ± 0.14 bits for calls of birds of group size 2; $F(2, 15) = 11.61$, $p = .001$. These uncertainty measures were not correlated with the number of calls obtained from each bird (Spearman rank-order correlation, $N = 18$, $r_s = -.027$, $p = .916$).

Findings from Freeberg (2006) indicated that birds in larger groups were using calls with more complexity than birds in smaller groups, in both nonmanipulated field settings and in experimental captive settings. Group size is one of the major components of social complexity (though there are other important considerations, as described further below). Larger groups, simply by having greater numbers of individuals, provide for the possibility of more diversity and complexity of social interactions among their members, relative to smaller groups. The Freeberg study did not collect information on actual interactions among members of a group; therefore, the relationship between social interactions and calling behavior could not be determined. We began to address this question with a study of the most basic social group in chickadees: a female-male pair.

Social Associations Correlate With Chick-a-dee Call Production

For this next study, 28 wild-caught adult male ($N = 14$) and female ($N = 14$) Carolina chickadees (*Poecile carolinensis*) were captured from one of two locations in eastern Tennessee. The study was conducted over a 2-year period, during the overwintering months when chickadees normally reside in flocks (six pairs tested between fall of 2004 and spring of 2005 and eight pairs tested between winter of 2005 and spring of 2006). One female and one male chickadee from a particular site were captured together at one of these locations. Just as in the Freeberg (2006) study reviewed above, female-male pairs were captured from the same site and closely in time on the same day, and so very likely were members of the same flock, if not actual mating pairs. In total, we had 14 female-male pairs. At time of capture, we uniquely color-banded birds for individual identification and measured their wing chords (mm) to determine sex.

In the laboratory, female-male pairs were housed in MED-Associates Large Monkey Cubicles; different pairs were isolated from one another. Cages ($0.5 \text{ m} \times 0.5 \text{ m} \times 1 \text{ m}$) within these cubicles were supplied with three natural perches (two near the top of the cage and one near the floor of the cage). Daily maintenance included providing the chickadees with ad libitum food (an equal mixture of black oil sunflower and safflower seeds, crumbled suet, and grit with crushed oyster shell). Fresh Bronx Zoo diet for omnivorous birds mixed with sprouted seed, chopped fresh fruit and vegetables, and 3–4 mealworms were supplied daily. Fresh vitaminized water was also given to the pairs on a daily basis. The lights were maintained on a light:dark cycle that was changed weekly to match sunrise/sunset times of the local environment.

After capture and transport to the laboratory, all pairs were provided with a 3-week acclimation period, allowing the birds to adjust to the new surroundings. After this acclimation period, we

observed the birds for two weeks. During this 2-week period, we focal sampled each male with its cage mate for eight 15-min observation sessions. During observations, the researcher sat in front of the chamber with the door closed in a darkened laboratory room. Observations began at least 30 min after the chamber lights automatically turned on in the morning and were completed by 1400 hours. The primary measures collected for the purposes of this study were instances of perching close (female and male situated within 15 cm of one another for at least 2 sec), supplants (an agonistic behavior between two individuals in which one bird, usually arriving via flight, takes the spot on a perch occupied by the other bird, causing the other bird to leave), and numbers of chick-a-dee calls produced (for more detail see Harvey & Freeberg, 2007).

We found that males who displayed greater rates of perching close to their female flockmates also produced higher rates of chick-a-dee calling (Figure 3; Spearman rank-order correlation, $N = 14$, $r_s = .641$, $p = .014$). Calling behavior did not occur systematically with close perching behavior during the sampling (perching close to a female did not automatically result in directing a chick-a-dee call to a female, or vice versa), however. Supplants were negatively correlated with rates of chick-a-dee calling, though the correlation was not statistically significant (Spearman rank-order correlation, $N = 14$, $r_s = -.336$, $p = .241$). These results indicate a relationship between extent of perching close with a female flockmate (which likely provides an important context for close-proximity social interaction) and extent of vocal signaling by these males. Although we must be cautious in extrapolating from the dyadic interactions here to the more complex social relationships in flocks, the results suggest that production of chick-a-dee calls, an important mechanism of social cohesion in flocks (Ficken et al., 1978), may be linked to the nature of the signaler's social relationships.

General Discussion

The two sets of studies point to the important role the chickadee social group can play on the vocal signals used by group members.

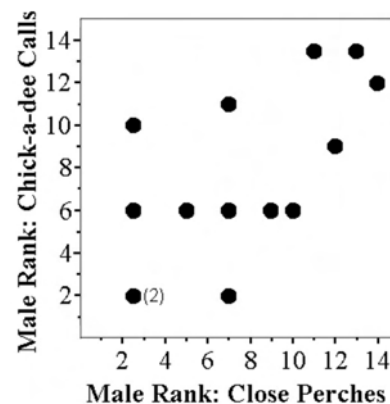


Figure 3. Association between ranks for close perching and ranks for chick-a-dee call production for the 14 males housed individually with females from their social flock. Each point represents an individual male. The (2) near the lower left hand point in the graph refers to two males who had scores of 0.0 times perched close to their respective female social companion and 0.0 chick-a-dee calls produced.

First, the Freeberg (2006) study we reviewed indicated that group size can influence the complexity (diversity of note compositions, and potentially of messages) of chick-a-dee calls produced by Carolina chickadees. Birds in larger groups produced calls with greater complexity. One potential explanation for this is that the manipulation of group size affected the frequency of social interactions and the overall group behavior, and as group size increased individuals needed to be able to produce a greater number of different messages with their chick-a-dee calls. Second, the study focusing on female-male pairs of chickadees found a positive correlation between rates of close associations between the female and male of a pair and rates of chick-a-dee call production by the male of the pair. Although not entirely surprising, given the general social function of the chick-a-dee call, this latter finding is important in that it is our first evidence in this species to suggest that social interactions are associated with the chick-a-dee call. Ongoing work in our laboratory is testing this association in larger social groups.

Understanding how the nature of social groups may influence the complexity of vocal signals used by group members has been an aim of recent comparative research efforts. For example, Wilkinson (2003) compared eight bat species and found that information in the isolation calls of infant bats was greater for species occurring in larger rather than smaller colonies. Presumably these species differences stem from an increased need for individual distinctiveness in infant isolation calls for species residing in larger colonies—greater information in these calls stems from greater variation in acoustic features across infant bats. McComb and Semple (2005) found that vocal repertoire size was strongly associated with group size in a large comparative study of nonhuman primates: species having groups with greater numbers of individuals had larger vocal repertoires than did species in which group sizes were smaller. In the first explicit test of a relationship between social complexity and vocal complexity, Blumstein and Armitage (1997) found evidence for such a relationship in ground-dwelling sciurid species: groups of marmot and squirrel species utilizing more unique social roles had a greater number of distinct alarm calls in their vocal repertoires, relative to species with groups having fewer social roles. The studies done to date have provided strong comparative evidence in support of the hypothesis of social complexity driving vocal complexity.

The studies described in the previous paragraph took evolutionary approaches to address the relationship between social and vocal complexity. The Freeberg (2006) study reviewed above took a developmental approach and provided experimental evidence for social complexity playing a causal role in vocal complexity in chickadees. The social organization of chickadees and related species offers a strong system to test questions of both proximate and ultimate causation in vocal complexity—similar arguments could be made for other avian groups with complex social structures, such as the corvids (Marzluff & Angell, 2005), jays (Dahlin, Balda, & Slobodchikoff, 2005; Hopp, Jablonski, & Brown, 2001), and parrots (Farabaugh & Dooling, 1996; Wright & Wilkinson, 2001). Features of the social group in chickadees have an influence on fitness of group members (Ratcliffe, Mennill, & Schubert, 2007; Smith, 1991), and will also serve as an important learning environment for members of the group, perhaps particularly for young birds joining a flock for the first time. Increased focus on the dynamics of social interaction between members of stable

groups would increase our ability to understand how social groups may constrain the vocal behavior of groups members (see King, West, & White, 2002; Miller, Freed-Brown, White, King, & West, 2006; see also Snowdon & Hausberger, 1997). Future work in our laboratory will aim to integrate proximate and ultimate approaches to understand the causal links between social and vocal complexity.

Much of the work that has been done to test the potential relationship between social and vocal complexity has relied on group size as the measure of social complexity. The Blumstein and Armitage (1997) study described above used a different measure of social complexity—the number of social roles in a group—raising an important point for future work on this question. Groups with a greater number of social roles (e.g., a species in which groups comprise reproductive females, reproductive males, adult nonreproductive males, adult nonreproductive females, juveniles, infants) are very likely to have a greater diversity of social relationships and social interactions than groups with a smaller number of social roles (e.g., a species in which groups comprise a reproductive female, a reproductive male, and their current set of offspring). Following from this approach, we believe increased effort should be devoted to assessing the nature and complexity of social interactions in groups to understand social pressures on vocal behavior better. We have taken the first step in this direction with chickadees, by demonstrating that a measure of social interaction—close spatial associations between two chickadees—correlates positively with rates of chick-a-dee call production.

