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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 bird*song*, 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-sematic 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

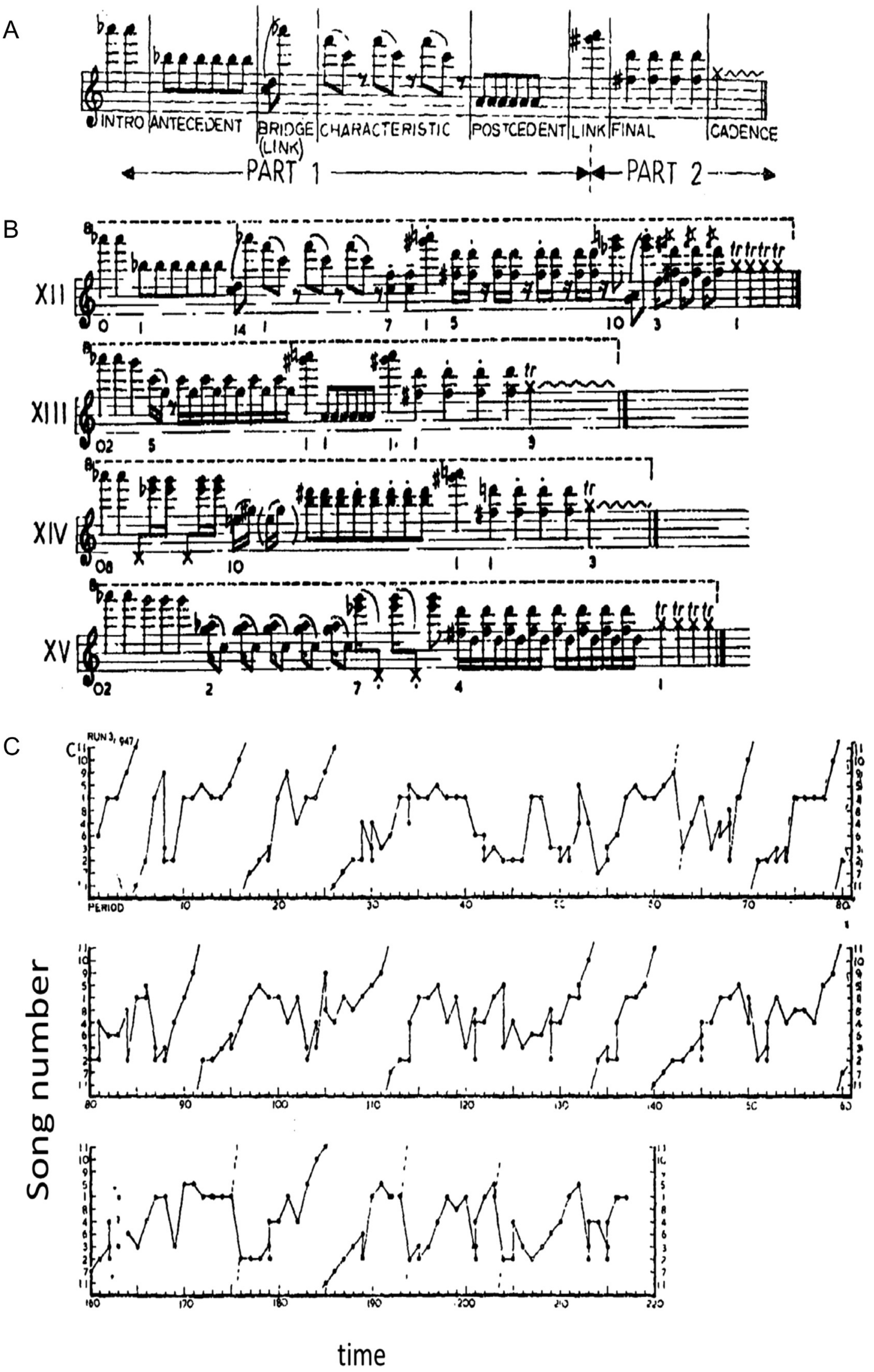

Fig. 1. Olavi Sotavalta's nightingale song analysis (Sotavalta, 1956). A, Generalized musical structure of each phrase. B, Excerpts from his catalog of all the phrases sung by his two study birds. C, Analysis of sequence of phrases in the nightingale song, showing a loosely patterned progression through the repertoire.

proposed for birdsong (reviewed by Riters, 2011). If this is true, it might become practical to use current techniques in music theory to design cross-species experiments.

However, current measures of structural aspects of birdsong are of limited use when it comes to investigating how song might drive its listeners' emotions. For example, showing that a male bird with the most number of syllables or the most complicated song has more mating success may work, but only in a small number of species, including the sedge warbler (Catchpole, 1980; Catchpole and Slater, 2008). It is therefore desirable to find a more nuanced but quantifiable esthetic sense that could work in species with more complex and refined songs such as nightingales, butcherbirds, thrashers, wrens and mockingbirds. As in human music, the most and the loudest is not always the best. As Darwin noted in a letter to Asa Gray, "birds have a natural esthetic sense. That is why they appreciate beautiful sounds." What are the sounds most beautiful to each species? We should strive to measure that.

3. A history of birdsong aesthetics

Ours is by no means the first plea for a more esthetic approach to making sense of birdsong. One of the most interesting attempts to apply musicological terminology to birdsong came from the process philosopher Charles Hartshorne (Hartshorne, 1973). Based on qualitative observations, he proposed that nearly every conceivable attribute of human music exists somewhere in the songs of birds: *accelerando* in the field sparrow (*Spizella pusilla*) and ruffed grouse (*Bonasa umbellus*) and *ritardando* in the yellow-billed cuckoo (*Coccyzus americanus*); *crescendo* in Heuglin's robin chat (*Cossypha heuglini*) of Africa and *diminuendo* in the Misto yellowfinch (*Sicalis luteola*) of South America; harmonic relations in the crested bellbird (*Oreoica gutturalis*) of Australia and the warblers of Fiji; and themes and variations in the Bachman's sparrow (*Peucaea aestivalis*).

