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Review

Investigation of musicality in birdsong

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ABSTRACT

Songbirds spend much of their time learning, producing, and listening to complex vocal sequences we call songs. Songs are learned via cultural transmission, and singing, usually by males, has a strong impact on the behavioral state of the listeners, often promoting affiliation, pair bonding, or aggression. What is it in the acoustic structure of birdsong that makes it such a potent stimulus? We suggest that birdsong potency might be driven by principles similar to those that make music so effective in inducing emotional responses in humans: a combination of rhythms and pitches—and the transitions between acoustic states—affecting emotions through creating expectations, anticipations, tension, tension release, or surprise. Here we propose a framework for investigating how birdsong, like human music, employs the above “musical” features to affect the emotions of avian listeners. First we analyze songs of thrush nightingales (*Luscinia luscinia*) by examining their trajectories in terms of transitions in rhythm and pitch. These transitions show gradual escalations and graceful modifications, which are comparable to some aspects of human musicality. We then explore the feasibility of stripping such putative musical features from the songs and testing how this might affect patterns of auditory responses, focusing on fMRI data in songbirds that demonstrate the feasibility of such approaches. Finally, we explore ideas for investigating whether musical features of birdsong activate avian brains and affect avian behavior in manners comparable to music’s effects on humans. In conclusion, we suggest that birdsong research would benefit from current advances in music theory by attempting to identify structures that are designed to elicit listeners’ emotions and then testing for such effects experimentally. Birdsong research that takes into account the striking complexity of song structure in light of its more immediate function – to affect behavioral state in listeners – could provide a useful animal model for studying basic principles of music neuroscience in a system that is very accessible for investigation, and where developmental auditory and social experience can be tightly controlled.

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1. Introduction

Birdsong is among the most striking vocal displays in nature and among the best studied communication systems in animals (Catchpole and Slater, 2008). Juvenile songbirds acquire their songs by imitating songs of adults. Usually only males sing but in some tropical birds both sexes sing duets in complex and melodious ways (Thorpe, 1972). Birdsong has provided a useful model system for vocal learning through research in ecology, animal behavior, neuroscience, physiology, psychology and linguistics and thus

provides widely used textbook examples. Many studies have shown that singing behavior in most species has a dual function by attracting females and by serving as a territorial signal to keep out rivals (Catchpole and Slater, 2008). Yet, it is not entirely clear why birds sing in such complex ways (Rothenberg, 2005; Mathews, 2001), and the amazing diversity in birdsong still raises questions with respect to the features that make it such an important biological stimulus. Most research on birdsong emphasizes its ultimate function rather than its structure. However, the vast differences in the length and complexity of species-specific songs cannot be easily explained in terms of functions like territory defense and mate attraction. As much as we know, the functions are by and large the same between species or individuals of a species, so why are the structural qualities so different?

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Much of the research into song structure has been content with accepting the signal structure as largely arbitrary (which is, of course, compatible with Darwinian processes including sexual selection). Classifying song syllables into arbitrary indiscriminate types followed by analysis of the statistical structure of those types has proven reasonable and useful. Based on this approach, in many species stable song types have been identified as production units so that repertoire sizes can be quantified (Catchpole and Slater, 2008). Statistical song characteristics such as repertoire size, singing versatility and production of specific song components have indeed been identified as salient to avian listeners (Catchpole, 1980; Forstmeier et al., 2002; Hasselquist et al., 1996; Kunc et al., 2005; Naguib et al., 2002; Podos, 1996; Podos et al., 2009) and as functionally relevant (Catchpole, 1983; Kipper and Kiefer, 2010; Naguib et al., 2011). While this statistical analysis of type classification has its uses, it tends to deflect analysis away from the formal relationship of adjacent types (i.e., notes or phrases) to each other. If birdsong and music share similar mechanisms in affecting the behavioral state of the listeners, such statistical features would not reveal much of it: first order statistical features of music (e.g., number of note types) have little to do with how music can evoke emotion (see also Huron, 2006; Sloboda, 2005; Egermann et al., 2013). Instead, it is more likely to be the dynamic structure, e.g., the building up an arc of suspense, confirming or violating the expectations of the listener, forming phrases containing a typical beginning, middle, or end, which make it work (Huron and Ollen, 2003; Meyer, 1956; Ng, 2003). Similarly, consideration of birdsong structure dynamics—for instance, how its rhythms or pitch intervals unfold through time—may reveal important aspects of its effects on the behavioral states of listeners. Further, for humans and possibly also for birds it is much easier to remember a melody than a random collection of notes (Deutsch, 1980). Such dynamic features might bind together several song elements into a cohesive percept. This might allow listeners to quickly assess a performance: otherwise a common nightingale (*Luscinia megarhynchos*) would need to listen to a male song for about an hour to assess its full song repertoire (Hultsch and Todt, 1981; Kunc et al., 2005; Kipper et al., 2006) and to compare several males would need to do so multiple times to assess each one's repertoire size. Yet, prospecting males and females initially spend very short periods near singers (Amrhein et al., 2004; Roth et al., 2009), suggesting that they quickly manage to extract principle features of the singing performance. On the side of the singers, focusing on such features makes sense for another reason: singing often happens in a noisy communication network where singers compete for attention by females (McGregor and Dabelsteen, 1996; Naguib et al., 2011). Song must therefore be designed to proximately attract and maintain the attention of its receivers, which the singers might achieve by manipulating rhythmic timing, amplitude, or other features.

