to suggest an additional chapter, it would have been on culture, the 'secret of our success' [7]. One could have wondered about the importance of the cultural environment for selecting particular learning abilities and cooperative behaviours [8]. For now, I am grateful to Solomon for not suggesting that robots will kill us all and pursuing a question no one wants to ask.

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Forum

Darwin, Sexual Selection, and the Origins of Music

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Humans devote ample time to produce and perceive music. How and why this behavioral propensity originated in our species is unknown. For centuries, speculation dominated the study of the evolutionary origins of musicality. Following Darwin's early intuitions, recent empirical research is opening a new chapter to tackle this mystery.

Darwin's Early Intuitions

Darwinian thought applied to understanding how music originated in humans has a conflicted history. Darwin originally proposed to apply his sexual selection framework to music [1]. However, except for a few theoretical perspectives acknowledging his contribution [2], it was commonly assumed that Darwin had little to say about music, and music research little to benefit from a Darwinian approach [1]. Recently, empirical research has tested Darwin's intuitions laid out as hypotheses almost two decades ago [2]. This research deals with the 'evolution of musicality', with musicality defined as a human biological predisposition to process music [3]. This is not to be confused with the study of the 'cultural evolution of music', where music is seen as a cultural product varying over history (Box 1 and Figure 1).

Old Hypotheses and New Empirical Work

Traditionally, hypotheses for the evolution of human musicality focused on one overarching question: why is music such a widespread behavior in our species if it does not seem to have an obvious adaptive function? For more than a century, the role of sexual selection in human musicality has been addressed from purely theoretical and anecdotal perspectives. By contrast, the past decade has seen a number of empirical, complementary efforts to test whether musicality could be a sexually selected trait in humans. Discovering genes associated with musical aptitude is a necessary prerequisite before any selective pressure (sexual or natural) can be invoked. Molecular studies have found a number of genetic correlates or expression patterns related to music processing, production, and perception [4]. In particular, alleles of the arginine vasopressin receptor genes are associated with memory for, among other things, musical motifs. In addition, music listening and performance influence upregulation of many genes affecting motor behavior, learning, memory, and dopaminergic pathways. At the population level, a large study used twin modeling to test predictions generated by the sexual selection hypothesis [5]. This study found

Box 1. Evolution of Music versus Musicality

In contrast to research about the evolution of human musicality [3], a second strand has investigated the evolution of music, intended as a cultural product of musicality. Darwin had a clear intuition that language and birdsong are shaped by learning and transmission (see Figure 1A in main text), and this intuition can be easily extended to music (see Figure 1B in main text). This second strand of empirical research tackles the question of how imitation, transmission, and 'selection' shape cultural and structural features of music (reviewed in [12]). Empirical, corpus-based research has shown how sets of musical behaviors are shaped by interindividual transmission across generations, display temporal trends and associations with other cultural variables, and are pruned via 'cultural bottlenecks' (reviewed in [12]). In addition, experimental efforts have replicated in the laboratory how musical patterns and cultures 'evolve': by building artificial cultural strains of participants who imitate unstructured sounds from their predecessors (see Figure 1B in main text), music-like patterns emerge (reviewed in [12]). Studying the evolution of both music and musicality is equally important, especially in light of the increasing scientific synthesis of biology and culture. This work on cultural transmission provides both a link between music and musicality, and a possibility to perform cross-species research (Box 2) using comparable paradigms (see Figure 1A vs 1B in main text).