The most complex birdsongs often include many such musical elements in a single song. Below, we present sonograms of thrush nightingale songs that illustrate this (Fig. 2). Similar analyses were made by Olavi Sotavalta, who made diagrams of the thrush nightingale's (*Luscinia luscinia*) song that resemble our sonograms but using modified musical terminology instead (Fig. 1A; Sotavalta, 1956).

Sotavalta segmented the bird's many phrases and musically notated them (Fig. 1B) before analyzing their sequence and concluding that the bird went through his phrases in a loosely patterned order (Fig. 1C). There was a sense of a periodic progression through the repertoire but no sequence of riffs was precisely the same as the next. Sotavalta's approach is an interesting hybrid between musical notation and quantitative statistical thinking. While he wasn't able to do multivariate statistical analysis yet, he developed hybrid visualizations that would make sense to musicians, with their sense of sound and order unfolding through time. Since then, there have been only a handful of studies that consider the musicality of complex birdsongs (Baptista and Keister, 2005; Brumm, 2012; Craig, 1943; Dowsett-Lemaire, 1979a,b; Earp and Maney, 2012).

Are these merely subjective evaluations or is this a window onto a species-wide nightingale esthetic? Here we propose a simple framework for investigating how the statistical structure of birdsongs can be described in terms that are not foreign to musicians, and then address the functional question of identifying which structural aspects affect a bird-listener's behavior. To achieve that, we will need to develop descriptive models of birdsong that are compatible with human music, including representations of pitch intervals and of rhythms that could reveal patterns of rhythmic timing, melodic course, etc. The approach is generic enough to avoid introducing human-music-centric (or even worse, western-music-centric) paradigms and biases into the analysis. Then, we discuss methods for testing whether putative musical features of the song activate neural loci and affect behavioral states in birds in a manner that is comparable to how music activates human brains and affects human behavior.

4. Searching for sound structures that have "emotive power"

When trying to identify which aspects of birdsong make it a powerful emotion-manipulator, our own esthetic sense may be useful as a first guide: humans are attracted to the songs of many bird species and often find them musical, organized, and esthetically pleasing. Many species' songs are characterized by a mixture of clearly-pitched whistle tones, rhythmic clicks and buzzes. Consecutive pitch intervals tend to differ in direction, in marked contrast to what is most common in human music (unpublished observation in European nightingale song). Human listeners who hear nightingale songs for the first time after having read of them in classical European literature are often surprised that they sound not quite like the pure melodies one would expect to be so celebrated by Keats, Wordsworth, and John Clare (Rothenberg, 2005). The beauty and power we perceive when listening to a nightingale singing on sunset comes in part from its otherworldly qualities.

When targeting structural features of birdsong for analysis, predetermining any particular feature bears the risk that this very feature might not play a major role in the esthetics of a particular bird species in question. A reasonable starting point would be to first look for any structure that is stereotyped but allows for some degree of variation. Such structures would be good candidates to generate expectations in avian listeners, with which comes the possibility of predictions, anticipations, delays, or surprises, which are believed to underlie the "emotive power" of human music (Huron, 2006; Meyer, 1956): recurring stereotyped structures will create in listeners an anticipation of what to expect next, which can be fulfilled (leaving the listener with a sense of satisfaction), delayed (first increasing tension that gives way to an increased degree of satisfaction) – or violated (creating surprise). Stereotyped yet varied structures can occur on all hierarchical levels: single notes (or subphrases of a few notes) can be repeated but modified slightly in timing or amplitude, for example, and entire phrases can occur repeatedly within a single performance with subtle variations in the order of some notes (as in European Nightingales). *Contrast* between adjacent materials – like for spectral differences between the mockingbird's successive phrase groups – are also thought to be a source of emotions evoked in the human listener (Huron, 2006). Such contrasts in birdsong, be it in the rhythmic, spectral, or dynamic domain, might be quantifiable and its use can be tracked across performances. We are presenting here an analysis of thrush nightingale songs in which contrast and variation become visually graspable. Once such putatively musical features of a species' song are identified, they can be tested for their emotive power: if avian listeners are presented with song samples containing these features versus song samples stripped of these features, the emotions elicited, and therefore their neural activation patterns, should differ if the feature in question is indeed biologically relevant to the bird. We will argue here that one potentially successful method for detecting differential emotive power is functional magnetic resonance imaging (fMRI).

5. A case study: assessing "musical" structure of the thrush nightingale song

Here we present a case study in which we developed a descriptive model of thrush nightingale songs that captures its

