

Birdsong: An evolutionary parallel to human language

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Abstract

We review the present knowledge of instrumental, developmental, and communicative parallels between birdsong and language. Birdsong and human language turn out to be convergently evolved 'adaptive profiles'. Such convergencies are indispensable for our understanding of why and how these properties came into being at all. The German philosopher Immanuel Kant emphasized in 1803 tradition in birdsong in parallel with human culture. We specify the role of tradition in birds' vocal repertoire, syntax, and semantics. Comparing birdsong with human language embeds the hitherto purely anthropocentric approach to language into a causal evolutionary framework and helps to identify the selective forces as well as the ecological factors that forged the evolution of language and language-like communication.

Introduction

According to the *Encyclopaedia of Human Evolution*, language is an adaptation unique to humans (Deacon 1992: 128). This conviction has a long history:

Ever since Aristotle, philosophers have been concerned to demonstrate, in the most convincing manner possible, that human beings are significantly different from all other forms of life. It was not enough to demonstrate that human beings were unique, for each species is evidently unique in its way; rather, it was necessary to show that the human form was *uniquely* unique. (Abram 1997: 77)

In our own time, language is most often used to demonstrate the excellence of humankind. Biologists will argue that the uniqueness of any spe-

cies or ability must not just be conceived but has to be shown to exist; this can only be done by thorough comparisons. Of course, comparisons should not be made impossible in that language is dressed up with a list of allegedly essential attributes like feelings, consciousness, or exchange of thoughts, none of which can be identified in other species.

Deacon (1992) admits that the uniqueness and the biological basis of language are notoriously difficult to define. But by calling language an adaptation, he implies some ecological (physical or social) factors and corresponding selective forces that forged the evolution of language. For the reconstruction of evolutionary pathways, it is helpful to compare similar traits in different species or populations where they occur either because of common ancestry (homology) or because of independent adaptation (convergency). The usual anthropocentric approach follows a homology reasoning, expecting to find either ancestral versions or essential precursors of language among our mammalian and primate relatives. (The *caveat* that homologous characters are bauplan-inherent carryovers and not necessarily designed by selection for their present function will be discussed below.)

Convergency reasoning, on the other hand, is based upon functional similarities that evolved independently in different species. This situation helps to identify the selective forces and ecological (social or environmental) factors that are likely candidates which channeled the evolution of an ability toward similarity. Because evolution selects only for outcomes, not for mechanisms, convergent similarity may be achieved with different mechanisms that thereby reveal their functional relevance for the property in question. Properties found to correlate with particular ecological conditions are called 'adaptive profiles' (Dewsbury et al. 1982), indicating that a species must exhibit these attributes for success in a particular ecological niche (Davey 1989). We understand language and language-like communication as part of an adaptive profile.

Looking for language-like communication in other species, Deacon (1992: 129) confines his view to the non-vocal dance of the honeybee, the songs of the humpback whale, and the alarm calls of birds and vervet monkeys. And who wonders: Neither case shows a close similarity to human language. Surprisingly, Deacon does not mention birds' songs though they resemble human language more closely than any other animal traditive communication system so far studied. In fact, the German philosopher Immanuel Kant (1803) recognized the parallel between bird-song and human language and proclaimed that 'birds' song tradition through generations appears to be the truest in the world' (our translation).

Now, two hundred years after Kant, we want to re-examine the role of tradition in birdsong. We ask whether the lexical song elements, their syntactic arrangement, and their semantic content are open to social learning from tutor individuals. We keep in mind that social learning comprises both perceptual learning (learning to know) and imitative learning (learning to reproduce). Language is here arbitrarily defined as a system of traditive acoustic symbols by which social individuals communicate. The term ‘traditive’ has been introduced by Wickler (1982) to denote the transfer of information units from brain to brain via social learning. We will show that evolutionary reasoning based on birdsong can be helpful in understanding human language as an evolved communication system.

