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Book review

Humans and other musical animals

Andrea Ravignani

The Evolving Animal Orchestra: In Search of What Makes Us Musical
Henkjan Honing (MIT Press, Cambridge, MA; 2019)
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Music is traditionally regarded as 'intellectual property' of the arts, humanities, and perhaps social sciences. Since when is music a topic for biologists? While Darwin and other naturalists had noticed cross-species similarities to human musical behaviors, realizing the importance of *musicality* has contributed enormously to linking music and biology [1]. In fact, while music is more of a cultural product, musicality denotes the neurobiological predispositions an organism uses to produce and process music. Henkjan Honing's new book *The Evolving Animal Orchestra: In Search of What Makes Us Musical* is not about animals listening to human music or the like. It is a journey through *cross-species musicality* — that is, the neurobiology underlying musical behaviors in humans and other animals.

Once we look at musicality through the lenses of biology and evolution, its presence and frequency in our species seem a real adaptive mystery. Most humans enjoy music and spend time performing or listening to it, but why did our capacity for musicality evolve? We still do not know — a shocking realization when compared with the well-understood adaptive function of other human traits, such as color vision, fainting, or even nail biting.

Luckily, Honing comes to the rescue, providing a succinct, informal though rigorous overview of what we know of cross-species musicality (and its historical milestones, see Figure 1). The author, with his polymath background, is particularly qualified to deliver what's promised. Honing's initial training in artificial intelligence was flanked by conservatory studies in music performance and theory — already a sign of exemplary multidisciplinarity. He then enthusiastically dove into the psychology and neuroscience of music, showing that human infants can feel the beat in music. As if this wasn't enough, Honing's interest in the evolution of musicality brought him to look into other species and to work with primates and birds. This book is about the last ten years of bio-musicality research around the world through the eyes of Honing in this 'third scientific phase', which conveniently coincide. This way the reader gets a fresh overview of a topic as explored by the author in real time. And I suspect the readers not already working or interested in biology will be irresistibly drawn to it thanks to Honing's stories.

The author is skilled at using narrative devices to keep the reader's attention. Emphasis is laid on the doubts and processes involved in scientific research, which nicely contrast with the shiny results one usually sees in published papers. From this perspective, the book provides a great educational resource for young generations of scientists. Most science happens as a tiresome journey, and what the public sees is only the splendidness of arrival – that is not the case of this book. This is a popular science book, intriguing and entertaining. Readers interested in a more academic treatment of (bio) musicality are redirected towards Honing's other recent, and equally excellent, effort [2,3].

In 10 short chapters, the author describes findings and scientific adventures, mostly from the last decade, which address two interconnected questions: What makes us musical animals? To what extent is this shared with other species? I will not spoil the book's beautiful narrative by recounting each chapter. Especially because the book felt like reading a modern-day Greek comedy, where some animals and scientists play the lead. For instance, the biologist Carel ten Cate appears as one of the main 'characters' of the book. ten Cate accompanies Honing on a journey through behavioral biology, which then enables Honing to walk the reader through the biology of music. But the most important main characters of the book are the individual animals whose musical capacities are recounted.

As a first example of one of these animals, we are introduced to Snowball the cockatoo, the first non-human animal shown capable of rhythmic entrainment. Snowball provides a great opportunity to illustrate a 'mini scientific revolution' for the field. Until 2008, several scholars believed humans were unique in their ability to move to the beat. Then, astonishing videos of a dancing parrot, Snowball, and