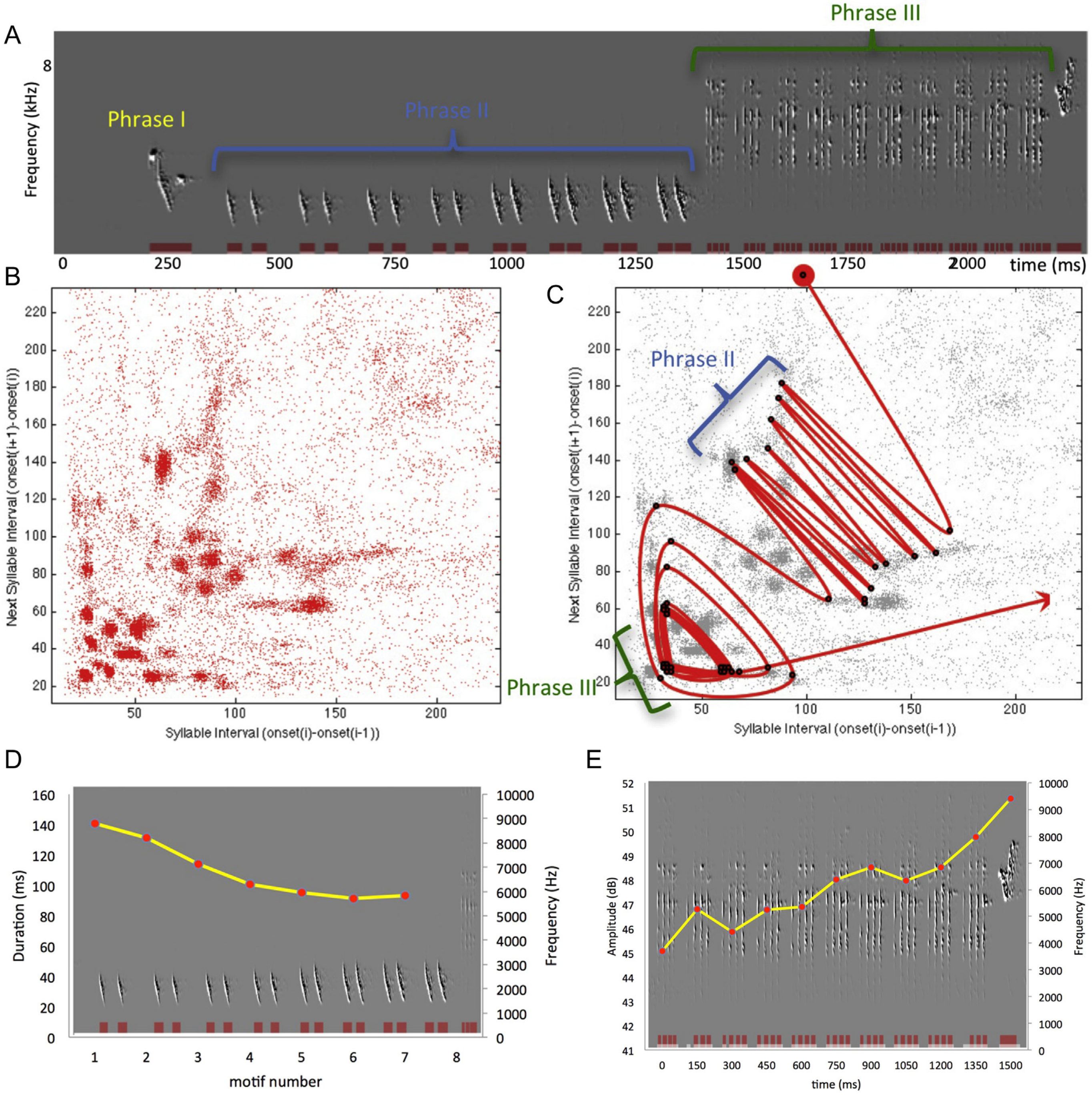

Fig. 2. Time structure of the song. A, One song motif with syllable outlines in dark red; B, phase plot of onset-to-onset time intervals for an entire performance. Each dot represents a syllable in its rhythm context, i.e. its temporal relation to the previous and the following syllable's onset. We call this a rhythm unit. Clusters indicate specific rhythm units that are recurring throughout the bird's performance; C, each song can be plotted as a trajectory in this phase plot, propagating from one rhythm structure into the next. D. Continuous escalation of the rhythm during the first part of the motif, curve indicates onset-to-onset intervals for pairs of downsweeps while spectral bandwidth increases; E, subtle escalation of amplitude during a trill of clicks leading to the next motif whistle.

putatively musical features. Thrush nightingales are among the most melodious singers, with large repertoires and versatile singing styles. The song of the thrush nightingale, found in Northern and Eastern Europe, is impressive: males often sing almost continuously for several hours, starting in the evening and continuing into the night (Naguib and Todt, 1998; Naguib and Kolb, 1992). They usually produce 15–20 different song types, often with many intermediate variants, delivered in variable order. Males learn those songs in their first year but some learning from neighbors later on in life also occurs (Griessmann and Naguib, 2002; Sorjonen, 1977). Studies in its sibling species, the Common Nightingale, showed that some song elements appear to be improvised (Hughes et al., 2002). Renditions of the same song type are often not identical, with subtle variations in the structure and number of elements and in rhythm.

We used audio recordings from two thrush nightingales who sang naturally in the field. Recordings were made at the Island Hiddensee in Northern Germany in 1996 (Naguib and Todt, 1998).

For each bird we used 30–50 min of continuous nocturnal singing. Male thrush nightingales sing at night over several hours, presumably until they attract a social mate for breeding as shown for their sibling species, the nightingale (Amrhein et al., 2002).

We then analyzed the entire singing behavior recorded for each bird (about 50,000 song syllables per bird). Using the Sound Analysis Pro 2011 software (SAP2011, Tchernichovski et al., 2000; SoundAnalysisPro.com), we performed multi-taper spectral analysis (FFT window 8 ms, bandwidth parameter 1.5, overlap 7 ms) and computed spectral derivatives (high-definition sonogram images). We automatically segmented the song data into syllables using an adaptive amplitude threshold (recorded amplitude filtered with a Hodrick–Prescott filter set to 400 samples, as implemented in SAP2011). We identified syllables (versus inter-syllable silence) as all sound where amplitude (filtered with a Hodrick–Prescott filter set to 50 samples) exceeded the threshold. Mean values of song features, including mean frequency and Wiener entropy, were computed for each syllable and saved in MySQL tables. Data were further analyzed using Matlab 7 (The Matworks, Inc., Natnick, MA) and Microsoft Excel 2011 (Microsoft, Inc., Seattle, WA).

5.1. *Analysis of thrush nightingale song time structure*

The building blocks of the thrush nightingale song are phrases of repeated syllables. Whereas Sotavalta used his own ear in musical notation and in manual enumeration of patterns, it is now technically feasible to visualize patterns in the raw song data in a manner that is compatible with his ideas. In Fig. 2A we present spectral derivatives of one song composed of four phrases: the first is a single syllable followed by a phrase of several down-sweeps which are delivered in pairs (chip–chip, chip–chip…), a third phrase composed of clicks, which are delivered in quartos, and a final single syllable. While the sonogram image clearly shows this coarse rhythmic structure, subtle modifications within these repetitive patterns, such as the slight acceleration in the second phrase, are more difficult to see: this is a case where the singer adds a systematic variation in timing to an otherwise stereotypically repeated note. This *accelerando* may possibly constitute a “musical” feature that is able to evoke emotions, expectations, and anticipation in thrush nightingale listeners. To capture such time structure, we analyzed the entire singing performance of one male during about 1 h of singing, including about 50,000 song syllables, and constructed a phase plot of the onset-to-onset time intervals of song syllables (Fig. 2B). While will call this temporal aspect of birdsong “rhythm,” please note that we do not intend to imply the existence of an underlying beat maintained throughout a song. Each dot represents one syllable in its rhythmic context. It shows two time intervals: between a syllable and the onset of the previous syllable (*X* axis), versus the time interval to the next syllable (*Y* axis, e.g., the duration from syllable 1 to syllable 2 versus the duration from syllable 2 to syllable 3). The clusters indicate that this bird sings using about 20 different rhythmic units, although some of those are harmonically related to each other (i.e., they represent versions of the same rhythmic motif in different speeds that are small fractions or multiples of each other). Within these plots, each song can be represented as a trajectory in rhythm-space (Fig. 2C). For example, by plotting the song presented in panel A we can see how the rhythm zigzags during the phrase of down-sweeps and then orbits into rapid three-state oscillations while performing the clicks.