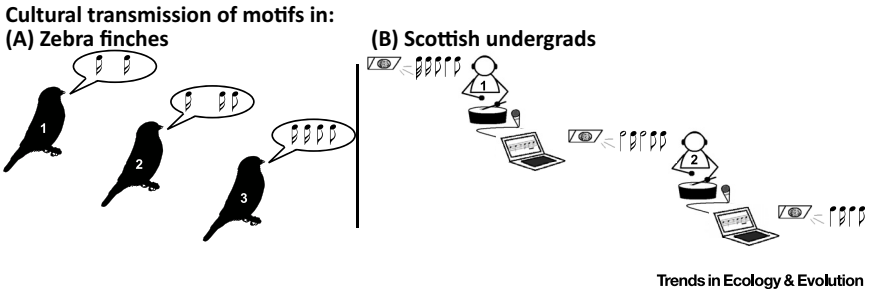

Figure 1. How Individual Learning and Interindividual Transmission across Generations of Learners Can Shape (A) Birdsong and (B) Human Music. In iterated learning experiments with zebra finches (A), a bird was raised in isolation and hence produced an aberrant song. This zebra finch (bird 1) constituted the only tutor for bird 2, which in turn tutored bird 3, etc. In the human iterated learning experiments, a non-musician (participant 1) was given random drumming patterns to imitate, and the imitated patterns were given to participant 2, again to copy. In both cases, signals became more structured over experimental generations: bird vocalizations converged towards wild-type songs, and drumming patterns converged towards rhythmic features found in most world musical cultures (see also universals and comparative method in Box 2). Both studies are reviewed in [12].

some, though weak, support that musicality is sexually selected for (see below). Another study found that during peak fertility, females preferred composers of more complex music as short-term partners [6]. These connections between genes, physiology, and behavior might seem straightforward at first. However, they are the first empirical efforts in a field traditionally dominated by 'Just So Stories'. A new chapter is being opened up by these recent empirical results.

Breaking Down the Evolution of Musicality into Individually Testable Hypotheses

The plurality of these empirical approaches and results suggests that the evolution of musicality should be broken down into individually testable subhypotheses (H1–4 in Table 1), which can be tested to probe the sexual selection framework. How do the empirical studies described above address the hypotheses in Table 1? There is ample evidence for H1: a number of genes are associated with, among other things, musical aptitude, creativity, perception, and production [4,5]. There is also some evidence for H2: musicality correlates with other measures of reproductive success, although this correlation does not seem to derive from overlapping genetic influences [5]. These first two hypotheses are expected to hold true not only for the case of sexual selection, but also for virtually any framework in which evolution plays a role in shaping musicality. Crucially, there is negative evidence for H3: musicality does not seem to predict mating success in a modern, Western society [5]. However, this finding must be contrasted with positive evidence for H4: women prefer more complex music and better performers. Women, more than men, would choose higher-quality performers for long-term relationships [7], and – around ovulation – they would pick a composer of more complex music for short-term relationships [6]. Notice that, while H1–3 would hold for a general natural selection framework, H4 would provide evidence for sexual selection in particular (but see [8,9]).

A Complex Picture: Mixed Support for Sexual Selection on Human Musicality

Together, these works provide a multifaceted picture: some data support while other data refute the role of sexual selection in human musicality; possibly because this evolutionary framework is more complex than usually surmised. Some caveats apply, which can inform and refine future research. First, sexual selection already displays nuances when applied to model organisms whose ethogram is well known (e.g., *Drosophila*). Applying sexual selection to early stages of human evolution is even trickier. Second, each one of the results above was obtained from modern, Western societies. Primordial conditions and selective

Table 1. Subhypotheses Supporting Hypotheses of Musicality as a Naturally Selected, Sexually Selected, or Nonadaptive, Purely Esthetical Trait[a]

	Hypotheses	Refs	Natural selection	Sexual selection	Nonadaptive esthetic trait
H1	Genes that code for abilities related to music perception and production.	Reviewed in [4]	+	+	+
H2	Population-wide associations between increased musicality and traits related to higher fitness.	[5]	+	+	–
H3	Greater mating success in musically skilled individuals – as long as this leads to increased fitness. Notice, however, that mating success does not always coincide with reproductive success, namely the number of surviving, second-generation offspring, or fertilization success.	[5]	–	–	–
H4	Sexual dimorphism in preference, operationalized as one sex preferentially choosing mates who show a particular musical trait, such as mates who produce more complex or conspicuous music, or are better performers.	[6,7]	0	+	+

[a]H1, H2, and H4 are mostly supported by the reviewed literature, while H3 is not. +, positive evidence; –, negative evidence; 0, neutral evidence.