2. Human sounds and bird sounds: how birdsong, bird calls, language, and music are related

In recent research, structural aspects of birdsong have more routinely been compared to human speech and language than music (Abe and Watanabe, 2011; Berwick et al., 2012; Bloomfield et al., 2011; Bolhuis et al., 2010; Fitch, 2011; Gentner et al., 2006, 2010; van Heijningen et al., 2009; Lipkind et al., 2013; Margoliash and Nusbaum, 2009, to just name a few). This might be so because both share the striking and rare trait of vocal learning through the acquisition of complex vocal sequences by sensory–motor integration processes through practice early in life (Doupe and Kuhl, 1999), involve homologous brain structures (Jarvis et al., 2005; Jarvis, 2007) such as a specialized telencephalic–basal ganglia–thalamic loop (Brenowitz and Beecher, 2005; Doupe

et al., 2005; Jarvis, 2007), and possibly even rely on similar genetics (reviewed by White, 2010).

However, the limitations of the language–birdsong comparisons are obvious, since birdsong lacks the semantics of language with its mapping of combinable syntactical elements on accordingly combined meaning (for reviews, see Berwick et al., 2011, 2012). Note that contrary to birdsong, the bird sounds classified as “calls” often have specific meanings, like “I’m hungry,” “Get away from my nest” or “Watch out everyone, there’s a predator overhead” (see Marler, 2004, for a review). These usually innate sounds are much closer to linguistic utterances than songs because they refer to specific messages (although they don’t seem to be combinatorial like language units; Hurford, 2011). In contrast, the songs of birds are repeated over and over again, like human songs. They are organized formal performances with a typical beginning, middle, and an end. The very structure, form, inflection, and shape of birdsongs are independent of both a concrete message or an ultimate function, which is reminiscent of human music and, indeed, it is not likely a coincidence that so many human languages call such sounds of birds “songs,” distinguishing them from the more speech-like calls. Further parallels between birdsong and music exist: 1) Humans find listening to music rewarding and are willing to spend time and money to hear it. Likewise, birds are attracted by birdsong and take some effort to hear it (Adret, 1993; Eriksson and Wallin, 1986; Gentner and Hulse, 2000; Riebel, 2000). 2) Like human musicians, birds distinguish between performing their song for others (directed song) and practicing for themselves (undirected song) (Dunn and Zann, 1997; Hall, 1962; Morris, 1954a,b): directed song is behaviorally different (often accompanied by dance, faster, more stereotyped) and relies on different brain activation and dopamine release patterns (Hara et al., 2007; Jarvis et al., 1998; Kao et al., 2008; Sakata et al., 2008; Sasaki et al., 2006; Stepanek and Doupe, 2010). 3) Birdsongs are transmitted vertically from parent to offspring as well as horizontally (between individuals of a population), leading to regional dialects that are subject to cultural evolution (Feher et al., 2009; Soha and Marler, 2000; West and King, 1985). This is paralleled by regional musical traditions and cultural evolution of musical styles.

Despite these numerous similarities, there have been fewer comparisons of birdsong structure to the structure of human music than language (Araya-Salas, 2012; Baptista and Keister, 2005; Dobson and Lemon, 1977; Fitch, 2006; Gray et al., 2001; Hartshorne, 2008; Kneutgen, 1969; Marler, 2001; Slater, 2001; Taylor, 2013; Tierney et al., 2011); attempts have sometimes been met with skepticism (see for instance Benitez-Bribiesca, 2001, and responses to Gray et al., 2001). A reason for this could be that musicality is a highly subjective concept. There are no simple quantifiable measures of musicality that can be extended across species. In fact, given that humans can make today music out of noises, gestures, patterns and textures, it has become hard to even find definitions that encompass only the total of human musicality. Not all music has a regular “beat” (birdsong rarely does) and only some music is based on regular sets of pitches known as scales.

Instead of deriving formal concepts from western music, trying to identify these predefined concepts in the songs of different birds, and then attempting to judge categorically if birdsong is musical or not, we can ask more generally how overall patterns in birdsong, including dynamic transitions from the expected to the unexpected, may affect a bird’s behavioral state and the behavioral state of its listeners. The proximate function of driving emotional responses through complex, structured, non-semantic sound streams might be a powerful parallel between music and birdsong. We expect that their structures would be shaped by and could be understood in terms of the function of driving emotional responses, as is assumed for music (Huron, 2006; Meyer, 1956) and has been

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