This phase plot reveals a graceful transition from one rhythm state to the next: the zigzag pattern gradually accelerates until it enters into the orbit of the click phrase. Fig. 2D shows a quantification of this transition. Further, although the rhythm of the clicks is very stable, another feature, in this case amplitude, increases during the clicks phrase, slowly approaching the amplitude of the next syllable, which is a high pitch sweep that terminates the song, like a *glissando* in music. Note that in both cases, a subtle gradual change (acceleration in phrase 2, amplitude increase in phrase 3) can be interpreted as preparing for and bridging a phrase boundary: the acceleration in phrase 2 leads over to an ever faster rhythm in phrase 3, and the increasing amplitude in phrase 3 culminates in the note of phrase 4. Is this way of linking different phrases part of a thrush nightingale aesthetics – i.e., does it elicit emotions and expectations, like the build-up of tension that releases when the phrase boundary is reached? We will later suggest an approach to such questions using functional brain imaging in avian listeners.

Note that a symbolic description of these songs, namely, categorizing syllable types and phrase types (essentially, what all previous studies have done in stage 1 of the analysis), does not take into account the subtle transitions we described above. Yet, removing these transitions from the signal makes it sound very different. According to Juslin (Juslin and Västfjäll, 2008; Juslin and Sloboda, 2010), in human music, what communicates emotion may not be melody or rhythm as exactly noted in the sheet but moments when musicians make subtle changes to those musical patterns. “Musicality” is a combination of all these elements of rhythm, melody, form, dynamics, timbre, and inflection. Perhaps birdsong, as in human music, combines these into coherent species-specific wholes. Stripping such subtleties from birdsong could affect neuronal and behavioral responses but such effects have not been tested in birds, though they have in humans (Chapin et al., 2010).

5.2. *Is exploring pitch space a matter of individual skill?*

A recent paper on the possibility of musical scales in the tonal-sounding song of the Northern nightingale wren (*Microcerculus philomela*) concludes that there are no musical scales in those songs (Araya-Salas, 2012). Another study by Tierney et al. (2011), however, finds evidence that some of the elements of musical structure are shared between humans and birds but those may be based on motor constraints on what possible sounds can be produced. Their study compares musical scores of nearly 10,000 folk songs, mostly European but also 2000 Chinese examples, with 80 species of birdsongs, hand-picking those that are primarily tonal with significant pitch variation. They purposely excluded birdsongs with noises, clicks, buzzes, and other sounds difficult to notate musically. Within this subset of songs they determined that the relative preference for consistency in melodic contour is remarkably similar between birds and humans, as well as the fact that phrases tend to lengthen toward their conclusions. Both birds and humans also tend to favor smaller interval jumps rather than larger ones. The authors hypothesize, in conclusion, that physical motor constraints lead to this similarity.

We are not sure what they would make of the songs of thrush nightingales, starlings, cowbirds, or lyrebirds that specialize in strange, glottal sounds and big contrasts between steady tones and rapid ratchety beats or wide-frequency bursts of precisely controlled noises. Other researchers have pointed out that physically the syrinx of birds is capable of far more sonic variation than most birds make use of (Zollinger and Suthers, 2004), so that the predilection for one species to have a far more complex song than another has more to do with selective pressures on the species song evolution than any physical limitation. Lyrebirds, which have one of the most complex and convoluted of all birdsongs, have a simpler syrinx than most songbirds (Robinson, 1991), yet they produce songs of astonishing complexity. This is not to say that motor constraints might not have some role in the fact that human and bird music contains many similar features but motor constraints tell only one part of the story. Investigating the form of the