Challenging parallels between language and song

When the Australian Macquarie Dictionary (1988) lists the ‘non-linguistic communication of animals, in particular the language of birds’, under the ‘Language’ entry, this refers to the vocal expressions called speech in humans and song in birds. A comparative approach in fact reveals non-trivial similarities between speech and song in (a) vocalizing apparatus, (b) development, (c) overt acoustic performance, (d) communicative social interaction, and (e) evolutionary perspectives of traditive songs.

The vocalizing apparatus

Humans and many birds make use of a rich vocabulary of sound units (‘morphemes’) for social communication. A sound unit is defined as a physically distinguishable unitary vocalization. Vocal sounds are produced in the larynx in humans and in the syrinx in birds. Both structures are functionally similar. But birds are much more versatile vocalizers than humans because the syrinx is bipartite and the two sides are capable of acting either together or independently. In two-voice singing, they can produce two harmonically unrelated sounds simultaneously (Suthers 1990, 1997).

Specialized brain areas are responsible for learning, memorizing, and producing vocalizations. They can be identified by their functional activity in humans, while in songbirds (oscines), parrots, and hummingbirds the interconnected nuclei of a special song-control system are also defined neuro-anatomically (Nottebohm 1976; Gahr 2000).

The ontogenetic development

The development of song in young songbirds largely parallels that of speech in human infants (Marler 1970, 1973; Marler and Peters 1981), in particular in the following respects:

1. Humans and songbirds socially transmit sets of vocalizations from adult tutors to young individuals; social isolation leads to abnormal vocal development.
2. In humans and birds, there is an early critical period of life during which the ability for vocal learning is at its maximum. While imitative learning ability in many bird species may be restricted to a critical period early in life, learning to know the vocalizations of other birds (of mates, offspring, territory neighbors) is not. Existing predispositions have the effect of guiding the learning in certain directions, e.g. of distinguishing language or song from inanimate sounds. Moreover, nearly all bird species studied possess some genetically predetermined foreknowledge about the species-specific acoustic morpheme universals.
3. Hearing the individual's own voice is a vital factor in normal development, in particular during a babbling phase in human infants and a corresponding sub-song phase in young birds. The processes of assimilating the individual's own vocalizations to the memorized model sounds seem to be self-reinforcing, i.e. basically independent of any kind of reward from the outside.

The overt acoustic behavior

Sound units of the vocabulary are ordered in sequences. In birds, morphemes are called syllables; ordered sets of syllables may form song phrases, and phrases may then be combined in various ways to song types. Syntactic rules govern the combination of syllables, of phrases, and sometimes also a sequence of song types to form a complex song.

For social communication, humans and birds assist their vocalizations by visible body movements that are not causally connected to the sound production. A close connection between speech and gestures as a body language is known for humans (Feyereisen and de Lannoy 1991); their facial expressions may even decide the precise meaning of spoken words. Similar composite audio-visual signals are barely considered by ornithol-

ogists although a well-known connection between singing and body movements exists in many birds. While singing, they may bow or stretch head and legs, wag the tail, and quiver or flap wings. They thus display conspicuous postures and movements whose communicative function is largely unknown but would deserve closer study.

Due to the different travel speeds of sound and light, and the corresponding desynchronization of the two components with increasing distance from the sender, composite signals of precisely coupled auditory and visual components have a limited range. In dense vegetation (as well as when using a telephone), those signals will split: the acoustic component will reach near and far recipients, while the additional optical component will affect only a nearby recipient and may modify a response to the isolated acoustic component.

The problem posed by composite signals is illustrated with some non-oscine birds who deliberately position themselves (e.g. on treetops) to be clearly perceivable over large distances, and then in rapid rhythmical repetition display vocalizations and movements at the same time (tailwagging in *Trachyphonus* barbets, wingflaps in *Halcyon* kingfishers, head and knee bends in *Tockus* hornbills). While sending such composite auditory-visual signals, they prevent the optical and the acoustic rhythm to be in phase or otherwise develop a stable time relationship that could catch a perceiver's special attention. The resulting random mix of both rhythms (not easy to achieve physiologically) keeps the signal unambiguous, independent of distance (Wickler 1978).

