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Editorial

Language and birdsong: Introduction to the special issue

By most accounts, language is uniquely human. No other species has a communicative system with such expressive power, one that allows us to transmit a seemingly endless set of meanings to our conspecifics. Every sentence we produce is composed of smaller linguistic units put together in a rule-governed manner. The standard view is that sentences are put together using syntactic rules that define hierarchical relationships within each sentence. These rules are claimed to contain recursive elements that permit sentences to be combined to form ever-longer sentences. As a consequence, language has a structure and open-endedness that is unlike the communicative systems of any other species, as far as we know (Hauser, Chomsky, & Fitch, 2002). Historically, considerations such as these have discouraged efforts to identify potential animal models of language, even though a comparative approach has been essential in ascertaining the neurobiology of other cognitive functions (but this has started to change in recent years; cf. Holy & Guo, 2005).

Even if language in its entirety is unique, however, certain aspects of it might not be. It is at least conceivable that useful homologies or analogies might exist between aspects of speech and language¹ and the communicative systems of other species. For example, one essential characteristic of human language is that it is based on a capacity for vocal learning with reference to auditory feedback. Humans are not born knowing the sounds that are relevant to the language they will speak. Vocal learning is itself a rarity in the natural world, but it is not unique. The short list of known vocal learners among animals includes parrots, some hummingbirds, bats, elephants, marine mammals such as dolphins and whales, and humans. But by far the most numerous vocal learning species (at about 4000) are the oscine songbirds. From an ontogenetic perspective, the acquisition of speech and birdsong have compelling parallels (Doupe & Kuhl, 1999). Humans and songbirds learn their complex, sequenced vocalizations in early life. They similarly internalize sensory experience and use it to shape vocal outputs, through sensorimotor learning and integration. Auditory feedback from self-generated vocalizations is necessary for vocal learning, as it is in humans. Songbirds show similar innate dispositions for learning the correct sounds and sequences; as a result, humans and some species of songbird have similar sensitive periods for vocal learning, with a much greater ability to learn early in life. These behavioral parallels at least make it plausible that there might be some non-trivial similarities between birdsong and speech, with respect to underlying neurobiological mechanisms.

Recent work has shown other compelling similarities. For example, songbirds rely on a specialized telencephalic-basal ganglia–thalamic loop to learn, produce, and perceive birdsong (Brenowitz & Beecher, 2005). Disruptions to this circuit disrupt the sensorimotor learning needed to acquire song, and also the sequencing skills needed to produce and properly perceive it. Other research has revealed a remarkable homology in this circuit between birds and mammals (Doupe, Perkel, Reiner, & Stern, 2005). This circuit in human and non-human primates involves loops connecting several regions in the telencephalon to the basal ganglia. Afferents from frontal cortex densely innervate the striatum of the basal ganglia, which also receives inputs from several other areas of the cortex. The striatum seems to control behavioral sequencing in many species (Aldridge & Berridge, 1998). Spiny neurons, the principal cells of the striatum, have properties that make them ideal for recognizing patterned sequences across time (Beiser, Hua, & Houk 1997).

Potentially important genetic similarities might also exist (see White & Mello, this issue). The much-discussed FoxP2 gene is similarly expressed in the basal ganglia of humans and songbirds (Teramitsu, Kudo, London, Geschwind, & White, 2004; Vargha-Khadem, Gadian, Copp, & Mishkin, 2005). A FoxP2 mutation in humans results in deficits in language production and comprehension, especially aspects of morphosyntax that involve combining and sequencing linguistic units (Marcus & Fisher 2003; Vargha-Khadem, Gadian, Copp, & Mishkin, 2005). Knockdown of FoxP2 expression in the avian striatum causes incomplete and inaccurate song learning (Haesler et al., 2007).

Importantly, the birdsong system offers a number of advantages as a model for identifying neural mechanisms underlying vocal learning and behavior (Brenowitz, Margoliash, & Nordeen, 1997). Song is controlled by a discrete and accessible neural circuit, and the basic details of the song control circuit are now reasonably well understood. If useful parallels do exist in the neurobiology underlying birdsong and language (or between birdsong and speech), then the full range of neuroscience methods could be applied to this model system.

Of course, there are limits to what this model system can tell us. Most fundamentally, humans combine their discrete speech sounds to form larger, more abstract representational units of meaning and structure (morphemes, words, phrases, clauses, sentences, etc.). The compositional syntactic structures we call sentences allow us to convey a huge set of equally compositional meanings. It is this mapping between syntactic structures and complex, compositional meanings that gives human language its communicative power. This is something that songbirds cannot

¹ Speech refers to the production and perception of speech sounds, whereas language also includes the levels of words, sentences, and larger units of discourse.

do. Even so, recent work has shown that white-crowned sparrows (at least under certain conditions) compose their song from smaller song phrases while singing (Rose et al., 2004), and that starlings can acquire an abstract rule that describes the patterning of familiar motifs (see Knudson & Gentner, this volume). These abilities are clearly more limited than human-type syntax but they are remarkable nonetheless: they suggest that the properties of compositionality and abstract rule learning, which are so central to language, are not beyond the capabilities of some oscine songbirds.

This special issue of *Brain and Language* is devoted to a consideration of birdsong and its potential relevance to speech and language. Several contributors to this volume provide useful descriptions of the birdsong circuit (for example, Margoliash & Schmidt), but a basic introduction is not included; interested readers might consult Brenowitz et al. (1997). The topics covered include song learning (Kirn), song production (Goller) and perception (Knudson & Gentner, Mello), brain development and song (Kirn), genetics (White, Mello), and sleep and song learning (Margoliash & Schmidt). Also included are commentaries by two eminent pioneers in the field of birdsong research (Konishi, Nottebohm). Finally, in order to place birdsong research in a wider context, we have also included contributions on vocal behavior in parrots (Pepperberg) and non-human primates (Seyforth & Cheney). The main goals of this special issue are to provide researchers who study human language with an up-to-date overview of the state of research on vocal learning and behavior in songbirds, to help build appropriate links, and to identify important limitations when relating this research to human speech and language.

Although definitive conclusions are probably not possible at this time, we believe that the time is ripe for a thoughtful consideration of possible links between birdsong and language, and, more generally, the prospective utility of a comparative approach to the neurobiology of communicative systems.

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