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### Synchrony and Rhythm Interaction: From the Brain to Behavioural Ecology

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**DOI**

[10.1098/rstb.2020.0324](https://doi.org/10.1098/rstb.2020.0324)

**Publication date**

2021

**Document Version**

Final published version

**Published in**

Philosophical Transactions of the Royal Society B: Biological Sciences

**License**

Article 25fa Dutch Copyright Act

[Link to publication](#)

**Citation for published version (APA):**

Greenfield, M. D., Honing, H., Kotz, S. A., & Ravignani, A. (2021). Synchrony and Rhythm Interaction: From the Brain to Behavioural Ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1835), [20200324]. <https://doi.org/10.1098/rstb.2020.0324>

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## Introduction



**Cite this article:** Greenfield MD, Honing H, Kotz SA, Ravignani A. 2021 Synchrony and rhythm interaction: from the brain to behavioural ecology. *Phil. Trans. R. Soc. B* **376**: 20200324.  
<https://doi.org/10.1098/rstb.2020.0324>

Accepted: 24 June 2021

One contribution of 17 to a theme issue 'Synchrony and rhythm interaction: from the brain to behavioural ecology'.

### Subject Areas:

behaviour, cognition, evolution, neuroscience

### Keywords:

animal signalling, chorus, communication, collective behaviour, musicality, coupled oscillator

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# Synchrony and rhythm interaction: from the brain to behavioural ecology

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This theme issue assembles current studies that ask how and why precise synchronization and related forms of rhythm interaction are expressed in a wide range of behaviour. The studies cover human activity, with an emphasis on music, and social behaviour, reproduction and communication in non-human animals. In most cases, the temporally aligned rhythms have short—from several seconds down to a fraction of a second—periods and are regulated by central nervous system pacemakers, but interactions involving rhythms that are 24 h or longer and originate in biological clocks also occur. Across this spectrum of activities, species and time scales, empirical work and modelling suggest that synchrony arises from a limited number of coupled-oscillator mechanisms with which individuals mutually entrain. Phylogenetic distribution of these common mechanisms points towards convergent evolution. Studies of animal communication indicate that many synchronous interactions between the signals of neighbouring individuals are specifically favoured by selection. However, synchronous displays are often emergent properties of entrainment between signalling individuals, and in some situations, the very signallers who produce a display might not gain any benefit from the collective timing of their production.

This article is part of the theme issue 'Synchrony and rhythm interaction: from the brain to behavioural ecology'.

## 1. Introduction

Repetitive expression of a physical action at regular cycles is a fundamental property of a wide range of behaviour. Music, dance and language in humans and movement and communication signalling in non-human animals often include prominent expressions of such repetition, a feature generally termed *rhythmicity* [1]. These expressions occur in solitary individuals, but within aggregations, the rhythms are normally sustained longer and more steadily [2], and they can be transformed into collective events exhibiting coordinated features that are not otherwise observed [3]. Such transformation is quite evident in highly social organisms, although it may arise in any situation where grouping in space affords opportunities for mutual perception and response between neighbours. Thus, much behaviour has the potential for collective rhythmicity.

In the behaviour of non-human animals, the most striking aspect of collective rhythmicity is an overall pattern in time and space created and experienced by individuals within the group but also perceived by individuals outside of it. Typically, the pattern is synchronization [4] in which multiple individuals align an ultradian rhythm (cycle period ranging from many seconds down to fractions of a second), although more complex timing formats, encompassing

anti-synchrony and even ‘musical canon’, are found. Synchronous phenomena fascinate us because of the sheer number of participants, the summed intensity of the display and the precision in time and space of the coordinated activity. Moreover, our perception may be drawn specifically to synchronous temporal patterns, possibly a sensory bias analogous to positive responses to spatial symmetry. However, in addition to its aesthetic appeal, synchronization poses major unsolved problems at several levels. What are the mechanisms with which neighbours adjust their timing? Are collective rhythmic displays ‘self-organized systems’ lacking central control or do ‘group leaders’ orchestrate the display? How did these displays evolve and how are they maintained? Do collective displays entail selection pressures acting at both individual and group levels? If yes, do these pressures reinforce one another or act in opposition? Do feedback loops arise where selection at one level favours traits that, in turn, influence selection acting at another?