In studying the complexity of social groups, we note that characteristics of specific individuals within a group have the potential to affect the dynamics of the larger group (Sih & Watters, 2005). For example, groups with a large proportion of “bold” individuals likely represent very different social structures than groups composed of a large proportion of “shy” individuals (Coleman & Wilson, 1998; Sih, Bell, Johnson, & Ziemba, 2004). We argue, then, that future research on social complexity and its possible link to communicative complexity should address the behavioral profiles of members within the groups of study. For example, Akert and Panter (1988) found that humans classified as extraverts (by standard psychological assessments of personality) were better able to interpret nonverbal communication of two people conversing than were humans classified as introverts. Akert and Panter argue that extraverts engage in a higher frequency of social interaction than introverts, and frequency of social interactions is directly related to an individual’s ability to signal efficiently and respond effectively to signals from group members (see also Lieberman & Rosenthal, 2001; Mehrabian & Diamond, 1971; Patterson, 1995; Wiener, Devoe, Rubinow, & Geller, 1972). Lieberman and Rosenthal argue that extraverts do not hold a general advantage over introverts regarding signal decoding, but are better able to do so in contexts of multitasking, when many different kinds of information need to be processed simultaneously. This argument would seem of relevance to nonhuman animals engaged in communicative interactions while also needing to be able to detect key environmental stimuli (e.g., predators) and solve other problems facing them. In short, we believe greater focus on these “personality” influences in nonhuman animal groups would aid our understanding of how characteristics of groups may influence communication in group members.

Finally, we wish to begin to address the basic question of why the complexity of a social group might influence the complexity of vocal signals used by group members. Potential answers to this question will depend largely on the specific natural history of a given species. Here, we offer two potential explanations that are in good accordance with the natural social structures and problems faced by chickadees and related species. The first, a more individual-centered view, stems from the Assessment/Management approach to vocal communication put forward by Owings and Morton (1998). Put simply, to be successful, individuals need to regulate the behavior of others in their environments, and a primary way many species do this behavioral regulation is with vocal signals. Thus, a first potential answer to our question is that an individual in a larger group, that has to manage successfully and efficiently the behavior of members of its group, may need a greater variety of vocal signals in its repertoire to do so, compared to an individual in a smaller group with a smaller number of individuals to manage. The second, a more group-centered view, stems from the idea that larger groups often provide substantial benefits to group members (Krause & Ruxton, 2002; Wilson, 1975). To be successful, a larger group may need to solve more problems (maintaining group cohesion when finding food, defending food, detecting predators, deterring predators, exploiting other necessary resources, etc.), compared to smaller groups or to solitary individuals. Vocal communication provides one mechanism for this sort of problem solving faced by larger groups (Bradbury & Vehrencamp, 1998; Maynard Smith & Harper, 2003). To communicate effectively about more stimuli in the environment and about group responses to those stimuli, members of a larger group may require a greater diversity of vocal signals than members of a smaller group.

Much more work is needed to test these hypotheses, and clearly there are other hypotheses regarding the potential links between social and vocal complexity. For example, if individual distinctiveness in vocal behavior is important and groups are large, there should be strong selection pressure for substantial amounts of acoustic diversity across individuals, as seen in the Wilkinson (2003) study with bat species varying in colony size. We believe that testing these potential links is an important topic for future research, as it points to a potentially powerful explanation for vocal diversity across groups of related species, and how that diversity may also help explain other social behavior (e.g., McComb & Semple, 2005). Furthermore, the notion that greater social complexity may cause greater vocal complexity is at the heart of recent arguments about the origins of language in our own species (Dunbar, 1996, 2003; Pinker, 2003), so increased efforts at understanding these social—vocal complexity links may also help inform theories of language evolution.

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Convergence of Calls as Animals Form Social Bonds, Active Compensation for Noisy Communication Channels, and the Evolution of Vocal Learning in Mammals

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The classic evidence for vocal production learning involves imitation of novel, often anthropogenic sounds. Among mammals, this has been reported for dolphins, elephants, harbor seals, and humans. A broader taxonomic distribution has been reported for vocal convergence, where the acoustic properties of calls from different individuals converge when they are housed together in captivity or form social bonds in the wild. Vocal convergence has been demonstrated for animals as diverse as songbirds, parakeets, hummingbirds, bats, elephants, cetaceans, and primates. For most species, call convergence is thought to reflect a group-distinctive identifier, with shared calls reflecting and strengthening social bonds. A ubiquitous function for vocal production learning that is starting to receive attention involves modifying signals to improve communication in a noisy channel. Pooling data on vocal imitation, vocal convergence, and compensation for noise suggests a wider taxonomic distribution of vocal production learning among mammals than has been generally appreciated. The wide taxonomic distribution of this evidence for vocal production learning suggests that perhaps more of the neural underpinnings for vocal production learning are in place in mammals than is usually recognized.

Keywords: vocal learning, vocal production learning, vocal convergence, noise compensation

The ability to modify the acoustic structure of a vocalization based on auditory input is called vocal production learning. Janik and Slater (1997, 2000) distinguish the ability to produce sounds that are similar or different from an acoustic model from contextual learning, in which an existing signal is used in a different context as a result of experience with how other individuals use the signal. A key distinction involves whether animals simply learn new contexts for the use of existing signals or whether they actually modify the acoustic properties of the sounds they produce to be more or less similar to sounds they hear. The best evidence for production learning has involved imitation of novel sounds, but evidence for this is limited, especially for mammals (see Table 1). Attempts to use geographic variation in signals has proven to be a problematic source of evidence for production learning, especially if such studies do not include detailed study of effects of the social and acoustic environment. Here I argue that growing evidence for vocal convergence as animals form groups suggests that vocal production learning may have broader taxonomic distribution than suggested by vocal imitation (see Table 1). But proving that convergence is true production learning requires careful quantitative analysis of acoustic features of calls before and after exposure.

The best data on production learning in nonhuman animals comes from the oscine songbirds (Catchpole & Slater, 1995; Kroodsma, 1982; Kroodsma & Miller, 1996). Evidence for pro-

duction learning in birds is strongest for males learning bird song. Once a male hatches, he listens to songs and forms memory traces of the songs that are closest to an inherited sensory template. Sometimes after a seasonal delay, he will produce a variety of sounds, slowly narrowing his song production to match those he has heard. Some songbirds have a song repertoire limited to this early period; others continue to learn new songs as adults. One of the classic methods to study the role of auditory input on vocal production is to raise animals in isolation. For many songbird species, if a male is raised in isolation or is deafened, his vocal production differs dramatically from birds with normal auditory input. This suggests that songbirds must compare auditory input to their vocal production in order to learn how to match their memory. Among birds, there is also evidence for vocal production learning in parrots and their relatives in the order Psittaciformes (Farabaugh et al., 1992; Todt, 1975) and hummingbirds of the order Micropodiformes (Baptista & Schuchmann, 1990).

Evidence for vocal production learning in mammals is much more limited than for birds. Janik and Slater (1997) conclude that evidence for imitation of new sounds is limited to humans and marine mammals. The dearth of evidence for production learning among nonhuman primates is something of a surprise, given the highly developed imitative skills of humans and given the profound impacts that deprivation from hearing speech has on vocal development in humans. For example, Hammerschmidt, Newman, Champoux, and Suomi (2000) reared rhesus macaques (*Macaca mulatta*) in two conditions: a) with their mothers or b) separated from their mothers at birth and housed with other infants. They report high variation within each individual in acoustic structure of calls during the 5-month period of study. There were some age-related changes in structure of all call types studied, but isolation

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Table 1

Summary of Species and References for Which Each Type of Vocal Production Learning Has Been Documented in Birds or Mammals