Another interesting aspect derives from the potentially different provenance of the signal components. The meanings of human symbolic gestures are traditive traits. Their culturally mediated diffusion results in 'gesture flow', which often is coupled to linguistic, religious, and other cultural features and may give rise to national or local gesture dialects (Morris et al. 1981). Whether birds' body gestures that accompany singing are socially learnt is unknown. If form (and syntax?) of the movements was genetically preprogrammed, then a combination of species-specific posture sequences with acquired foreign songs could create new or distorted signals and provide new insight in their communicative function.

With all this in mind, we strongly suggest that future research into birds' and other animals' language-like communication should take into account both acoustic and visual components, as has been urged already a century ago by Craig (1908: 100): 'The song ought never to be studied (as hitherto it has been studied) without reference to the whole system of vocal and gestural activity'.

Communicative social interaction

Most birdsong studies concentrate on analyzing song as vocal monologue, sometimes complemented by an analysis of a recipient bird's reactions to the perceived song. But in many tropical bird species, individuals regularly exchange vocalizations and song phrases in duets, comparable to human individuals who take turns when talking. The systematics of dueting birds' turn-taking is largely the same as described in Conversation Analysis for human talk (Sacks, Schegloff, and Jefferson 1974; Levinson 2000). Dueting in birds is a very prominent socially organized vocal behavior, by definition of two participants who in the majority of known cases are pair mates.

The organization of taking turns in dueting differs between species and sometimes also between pairs of the same species. A simplest duet occurs in the dabchick *Podiceps ruficollis* (Bandorf 1968); it is built by both partners uttering an identical vocalization in strict (and very rapid) alternation. Here, as in many other species, turn-taking is predetermined in a species-specific way. In other species, however, turn-taking may be open to the individuals' own decisions and mutual agreement. If individuals have several song types available for dueting, turn-taking may become song type-specific (Wickler 1972). A dueting individual in any case elicits explicit vocal answers from its partner. On top of this, in the slate-colored boubou *Laniarius funebris*, the two sexes have different non-overlapping morpheme repertoires. The species' total vocal repertoire thus subdivides into an 'overt' repertoire, comprising the vocalizations produced by a given individual, and a 'silent' repertoire, comprising the vocalizations of the other sex, which the individual typically responds to, but which it never utters. This requires a memory in every individual for both gender repertoires (Seibt and Wickler 2000). A duet in this species may be compared to a dialogue between two persons who strictly stick to their different mother tongues but nevertheless understand each other.

Once dueting has become firmly established in a pair, its sequences of vocal utterances may become highly predictable (as if telling time and again the same proverbs). But duets of other species reveal a much more complex structure. Pair mates of the African drongo *Dicrurus adsimilis*, for instance, use different non-overlapping morpheme repertoires. In a duet, the elements produced strictly alternate between the birds. The occurrence of a particular element in a given moment depends on the previous elements of that individual's own repertoire and the preceding element of the partner. By presenting its own elements, the leading bird alters the probability of appearance of certain elements of the responding

partner. Drongo partners while dueting keep fluctuating between leading and responding, showing that both continuously monitor their respective partner's vocalizations (v. Helversen and Wickler 1971). Fluent dueting for more than a minute is indicative of a well-established drongo pair, while during pair formation short sequences are repeatedly initiated and may soon break off. Obviously, pair partners have to build up a common grammatical duet-framework and only then are ready for an interactive alignment process while dueting.

Evolutionary perspectives

Historical strains of socially learned vocalizations tend to diverge due to cultural drift and give rise to local dialects in humans and in birds. It follows from taxonomy that dialects in a bird species correspond to languages within the human species. Communication between representatives of the diverging strains may become increasingly difficult, rendering mating ever less likely. Where dialects limit gene flow, genetic evolution becomes constrained by tradition, and culture starts to keep genes on a leash (Salwiczek 2001).