Similar questions arise for synchronous phenomena in biological organs, e.g. heart and brain, and in long-term (circadian, monthly, annual and multi-year) activity cycles observed within and between populations. Humans engage in a vast array of synchronized activities in verbal and non-verbal communication, social interaction, movement and the performing arts, all of which present many problems. For example, what are the cognitive, motor and environmental factors that shape rhythm interactions in music and dance?

The above issues are currently being addressed in novel ways that generally entail cross-disciplinary effort. Thus, scientists now ask the following: what are the genetic and evolutionary bases for synchrony and rhythm interaction in humans and non-human animals? Is synchrony necessarily an adaptation, or can it also arise as an emergent property? Are there common neural bases for rhythm interaction in language and music? And are there common bases for synchrony and rhythm interaction across animal species, including humans? Can models used in physics and applied mathematics to describe synchronous phenomena help us to understand synchrony as it occurs in animal behaviour at different time scales? Can cognitive scientists studying language, music, dance and other social interactions adapt and apply models used to describe synchrony in animal behaviour and vice versa? How should we incorporate the spatial dimension when modelling synchrony between mobile ‘entities’ and what are the special features of synchronous phenomena where mobility occurs? Our theme issue assembles review, opinion and research articles that address these key questions across a wide range of species. From an organizational perspective, the articles can be arranged in four different, but linked, sections.

## 2. Neural and genetic bases

Interest in the neural and genetic control of synchrony arises from the high precision of these interactions and their occurrence across a broad array of species. Musical performance in humans is arguably the most complex case of synchrony and rhythm interaction in the living world, and it is not surprising that a great many studies have focused specifically on the neural bases of the human capacity for music, i.e. *musicality* [5]. The evolution of this seemingly unique capacity has attracted a similar level of attention, and with

that interest come questions on the genetic bases. While there is still much debate on the cultural versus biological origins of music, evidence that musicality has deep biological foundations is growing. Genetic variation for this human capacity is now known to exist [6], and we have yet to identify a human culture that does not include music in its repertoire of expression. Here, comparison with human language—another universal capacity in which rhythm and rhythm interaction play critical roles—can be helpful. Both capacities integrate innate and cultural factors, the latter leading to expression in myriad ways [7]. Musical and language expression also require exposure and practice during development, but, unlike language, musical practice is very uneven among individuals, which probably generates extreme intra-population variation in musical ability. Thus, one may be led to underestimating those universal, innate factors or overestimating genetic variance for ability in music.

Just how unique is human musicality, particularly in terms of rhythm interaction? This age-old question came to the forefront again in 2009 with a report [8] on a parrot, a sulfur-crested cockatoo named Snowball, that moved—danced—to musical rhythm apparently without any prior training. The observation bolstered a hypothesis that synchrony and vocal learning are inextricably associated. However, more recent evidence suggests that only a few non-human animals share Snowball’s talent—much against Darwin’s intuitions. Hence, vocal learning may not be sufficient for the ability to synchronize. Furthermore, other animal species that do synchronize their acoustic signals are not vocal learners at all. In this theme issue, Patel [7] revises the hypothesis based on a range of empirical studies with parrots and other animal species, and our current understanding of the complex way in which vocal learning is implemented in the brains of parrots and humans; i.e. specialized auditory–motor forebrain circuitry. It is claimed that this circuitry—only found in species with very advanced vocal learning—is responsible for the finely tuned coordination needed to perceive a regular pulse, the ‘beat’, in an auditory signal and synchronize with it. Humans may have taken the process a step farther via the occurrence of a ‘Baldwin-like effect’ of gene-culture coevolution.

Lenc *et al.* [9] broaden the cross-species comparison by proposing a general model that encompasses four levels of synchrony and rhythm interaction. The model assumes three components: (i) sensory input, (ii) representation of that input by neural activity in the brain, and (iii) behavioural output. Sensory input is the unadulterated sound and rhythm reaching the ears, while neural representation is the transformation of that raw input into what is typically called ‘meter’ in music and poetry. Level 1 synchrony entails entrainment of behavioural output to the sensory input rhythm, but no more. That is, the interaction is not a simple series of responses to each individual pulse of the input rhythm, but there is no modified representation of that rhythm in the brain that serves as a template for comparison with behavioural output. At the other extreme, level 4 synchrony involves flexible learning, as in culturally transmitted music in humans. The intermediate levels 2 and 3 include some transformation of raw input into modified neural representations in the brain and would be found in species with competent to advanced vocal learning; e.g. passerine birds and parrots. The model is supported, in part, by electroencephalogram measurements, and data from a non-human primate, the Rhesus monkey

(*Macaca mulatta*)—which is not a vocal learner—are consistent with level 1. Thus, there does appear to be a fundamental neural base in primates from which human musicality might have evolved and converged with its counterpart in parrots.