Type of vocal production learning	Species	Reference
1 Production of call similar to model		
1.1 Imitation of sound not in species typical repertoire		
1.1.1 Sounds used for communication	Oscine songbirds	Kroodtsma, 1982
	Parrots and relatives (Psittaciformes)	Todt, 1975
	African elephant	Poole et al., 2005
	<i>Loxodonta africana</i>	
	Asian elephant	Holden, 2006
	<i>Elephas maximus indicus</i>	
	Harbor seal, <i>Phoca vitulina</i>	Ralls et al., 1985
	Bottlenose dolphin	Richards et al., 1984
	<i>Tursiops truncatus</i>	
	Killer whale, <i>Orcinus orca</i>	Foote et al., 2006
	?	?
1.1.2 Sounds used for echolocation		
1.2 Copying of conspecific acoustic model is part of normal vocal development		
1.2.1 Sounds used for communication	Oscine songbirds	Catchpole and Slater, 1995
	Parrots and relatives (Psittaciformes)	Kroodtsma and Miller, 1996
	Anna hummingbird	Farabaugh et al., 1992
	<i>Calypte anna</i>	Baptista and Schuchmann, 1990
	Bottlenose dolphin	Sayigh et al., 1990
	<i>Tursiops truncatus</i>	Fripp et al., 2004
	Humpback whale	Payne et al., 1983
	<i>Megaptera novaeangliae</i>	Noad et al., 2003
	Greater Horseshoe bat	Jones and Ransome, 1993
	<i>Rhinolophus ferrumequinum</i>	
1.2.2 Sounds used for echolocation		
1.3 Vocal convergence of conspecific sounds		
1.3.1 Sounds used for communication	Anna hummingbird	Baptista and Schuchmann, 1990
	<i>Calypte anna</i>	
	Black-capped chickadee	Mammen and Nowicki, 1981
	<i>Parus atricapillus</i>	
	Budgerigar	Farabaugh et al., 1994
	<i>Melopsittacus undulatus</i>	Hile & Striedter, 2000
	Australian magpie	Brown et al., 1991
	<i>Gymnorhina tibicen</i>	
	Greater spear-nosed bat	Boughman, 1997
	<i>Phyllostomus hastatus</i>	Boughman, 1998
	African elephant	Poole et al., 2005
	<i>Loxodonta africana</i>	
	Pygmy marmoset	Elowson & Snowdon, 1994
	<i>Cebuella pygmaea</i>	Snowdon & Elowson, 1999
	Cotton-top tamarin	Weiss et al., 2001
	<i>Saguinus oedipus</i>	Egnor & Hauser, 2004
	Chimpanzee	Mitani & Gros-Louis, 1998
	<i>Pan troglodytes</i>	Marshall et al., 1999
		Crockford et al., 2004
	Bottlenose dolphin	Smolker & Pepper, 1999
	<i>Tursiops truncatus</i>	Watwood et al., 2004
2 Production of call different from model		
2.1 Development of individually distinctive signal	?	?
2.2 Shifting call frequency out of noise band		
2.2.1 Sounds used for communication	Great tit, <i>Parus major</i>	Slabbekoorn & Peet, 2003
	Beluga whale	Lesage et al., 1999
	<i>Delphinapterus leucas</i>	
2.2.2 Sounds used for echolocation	Greater horseshoe bat	Schnitzler, 1973
	<i>Rhinolophus ferrumequinum</i>	Trappe & Schnitzler, 1982
	European free-tailed bat	Ulanovsky et al., 2004
	<i>Tadarida teniotis</i>	

from adults did not appear to affect these changes; variation in weight explained variation in all but one acoustic parameter for macaque coo calls.

Rearing in isolation from conspecific adults could interfere with so many general developmental processes that some have studied the effects of deafening to study how lack of auditory input alone may affect vocal production. Talmadge-Riggs, Winter, Ploog, and Mayer (1972) found no differences in calls of normal versus deafened adult squirrel monkeys (*Saimiri sciureus*), suggesting that auditory feedback is not required for normal vocalization in this species. Winter, Hardley, Ploog, and Schott (1973) reported no differences in acoustic parameters for calls of one deafened squirrel monkey that had been reared in isolation compared to normal monkeys. Hammerschmidt, Freudenstein, and Jürgens (2001) extended the earlier study of Winter et al. (1973) by rearing squirrel monkeys in three conditions: normal, raised with a mother who could not call, and congenitally deaf. For all 12 call types studied, they found age-related changes in one or more acoustic parameters. There was a high level of variability in calls throughout the 20 month study, and the calls of both animals deprived of hearing adult calls fell within the range of calls produced by normally raised monkeys. This suggests that auditory input had little effect on call production, and that age-related variation in calls seemed to be primarily caused by physical growth.

Vocal Imitation

Perhaps the most direct evidence for production learning involves animals that can imitate unusual signals, such as when parrots imitate human speech. This kind of evidence for imitation is well documented for several avian taxa, including oscine songbirds and parrots and their relatives in the order Psittaciformes. However, attempts to train nonhuman primates to imitate speech have provided primarily negative evidence (Hayes, 1951; Hayes & Hayes, 1952). Among other mammals, there is a case of a harbor seal (*Phoca vitulina*; Ralls, Fiorelli, & Gish, 1985) and an Indian elephant (*Elephas maximus indicus*; Holden, 2006) imitating speech. African elephants (*Loxodonta africana*) have also been reported to imitate the sounds of a truck or of Asian elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005). Bottlenose dolphins (*Tursiops truncatus*) have also proven skilled at imitating synthetic computer-generated frequency modulation patterns (Richards, Wolz, & Herman, 1984). Foote et al. (2006) report that killer whales (*Orcinus orca*) imitated the barks of California sea lions (*Zalophus californianus*). In general, when animals can be shown to produce precise imitations of sounds that are not part of the normal repertoire of their species, that provides solid evidence that auditory input is influencing vocal output. Such evidence is limited to very few mammalian species.

Janik and Slater (2000) point out the difficulty in demonstrating vocal production learning unless the subject produces a novel vocalization. When a bird, elephant, or a seal precisely imitates human speech, the evidence is quite strong. When an animal makes slight modifications to an existing sound, the case may be less clear. However, if we only accept as evidence for vocal production learning, cases where animals can be raised in artificial settings and tested for their ability to imitate arbitrary anthropogenic signals, we may err on the side of not understanding all of the taxa that may be capable of production learning.

Production of Calls That Differ From an Auditory Model

Most work on production learning has focused on evidence that animals learn to produce vocalizations that match an auditory model, but several problems might select for learning to produce a sound that diverges from a model. For example, if vocal learning were used to facilitate the development of individually distinctive vocal signatures, animals might learn to produce signals that differed from those it heard (Tyack, 1997). However, Fripp et al. (2004) suggest that dolphins develop signature whistles that are distinctive with respect to their common associates by imitating the whistles of a member of the population with whom they associate rarely. Another reason to produce a sound that differs from auditory input involves shifting the frequency of a call outside of a noise band. Slabbekoorn and Peet (2003) have shown that great tits (*Parus major*) increase the frequency of their songs when in urban noise, which emphasizes low frequencies. Lesage, Barrette, Kingsley, & Sjare (1999) report a similar increase in the frequency of calls of beluga whales in the presence of low-frequency vessel noise. This kind of frequency shift has been described before in the context of Doppler compensation (Schnitzler, 1973; Trappe & Schnitzler, 1982) or jamming avoidance (e.g., Ulanovsky, Fenton, Asaf Tsoar, & Korine, 2004) in bats, but this well-known phenomenon has not typically been considered in discussions of vocal production learning. This lapse may stem from the tendency of those interested in vocal production learning to focus on development of communication signals rather than shorter term accommodation of calls, especially those used for functions other than communication. However, the problem of communicating in noise is ubiquitous and should not be ignored in discussions of vocal production learning.

Use of Vocal Production Learning to Compensate for Varying Noise

Some of the solutions to the problem of communication in varying noise, which is faced by all animals with sensitive hearing, may also involve vocal learning mechanisms. There has been growing awareness that animals may have evolved mechanisms to compensate for varying ambient noise. Potential mechanisms for increasing the detectability of signals include waiting to call until noise decreases, increasing the rate of calling, increasing signal intensity, increasing the signal duration, and shifting the frequency of a signal outside of the noise band. Even though the first two of these mechanisms indicate that auditory input modifies vocal behavior, they do not involve production learning by the definition of Janik and Slater (1997, 2000) because they do not involve novel vocalizations, but the last one, involving a shift in frequency out of the band of an auditory model, certainly does. Whether increasing the level or the duration of a signal in response to increased level or duration of noise represents vocal production learning is debatable. Janik and Slater (1997, 2000) suggest that there may be several different levels of complexity in production learning. They suggest that changes in the amplitude or duration of a signal may stem from relatively simple changes in the state of muscles of the respiratory system. By contrast, they suggest that changing frequency parameters of a signal may require more complex changes of the sound production apparatus, including the acoustic source and filters in the vocal tract. The ability of animals to shift the

frequency of a call out of a noise band mentioned in the last section clearly qualifies as a complex form of vocal production learning as defined by Janik and Slater (1997, 2000). By this standard, changes in the amplitude or duration of a signal represent vocal production learning, but of a simpler sort than shifting frequency. Responding to noise by increasing the intensity of signaling is well known in humans as the Lombard effect. It has been demonstrated in nightingales (*Luscinia megarhynchos*) in response to traffic noise by Brumm (2004) and in beluga whales (*Delphinapterus leucas*) in response to shipping noise by Scheifele et al. (2005). Foote, Osborne, and Hoelzel (2004) have shown that killer whales (*Orcinus orca*) increase the length of their calls in the presence of more vessels. They did not measure noise directly, but they assume that the increase in number of vessels increased vessel noise. These mechanisms that modify vocal behavior to compensate for varying noise may be an important function of vocal production learning and of simpler versions of modifying vocal output based on auditory input, such as increasing calling rate when noise is elevated or waiting to call until noise has declined. These mechanisms for timing calls with respect to interfering noise are well developed in anurans (Zelick & Narins, 1983), as well as birds (Brumm, 2006) and mammals (Egnor, Wickelgren, & Hauser, 2007). I believe that the role of noise compensation mechanisms in the evolution of vocal learning may have been underestimated.