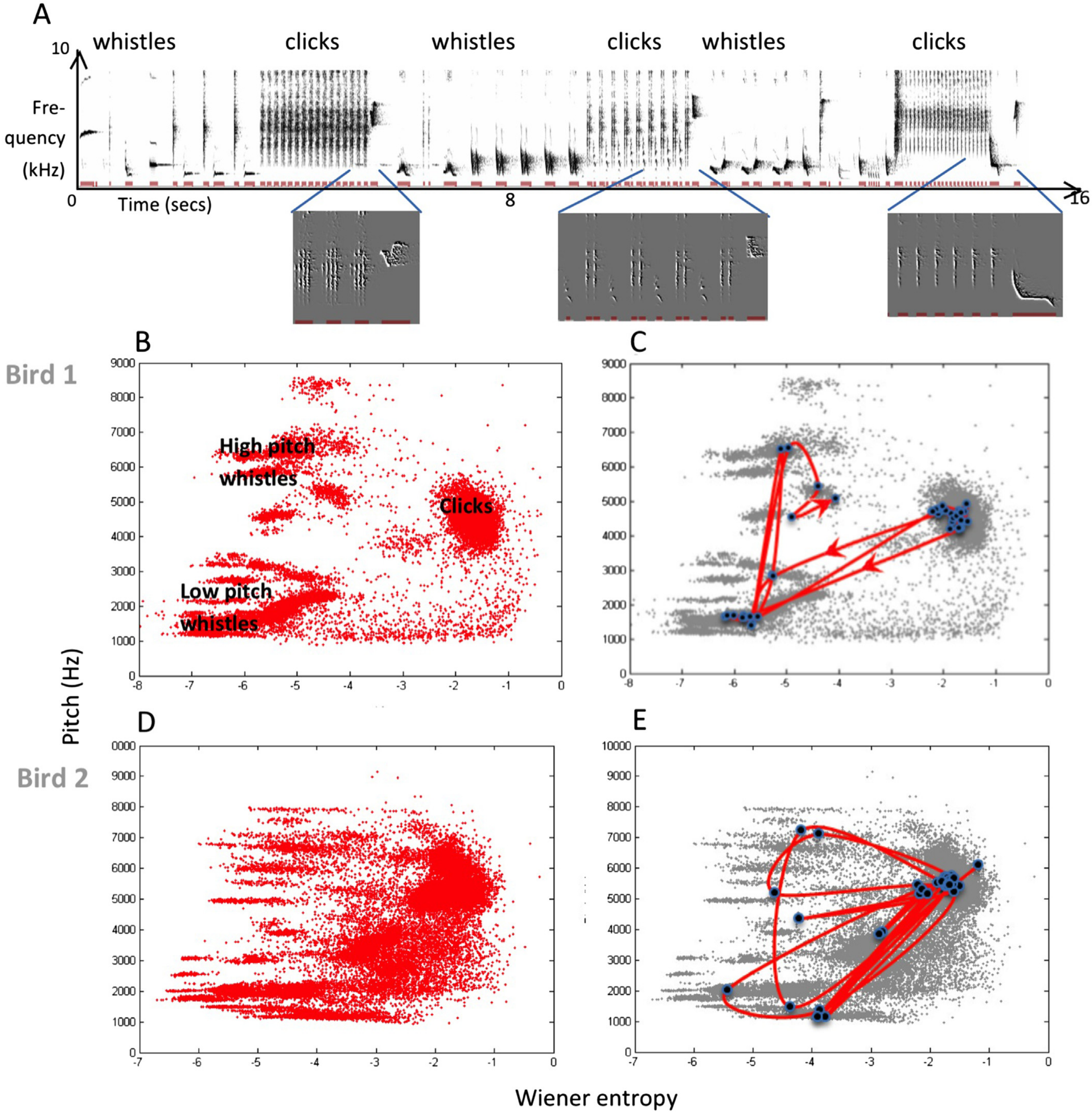

Fig. 3. Songs depicted as trajectories through spectral space. A, An example of three consecutive songs produced by a thrush nightingale, each song including phrases of whistles and clicks. Below the sonogram, zooming in using spectral derivatives shows that the click trills include a complex fine structure, produced in sets of 4, 2 or 1, sometimes with low pitch whistles in between (second panel); B, to summarize an entire singing performance over about 1 h of continuous recording, we present a scatter plot of syllable features, where each dot represents the pitch versus Wiener entropy of one syllable; C, a trajectory of one song in this space. D–E, Same representation for a different bird.

rhythmic, harsh phrases uttered by thrush nightingales as we have attempted here might complement the tonal and melodically-expectant approach of Tierney, Russo, and Patel.

Here we propose an alternative approach of exploring the space of tones and tonality more generally. As we did with analysis of rhythm, we examined songs as *trajectories* in that frequency space, searching for musical features in those trajectories. As in our preliminary investigation of rhythm, the putative musicality we are positing in birdsong emerges through analysis of the structures of the birds' songs themselves. Thrush nightingale syllables are rarely pure tones; instead, their syllables are usually frequency modulated whistles or clicks (Fig. 3A). However, zooming into the spectral derivatives (Fig. 3A inserts) reveals that even the clicks may have a more complex frequency and rhythm structure than the human ear first picks up. Therefore, we use two features to summarize their frequency structure: one is the mean frequency of the syllable, which is an estimate of pitch. The other is Wiener entropy, which is an estimate of tonality, ranging from white noise (high spectral entropy) to pure tone (low spectral entropy). Note that we are using the term "tonality" here in the sense of "tone-like" as used in signal analysis as opposed to its use in music theory to denotes relationships of different tones on a scale. Fig. 3B presents a scatter plot of mean frequency versus Wiener entropy for an hour of singing performance of one bird. As shown, the song is composed of distinct classes of vocal sounds: clicks of high Wiener entropy and syllables composed of tonal elements with no overtones (whistle) or of low or high pitch.

As for rhythm, we plotted each song as a trajectory in feature space (Fig. 3C). Comparing two birds (Fig. 3B and D), we see that one bird (Fig. 3B) has more distinct classes of vocal sounds with significant gaps between them. The other bird, although having similar categories of sounds, produces syllables that fill the feature space much more continuously, e.g., including many intermediate forms between clicks and low pitch whistles. Interestingly, song trajectories of the first bird tend to be more linear, e.g., starting from a phrase of low pitched whistles followed by a phrase of clicks (as in Fig. 2A). The other bird, however, shows also circular trajectories, making complete cycles from a click to a low pitch whistle, high pitch whistle, and back to a click, such as the one shown in Fig. 3E. Do such transitions indicate virtuosity, suggesting that one of the birds exploits the pitch space more skillfully than the other bird? When focusing on musical features of birdsong, we have to assume that eliciting in the listeners suspense, surprise, and pleasant tension release requires skill and that such musical skill differs between individuals (just as it does between human musicians). How would avian listeners respond to synthetic playbacks of songs where the degree of pitch and entropy contrast is systematically altered, in a way similar to what is different between the songs of our two birds? Previous studies showed that birds will calibrate their performances when presented with song models that include trills that are too fast for them to produce (Podos, 1996) and females find trills produced at the species' performance limit as being more attractive (Ballentine et al., 2004). Here, we suggest another way of looking at complex performances, which is summarized in Figs. 2 and 3: first, present songs as trajectories in continuous rhythm space and in frequency–entropy space instead of using symbolic notations based on cumulative statistics. Then, explore entire performances, looking for systematic variations between performances of different individuals or between one individual's singing in different social contexts. Some structures will be shared across all performances (e.g., the general tendency to alternate trains of clicks with trains of whistles in the case of the thrush nightingales). Such shared structures most likely reflect species-typical song features that might be interpreted as a "default." Systematic variations between individuals, on the other hand (such as the different use of entropy-frequency space of the two thrush nightingales shown), are what might carry information about virtuosity and thus affect a listener's attention and response. Once variants are identified, we can quantify the auditory and behavioral responses they elicit and create new variants with over- or under-emphasized distances to the default. These can be tested for auditory and behavioral responses. What are we missing when looking at song symbolically? We are missing the transitions in acoustic space, which are, to a large extent, what makes music work. The arbitrary naming of phrases or states (A, A1, B, C, etc.) does not reveal musical structure. The analysis of analog features such as variations in amplitude and rhythm suggest musicality in the details of the song, perhaps generating tension and expectation in manners be comparable to human music.