Lense *et al.* [10] take a different, somewhat reverse approach by focusing on variants or disabilities in rhythm interaction that occur in some humans. These variants entail movement disorders, problems in turn-taking during speaking with others, and lack of response to musical rhythm, and they typically appear at a young age. The authors' approach has two main objectives: first, they propose that early intervention using 'rhythm therapy' may head off, or at least lessen, more severe problems expected to arise later. To some extent, the interventions are based on the notions that rhythm interaction in daily life is fundamentally a sensorimotor activity [11–13] and typically multimodal [14]. Second, determining the specific nature of these variants may improve our understanding of the neural and genetic bases of rhythm interaction in movement, language and musical performance.

The above articles do not ignore genetics and evolution, but it is this section's final article by Gordon *et al.* [6] that explicitly addresses the origin of rhythm interaction in humans and specifically relates it to our capacity for music. The authors made use of a large human genetic database which included information on musical beat perception: a binary response to the question 'Can you clap in time with a musical beat?' Applying genomic techniques, e.g. genome-wide association scans, to these data, they determined the genes that may be responsible for the mechanisms of synchrony, and then their orthologues in the zebra finch (*Taeniopygia guttata*), a passerine bird that is a competent vocal learner. These orthologous genes appear to be involved in regulating song production in the zebra finch. The article is a landmark indication that the long-sought genes influencing musicality probably exist.

### 3. Cognitive mechanisms

Synchrony and rhythm interaction are elaborate behaviour, and particularly so in social groups. An individual must not only be concerned with the timing of its sensorimotor activity, but often needs to decide on whom to ignore, whom to pay attention to, and how [15]. A large body of experimental work and modelling has taken a cognitive science approach to understand how these coordinations and decisions are made in humans and non-human animals. As with work on neural and genetic bases, some studies have concentrated on human musical performance. These investigations have indicated how some exceptional feats are accomplished and also have revealed some surprising constraints limiting what we can do.

Beginning with the most basic of musical interactions, a duet, Heggli *et al.* [16] remind us of the three possibilities for dyadic coordination: one individual leads while the other follows, both (attempt to) lead, and mutual adaptation. Given these three arrangements, the authors develop a general cognitive model based on each individual's perception of the joint musical output. It is assumed that the one who leads or attempts to lead segregates its own musical stream from the other's, whereas the one who follows or mutually adapts integrates both streams into a single entity. The model can be extended beyond a duet, and, more importantly,

makes testable predictions about the brain and behaviour during the performance.

Can a cognitive approach help identify the factors influencing the precision of synchrony in musical performance? What are the minimal phase angles that can be sustained between performers, and what are the fastest rhythms that can be synchronized? Jacoby *et al.* [11] recognized that identifying these limits would require a wide survey of musical genres, notably non-Western ones. The extreme studied thus far is the Malian ensemble drumming termed Jembe, which consists of three players. Its organization is a balance between 'democracy', which could be chaotic, and a strict hierarchy ruled by a stern conductor. One player is relatively invariant, a sort of metronome whose rhythm occasionally changes in response to the other two players, who regularly do shift small phase angles—asynchrony averaging only 17 ms—with each other. Modelling in which coupling between the several players was varied showed that this asymmetric balance yields higher precision than the tested alternatives.