Geographical and Temporal Variation in Calls

One indirect method to look for evidence of production learning involves studying temporal and geographical variation of calls. For example, the songs of the humpback whale (*Megaptera novaeangliae*) differ across different ocean regions (Winn et al., 1981), and within a population all of the singing males track continuous changes in the song (Payne & Payne, 1985; Payne, Tyack, & Payne, 1983). At any one time, the songs of one whale will be more similar to those of others nearby than its own song several months later (Guinee, Chu, & Dorsey, 1983). Most biologists have concluded that this process of continuous change requires production learning, but Cerchio, Jacobson, and Norris (2001) speculate that humpbacks might inherit a set of rules governing song change. In my view, the clincher for production learning in humpback whales is the observation by Noad et al. (2000) of what they call a "cultural revolution" among humpbacks. When a few humpbacks singing the song from the west coast of Australia swam to the east coast, the east coast song was rapidly and completely replaced by the west coast song. This means that nearly all of the humpbacks in the east coast population must have abruptly ceased the slow process of change ongoing in the east coast song and adopted an entirely different song. The combination of geographical and temporal change in humpback song is very difficult to explain by any mechanism other than a sophisticated form vocal production learning that remains active in adults.

The history of using geographical variation in calls as evidence for production learning illustrates pitfalls. For example, early papers on geographical variation in pant hoots of chimpanzees (*Pan troglodytes*) suggested that this variation was evidence for production learning in this species (Arcadi, 1996; Mitani & Brandt, 1994; Mitani et al., 1992). Mitani, Hunley, & Murdoch et al. (1999) reassessed the interpretation of geographical variation in chimpanzee calls. They concluded "The preceding observations

suggest that genetically based rather than cultural (sensu McGrew, 1992) differences are likely to underlie any vocal variations that exist between Mahale and Kibale chimpanzees" (p. 147) and that "Ecological factors related to differences in habitat acoustics, the sound environment of the local biota, or body size are likely to contribute to the observed macrogeographic variations in chimpanzee calling behavior" (p. 149).

Elephant seals (*Mirounga angustirostris*) provide another cautionary tale regarding the use of dialects as evidence for vocal learning. Le Boeuf and Peterson (1969) described well defined local dialects in the pulse rates and other acoustic parameters of threat vocalizations of male elephant seals from various islands off the California coast. They drew analogies to dialects in songbirds and humans, suggesting that young elephant seals copied the vocalizations they heard on their own island. However, once these authors were able to record more longitudinal data, the story became more complex. Le Boeuf and Petrionovich (1974) found that the pulse rates of individual seals did not vary across years, but that the mean pulse rate at a newly colonized island slowly changed from year to year, moving closer to the rates found on large established colonies. They found that most of the breeding males at the new colony were recruited from established ones, and they hypothesized that the original founders of the new colony happened by chance to have pulse rates at the low end of the normal distribution from the established colonies. As more males came from the established colonies to the new one, the pulse rates recorded at the new colony were less affected by the initial sampling bias, and the initial differences were reduced.

In both the chimpanzee and elephant seal cases, initial enthusiasm to interpret geographical variation in calls as evidence for production learning became tempered by new data and a growing appreciation of alternative hypotheses. I argue that the effort to use dialects as evidence for vocal production learning has been problematic. Very different phenomena have been called dialects, with geographic scales from ocean basins or continents to boundaries with scales of meters. Differences in call structure may tempt early observers to draw analogies with dialects in humans or birds, but many mechanisms other than production learning may lead to such differences. As Janik and Slater (1997, 2000) point out, these differences may stem from contextual learning. Animals may also differ in their usage of communication signals based upon differences in social setting and behavioral context, differences that may not be obvious at the early stage of defining dialects. There has also been increasing appreciation that subtle differences in habitat can select for differences in call structure. Animal vocalizations may be selected so that the signals can better be detected given the ambient noise and sound transmission characteristics of the habitat (Slabbekoorn & Smith, 2002). Even for sympatric animals, small differences in location of calling or receiving may change the desired qualities of a signal (Parris, 2002).

Vocal dialects have been described among killer whales (Ford, 1991) and sperm whales (Whitehead et al., 1998). Dialects in these highly mobile animals not only occur across broad geographical regions, but also are defined by sympatric social groupings. Differences in killer whale calls closely follow matriline, and there is a correlation between coda repertoire and mitochondrial haplotype in sperm whales. The correlation between call variation and genetic variation in these cases makes it difficult to rule out genetic influences on call variation.

I would argue that the only way to address these problems is to take a more fine-grained look at the auditory environment of individual animals and the process by which they modify their vocal behavior. Sanvito, Galimberti, and Miller (2007) show how more detailed longitudinal data on vocal development in elephant seals provide much stronger data on production learning than does study of dialects. Sanvito et al. (2007) recorded 29 male elephant seals throughout vocal development. The observed changes in vocalizations observed are well explained by vocal learning, with young peripheral males imitating vocalizations produced by established successful males. In this case, the initial interpretation of dialects as evidence for vocal learning (LeBoeuf & Peterson, 1969) did not stand up to further analysis (LeBoeuf & Petrinovich, 1974), but it would have been incorrect to interpret this problem as evidence against vocal production learning in elephant seals.

Vocal Convergence

Evidence for production learning that derives from convergence of acoustic features of calls among adults has a broader taxonomic spread than either evidence of vocal imitation or effects of auditory deprivation in early vocal development. This may surprise some readers because a dominant model for vocal development has emphasized critical periods early in development for forming auditory memories, followed by vocal practice, with narrower, more stable vocal repertoires among adults. However, many studies have shown that when adult animals are caged together or form natural groups, their calls become more similar than neighbors in different cages or groups. One of the earliest of these studies involved the black-capped chickadee (*Parus atricapillus*). Mammen and Nowicki (1981) recorded the calls of chickadees from four wild winter flocks. Each group was captured and put in an aviary. Birds from three of the aviaries were rearranged to form new flocks, and the calls of members of each new flock converged in acoustic features within a month. Similar convergence among vocalizations of birds caged together come from the Anna hummingbird (*Calypte anna*; Baptista & Schuchmann, 1990), budgerigars (*Melopsittacus undulatus*; Farabaugh, Brown, & Booling, 1994; Hile & Striedter, 2000) and Australian magpies (*Gymnorhina tibicen*; Brown & Farabaugh, 1991).

Poole et al. (2005) analyzed calls of many African elephants, including a male that was housed with female Asian elephants. The calls recorded from this male were more similar to the chirp vocalization of the Asian elephant females than any of the normal calls recorded from African elephants. This seems to represent a case of interspecific vocal convergence.

In spite of the lack of evidence for vocal imitation and for effects of auditory input on vocal production during development in most nonhuman primates, there is evidence of call convergence among adults of the following species: pygmy marmosets (*Cebuella pygmaea*; Elowson & Snowdon, 1994; Snowdon & Elowson, 1999), cotton-top tamarins (*Saguinus oedipus*; Egnor & Hauser, 2004; Weiss, Garibaldi, & Hauser, 2001), and chimpanzees (*Pan troglodytes*; Crockford, Herbinger, Vigilant, & Boesch, 2004; Marshall, Wrangham, & Arcadi, 1999; Mitani & Gros-Louis, 1998). Elowson and Snowdon (1994) tracked changes in trill vocalizations of two groups of pygmy marmosets that were recorded before and after they were put into acoustic contact in separate cages in the same room. Acoustic measures of frequency

and bandwidth shifted "as if the animals were tracking one another's acoustic production" (p. 1273). Snowdon and Elowson (1999) followed up this study by tracking the trill calls of pygmy marmosets as they paired with a new mate. Three of the four pairs showed convergence in acoustic features of trills during the first six weeks following pairing. Two of these pairs could be recorded three years later, and the degree of change in trills was higher in the six weeks after pairing than in the following three years. Weiss et al. (2001) and Egnor and Hauser (2004) reported that male and female cotton-top tamarins had more similar calls within a cage compared to between cages. Marshall et al. (1999) compared pant hoot calls of male chimpanzees from two captive colonies and from a wild site. The acoustic features of pant hoots from each colony and site converged enough so that there were distinct differences in pant hoots from each group. After one chimpanzee arrived at a colony producing an unusual variant form of the pant hoot, other males in this colony started to produce the variant form. Marshall et al. (1999) argue that these data show that male chimpanzees modify their pant hoots to converge on versions that are shared within a group.

This process of vocal convergence has been monitored among wild chimpanzees as they form social bonds. Mitani and Gros-Louis (1998) studied pant hoot choruses in wild chimpanzees. They showed that individual chimpanzees modified features of their pant hoot to match those of the individual with whom they were chorusing. Crockford et al. (2004) measured pant hoots and genetic distance of wild chimpanzees of two neighboring communities and a more distant community. They found no support for genetic differences explaining variation in acoustic structure of the calls. Pant hoots from chimpanzees of each of two neighboring communities were more distinctive than those from the distant community, leading Crockford et al. (2004) to argue not only for vocal convergence within a group, but also vocal divergence between neighboring groups.