This case study demonstrates that looking at a single species in sufficient detail and considering continuous feature space may reveal acoustic attributes that are most meaningful to this species: instead of testing in general if music and birdsong are similar, it might be more useful to take some obvious commonalities between the two series and explore points of view that are more traditionally found in contemporary music theory.

6. What music tickles bird brains?

Humans are consistently impressed by musicality heard in birdsong. But are birds impressed by features humans perceive as musical? Above, we presented an approach for detecting musical features of birdsong. How might we examine what these features mean to the minds of the birds themselves?

We can look for activation of neuronal mechanisms and the alteration of behavior by i) synthesizing songs that are stripped of those features (e.g., constructing thrush nightingale songs without accelerations leading to transitions); ii) detecting homologous features in human music; and iii) comparing changes in brain activation and behavioral patterns across songbirds and humans when listening to the two original versus synthetic sounds. We focus on the feasibility of the attempt to identify shared mechanisms by which sounds can alter behavior and for determining whether they are shared between birdsong and human music. In humans, listening to an expressive performance of music activates different brains centers than listening to a mechanical performance of the same piece (Blood and Zatorre, 2001; Chapin et al., 2010). Such differences can be seen not only in auditory areas but also in reward and emotion-related areas such as the ventral striatum, midbrain, amygdala, orbitofrontal cortex, and ventral medial prefrontal cortex, as well as in motor and "mirror-neuron-" rich areas (including bilateral BA 44/45, superior temporal sulcus, ventral premotor cortex, inferior parietal cortex, insula).

What features of birdsong activate brain centers and affect behavior in a manner that might be comparable to human music? We will review and compare the literature about auditory responses to song in songbirds and how they resemble auditory responses to music in humans. We then argue that methods allowing direct comparative studies are already in place, focusing on recent fMRI studies in songbirds. Those demonstrate that non-invasive techniques can capture song-specific patterns of brain activation which relate not only to acoustic structure but also to the social significance of the song and to the developmental history of the bird. Finally, we suggest a roadmap for combining these approaches and discuss the potential and difficulties of attempting direct comparisons between human and avian systems.

Note that fMRI is just one of many possible readouts for effects of musical features on listeners' brain and behavioral states, and a number of possible alternatives are conceivable. Behavioral assays like learning experiments can reveal preferences for certain musical features: a young bird who is acquiring his song can be presented with two models, one of which contains while the other lacks the musical feature in question (in the same way as described above). The bird will reveal his preference by copying one of the models. Behavioral female choice experiments can tell what kind of song is preferred by female avian listeners. Electrophysiology can be used to record brain responses to different song samples with high temporal resolution (although at the expense of a good spatial resolution). An interesting technique to assess the role of dopamine in the processing of such "musical" versus "non-musical" song stimuli are PET scans using radioactive dopamine antagonists: they can reveal whether the two kinds of stimuli lead to different amounts of dopamine released. We will here discuss in detail – as one possible option – fMRI, which with stronger (7T and 9T) scanners now becoming available, has the advantages of being a non-invasive brain imaging technique with a good spatial resolution even for small brains. However, the temporal resolution of fMRI is orders of magnitude slower than short time scales in

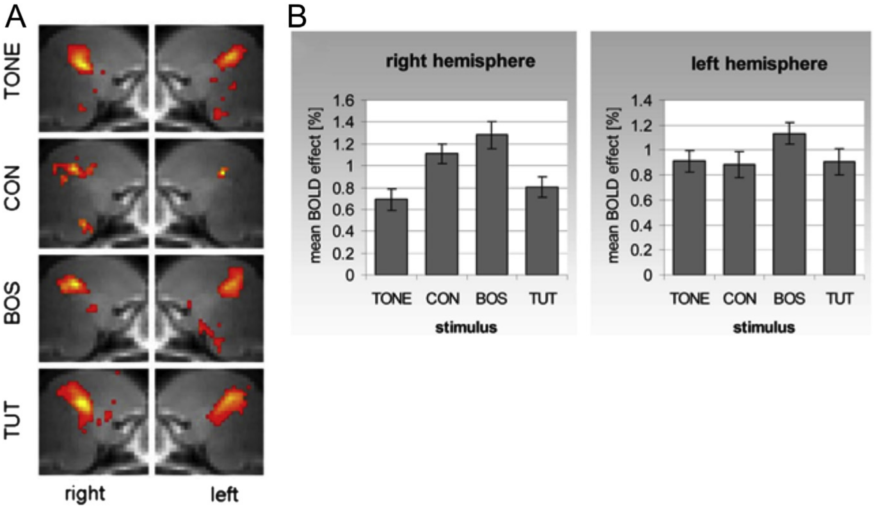

Fig. 4. Auditory responses in the zebra finch brain are stimulus specific. A, BOLD responses to different stimuli at the medial portion of right and left hemispheres in zebra finches; B, summary of BOLD effects across birds. TUT tutor's song, BOS bird's own song, CON a song of unfamiliar zebra finch, TONE a 2000 Hz tone. From Voss et al. (2007a,b).

birdsong. In fMRI experiments, we are constrained to assessing the time-averaged regional response of the brain to these modified stimuli. In this sense, it might be that a modified song activates other regions than the unmodified song, that the amplitude of activation systematically differs, or that the shape of the response over time changes with the stimulus.