In music and a host of other activities among humans and non-human animals, we know that rhythm interactions include synchrony or near-synchrony (phase angle  $\approx 0^\circ$ ) and anti-synchrony ( $\approx 180^\circ$ ), also termed alternation, but do other phase relationships, e.g.  $60^\circ$  or  $120^\circ$ , occur? If not, what could account for their absence? Dotov & Trainor [17] recognized this curious problem and approached it experimentally as well as via modelling. The classic 'finger tapping test' showed that human subjects were unable to sustain other phase relationships, e.g.  $72^\circ$ , with a stimulus rhythm after being primed with two rhythmic stimuli offset by that given phase, and they often veered toward anti-synchrony. It is reasoned that these other phases are unstable because they do not stimulate 'cross-frequency coupling' in the brain. Interestingly, phases that represent the  $360^\circ$  cycle divided by a small integer value, e.g.  $120^\circ$  ( $=360^\circ/3$ ) and  $90^\circ$  ( $=360^\circ/4$ ), in addition to  $180^\circ$ , exhibited modest stability during testing. These phases may stimulate a small amount of cross-frequency coupling, and they are observed in some animal choruses, as when three or four male frogs call together, each male offset by  $120^\circ$  or  $90^\circ$ , respectively, following one of his neighbours [15].

It is increasingly apparent that much of the transmission and perception of communication messages in both humans and non-human animals is multimodal; e.g. acoustic and visual. The rhythmic properties of communication messages are therefore multimodal as well, and Pouw *et al.* [14] take the logical next step by examining how rhythms of the several modalities interact, from the perspectives of the signaller and of the receiver. A survey shows that synchrony of the separate rhythms is generally critical for effective communication. For a personal example, consider the annoyance that some viewers of foreign films experience while being distracted by the asynchrony between the rhythm of speech and that of lip movement when voices are dubbed. In many situations, synchrony of the several modalities is trivial, as when sound is a direct by-product of movement. However, such linkage is not necessarily the case, and we must generally ask how separate rhythms mutually connect at neural, anatomical and social levels. These connections remain poorly known at present.

The two final articles in this section, focusing largely on non-human animals, point out how overlooking key biological factors has restricted our understanding of rhythm interaction. Bouwer *et al.* [12] emphasize that synchrony is essentially a sensorimotor process, but find that very few studies address both

parts adequately. Moreover, many investigations are rather context specific, e.g. mating communication, and never determine the basic elements of the synchronization mechanism and abilities. Studies of synchrony are concentrated on several animal groups with displays of rhythm interaction that are highly conspicuous to human observers, which has created a very uneven distribution of our knowledge across animal clades and modalities. These gaps hinder our efforts to apply the comparative method effectively and to understand the evolution of synchrony.

Henry *et al.* [13] continue the emphasis on the sensorimotor nature of synchrony, noting that we have generally failed to appreciate physiological constraints on the motor part: in most cases, this part is essentially a co-option of the animal's bodily or appendage movement, its respiration, or another physiological activity, and these activities typically have characteristic rhythms. That behavioural synchrony mostly entails ultradian rhythms ranging from 0.1 to 5 Hz is probably not chance coincidence but reflects properties of these basic activities. We have also failed to recognize the importance of context and motivation in synchronous behaviour, which is often associated with courtship and other reproductive activity. Considering these contexts more carefully during observation and testing may expose many new cases of synchrony.

#### 4. Animal communication

Displays of animal communication signalling include many of the pre-eminent examples of synchrony in biology. Moreover, they are often amenable to experimental probing, in the field or laboratory, and thus afford opportunities to test the adaptive value of synchrony. In some species, there are multiple adaptive factors favouring synchrony, but in others synchrony emerges as a by-product of signalling behaviour and offers no selective advantage to the signallers. Above all, the study of synchrony in communication reinforces the importance of understanding the animal in its natural milieu, its social environment and its sensory ecology.

De Reus *et al.* [18] open this section with a review devoted to rhythm interaction in dyads, pairs whose members are distinguished by a particular social relationship. Dyads are generally considered as comprising individuals with largely parallel interests, e.g. parent–offspring pairs, male–female conjugal pairs, or social partners within a local population. However, some adversarial pairs, e.g. contestants over territory ownership, may also be considered if the two individuals maintain a specific relationship over an extended bout. In humans, dyads typically exhibit synchrony in the context of music or social interaction, and alternation when speaking. In non-human animals, the interactions are mostly alternation in all contexts save a few cases where a pair synchronizes their signals. Alternation shaped by rules for avoiding coincidence is believed to facilitate clear communication for both the signaller and receiver, as overlapping sounds physically mask each other. Overlapped visual signals too may pose problems for clarity, as an individual pre-occupied with transmitting its own signal may be cognitively limited from attending to its partner's. The few occurrences of synchronized signals may be a means by which a pair communicates, to the local population, the strength of its bond. The review emphasizes that most of our knowledge concerning dyads is taken from

acoustic communication. Thus, our understanding is likely to increase with more attention to optical, movement and multimodal signals.