The process of vocal convergence has been followed as wild bottlenose dolphins (*Tursiops* sp.) form social bonds. In several field sites, it has been observed that as male *Tursiops* mature, they form alliances with one or two other males. Allied males are sighted together 80% of the time or more, and the alliances typically last for many years, often until one partner dies (Connor, Smolker, & Richards, 1992; Wells, 2003). Smolker and Pepper (1999) studied the whistle vocalizations of three male bottlenose dolphins as they formed an alliance. Over the course of four years, the whistles of all three dolphins, which initially were quite different, converged and became more similar. Watwood, Tyack, and Wells (2004) were not able to study the convergence process, but they were able to confirm that pairs of males within an alliance had whistles that were more similar than comparisons to males from a different alliance.

Boughman (1997) describes similar group-distinctive calls in foraging groups of greater spear-nosed bats (*Phyllostomus hastatus*). During their second year, female greater spear-nosed bats join a social group of unrelated females that is defended by a single male. Females in these social groups will sometimes forage together. When they leave on a foraging trip and when at the foraging sites, they make screech calls that are more likely to recruit group members than bats that are members of other groups. Boughman (1997) shows that the screech calls of bats within a group are group-distinctive, and Wilkinson and Boughman (1998)

argue that the bats use these calls to maintain contact with long-term associates traveling to and within feeding areas. Playback of screech calls outside of the roosting cave and at foraging sites shows that bats respond to screeches by calling and approaching the speaker (Wilkinson & Boughman, 1998). After having found these results in wild bats, Boughman (1998) studied vocal convergence during experimental transfers of captive bats from one group to another. She used two groups of wild-caught adult bats and their offspring, each group of which was maintained in a separate room. Before transfer, the offspring formed a separate roost from the adults in each room, and their calls had begun to differ slightly. She recorded screech calls of some of the younger bats, then transferred them from one room to another at the age at which bats will typically join a social group. Before the transfer, calls of the transfer bats differed from those of the group that they joined. Within a month after the transfer, calls had converged, and after five months, they were almost indistinguishable. This demonstrates that call convergence in these bats occurs through production learning, with both residents and transfers modifying their calls to come up with a new shared group-distinctive call.

One of the striking things about convergence of calls among adults as they form a group is that evidence for this capability appears to be so much more widespread than evidence that auditory input influences early vocal development. The ease of manipulating the social environment of captive animals and testing for convergence suggest that this is a useful method for comparative studies of vocal production learning. Janik and Slater (2000) highlight the importance of discriminating between vocal production learning, in which an animal modifies the acoustic structure of its vocalization to create a signal that is more or less similar to the model, versus contextual usage learning, in which an animal learns to produce an existing signal in a new context as a result of learning about usage of the signal by other individuals. The production of chirps typical of Asian elephants by an African elephant that was housed with Asian elephants seems to be a clear case of vocal production learning, because the chirp sound does not seem to be part of the normal repertoire of African elephants. But more subtle convergence of acoustic features within a call type is harder to define as vocal production learning by the Janik and Slater (2000) definition. As long as studies show that an animal changes a call to use a previously unused area of acoustic feature space after hearing calls in that area, I would argue that this provides evidence for a more subtle form of vocal production learning than that shown by evidence of imitation of highly unusual sounds. For example, Jones and Ransome (1993) showed that the resting frequency of the echolocation calls of the greater horseshoe bat, *Rhinolophus ferrumequinum*, increases over the first few years of life, and then decreases over the rest of the life span. There is a strong correlation between the frequency of an infant's echolocation call and that of its mother, suggesting that the infant fine tunes the frequency of its echolocation call by listening to its mother and modifying its call accordingly. Greater horseshoe bats can adjust the outgoing frequency of their echolocation calls so that the Doppler-shifted returning echo arrives within a narrow frequency window. Jones and Ransome (1993) argue that this is the most precise regulation of vocal behavior known among animals. Methods to quantify this kind of subtle usage of acoustic feature space may need to be improved for communication signals, but I would argue that understanding the function and taxonomic breadth of

vocal production learning requires the inclusion of this phenomenon as well as imitation of completely novel sounds.

Possible Functions of Convergence

Group Cohesion

Most studies of vocal convergence suggest a role for providing group recognition and maintaining cohesion of groups. Among early papers on vocal imitation in mammals, Andrew (1962) suggests "it may have been advantageous for an individual to be able to distinguish his own group from others at a distance. In this way disastrous attempts to join the wrong group could be avoided" (p 586). Mundinger (1970) in the first description of vocal convergence in bird calls suggests "Taken as a whole the data provide support for the hypothesis that avian vocal imitation is sometimes employed for recognizing and maintaining contact with other members of the species" (p 482).

More recent research provides several mammalian examples, including primates and marine mammals, of group-specific calls used to maintain contact. For example, the coo call of Japanese macaques (*Macaca fuscata*) has been reported by Sugiura (1998) to function to maintain contact. Coo calls are often produced when macaques are in dense vegetation, and when a group member hears a coo, it usually responds by cooing back. Sugiura (1998) conducted a playback experiment and found that macaques modified their contact call to match acoustic features of the played back contact call. Tanaka, Sugiura, and Masataka (2006) compared coo calls from two groups of Japanese macaques from the same population. A cross sectional study showed consistent differences in frequency of coo calls between the two sympatric groups. Two frequency parameters did not differ among 4–5 month olds but did differ in 7–8 month olds, suggesting that 6–7 month olds learn to modify their calls to match those of their group.

Killer whales (*Orcinus orca*) are another species where group-distinctive calls are reported to function to maintain contact. Research on wild killer whales in British Columbia, Alaska, and Norway confirm that killer whales have very stable social groups, called pods, and each pod has a group-distinctive repertoire of discrete calls (Ford, 1989, 1991; Strager, 1995; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). Killer whale pods frequently interact with other pods and forage together. Ford (1989) argues that individual discrete calls have little context-specific meaning, but that the pod-specific repertoire of calls functions for maintaining contact between members of the pod to maintain long-term integrity of the pod. As with the Japanese macaques described above, when one killer whale produces a discrete call, other whales tend to respond by producing the same signal (Miller, Shapiro, Solow, & Tyack, 2004). Further evidence that killer whales use discrete calls to maintain spatial cohesion is provided by Miller (2002), who showed by comparing the amount of energy in high versus low frequencies in discrete calls that a killer whale not only should be able to tell where another whale is, but also whether it is swimming toward or away from the listener. The low frequency components of killer whale calls are less directional than the high frequency components, with more high frequency energy emitted in the forward direction. Thus, if a receiver hears a high ratio of the high to low frequency energy in a call, this means that the caller is likely pointed toward it. There is likely more of this kind of

complexity in how animals use calls for coordination of movement and for maintaining cohesion than has been demonstrated to date, especially for animals that move in three dimensions and are often out of sight of one another.

Mammen and Nowicki (1981) demonstrated that some acoustic features of chickadee calls are individual-specific while others converge as birds form temporary flocks. They point out that the contexts when the chickadee call is used suggest a role for individual recognition and flock cohesion—the chickadee call is used as a contact call during group travel or as birds separate while foraging, when one bird separates from the flock, while the flock mobs a predator, and during interflock encounters at group territory boundaries. Mammen and Nowicki (1981) discount the idea that flock calls would help chickadees maintain contact. Chickadee flocks are small and calls are so individually distinctive that Mammen and Nowicki (1981) argue that convergence is not necessary for this contact function. They do suggest that convergence might speed up recognition of flock members, which might be useful in interflock competition or in the presence of a predator.

The whistles of allied male bottlenose dolphins show a pattern of initial individual distinctiveness and convergence similar to that described by Mammen and Nowicki (1981) for chickadee calls. Janik and Slater (1998) showed that bottlenose dolphins tend to produce individually distinctive whistles when separated from other members of their group, and they argue that this supports the hypothesis that individually distinctive whistles are used to maintain group cohesion. Smolker and Pepper (1999) follow Mammen and Nowicki's (1981) argument that it is unlikely members of an alliance require converged whistles in order to recognize one another. Rather they suggest that alliance signatures are directed toward other males to signal a greater threat or toward sexually receptive females, who might either be more likely to select the alliance for mating or to be less likely to try to leave the alliance.