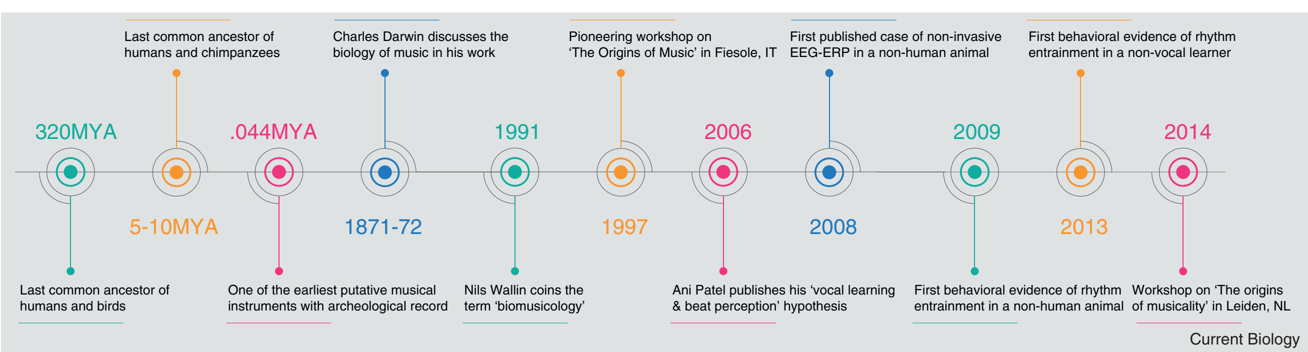

Figure 1. Timeline of some events in our evolutionary history and some scientific discoveries relevant to the biological study of musicality. Based on a template originally designed by Freepik.

Figure 2. A fishy kiss.
A ‘kiss’ between Henkjan Honing, the author, and Ronan the sea lion, the first mammal shown capable of flexible rhythmic entrainment. Photo (edited) courtesy of C. Reichmuth, NMFS marine mammal research permit 14535.

meticulous statistical analyses changed everything [4], and started driving animal musicality from armchair speculation to empirics-based discussion.

We also meet Ai and Ayumu, two chimpanzees in Japan who show some, though very limited, capacity for rhythmic entrainment. During Honing’s travels to Mexico and Japan, we get to know several individual apes and macaques, the first non-human animals with whom non-invasive electrophysiology work was performed [5]. Getting to know these animals is not only a way to learn about biomusicology, but also to let the reader ponder over neurobiology and ethics. The reader can hear about EEG–ERP techniques, which reliably measure, *in vivo* and non-invasively, how surprised an organism is of a sensory event. The reader can also independently reflect about invasive vs. non-invasive research — a topic of heated debate in neuroscience during the last few years.

Based on cross-species evidence, Honing briefly discusses relative support for alternative hypotheses on the evolution of musicality, and specifically, rhythm. There is the classical ‘auditory cheesecake’ hypothesis, which gets explained in ethological terms by using Niko Tinbergen’s concept of supernatural stimulus — when a normal stimulus is exaggerated, it gets more attractive and elicits increased behavioral responses. The auditory equivalent of this constitutes, for some, the baseline ‘adaptive’ model of human musicality: a suite of soft spots for auditory stimulation which get tickled particularly well by human music, although none of them is functionally adapted to music specifically. A second hypothesis suggests that rhythmic entrainment can only – but will not necessarily – be found in animals capable of vocal learning [6]. This hypothesis has been powerful in spurring research on animal vocal learning and rhythmicity. So, although the current support for it is quite mixed [7], and vocal learning may be a graded trait, rendering all rhythm/vocal learning inferences more difficult, this hypothesis remains a cornerstone for the field.

While the interested reader can read about all other hypotheses elsewhere [1,2], one last one is worth mentioning. The gradual evolution hypothesis for rhythm is radically different from the previous two [8], suggesting that rhythmic entrainment can be found mostly in the primate lineage — the more developed this ability in a species, the closer its phylogenetic proximity to humans. It is important to state that this hypothesis is not an example of bad anthropocentrism. On the contrary, the whole book subtly hints at the idea that humans, after all, are not that special. For instance, absolute pitch, something rare and sought after in a musician, is incredibly common, actually the norm, across animal species. Relatedly, the book touches upon the connection among birdsong, music and language in evolutionary terms, hinting at the idea that human musicality may actually predate language. Crucially, however, Honing does not show partisanship for a particular hypothesis, which is quite honorable considering one hypothesis is his own.