Auditory responses to birdsong have been studied intensively, from auditory brainstem responses and activation by songs (Henry and Lucas, 2008; Poirier et al., 2009) to investigations of song-specific responses in the auditory mid- and forebrain (Woolley et al., 2005, 2006), in secondary auditory and integration areas (NCM), and also in motor and sensory–motor song nuclei (Chew et al., 1995; Vicario and Yohay, 1993). The auditory representation of the song transforms from simple feature detectors in the brainstem to complex, song-specific responses in higher brain areas (Woolley et al., 2005, 2006). There are strong auditory responses to songs in all the motor song nuclei (Doupe, 1997; Margoliash and Konishi, 1985), which are strongly modulated by behavioral state (Cardin and Schmidt, 2003). Overall, the auditory responses to songs are strongly stimulus specific, depending on the overall time and frequency structure of the song.

Most remarkable are the auditory responses to the Bird's Own Song (BOS): the song nuclei usually respond very strongly to playbacks of BOS compared to any other song (Doupe, 1997; Solis and Doupe, 1997). Even small acoustic modifications might suffice to eliminate BOS specific responses (Theunissen and Doupe, 1998). Further, when the bird sings, corollary discharges of the premotor song patterns propagate into the anterior forebrain pathway, suggesting sensory–motor mirroring (Mooney and Spiro, 1997; Mooney et al., 2002). It is the same neurons in the song system that can switch, within seconds, from premotor to auditory responses of very similar patterns (Prather et al., 2008). Therefore, sensory–motor auditory responses to birdsong are similar to sensory–motor responses to music in humans (Callan et al., 2006; Hickok et al., 2003; Pa and Hickok, 2008). As in humans, both auditory and motor song-related brain activity is lateralized (Cynx et al., 1992; Espino et al., 2003; Floody and Arnold, 1997; George et al., 2005; Halle et al., 2003; Hartley and Suthers, 1990; Moorman et al., 2012; Nottebohm, 1971, 1972; Phan and Vicario, 2010; Remage-Healey et al., 2010; Van der Linden et al., 2009; Voss et al., 2007b; Williams et al., 1992).

This evidence indicates that auditory responses to song playbacks are specific enough to test the effect of subtle manipulations in song structure. However, most of the methods mentioned above were obtained by recording from single units or by analysis of gene expression patterns in brain areas after song playback. These ways of measuring neuronal responses are not directly comparable to studies of music and, in most cases, they involve acute or terminal preparations. An alternative approach, which is more comparable to human studies, uses non-invasive imaging techniques such as fMRI. Recent studies by our groups (Maul et al., 2010; Voss et al., 2007a,b, 2010) and by others (Boumans et al., 2005, 2007, 2008a,b; Peeters et al., 2001; Poirier et al., 2009, 2010, 2011; Van Meir et al., 2003, 2005) showed that the specificity of auditory responses to particular songs can be detected by looking at BOLD responses. These fMRI studies show that, as in human music, brain activation in response to birdsong can be lateralized and strongly depends on the social significance of song (Fig. 3): comparing BOLD responses to songs versus tones, there are significant differences only in the right hemisphere, with Bird's Own Song (BOS) inducing the strongest BOLD responses. The left hemisphere show strong BOLD responses as well, but those are less stimulus-specific. Note, however, that all those studies were performed in a single species (zebra finches) (Fig. 4).

6.1. The development of auditory responses to songs

One issue that complicates musical analysis are the effects of development and culture, which is very difficult to segregate in humans. Using songbirds as animal models for studying basic mechanisms of music neuroscience could circumvent these complicating factors: first, in songbirds auditory experience during development can be tightly controlled. Second, early auditory exposure has strong effects on the specificity of fMRI responses to songs, so that the effects of development and culture on auditory processing could be accessed with this technique.

To demonstrate this point we present data from our recent study comparing BOLD responses to two stimuli: playbacks of the bird's own song (BOS) versus a repeated song syllable (i.e., a simple repetitive song). Colony-raised birds show much stronger responses to BOS, which is expected (Fig. 5A). However, this stimulus-specific response depends on early experience and perhaps also on normal song development: in birds that were raised in complete social and auditory isolation during the sensitive period for song learning we see strong responses to both stimuli (Fig. 5B). Comparing several stimuli, including the tutor song (TUT), conspecific song (CON), and tones across several birds (Fig. 5C and D), we can see that this effect generalizes. We conclude that the auditory responses are specific to songs of different social significance (keep in mind that the particular BOS and TUT songs are different in each bird) and that this stimulus specificity is therefore an outcome of early experience. Since BOLD responses reveal these experience-based effects they are a promising means to explore the subtle differences between songs that have been musically manipulated (such as containing versus being stripped off timing subtleties, as in Fig. 2).

6.2. Challenges in comparative studies of music and birdsong

The results above suggest that the gap between birdsong research and human music neuroscience research might be bridgeable. Of particular interest is a direct comparison when some aspects of the musical features are removed and when listeners' brain activation patterns are analyzed as they listen to music stripped of dynamic variation, expression, and other emotionally-evoking acoustic features (Chapin et al., 2010). A parallel study in thrush nightingales would include subtle adjustment of the dynamics and micro-tempo (acceleration) of phrases, similar to those shown in Figs. 2 and 3. One can then use fMRI as in Voss et al. (2010), perhaps in addition using heart rate as a proxy for changes in internal state.

One conceptual difficulty in comparing auditory responses between birdsong and human music is that there is no simple way to distinguish auditory responses to music and auditory responses to other natural sounds. There is no simple answer to this question because the perception of music is, to a large extent, built upon natural time scales of responses to stimuli we have evolved to respond to. However, in order for music to "work" it must meet some conditions: first, there should be some balance between anticipation and suspense; otherwise, the music would become boring or incomprehensible (for discussion see Huron, 2006). Second, music has a strong sensory—motor aspect: this is true not only for musicians, who can often inverse the perception of music into motor gestures, but also for non-musicians, who perceive some aspects of the music via their motor system (Haueisen and Knösche, 2001). The association between music and movement can explain some of its power in driving emotion, namely, by activating motor centers that are associated with different types of actions (i.e., motor correlates of marching, having sex, or feeling weakness). Finally, the perception of music has a strong developmental component and people from different cultures might differ in some very basic perceptual aspects of music including the notions of consonance and dissonance, time scales and rhythms. As elaborated above, all those aspects can be found in birdsong, including studies showing that female song preference are shaped

