

# The Design of Animal Communication

edited by Marc D. Hauser and Mark Konishi



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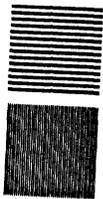
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The Design of Animal Communication



# I MECHANISMS OF COMMUNICATION

**Mark Konishi**

Animals use many different methods to produce communication signals even within a single sensory modality. For example, sounds may be produced by the passage of air through special organs as in the mammalian larynx and avian syrinx, by rubbing appendages against each other like insect legs and wings, and by striking objects in the environment as in woodpeckers.

Recording bodily movements or their products in naturally behaving animals has been the main method of studying how signal-producing organs work. For example, the spectral and temporal analyses of sound signals can reveal some of the properties of sound production as exemplified by the discovery of the simultaneous production of two different sounds by birds, which led to the two voice theory (Greenewalt 1968; Stein 1968). In the study of insects, fish, and frogs, this approach has progressed to the neuromuscular level. Chapter 1 by Kelley and Tobias is a good example of this approach (see also chapter 17 by Bass et al.). In the past, this level of analysis appeared unobtainable in songbirds despite extensive descriptive and developmental studies of birdsong. This situation has, however, changed dramatically in recent years. Use of an angioscope for inspecting the inside of human blood vessels allows viewing of the inside of the syrinx during phonation. This approach has revealed that the labia instead of the internal tympaniform membranes produce sounds (Goller and Larsen 1997). This finding radically changes the long-held view that these membranes are the source of sounds. Suthers reviews these and other developments in the study of avian phonation in chapter 2.

Of many issues, the relationships between respiration and vocalization are particularly interesting. Suthers and his associates succeeded in recording simultaneously song, air flow, and sounds in the trachea or bronchi, pressure in the air sac system, and electrical activities in abdominal and syringeal muscles. Their results have resolved some of the outstanding questions and hypotheses concerning the methods of breathing during song and also uncovered many interesting new facts. The two-voice theory is one of the hypotheses. Simultaneous recordings of air flow and sound in the left and right bronchi of catbirds, brown thrashers, canaries, and cowbirds show that birds do produce different sounds from the left and right halves of their syrinx. The two sides often generate different sounds either simultaneously or in sequence within a syllable. The timing relationships between the two sides are particularly interesting. Birds can close one side while singing with the other side, and they can rapidly switch from one side to the other between syllables and within a syllable (Suthers 1990). This dynamic control of respiration during song suggests

that the vocal system sends control signals to the respiratory system. The anatomical bases for this control involve neural pathways from the forebrain song-control circuit to the hindbrain respiratory center (review in Wild 1997).

Lateralization is another important phenomenon for which physiological evidence has become available. In *Wasserschlaeger* canaries, cutting the left syringeal nerve or lesioning the left nucleus HVC causes the disappearance of a majority of song syllables (Nottebohm and Nottebohm 1976; Nottebohm et al. 1976). This finding led Nottebohm to the hypothesis that there is hemispheric lateralization in song production as in human speech. Air flow and sound recording does show that a majority of syllables are produced by the left side. However, examination of the brain areas that control song production shows no size differences between the hemispheres, whereas the left half of the syrinx is much larger than the right half. Suthers and his coworker found that while a bird is singing with the left side, the dorsal syringeal muscles contract to stop the air flow in the right side (Goller and Suthers 1995). Since other muscles are active on both sides, the difference is not reflected in the size of the song nuclei.

The “mini breath” theory is yet another hypothesis that has been confirmed. Calder (1970) used behavioral methods to show that canaries take a short breath before each song syllable when they are singing fast. Air flow and pressure measurements clearly showed the validity of this interpretation. Suthers and his coworker further demonstrated that canaries produce fast-song syllables without inspiring between the syllables (Hartley and Suthers 1989). They can sing using the air stored in the air sac system. This finding is important for understanding the evolution of vocal signals in birds. It is safe to assume that vocalization evolved from respiration. The question then is how the vocal system was “emancipated” from the constraints of the respiratory rhythm. The air sac system working as a bellows partly frees the vocal system from these limitations.

Only a few years ago we knew more about the brain mechanisms of birdsong than about its syringeal mechanisms. Now, we have many interesting findings about the syrinx, some of which need to be explained in terms of central mechanisms. The discovery of the song control system by Nottebohm and his associates in 1976 marked a new era in birdsong research. It brought birdsong research into the realm of neuroscience. Few vertebrate neural systems with known function are so discrete as the song system. This property allows the investigator to compare the song system between different species, sexes, ages, seasons, and normal and experimentally manipulated individuals. All these comparisons have yielded exciting results including the absence of the forebrain song nuclei in suboscine birds, the rudimentary state of the forebrain song nuclei in the female of species in which only the male sing,

developmental and seasonal changes in song nuclei, and growth and differentiation of forebrain song nuclei by hormonal manipulation. Finer analyses of song nuclei have also produced surprising results such as the migration of new neurons into forebrain song nuclei in the adult brain, formation of new synapses in response to testosterone in the adult brain, and the expression of early immediate genes that is correlated with song behavior. Nottebohm (chapter 3) and Ball (chapter 8) provide extensive discussions of these topics.