The convergent evolution of language-like communication can be studied at two taxonomic levels: Between birds and mammals, and also within the birds among parrots, hummingbirds, and songbirds. These three unrelated bird orders developed very similar vocal systems, consisting of an elaborate syrinx structure, a specialized song control system in the brain, and the ability for both to copy vocalizations from tutors and to combine the learned vocal elements into complex sequences.

Impacts of tradition on birdsong

A methodological remark

If one wants to trace the path, the possible transformation, or final destination of a given structural or physiological element inside an organism, one has to mark that element in order to ensure its correct identification. The same applies when one wants to analyze the significance of traditive characteristics within a species' communication system. A convenient way to have vocal elements marked is to borrow them from a foreign species. This trick helps in analyzing the lexicon (vocabulary), the syntax, and the semantics of birds' vocal communication.

Lexicon and syntax

While the vocalization patterns of most bird species are genetically pre-programmed, all songbird species have to learn their songs, as described above. But most songbirds copy only their own species songs, due either to the social learning conditions or to a genetic predisposition (Davey 1989: 268). Young chaffinches, for instance, are unable to produce the chaffinch song unless they hear it, but naïve individuals will unfailingly identify and copy chaffinch song presented among a sample of foreign birdsongs.

Heterospecific natural birdsongs as well as man-designed tone sequences have been used to analyze the details of the song-learning process and its limitations. Güttinger (1979) studied greenfinches (*Chloris chloris*) and canaries (*Serinus canaria*) who possess a similar sized vocal repertoire of up to 40 syllables, though syllable shape and duration as well as the temporal structuring of syllable sequences are species-specific. Güttinger had greenfinches raised by canary foster parents. They copied more than 50 percent of the canary syllable repertoire precisely in shape and duration, but did not follow the canary's syntactic principles of temporal organization. Instead, the greenfinches arranged the canary syllables according to their greenfinch-specific temporal song architecture. This shows that the greenfinches did not blindly imitate what they heard from the canary but copied syllables as separate units to be filled in to their existing, but empty, syntactic structure.

In greenfinches, a song syntax seems to be predetermined, but it is not in other species. For centuries, European bird fanciers hand-raised bullfinch nestlings (*Pyrrhula pyrrhula*) and trained them to copy folk song melodies whistled by the human tutor. If the chosen melody lies within the natural range of wild bullfinch song, the birds will copy the whole series of notes exactly in duration, pitch, and rhythm (Güttinger et al. 2002). Offspring eventually raised by a 'folk-song bullfinch' learned the melody from the parent and will in turn transmit it to their own young. Once started, a foreign-song tradition may thus continue for several generations without renewed human intervention (Nicolai 1959). Here, as in other bird species able to copy foreign species songs, both song morphemes and song syntax are open to social learning.

Several bird species are called mimics because throughout life they are able to imitate vocalizations from other species. Ravens (*Corvus corax*) are known to copy a variety of sounds like a dog's bark, a turkey's gobble, a stork's bill-clap, and a human's cough (Gwinner 1964). When the British Post Office in 1965 introduced a new 'trimphone' receiver, thrushes (*Turdus philomelos*, *T. merula*) soon copied its distinctive ring to

the great displeasure of the phone owners (Slater 1983). Marsh warblers *Acrocephalus palustris* in their winter quarters pick up songs from African birds and utter them in their European breeding areas, thus telling the knowledgeable listener where they have been (Dowsett-Lemaire 1979). Thus, adoption of foreign song elements does occur under natural conditions in various songbird species.

Sufficient evidence has now accumulated to state that the neural song control system of songbirds is capable of acquiring, memorizing, and reproducing most sounds that the birds' ears can perceive. And the adult bird may imitate a huge variety of animate and inanimate sounds irrespective of their origin.

Biological functions of vocal copying

We know much about birds' vocal copying capacity but only very little about its biological relevance. In some instances it is used as a kind of address. Birds able to precisely copy individual vocalizations can also imitate idiosyncratic vocal characteristics of another individual. In territory disputes, rivals commonly start a vocal duel with a song phrase of the opponent and thus address their aggression. Such song type matching between neighbors during countersinging is known from many different species (Verner 1975). It indicates the significance of paying attention to available vocal information. Both countersinging between neighbors and dueting between pair mates may be structured as a dynamic system if the calls heard affect the calls made (Bertram 1970).