Badge or Password

Several studies on vocal convergence suggest that group-distinctive vocalizations may be used as a password for access to shared resources. Feekes (1977, 1982) found that male yellow-rumped caciques (*Cacicus cela*) share a group-specific song within a breeding colony, and she suggests that "colony-specific song may be a 'password' distinguishing strangers and familiar inhabitants" (Feekes, 1982, p. 147). She specifically suggested that colony-specific songs might allow "strange males to be immediately recognized and expelled" (p. 147). Wilkinson and Boughman (1998) argue that greater spear-nosed bats use a group-distinctive screech call as a badge to exclude nonmembers from access to food resources. They found that greater spear-nosed bats tended to call more and to forage in larger groups when feeding on concentrated rather than dispersed resources. Tracking of movements showed that females from more than one group were found at a feeding site, but that females from the same group foraged more close together compared to females from different groups. Wilkinson and Boughman (1998) argue that females can defend rich feeding sites and that a group should be more effective for this defense than an individual. They suggest that when a bat hears an approaching bat at a feeding site, the guarding bat could call to announce discovery of the approacher, and the approacher might be required to produce the same call as a password. For screeches

to be honest indicators of group membership, they would have to be difficult to imitate spontaneously. The pattern where it takes months for bats to learn to converge (Boughman, 1998) suggests a potential obstacle to rapid imitation.

Rendell and Whitehead (2003) suggest that sperm whales may use a vocal badge of clan identity in their decisions of how to allocate social benefits. Sperm whales produce group-distinctive repertoires of rhythmic patterns of clicks, called codas. Weilgart and Whitehead (1997) found no coda types were unique to a group, but that each group had a distinctive repertoire of these codas, a repertoire that was stable for years. The basic social unit of sperm whales is the family unit comprised of adult females and their young. Most social groups of sperm whales are comprised of two family units that associate temporarily for about a week, but the individuals within a family unit associate for years (Christal & Whitehead, 2001; Whitehead, Waters, & Lyrholm, 1991). Rendell and Whitehead (2003) suggest that groups of sperm whale units may form vocal clans, where all of the units within a clan tend to produce similar coda types. They report that units prefer to form a group with other units that share codas within the same clan. Sperm whales rely upon social coordination to defend against predators, especially to protect calves (Arnbom, Papastavrou, Weilgart, & Whitehouse, 1987; Whitehead, 1996). Rendell and Whitehead (2003) suggest that sperm whales may restrict the provision of this defense to members of the same clan, using coda repertoires as a marker of clan membership.

Ford (1989) argues that group-distinctive repertoires of calls in killer whales "may provide a more reliable or detailed 'badge' of group identity than would be possible with a single pod-specific call" (p. 743). Brown and Farabaugh (1997) support this idea for Australian magpies (*Gymnorhina tibicen*) where each member of a group, both males and females, sings specific elements of its song to form a communally sung group-specific chorus-song for territorial defense: "Presumably, group-specific chorus song may aid magpie's recognition of groupmates versus intruders during the melee of a territorial battle, as well as aiding in synchronizing their aggressive activities" (p. 119). I understand this argument if the birds cooperate to produce one synchronized chorus song, like a group version of duetting song. By contrast, it seems to me that relying on a complex and large repertoire of separate calls as in the killer whales and sperm whales would be less effective for identifying group membership than a single group-distinctive call. The functions of maintaining cohesion, recognizing groupmates during a fight, and catching nongroup members before they benefit from costly support would seem to usually require a rapid communication system. Detection of an inappropriate single group-specific call would require just one exemplar. But since many sperm whale and killer whale groups share calls, an individual might have to wait for tens of minutes to be sure whether it is hearing the same or a different group. To give a human analogy, teams in a sport usually wear the same basic kind of jersey, but each team has a distinctive color. By contrast, teams of sperm or killer whales would wear the same jersey, with a team-specific assemblage of patches, but for which most individual patches are shared across several teams. This does not seem like a system designed to simplify cohesion or to coordinate group cooperative or competitive activities under time pressure. It seems particularly ill-suited to fulfill a badge or password function.

There are several alternative hypotheses for the functions of group-distinctive call repertoires. Krebs (1977) suggested that an animal defending a territory might benefit from producing a large repertoire of calls if the repertoire created an impression of more inhabitants. The same logic might apply if a large repertoire created the impression of more members of the group. Another hypothesis is that a complex group-specific repertoire may provide better protection against cheating in species that are skilled at vocal imitation. It is notable that these group-specific repertoires are reported for animals that appear to be skilled at vocal imitation. Brown and Farabaugh (1997) provide evidence that Australian magpies can imitate human sounds as well as use vocal learning to produce conspecific sounds. There are limited data on vocal production learning in killer whales, but they have been reported to imitate the sounds of sea lions (Foote et al., 2006). There are even fewer data on vocal learning in sperm whales, but imitation of codas may require little more than matching the timing of coda clicks, and Backus and Schevill (1966) showed that a sperm whale was able to match the timing of a ship's depth sounder with great precision. If these species are adept at imitating a group-specific call immediately after exposure, the development of a complex repertoire of group-specific calls could be used to make cheating more difficult. A third hypothesis suggests that the repertoires of calls in killer and sperm whales may enable recognition of different levels of group affiliation. The smallest social unit of killer whales is the matrilineal group, comprising a mother with her offspring. Neither sex disperses, so these are very stable groups (Ford, 1990). Related matrilineal groups often associate together to form pods, and different sympatric pods form a community (Ford, 1990; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). The calls of killer whales change enough that the calls of different matrilineal groups differ even within one pod (Miller & Bain, 2002), different pods differ even more (Ford, 1989), and communities even more. Different pods that share calls are called part of the same vocal clan (Ford, 1990; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). Sperm whale groups that share extensive parts of their coda repertoires are also considered part of the same vocal clan, and sperm whales share more codas within than between units and vocal clans (Rendell & Whitehead, 2003). The pattern of call repertoires in killer and sperm whales may be too complex to serve well as a simple password, but Miller and Bain (2002) suggest that "repertoires of sounds may be particularly efficient for encoding information about multiple levels of social affiliation" (p. 625).

Affiliation

A different view of vocal convergence emphasizes the role of imitation as an affiliative signal to ease the integration of new members into a group (Mammen & Nowicki, 1981). There is a rich literature showing that when a human wants to establish a social relationship with another, s/he will modify many aspects of his or her communication to match the partner (Giles, 1984). A speaker will be particularly likely to accommodate and match the speech of a more powerful or influential partner. Communication accommodation emphasizes a process that, unlike the password function discussed above, would be expected to take place quickly as parties begin to interact, and for there to be little aggression against animals that accommodate but do not match perfectly at first.

Many animal studies have pointed out the similarities between the predictions of communication accommodation theory for humans and observations in animals as diverse as nonhuman primates (Mitani & Gros-Louis, 1998; Snowdon & Elowson, 1999), dolphins (Tyack, 2003), parrots (Vehrencamp, Ritter, Keever, & Bradbury, 2003), and several other avian species (Brown & Farabaugh, 1997). Vehrencamp et al. (2003) conducted playback experiments with orange-fronted conures (*Aratinga canicularis*) and suggest that conures increased the similarity of the calls they used to respond to playback calls as an affiliative signal during the initial exchange. Mitani and Gros-Louis (1998) conducted a study to test three hypotheses about call convergence in chimpanzees. Chimpanzees use pant hoots to recruit allies and to maintain cohesion (Mitani & Nishida, 1993). Mitani and Brandt (1994) showed that males who are associating and producing a chorus of pant hoots tend to produce acoustically similar calls. One possibility was that the chorusing context might trigger a particular type of call in all of the males. Another was that low-ranking chimpanzees might mimic high-ranking ones, producing calls that converge on those of high-ranking chimpanzees. The third hypothesis was that chimpanzees actively modify their calls to match those of the chimpanzees with which they are chorusing. This hypothesis predicts that when chimpanzee A is chorusing with chimpanzee B, he would produce calls more similar to B than when he is chorusing with another chimpanzee. Mitani and Gros-Louis (1998) did not find a significant difference in pant hoots produced by chimpanzees when they were alone compared to when they were chorusing. They also found that low-ranking males did not often chorus with high-ranking males, and low-ranking males did not tend to produce calls more similar to the alpha male than to each other. There were two pairs of male chimpanzees with sufficient calls to compare similarity when they chorused with each other versus with other chimpanzees. Both pairs produced calls that were significantly more similar when chorusing together versus chorusing with other males. Mitani and Gros-Louis (1998) suggest for chimpanzees and the many cases listed above that vocal accommodation functions to strengthen social bonds between individuals.

There are several aspects of speech accommodation that are quite similar to vocal convergence. Some of the literature on speech accommodation focuses on short dyadic interactions but the concept is equally appropriate for longer term development of shared communication patterns as a group forms. In both speech accommodation and vocal convergence, as interactants form social relationships, features of their vocal communication may converge. If the theory of communication accommodation were broadened to include vocal convergence among animals, it would predict that animals would converge as an affiliative gesture, to facilitate social integration and cohesion. This is quite similar to the predictions of a group cohesion function for vocal convergence in animal calls. This view seems entrenched enough in our culture for the movie *Close Encounters* to be able to assume the audience would understand that imitating sounds of an extraterrestrial should be viewed as a friendly act.