One aspect of the song system that has received much attention is its role in song imitation. The forebrain part of the system including HVC, RA, X, and LMAN occurs only in oscine songbirds (which can imitate song) and is absent in suboscine songbirds (which sing but do not imitate song). Oscines include such birds as canaries, finches, and sparrows, whereas suboscines include flycatchers and many South American passerines. This observation led Nottebohm (1980) to suggest that the forebrain song nuclei evolved to accommodate song learning (cf. Kroodsmma and Konishi 1991). If this theory is true, this example is the only case in which conspicuous differences in the brain are correlated with the ability and inability to learn. Thus the song system is a good model for the study of learning. Some of the changes in the song system mentioned in the preceding paragraph are likely to be involved in song imitation, although ultimately one has to discriminate between maturational and renewal processes, and those that are essential for song imitation. In chapter 3, Nottebohm discusses the significance of anatomical and physiological changes with reference to the critical period of song learning (see also chapter 12).

The discovery of seasonal changes and the effects of sex hormones made the song system a very attractive subject for neuroendocrinological research. In chapter 8, Ball reviews recent advances in this field. In addition to endogenous circannual rhythm, photoperiod plays an important role in avian reproductive behavior of which song is a component. Long spring days following short winter days stimulate the secretion of gonadotropine-releasing hormone from the hypothalamus, gonadotropines from the pituitary, and eventually sex steroids from the gonads. Measurement of testosterone in wild songbirds shows a strong correlation between hormone levels and different phases of the reproductive cycle including singing. Since an increase in testosterone is known to induce the growth of song nuclei, long days should have the same effects. Indeed, relatively short exposure, such as one week, to long days increases the volume of some of the song nuclei. This growth may involve an increase in cell number, growth of dendrites, somata, and intercellular distance. Ball carefully analyzes the existing results to determine which of these events really occur. The action of a single hormone on the song system is, however, by no means simple. For example, growth and regression in the song system can occur without changes in

testosterone titre. Some of the song nuclei grow in response to testosterone in the absence of steroid receptor containing cells. This is because cells with steroid receptors influence the growth of other cells by transsynaptic action.

The discovery of gender difference and plasticity in the adult avian brain surprised everyone and stimulated new efforts to look for the same phenomena in other animals, particularly laboratory mammals. Both neurogenesis and seasonal changes in the adult brain were subsequently found in mammals (Gaulin and FitzGerald 1986; Louis and Alvarez-Buyalla 1994; Jacobs and Spencer 1994). Large gender differences were also found in the brain and spinal cord of laboratory mammals (review in Breedlove 1993). Wherever there are innate gender differences in behavior, there are gender differences in the nervous system. Kelley and Tobias review their work on the African clawed frog *Xenopus laevis*, whose males and females produce different calls. Both the vocal organ and the neural circuits for vocal control are different between the sexes in terms of cell number, biochemical properties, and connectivity. One of the most interesting findings discussed in this chapter is the fact that sex differences in the larynx and its muscles can explain why males and females produce different calls. The male larynx is equipped with fast-twitch muscles to produce fast trills, whereas the female larynx is controlled by slow-twitch muscles to accommodate only slow clicks. During development the laryngeal muscles change from slow to fast type in the male under the influence of androgen. However, this conversion does not occur in other muscles of the body. This difference is due to a special gene that is expressed in the laryngeal muscles. The synapses between the motor neurons for these muscles are also different in the sexes. Male synapses have a property suitable for producing male-specific amplitude-modulated trills. The sex difference in laryngeal synapses emerges during ontogeny. Here male synapses retain the juvenile state, whereas female synapses undergo changes in response to estrogen. This body of work constitutes the most thoroughly studied example of sexual differentiation of signaling behavior and its neural substrates.

The methods of signal detection match the diversity of signal production. For example, relevant auditory signals may be detected by the resonant property of peripheral sensors as in the antennae of mosquitoes (Roth et al. 1966), by specialized segments of the basilar membrane as in certain bats (Suga et al. 1975), and by higher-order neurons as in space-specific neurons of barn owls (Konishi 1995).