In several species of finches, pair mates adopt an almost identical flight call, which is typically given when in flight or just before or after flight. Both sexes are able to imitate the partner's flight call, and in a mixed-species pair (male pine siskin *Carduelis pinus* with female Eurasean siskin *C. spinus*), one partner copied the flight call from a foreign species (Mundinger 1970).

A special form of addressing an individual is found in ravens (*Corvus corax*) and common shamas (*Copsychus malabaricus*). In both species, individuals develop their personal vocabulary, but pair mates make use of vocalizations that 'belong' to the partner to call their mate 'by name', when for instance he or she should return to the nest (Gwinner and Kneutgen 1962).

The possibility to address particular individuals is a major advantage over anonymous signaling in birds as it is in humans. In our telephone network, we pay for the ability to select one addressee without bothering

a hundred others. And on the other hand, we happily limit our attention to our private phone's ring — though not without exceptions when we try to gain information by listening to other individuals' vocal interactions. Such 'eavesdropping' has also been shown to occur among birds (McGregor et al. 2000).

An important evolutionary consequence of vocal copying

Vocal copying of brood-parasitic widowbirds is of special evolutionary relevance (Nicolai 1964). Each species of widowbirds is a brood-parasite of a certain species of waxbills (Estrildidae). Unlike our cuckoos, a widowbird hatchling does not throw the host's young out of the nest but stays among them. A characteristic feature of waxbills' nestlings is a very conspicuous pattern of colored tubercles at the corner of the bill, as well as colorful markings inside the mouth and spots on the tongue and palate. This pattern is species-specific and intensively displayed to the parents when the nestling begs for food. Host parents will not feed any young that does not show the correct species-specific signal. However, as one of the most impressive cases of interspecific mimicry, each widowbird species has evolved an exact parallel to its host's mouth markings such that host parents cannot distinguish their own young from those of the parasite and consequently care for the parasite as well.

Now this situation sets the stage for an exciting case of co-evolution of genetic and traditive characters. Different populations of the paradise whydah (*Steganura*) have specialized on different waxbill host species with different nestling mouth markings, and the respective paradise whydahs evolved different genetic programs for producing their respective host species' mouth markings. However, adult paradise whydahs from different populations look very much the same and could easily interbreed. But matings between paradise whydahs with genetically different mouth markings would result in offspring with a hybrid pattern that would not be accepted by any host bird; so these young would be doomed to starvation. In nature, hybridization is prevented by the fact that whydah nestlings learn the entire species-specific song of their foster parents. Male whydahs later use this foreign song in courtship. A female can therefore recognize from that song by what species of waxbill a male was raised. Song thus serves as a socially acquired marker for the individual's genetically determined mouth colors. As a result, mating takes place only between adult paradise whydahs that have learned the same waxbill song and thus must carry identical mouth marking genes.

If host birds develop local dialects, these are faithfully copied by the parasites. Foreign song learning thus links cultural to genetic evolution, which occurs in parallel in two taxonomically different bird families. This is the most impressive example within the animal kingdom that traditive elements direct genetic evolution. Less conspicuous are various other cases where traditive characters guide mate choice, to the effect that potential mating partners' genotypes are disfavored due to being linked to a foreign non-genetic trait, be it imprinted food preferences, learned preferences for nesting site, etc.

Birdsong semantics

A methodological remark

In the introduction to their book on learning, Friederici and Menzel (1999) state that, unlike human language, birdsong is not a recursive system allowing an indefinite number of phrases. This may be true, but to verify this statement we would need to know the meanings attached to birdsong elements. There is only one way to identify the meaning of a signal under natural conditions, and that is to analyze how the signal affects the receiver's behavior (Cherry 1966). According to Craig, 'an influence of one bird over the behavior of another is social control', and 'the song is one means of social control' (1908: 88 and 99).