Escalating Threat in Agonistic Encounters

An alternative interpretation to the idea that vocal matching is affiliative, stems from studies of how songbirds can use song matching to escalate aggressive interactions. One of the first ef-

fects of aggressive song matching noted was that some song birds may match a song played back in their own territory, and that the probability of matching a rival song correlates with the probability or intensity of attack (Krebs et al., 1981). This result suggests that matching an opponent's song can heighten the warning or escalate the threat. As adult male songbirds establish their breeding territories, they familiarize themselves with the calls of their neighbors. Playback of a neighbor's song from the neighbor's territory elicits weaker responses than either playback of a stranger's song from the same place, or of the neighbor's song from outside its territory (Falls & Brooks, 1975). This shows that by listening to song and by locating where it is coming from, a male songbird can determine whether a stranger is present in a neighboring territory. This observation suggests that a newcomer might benefit by being able to copy the songs of local males. Wilson and Vehrencamp (2001) tested this idea by playing back to a male song sparrow (*Melospiza melodia*) either a neighbor's song (neighbor), the same song produced by a stranger (mimic), or a novel song produced by the stranger (stranger). They found that male sparrows tended to respond as strongly to the mimic song as to the stranger song, suggesting that territorial males were able to discriminate whether the same song type was sung by a neighbor or by a stranger. When a bird hears a neighbor singing from its normal territory, it may reply not by matching the same song, which might escalate the interaction, but rather by selecting another song that the two share within their song repertoires which seems to signal recognition of the neighbor with a reduced threat when he is on his own territory (Beecher, Stoddard, Campbell, & Horning, 1996). If the bird instead hears the song of a stranger, it is more likely to match the song and escalate the interaction.

The results described in the preceding paragraph have been described by Lachlan, Janik, and Slater (2004) as behaviors that function to enforce conformity in the songs of neighbors. Lachlan et al. (2004) used a spatial simulation model to study the evolution of conformity-enforcing behavior. In this model, each individual produces one song type, has a fixed number of neighbors and a fixed benefit of winning a contest against a neighbor. The choice available in the model was either to attack a neighbor at random or to attack one that produces a different song type. Lachlan et al. (2004) show that under many conditions, an effective strategy is to select opponents that sing uncommon songs. This conformity-enforcing behavior helps neighbors that share songs to gang up on intruders. While the Lachlan et al. (2004) model involved territorial males, a similar logic might hold for animals within a social group instead of holding stable territories. If members of a group discriminated against a member that produced a different signal, this could lead to the development of group-distinctive call repertoires.

The idea of vocal accommodation theory that vocal matching should be interpreted as affiliative stands in sharp contrast to the idea that song matching in birds signals an escalation of the threat and that deceptive mimicry elicits retaliation. The one theme that strikes me as common between these two situations, however, is that the signaler can match the call of another in order to communicate that the response is meant to target the specific earlier caller. This interpretation was highlighted by Thorpe and North (1965) for imitation of song in birds. This commonality may stem from sensory systems that are more likely to detect or weight signals similar to those just sent out. Miller et al. (2004) and Sugiura

(1998) suggest that by rapidly responding to a call with a match, a respondent can direct the response directly to a specific caller. One of the intriguing questions about this kind of matching is whether such a signal can functionally refer to the associated signaler. If a signal takes on a predictable association with an individual as in the case of individual signatures or a group as in the case of vocally converged group signals, it may form the basis for a learned and arbitrary signal that becomes associated with a social referent. The question of how rich such reference is for nonhuman animals has barely begun to be addressed.

Selection for Innovation Versus Conformity

One of the puzzles of vocal learning is why some animal species that are capable of vocal convergence as adults show so little evidence for vocal learning in development. Vocal learning can be harnessed to solve a variety of very different problems—for echolocation, examples include Doppler shift compensation and matching a mother's echolocation call; for communication, examples include producing group- or individual-specific calls and producing a variety of patterns of reproductive advertisement displays—from a single stereotyped song never changed from early life to an adult repertoire that continuously grows or changes. It stands to reason that selection is constantly acting on the timing and extent of modifiability of vocal repertoires. Many species may inhabit social and ecological niches where selection may not favor highly variable vocal repertoires, and modifiability may not be obvious in these taxa. For example, many songbirds with vocal production learning inherit templates that restrict the kinds of sounds they copy. It may require particularly predictable social and acoustic environments for the young to be freed to have a broader innate template for what sounds to learn. There is no reason to expect that species where individuals raised by humans in captivity will spontaneously imitate exotic sounds would not be a small subset of all species capable of vocal learning.

Species requiring mechanisms to manage grouping in fission-fusion societies may develop specific forms of modifiability that are likely to enable the development of group-distinctive calls. Development of group-distinctive calls may require specific parameters for vocal learning, depending upon the patterns of association typical of a population. Too little influence of auditory input on vocal output and there might not be enough change to allow convergence. Too much of a tendency to copy what you hear could lead to a cultural revolution instead of distinctive calls within small groups. For example, the humpback whales of the eastern Australian coast studied by Noad et al. (2000) shared a vocal tradition of a song that was shared among the population. When the song of western Australia arrived on the east coast, it swept through the eastern population with such popularity that it completely replaced the east coast song, removing the distinctiveness not just between groups but also between whole populations.

In the case of bird song, the question of whether dialects might stem from random copying processes gave rise to a series of models to predict dialect patterns based upon the number of neighbors and error rates for copying (e.g., Goodfellow & Slater, 1986; Lachlan & Slater, 2003). Because these models were designed to understand geographical dialects, they were organized in terms of spatial distribution. For animals as mobile as marine mammals, it would be important to model social structure as well

as space. This kind of modeling to test whether specific matching patterns and error rates coupled with association patterns lead to individual- and group-specific repertoires may help test ideas for functions of vocal production learning in mammals and specify critical measurements, such as patterns of association, vocal development, lifetime patterns of vocal matching, and rates of copying errors.

Rather than having a single group-distinctive signal, killer and sperm whales have complex patterns of group-distinctive repertoires of calls. The functions of these repertoires have been studied less than song repertoires of songbirds, where a variety of hypotheses have been tested. If behavioral phenomena as complex as matched countersinging are used by whales, then much more detailed behavioral study will be required to uncover the functions of group-distinctive call repertoires. Current research on sperm whale codas and killer whale calls suggest that the calls do not depend much on behavioral context and may be interchangeable. The development of call repertoires where call types are shared across groups might result from differing rates of copying and copy error. Ford (1991) studied 16 pods of killer whales off British Columbia and reported that they formed four different acoustic clans, with some call sharing within a clan, but no sharing across clans. Yurk et al. (2002) studied calls and genetics of seven pods in Alaska, and showed that each vocal clan was a distinct matriline. Ford (1991), Miller and Bain (2000), and Yurk et al. (2002) suggest that new pods are formed as one pod splits after growth, and as two pods separate, their calls will diverge through processes of copying errors, call innovation, and call extinction. Deecke, Ford, and Spong (2000) studied how two calls changed over 12–13 years in two different pods of killer whales. One of the calls did change significantly over this time in both pods, but changed in the same direction, so that the calls from the two pods did not diverge. The other call did not show significant change over this time period. Deecke et al. (2000) suggest that these results can best be explained by cultural drift with animals matching changes not just within, but also across pods. The lack of such matching across vocal clans, even for groups that associate often, indicates that there are social barriers to matching. Some features of sperm whale codas, such as the wide spread of coda repertoires shared across groups, might be explained by a different pattern of rules for copying coupled with their different pattern of grouping. Thus group-distinctive dialects appear to be maintained by a process of vocal production learning with a complex set of socially mediated constraints and patterns of modifiability.

Conclusion

Evidence for vocal convergence as animals form groups suggests that if group-distinctive calls are important, this might be an important function for vocal learning. Few animal groups split precisely along reliable patterns of genetic variation, so it is difficult to imagine a mechanism by which animals could inherit group-distinctive calls. Vehrencamp et al. (2003) argue that “While a system of recognition based on memorization of individual- or family specific call variants does not depend on vocal learning by senders, a system of group recognition based on the convergence of call structure among strongly associated group members does require vocal learning (Bradbury & Vehrencamp, 1998). Thus understanding the mechanisms used to organize

fission-fusion societies may have broad relevance to the evolution of vocal learning in general” (p. 38).

Andrew as early as 1962 pointed out:

... it may well be that song learning has evolved purely as a simple means of insuring the transmission of complex species-specific song, and that the existence of dialects is a functionless by-product. That this method of transmission appears to allow enough variability to permit individuals to be recognized by slight differences in the form of their song (10) is probably also important.