Mechanistic studies can be carried out on several different levels. Behavior is the first level at which signal detection can be analyzed. For example, in his classic work, von Frisch showed how honey bees communicate through dance the direction and distance of food sources. The “waggle run” part of waggle dances indicates the direction of a food source relative to the sun. Bees can communicate this informa-

tion by dancing on a vertical surface of their hive in total darkness. In chapter 4, Michelsen addresses the problem of how new recruits extract this information from the dancing bee. Recruits may derive it from the vibration of the comb by the dancing bee or from touching this individual. These methods do not seem likely. Michelsen casts doubt on even his own theory in which rhythmic airflows created by wing movements are supposed to provide the information. If one could manipulate either dancers or new recruits, one could analyze the dance language; therefore, it had been a dream to build a robotic bee. Most models had failed until Michelsen designed and built one. Studies of this robotic bee showed once again that bees need not use odors to locate food sources (cf. Gould 1975). The robotic bee also allowed the investigator to manipulate different components of dances, such as the direction and duration of waggle runs and sounds produced by the wings. The results confirmed the original hypothesis that the direction and duration of waggle runs encode the direction and distance of food sources, respectively. However, the direction of simple runs with sounds was also interpreted to indicate the direction of food sources. Thus bee dances appear to contain coding redundancy. This is an exciting first step in elucidating how new recruits read the codes contained in the dance language.

To communicate one's emotional states to other individuals is perhaps the oldest function of animal communication. Following on the footsteps of Darwin's major treatise on this topic, ethologists have studied the communicative function of facial and bodily expressions. The elaborate ethograms showing expression of threat and fear in wolves and cats are well known (Schenkel 1947; Leyhausen 1956). The recent advent of brain-imaging techniques has made it possible to correlate human sensory perception with the brain areas involved. Adolph reviews work on people whose amygdala is bilaterally lesioned for various reasons. These people fail to recognize facial expressions showing fear, although they have no problem in discriminating between individuals by face. The study of people with lesions in specific areas is likely to yield much information about the functional organization of the human brain. There are, however, constraints on this approach. One of them is the impracticality of single neuron recording in the human brain, although there have been a number of cases in which single neurons were recorded in patients during preoperative explorations. In fact, some studies show that the human amygdala contains neurons selective for faces expressing fear (see chapter 6).

It would seem naive to expect to find neurons selective for faces, because these stimuli could be encoded by ensembles of neurons in which each member is not specialized for any stimuli. Encoding of complex stimuli by single neurons appears to be the dominant method at least in the visual and auditory systems (see chapter 12). However, the reader must first understand how selectivity for such complex stimuli is

created. These sensory systems use parallel pathways to process different components of the stimulus. The codes for complex stimuli are then synthesized by collecting processed information from all parallel pathways. These “complex” neurons, therefore, represent the results of all processes that take place in the pathways leading to them. Since these pathways are designed to process biologically relevant stimuli, it is not surprising to find neurons selective for these stimuli at nodal loci of the entire network. The temporal cortex of the macaque monkey contains neurons selective for facial expressions and bodily movements. This makes sense, because facial expressions and bodily movements are biologically important signals in the social life of primates, as Perrett points out in chapter 6.

The biological relevance of stimuli is the most important prerequisite for sensory physiology. To show or infer biological relevance is relatively easy in animals that are adapted for extreme lifestyles such as hunting in the dark. Since bats navigate and hunt by echolocation, processing sonar signals must be important for them. This simple logic has led Suga and his associates to the fruitful exploration of the auditory cortex of bats (Suga 1992). In moustached bats, they charted the auditory cortex according to the stimulus selectivity of neurons. This map is now well known. However, auditory signaling in bats is not restricted to echolocation, as many species, including the moustached bat, have a substantial repertoire of social calls. How are these signals represented in the brain? Are there separate brain areas for echolocation and communication? Kanwal reviews the results of preliminary work to answer these questions. Two of the areas in the sonar map contain neurons that respond well to some of the calls. Some of these neurons are selective for a specific call or a class of calls, either because these calls contain an appropriate combination of excitatory and inhibitory frequencies or because they contain particular temporal patterns or both. These findings raise important questions as to how the bat interprets the response of these neurons, because they appear to represent both sonar and social signals.

Social relationships influence many aspects of communication. The nature of this influence and what mediates it have mostly been studied in laboratory settings and captive animals. For example, the effects of serotonin in establishing and maintaining social hierarchy have been extensively studied in captive animals including crayfish, lobsters, and monkeys (Raleigh et al. 1991; Edwards and Kravitz 1997). Wingfield and his associates (chapter 9) have made heroic and successful efforts to dissect the relationships between the sex hormones and the reproductive behavior of wild songbirds. One of the most interesting findings is the effects of behavior on the serum concentration of testosterone. The testosterone titre of territorial males rises when old neighbors are replaced by new ones and when their mates show precop-

ulatory soliciting behavior in response to injection of estrogen. This rise in testosterone titre occurs even when it is normally low, as during the care of nestlings. These and other findings indicate that the interactions between the endocrine and behavioral control systems change dynamically in different stages of the life cycle and that communication plays an important role in these regulatory mechanisms.

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