However, communication involves both a signal sender and a signal recipient, both playing different roles. Natural selection therefore may act against conveying accurate information, as Krebs and Dawkins (1984) have shown. Signaling is costly, so the signaler must benefit from sending a signal. And the benefit obviously must come through a recipient's response to that signal. A signal therefore will be designed to manipulate a recipient's behavior according to the sender's interest. On the other hand, being attentive and responding to a signal is costly, too, and the receiver should not react to a signal unless it is also in his interest. Recipients therefore will be selected to be resistant to the manipulative intent of the signaler. Due to this evolutionary arms race, the resulting communicative function of any signal will be a situation-specific compromise between the sender's and receiver's interests. (This point seems particularly relevant for dueting birds.)

Two types of natural birdsong signals have been identified: those relating to an outside event, and others that announce a particular behavioral preparedness of the signal sender.

Vocalizations that indicate an outside event

Best-known examples are the warning calls that announce an immediate threat by a predator. Different calls are used with respect to aerial and ground predators, and the birds respond differently to each alarm call type; they look up and run for cover following aerial alarms but scan horizontally following ground alarms. Special experiments are required to clarify whether a call stands for the dangerous animal, or for the situation, or for the appropriate counteraction, i.e. whether a call should be understood as 'raptor in the air', or 'danger from above', or 'rush under a bush' (Evans and Marler 1995).

A special case is the mobbing behavior performed by experienced individuals when a known predator is visible. The behavior combines conspicuous vocalizations with movements that unmistakably point toward that predator. Studies by Curio (1988) revealed that mobbing attracts inexperienced individuals and serves to socially transmit recognition of local predators to them. In the critical experiments, naïve European blackbirds (*Turdus merula*) were exposed to some neutral object, e.g. a multicolored plastic bottle, while an experienced bird was tricked into mobbing a resting owl that was shielded from view of the naïve birds. So the naïve birds connected the predator harassment to the neutral object and from there on habitually mobbed this object. They also handed this mistaken information on to their own offspring.

Mobbing behavior patterns including mobbing vocalizations seem to be genetically preprogrammed. The general meaning of the vocalization as an indicator of immediate danger is known to the birds from the beginning. But they have to be instructed about the source of danger in order to react properly. Because of a general similarity between different species' warning calls, birds can use foreign species' mobbing calls to acquire knowledge about the referential object, which proves cross-species tutoring of enemy recognition.

Vocalizations that relate to the individual's state and motivation

As nutritional stress in early development just before and after independence interferes with the development of brain nuclei underlying song learning and production, song may be a reliable indicator of general male quality (Nowicki et al. 1998). Repertoire size may index male age (having had a long time available for learning), and song rate can indicate good condition (as singing is energetically costly); so a female can read from a male's song whether he is healthy, experienced, and owns a resource-rich

territory (Vehrencamp 2000). Of course, male song parameters may meet different interests of, and indicate different things to, male and female receivers.

There are birdsong phrases that correlate with the singer's current physiological state; thus by being context sensitive they allow an attentive conspecific to infer the singer's motivation from its vocal utterances. Tyrant flycatchers (genus *Sayornis*) produce a number of different combinations of vocal elements. The combinations not only identify the communicator but furthermore indicate different probabilities that he will fly, attack, or escape, be non-aggressive, or associate with the individual at whom his song is directed (Smith 1970). Some song themes of an individual tufted titmice (*Parus bicolor*) male's repertoire likewise indicate a tendency to escalate an encounter while others indicate a low probability of aggression or a tendency to terminate an encounter (Schroeder and Wiley 1983). This information thus comprises the messages of the vocalizations (Smith 1970).

Furthermore, some sex-specific vocal repertoires of songbirds are copied only from the consensual parent (sons learn from their fathers, daughters from their mothers). Traditive vocalizations of the stripe-backed wren *Campylorhynchus nuchalis* are both family-specific and sex-specific, to the effect that males in the same patriline have nearly identical repertoires, and females in their same matriline also have nearly identical repertoires. Thus, as vocal traditions separately follow patrilines and matriline, vocal cues reflect both sex and kinship (Price 1998).