The matter is complicated by the fact that it is not yet possible to establish the course of evolution of song learning in any line of passerine evolution. It is even possible that extensive learning is primitive within the group, and that this faculty has been lost in some lines (11). However, it is clear that mimicking can be evolved in the absence of any very high level of intelligence when there is a need for the acquisition during development of complex species-specific, group-specific, or individual-specific patterns of vocalization. (p. 586)

The point brought up by Andrew (1962) with respect to geographical dialects in birdsong suggests a parallel null hypothesis that perhaps some correlations of communication signals with various levels of grouping or social association might also represent functionless byproducts of vocal learning. As suggested above, patterns of vocal repertoires result from a complex interaction between learning rules and capabilities internal to a developing animal with the spatial and social patterning of the population in which an animal develops. This highlights some of the complexities of studying the functions of vocal learning today. For example, given a pattern of production learning in vocal development throughout the lifetime, different patterns of sociality could lead to different patterns of communication signals. For example, inshore dolphins that rely upon strong individual social bonds living within highly fluid social groupings might be expected to develop individually distinctive calls that converge on calls of close associates. Coastal killer whales that live in highly stable groups from which neither sex emigrates might use the same pattern of vocal development to develop a group-distinctive repertoire of calls. Sperm whales, which are highly mobile pelagic animals usually sighted in groups formed of two more stable units, might be expected to form a more geographically dispersed set of groups sharing call repertoires. We know that these species have very different social organization; we do not yet know whether the same learning mechanism in these different social settings could lead to the different repertoires observed, or whether vocal learning mechanisms may have been selected to produce the communication system of each species. In addition to these problems, Catchpole and Slater (1995) raise additional concerns about how much current utility can tell us about evolutionary origins.

Andrew (1962) suggests that perhaps vocal learning may have been more widespread taxonomically at an earlier stage of evolution and has been lost in some lines. Another way to look at this is to recognize that the pattern of presence or absence of vocal learning depends heavily upon the criteria for presence and absence and for what assumptions to make about taxa for which relevant data are not available. The phylogeny of vocal learning would look very different depending upon the evidence required to demonstrate its existence. Pooling the data on vocal imitation and vocal convergence suggests a wider taxonomic distribution of vocal production learning among mammals than is generally ap-

preciated. Spontaneous imitation of novel sounds, often speech sounds produced by animals raised with humans, has a relatively narrow distribution. Among mammals, imitation of anthropogenic sounds has been reported for elephants, harbor seals, and dolphins. But vocal convergence seems to be much more widespread among mammals. Vocal convergence has been reported for bats, humpback whales, several species of toothed whales, African elephants, and several species of nonhuman primates. The wide taxonomic distribution of this evidence for vocal production learning suggests that perhaps more of the neural underpinnings for vocal production learning are in place in mammals than is usually imagined. It may also be that the genetic underpinnings for neural mechanisms linking vocal output to auditory input are even more widespread for ubiquitous problems such as adapting signaling to compensate for noise. Such relatively simple mechanisms have not normally been included in discussions of vocal production learning. But as long as they provide neural pathways to link auditory input with vocal motor output, they might form the substrate for evolution to work on in taxa that encounter niches with added uses for vocal learning.

It is sobering that after more than 40 years of work in this area, the questions raised by Andrew (1962) are still so open. While behavioral research on imitation helps us to understand some current functions of vocal learning, I think that a broader view is required to understand its evolution. The more complete an inventory of the taxonomic distribution of different mechanisms for vocal production learning from simple to complex, the better we will understand its functions and its evolution. Research on the genetic underpinnings of the neural mechanisms will be required to understand the evolutionary origins of vocal learning in birds and mammals. Without such information, it is difficult to predict how many times vocal learning may have originated in evolution, what selection pressures led to its development, and how difficult and unlikely such origins may be.

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Updating von Uexküll: New Directions in Communication Research

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The study of communication in all its forms has come a long way conceptually and methodologically in the last decade, and this is more true of auditory communication than of the other sensory modalities. In considering the issues involved in communication, it is clear that simple dyadic considerations leave out too many important issues. Background noise, eavesdropping, and deception represent important neglected factors driving the evolution of the mechanisms, development, and ecological adaptiveness of communicatory processes in natural environments.

Keywords: von Uexküll, communication, Darwin

I was very pleased when the editors of this special issue approached the *Journal of Comparative Psychology* about the possibility of publishing a special issue based on the 2006 symposium on auditory communication in animals held in Baltimore under the aegis of the Acoustical Society of America. This issue of the *JCP* should be most useful for students and researchers interested in a timely introduction to the diversity of this rapidly advancing field. Recent progress in auditory recording, and especially in computerized analysis of massive streams of data, should amaze those, who like me, were proud of having, at the start of our careers, a bulky sonograph that would burn a few seconds of sound on paper, which then had to be manually measured, evaluated, summarized, and treated statistically.

However, there are more than technical advances in these papers. Our entire perspective on animal communication and the richness and complexity of the content of animal “signals” has changed in a remarkable sense. For comparison, we can look back at what was one of the most comprehensive of the animal behavior texts from decades ago, *Mechanisms of Animal Behavior* by Peter Marler and William Hamilton (1966). This massive book was the reference text of the era and the primary text in the joint Psychology/Zoology course I cotaught in my first year at The University of Tennessee 40 years ago in 1968. Note the title, with its focus on mechanisms, and the first author, who was, and still is, a major figure in the study of vocal communication frequently cited in the preceding papers. This book was written before the growth of sociobiology, behavioral ecology, and study of sexual selection, fields that initially eschewed an interest in “mere” mechanisms as old fashioned and largely irrelevant in the light of functional analysis and evolutionary theorizing (e.g., Wilson, 1975).

How the field of animal behavior has changed! Calls for a renewed emphasis on mechanisms have come from varied quarters (e.g., Ryan, 1994). In truth, many scientists interested in the intricacies of animal communication never wavered from asserting

the need for a balanced attention to all of Tinbergen’s (1963) aims of ethological analysis—mechanisms, ontogeny, adaptive function, and evolution. However, the 20 year or so detour did have its benefits in that it encouraged a more naturalistic focus on field as well as laboratory studies, and a more sophisticated agenda for more mechanistic (sensory, motor, physiological, neural) approaches. The positive consequences are very evident in the preceding papers.

Charles Darwin, in his two primarily behavioral books on the emotions, mental continuity, and sexual selection (Darwin, 1871, 1872), set the stage for the evolutionary comparative approach to animal communication research (Burghardt, in press). He discussed the proximate mechanisms involved in signaling, foraging, predation, and emotional expression as well as the importance of inter- and intraspecific selection in mate choice and competition. Darwin focused largely on visual signaling due to the lack of methods to record and analyze vocalizations. In the decades after Darwin much animal behavior was studied, but communication was de-emphasized as compared to other issues such as sensory perception, motivation, and learning. It was not until Jacob von Uexküll (1921) pointed out that we need to view the salience of stimuli from the animal’s sensory, instinctive, and experiential perspectives that integration of sensory and naturalistic communicatory processes became fashionable via the rise of European ethology. About the same time Schjelderup-Ebbe (1935) discussed the importance of social setting and other factors on social interaction and social relationships, pointing out in the first sentence of his review that “Every bird is a personality” (p. 947). In 2002 this journal published a special issue on the impact of von Uexküll on communication research (Green, Owings, Hart, & Klimley, 2002).

This special issue extends the thrust of the earlier effort into new territory (but see Shier, 2002) as well as focusing exclusively on sounds. A major theme throughout many articles in this issue is that auditory stimuli between signalers and intended recipients can be compromised, disrupted, degraded, usurped, and otherwise rendered less than effective by the conspecific social environment and not just the vagaries of the physical environment. Indeed, this social environment is increasingly viewed as a social network (McGregor, 2005). As Terry and Lachlin (2005) wrote: “the decisions that both signalers and receivers make about their future behavior are thus contingent not only on each other’s behavior but

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also on a wider network of individuals" (p. 604). This understanding, so foundational to the theoretical context of this special issue, merits another modification in the seminal and famous von Uexküll functional cycle diagram integrating stimuli and their perceptual and effector relations mediated by "inner world" (neural) pathways (von Uexküll, 1921). I expanded this diagram to include another organism entering into a dyadic relationship as more than a "mere" stimulus (Burghardt, 1998, p. 90). However, the message of this issue is that the decision-making "inner world" of an animal is affected by a far more complex stimulus environment than we have appreciated in our experimental science. A start on providing a heuristic diagram capturing this complexity has been provided by Oliveira (2005, p. 495), and other useful conceptual models will be undoubtedly forthcoming.

Embedding visual features in the natural context are the essence of studies on camouflage. Although visual noise and disruption are thus well-known and discussed in many contexts (e.g., Thayer, 1918), it is in the auditory and chemical environments that this astounding complexity is greatly expanded and for which the work in this *JCP* issue and other recent studies are providing guidance. In terms of the chemical senses we are just starting to study interactions among discrete and overlapping signals and background stimuli, as we have so much difficulty appreciating chemical signals both analytically and critically anthropomorphically.

There was an earlier movement in animal behavior, social ecology, which included in its agenda the importance of analyzing differences in reliance on communication cues by related species inhabiting different ecological settings, such as forest or savannah dwelling birds and nonhuman primates (e.g., Crook, 1970). Some of these studies and their rich examples might well be revisited with the tools and perspectives outlined in this issue. Certainly, more expansive and integrative developmental and phylogenetic perspectives will prove necessary as the field progresses. The importance of the work reviewed in this issue however, cannot be overestimated in terms of concepts, theory, and methodology. Even beyond sound, there need not be much fury.

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