The last animal character we encounter in the book is Ronan the sea lion — the first mammal and the first non-vocal learner shown capable of flexible rhythmic entrainment [9]. Finding a non-vocal learner with rhythm constitutes a turning point for the study of musicality, suggesting that the reason why we are musical animals may be more complex than surmised by any single hypothesis. Still, Ronan’s skills provide indirect support for Honing’s gradual evolution hypothesis [8], so no wonder that the book ends on a kiss between the two (Figure 2).

How does the future of this field look? The intriguing hypothesis by Patel [6], connecting rhythmic entrainment and vocal learning, might be refuted. Even if that were the

Figure 3. Three vocal learning underdogs.
A greater sac-winged bat (*Saccopteryx bilineata*), an African elephant (*Loxodonta africana*) and two Eastern Atlantic harbor seals (*Phoca vitulina vitulina*). Photo credit: Michael Stifter (left), Angela Stöger (center), Andrea Ravignani & Sealcentre Pieterburen (right).

case, comparative work probing for rhythm and vocal learning in different species would still be needed. From a bioacoustics perspective, temporal and spectral flexibilities in animal vocalizations map respectively to rhythm and spectral features in our own voice and behavior. To map which species are good at modulating spectro-temporal features of their voices, three animal taxa will need special attention and resources: bats, elephants, and phocid seals (Figure 3). Each of these groups features one or more species shown capable of vocal learning, by modulating either fundamental frequency (roughly corresponding to the 'pitch' of our singing voice) or formants (roughly mapping to the syllables articulated by, for example, an opera singer). Unfortunately, evidence of rhythm in bats, elephants, and seals still remains scarce, indirect [10–12], or even absent for the particular case of elephants.

To conclude, the interdisciplinary field of animal musicality and music origins is booming. It is a field concerned with biological processes which were set in motion millions of years ago, possibly defined human nature in the last thousands of years, but were the object of pure speculation over the last centuries. In the last few decades, however, the field has taken a strong empirical turn. Animal musicality and music origins are gaining scientific respectability, cohesiveness, and maturity. The field is also ripe with questions and low-hanging fruits, which are ready to grasp for all colleagues interested in joining us.

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Artificial Intelligence Laboratory, Vrije Universiteit Brussel, Pleinlaan 2, 1050 Brussels, Belgium; Research Department, Sealcentre Pieterburen, Hoofdstraat 94a, 9968 AG Pieterburen, The Netherlands.
E-mail: andrea.ravignani@gmail.com

Quick guide

Trichomes

Martin Hülskamp

What are trichomes? In plants, trichomes are single or multicellular epidermal appendages on the aerial parts of the plant (Figure 1A). They have diverse biological functions, including helping the plant protect itself against herbivores, UV irradiation and water loss. Depending on the function in a given species, trichome density and morphology display a wide range of structural adaptations. In addition, trichomes may show physiological adaptations and produce special metabolites or play a role in detoxification of the plant by accumulating toxic components.

What can we learn from trichomes? Study of trichome development in *Arabidopsis thaliana* has produced a rich knowledge on the developmental program of this cell type. Except for one gene, all trichome genes turned out to be involved in other tissues and cells as well. Consequently, in studying trichome genes, we have learned about general aspects of cellular and developmental processes.

What makes trichomes a good experimental system? The aim of model systems is to derive general biological principles from the analysis of specific cases. This is particularly challenging for the function and morphogenesis of single cells. For this purpose, trichomes in *Arabidopsis* are ideal, as they are single cells with a complex but predictable three-dimensional structure. Moreover, they are dispensable under laboratory conditions. It is therefore possible to isolate mutants for every developmental step in trichome formation — at least if the corresponding genes are not essential for other processes in the plant.

What can we learn from trichome mutants? The development of trichomes is a continuous process throughout the plant life cycle. With the help of mutants that are defective in specific steps of trichome