Meaningful duets

Both the sender and receiver could benefit if the receipt of a signal was acoustically confirmed. In view of the fact that several senders may be active simultaneously, it would be useless to broadcast a general 'thank you' signal anonymously to whom it may concern. Instead, birds able to copy song elements from one another develop specific vocalization patterns between sender and receiver to acknowledge the signal receipt. This is common practice among pair mates in several species in that one bird simply echoes the partner-specific vocalization. It may be seen as a primitive type of duet.

Some birds perform more complex 'song reply-games', which are most conspicuous to us if the birds use folk melodies that they copied from a human tutor. An early example was described by Henschel (1903). He had a young canary that copied the melody 'God save the King' from a bullfinch that had previously learned the melody by human instruction. If

the bullfinch increased a time interval as though it were stopping, the canary would take up the tune where the bullfinch had stopped and properly finish it. A parallel case was reported by Waite (1903) from Australian magpies *Gymnorhina tibicen*. One bird had as a nestling been taught a simple 15-note flute melody containing a pause after the eighth note. Several years later, a second individual copied that melody from the original magpie. After some time, the birds produced the melody together; one commenced the melody up to the pause, then the other finished the strain. When the second bird died, the original one produced the whole melody alone, as was its original custom. Obviously, in several bird species, individuals tend to cooperate in vocal behavior indicating that not only pair mates benefit from vocalizing together in a coordinated manner.

This occurs as well under natural conditions if partners divide their typical song types between them such that one bird adds the particular part of a given song which the partner left out. Some tropical shrike species thus perform perfect song phrase partitioning (Wickler and Seibt 1982). These cooperative vocalizations may easily become meaningful duets if composed of song phrases that correlate with the singer's current physiological state. Through vocal communication, pair mates may then mutually influence each other and coordinate their behaviors for cooperative enterprises, like reproduction, broodcare, and territory defense (Sonnenschein and Reyer 1983).

The vocalizations of an individual uttered during elaborate dueting may become highly informative in that they tell (a) the identity and (b) the sex of the singer, (c) that the singer is engaged in a pair, (d) to whom the singer is mated, and (e) if complexity of dueting is refined over time (as in the drongo mentioned above as well as in the African parrot *Poicephalus gulielmi*; Venuto et al. 2001), the degree of vocal synchronization indicates the stability of the pair bond.

Vocalizations connected to cognitive concepts

By teaching birds words from our own language as well as their meanings, we come to understand that they are in fact able to connect cognitive concepts to specific vocalizations. Parrots, for instance, can be trained to copy human words and use them in a 'naming' game, associating a word with a specific object or category. The most sophisticated studies in this context have been performed by Pepperberg (2001) with African gray parrots (*Psittacus erithacus*). A bird of this species can label many objects and categorize them according to shapes or colors, using

human words as labels. Confronted with collections of unique combinations of items that differ in color and shape, the bird on a vocal query of ‘What color?’ or ‘What shape?’ has to categorize the same item with respect to color at one time and shape at another. Furthermore, the bird proved able to correctly answer when queried ‘What color is object X?’, ‘What shape is object Y?’, ‘What object is color-A?’, ‘What object is shape-B?’, and even ‘What object is color-A and shape-C?’. Thus the bird understands all elements in the query and categorizes conjunctively. Drawing a comparative conclusion, Pepperberg provocatively states ‘that a nonhuman, nonprimate, nonmammal has a level of competence that, in an ape, would be taken to indicate that equal to a human’ (2001: 59).

These experiments test the animals’ cognitive ability to cope with human categories that may not be theirs and to name objects that they do not encounter under natural conditions. On the other hand, we know that birds under natural conditions do identify and name individuals, but there is no test available to find out whether they also categorize individuals.