Box 2. Darwin's Legacy beyond Sexual Selection

Going beyond sexual selection, researchers have tested three of Darwin's ideas that are indirectly linked, though clearly connected, to the evolution of musicality. One concept relates to the universality of music and musical skills. The biological predispositions of a species define the set of behaviors and behavioral artifacts they produce, and musicality is no exception [3,11,12]. This concept was subtly introduced by Darwin but needed to develop in the 20th century before being tackled empirically [1,12]. A second concept is the comparative method [2,3]: looking for homologies and analogies of traits underpinning human musicality in other animal species. This has proved a fruitful strand of research [12]. Third, a recurrent theme in Darwin's work is the association between vocal modulation and emotions [11]: this concept has been empirically tackled via prosody. Perceptual experiments have tested how this musical aspect of human language links speech, emotions, and referential meaning [11].

forces might be removed or reversed in present-day humans (e.g., contraception and relaxed selection), making concepts like fitness and mating advantage difficult to test reliably. Third, across animal species, females can be either the choosing or the chosen sex [8]: if musicality were sexually selected for in our lineage, males should not be assumed as those systematically engaging in displays. Fourth, sex differences in human cognition are sometimes attributable to culture, rather than purely biological sexual dimorphism. The same might hold for musicality. Finally, sexual selection is only one of the many hypotheses suggested for how music might have originated in humans. Some alternative hypotheses invoke, for example, kin selection, group bonding, or coordinated behavior [2,7,9]. Other hypotheses seek less functionally driven explanations [10], or propose that musicality would not have evolved under functional selective pressures, but rather be a byproduct of other traits such as language [7,11,12]. In support of this hypothesis, most genes related to music processing [4] are equally related to phonological processing. In such cases, it is impossible to know whether music, speech, or both influenced the prevalence of a particular gene.

Human Sensory Biases and Alternative Evolutionary Hypotheses

A possible solution to this riddle could be offered by the biological framework of sensory biases [2,10]. This framework suggests that not all traits and perceptual preferences are amenable to selective pressures. Preference for some patterns is a mere byproduct of sensory biases, and production of specific patterns is a way of exploiting those biases. In particular, the idea from avian vision that evolution can be driven by esthetics, rather than functionality [10], is readily extendable to other species (humans) and domains (musicality). Empirical evidence for sensory biases that lack a straightforward function [10] should be sought for human musicality. For instance, the small-integer ratio bias in rhythm processing is a potential candidate for nonfunctional sensory biases. When humans perceive or imitate musical rhythms, they tend to alter note onsets in a way that interonset durations are integer multiples of each other's (Figure 1B and references in [12]). This approach seems particularly worthy of more investigation in humans; also because a substrate of sensory biases (Box 1) could fit most evolutionary frameworks, and link behavioral predispositions with culturally transmitted behaviors (Figure 1).

A Multicomponent Approach to Empirically Test the Origins of Human Musicality

In brief, it remains unclear whether sexual selection might have shaped musicality in our ancestors [3,8,9]. What appears clear is that several strands of research are starting to actively test evolutionary hypotheses empirically. Armchair speculation is finally turning into data-driven debate. Methods used include comparative experiments on precursors to musicality in other species (Box 2), genetics of human populations, and paleo-anthropology reconstructing early hominid behavior. An empirical approach to Darwin's longstanding intuitions (Box 2) should allow testing whether sexual selection, or other evolutionary mechanisms instead, drove the emergence of musicality. Crucially, musicality should be deconstructed in its constituent components, for example, the neurobiological bases for preferring consonant intervals, processing temporally structured rhythmic sequences, or synchronizing to a beat (Box 1) [12], and each tested independently. Several complex behaviors in animals can be dissected into simpler unrelated mechanisms, each with a distinct evolutionary path. Likewise, distinct evolutionary paths might underlie different components of human musicality.

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