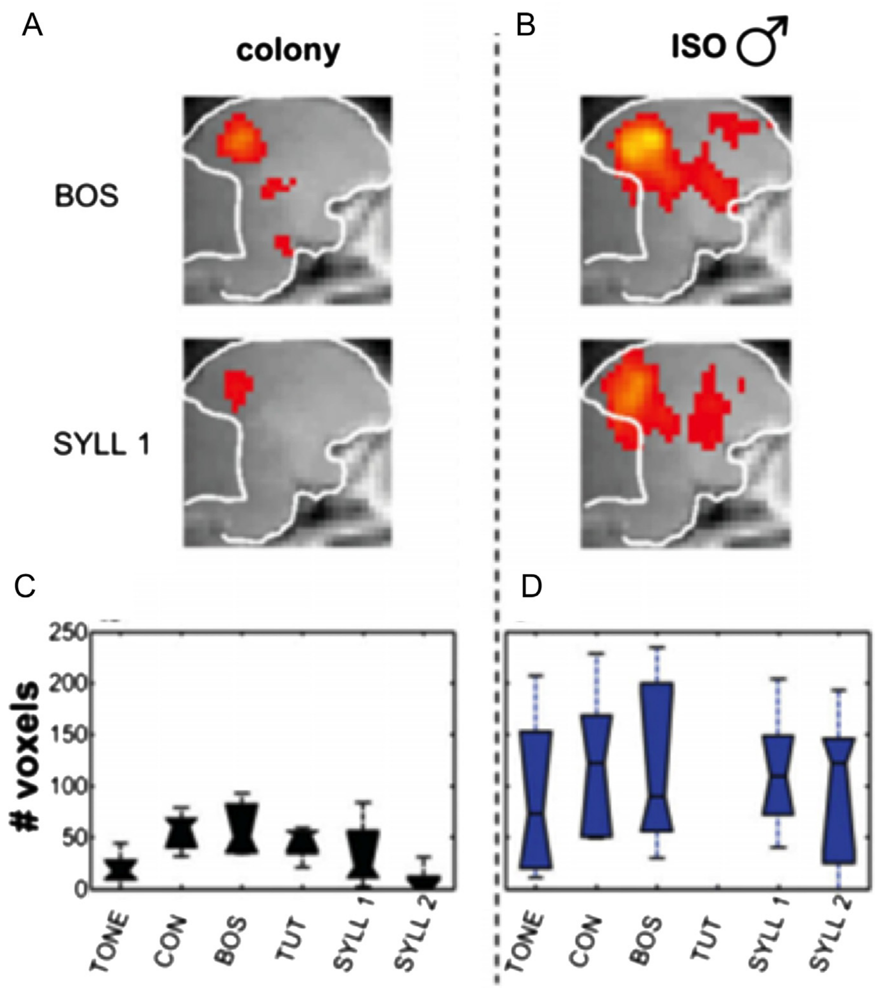

Fig. 5. Auditory responses depend on developmental experience. A, BOLD responses in colony raised birds show strong differences comparing the bird's own song (BOS) to a repeated syllable, but not in isolate males. B, A summary across stimuli shows stimulus specific responses only in colony raised males, but not in isolate males, whose responses are highly variables. From Maul et al. (2010).

by the early developmental conditions (Holveck and Riebel, 2010; Riebel et al., 2009). However, to show that birdsongs are truly musical one must be able to find specific features of performance that, independently from the coarse song structure, may affect behavioral responses in an interesting and functionally relevant manner. There is no empirical evidence for the emotive power of specific features of the song but Earp and Maney (2012) were able to show that the same reward related brain circuit that is active in humans listening to music – the mesolimbic reward pathway (Blood and Zatorre, 2001; Koelsch et al., 2006; Mitterschiffthaler et al., 2007; Montag et al., 2011; Pereira et al., 2011; Salimpoor et al., 2011) – is activated in birds listening to birdsong. The approach we suggest here – presenting avian listeners with more or less "musical" birdsongs and assessing their brain response – might lead to similar results as have been found in humans: hearing your favorite music activates the brain differently than other similar music (Blood and Zatorre, 2001; Montag et al., 2011; Salimpoor et al., 2013). Brain dopamine levels increase when listening to music and the level of increase correlates with the number of chills experienced while listening (Salimpoor et al., 2011). We do not know yet if and how hearing song increase dopamine in the bird brain but singing behavior certainly does (Kubikova and Kostal, 2010; Sasaki et al., 2006; Hara et al., 2007; Simonyan et al., 2012). If hearing song does, as well, detecting putatively musical features of songs that can alter dopamine levels could be an important breakthrough in establishing a comparative approach.

As noted above, music perception in humans depends strongly on development, previous listening experiences, and culture. One great advantage of studying birdsong is that the development of many species is short and observable under laboratory conditions, where one can fully control auditory and social experience. No detailed studies were done to directly relate humans' musical preferences to birds' song preferences with respect to development but it is well established that birds' neural responses to song change strongly over development. One simple manipulation is comparing auditory responses to song across birds that were raised in a normal auditory and cultural environments (namely, in a semi-natural colony), to those in birds that were raised in complete social and acoustic isolation during the sensitive period of their development. Fig. 5 presents a summary of differences in BOLD responses to different song and call stimuli, comparing colony birds to isolates. As shown, isolates often show strong responses but those are not stimulus-specific. Namely, as much as can be judged by fMRI, the isolate males who never had an opportunity to imitate a song from another bird (tutor) do not develop specific brain activation to different stimulus types.

7. Conclusion: a framework for identifying musicality in birdsong and how it affects behavioral state

Taken together, the approach we outline here identifies new avenues to study animal communication and specifically the proximate factors that could attract and maintain attention by listeners. Dynamic song features such as rhythm, timing and frequency–time relations across a singing performance, which we outline here for the melodious thrush nightingale song, expand on the most commonly statistical approach to study complexity of birdsong. Such musical features may lead to a better understanding about the mechanisms making song such a potent and biologically significant social stimulus. Combining this approach with techniques such as fMRI visualization of brain activity may provide insights into features birds are actually attending to and help obtaining a more objective assessment of the relevance of musicality in animal communication.

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