Conclusive suggestions

We want to stress the importance of studying convergencies as independently evolved functional similarities. Even if implemented differently in detail in different species, such convergently evolved properties are indispensable for our understanding of why and how they came into being at all. This will also help to identify the selective forces as well as the ecological factors that forged the evolution of language-like acoustic communication three times among birds, once among human primates, and presumably once in nonprimate mammals — whales. Comparing bird-song with human language should thus help to embed the hitherto purely anthropocentric approach to language into a causal evolutionary framework. For instance, among birds, language-like phenomena correlate with sociality, but not with the ability to use tools or master technical problems. Thus language(-like) phenomena may be connected to social rather than technical intelligence. Furthermore, parrots and some other social birds normally copy only vocalizations within their group (Nottebohm 1970; Price 1998). This suggests that the original advantage of vocal copying was to address individually known conspecifics and to name them rather than objects.

To get insight into how an animal communication system becomes structured, and how meaning may be attached to vocalizations, we

maintain that it is methodologically important to install foreign vocalizations (including human words) into the vocal system of the species under study.

From a consideration of animal proficiencies that became apparent only under laboratory conditions, Rensch (1970) concluded that the brains of higher animals are generally pre-adapted to higher cognitive capabilities than required for their life under natural conditions. In order to enable explanation of animals' behavior in their natural environment, so-called Cognitive Ecology aims at integrating cognition, evolution, and behavior (Healy and Jones 2003). But it is important to realize that natural selection does not precisely tailor an organism to the requirements in its environment. Not all characteristics of an organism evolve to subservise some adaptive function. This becomes apparent by experimental selection for a given behavioral trait when correlated effects appear on other overt characters. For example, selection for positive or negative geotaxis in *Drosophila* affects courtship duration, locomotor activity, and arisal morphology as well (Pyle 1978); and selection for tameness in arctic foxes resulted in extra-seasonal estrus in females, altered vocalizations, and coat piebaldness in addition (Belyaev 1979). Natural selection on special abilities, e.g. learning to adopt new foraging patterns, may well favor other learning abilities too. But those abilities may remain hidden in the individuals that possess them because the experiences necessary for them to be revealed in development will not be provided by the environment in which the population lives. Abilities that make no contribution to the animal's ontogenetic adaptation to its environment are therefore called 'ecologically surplus abilities' (Johnston 1981). If circumstances change, such surplus abilities may be available as proto- or pre-adaptations (Bock and von Wahlert 1965; Gans 1968) and may then turn up only in experiments on animal learning that constitute a new, though artificial environment. Complex communication systems may well be predisposed in many species without becoming apparent as long as they are neither favored by selection nor rewarded in a learning individual.

Surplus abilities will also relate to brain function. Language-like acoustic communication is linked to certain brain areas that deal with complex cognitive abilities. Several brain areas have taken on new roles that they were not originally designed for by selection. If an area serves different functions, such as planning and language in humans, we cannot be sure which was the primary one. The role that an area presently plays (e.g. in language-like communication) may not have arisen from selection for that purpose but may represent a property that emerged secondarily. Testing this possibility will require identifying the function that selection initially designed that area for.

While laboratory studies are normally designed to achieve a better understanding of a supposedly adaptive behavior that was first encountered under natural conditions, a reverse situation arises in cognition research, if laboratory experiments expose an ability which clearly is an epiphenomenon of some biologically relevant performance. Then, in a second step, we have to identify the pertinent behavioral context in the field. This touches upon a central problem of present cognition research: The vertebrate brain is energetically a very expensive organ, and selection will unlikely equip a species with the burden of excessive brain capacities. From an evolutionary point of view, one would favor the hypothesis that any proficiency for a task exhibited in the laboratory is a side effect of a cognitive ability that evolved for some other purpose in the species' natural environment. Assuming that learning abilities and intelligence will evolve largely because the animal requires them in its own environmental niche, we can foresee an increasing demand of ethological field studies to supplement the results obtained with psychologically oriented laboratory studies.

The 'ecological intelligence' approach (see Bshary et al. 2001) to language as a specific cognitive ability should include birds in particular because, in contrast to primates, they include numerous closely related species that differ in their social and environmental specializations as well as different versions of ecologically related communication systems.

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