Greenfield *et al.* [15] take the rather opposite approach by focusing specifically on communication in animal groups, i.e. assemblages of three or more individuals. Here, the critical limitation is that most of what we know about synchrony and rhythm interaction in non-human animals comes from the study of pairs, either dyads or duos simply isolated from the larger population. This limitation is certainly recognized, and it can be attributed to the difficulty of testing larger groups, either in the field or laboratory. However, signalling in groups is the rule, not the exception, and an understanding of rhythm interaction demands that we determine how animals deal with multiple neighbours. A survey shows that arthropods and anurans generally accomplish the task via selectively attending to only a subset of the neighbours that they can physiologically perceive, and that such attention is found in species that synchronize or alternate, that use various interaction mechanisms, and that signal in different modalities. Birds and mammals, among which information is scant, may solve the multiple neighbour problem by transmitting shorter signals at slower rhythms and by specialized rules for signal timing. A 'communication network' approach is expected to be particularly useful in addressing the group signalling problem.

The next two articles in this section report research testing how rhythm interaction in non-human animals may be favoured by selection. Legett *et al.* [19] studied a Japanese tree-frog species (*Buergeria japonica*) whose males call in synchronous choruses that may afford advantages in attracting females and avoiding phonotactic natural enemies. But some of the males who join choruses might attract fewer, not more, females by virtue of calling immediately following a neighbour(s). A series of field recordings and playback experiments resolved these questions. A group of males who synchronize their calls do transmit a more intense collective signal than a group who time their signals randomly, and overall they will attract more females by broadcasting over a greater radius. Synchrony in a group is quite good, but not perfect, and some males inevitably call slightly later than others, a relative timing that attracts fewer blood-sucking midges. Unlike many acoustic species, late callers in *B. japonica* do not attract fewer females. Thus, males who synchronize gain a fitness advantage regardless of the relative timing of their calls. Nonetheless, one may ask how changes in predator behaviour, population density and female choice could influence the overall status of synchrony.

Perez *et al.* [20] studied an Australian fiddler crab species (*Austruca mjobergi*) in which advertising males synchronize optical and movement signals generated by waving an enlarged front leg. Here too the synchrony is imperfect, being characterized by leaders and followers. Females do prefer leading signals, but it is not clear if males who tend to lead are necessarily of higher 'quality'. Rather, males who wave faster are more likely to lead, and synchrony may simply emerge when males who are similarly matched for a fast rate wave together in a competitive signalling display. Females also prefer faster signal rates, which might be an indication of 'condition', potentially a proxy for quality. Because leaders are generally fast signallers, when a female identifies a leading signaller and responds to him, she may indirectly choose a high-quality mate.

## 5. Long-term rhythm

Rhythms with periods much longer than the ultradian cycles treated in the first three sections also occur in living organisms, and some long-term rhythms influence overt behaviour and exhibit synchrony, most notably in reproductive and social activity. Long-term rhythms originate in a 'biological clock' that keeps 'real time'. In mammals, the clock is known to reside in the superchiasmatic nucleus of the hypothalamus in the brain. The best known long-term rhythms are circadian, i.e. approximately 24 h, but tidal, monthly and annual rhythms also function. As in the ultradian rhythms that regulate communication signalling in animals, long-term rhythms are endogenous, i.e. free-running, and entrained by the activity of neighbours. However, in long-term rhythms external environmental signals, typically reliable *zeitgebers* such as photoperiod, also play a major entrainment role. The endogenous rhythm, sharpened by entrainment to neighbours' activities, is particularly critical in species inhabiting dark zones where exposure to photoperiodic *zeitgebers* is infrequent or absent [21]. Thus, an individual can anticipate and prepare itself physiologically before a critical activity must begin at a certain hour of the day or month of the year.

Siehler *et al.* [21] report a study on synchronization of activity rhythms in colonies of the western honeybee (*Apis mellifera*). This social species is a cavity nester both in nature and when kept in commercial hive boxes, implying that most of the non-foraging workers do not have direct access to environmental *zeitgebers*. Synchrony of the workers' daily activity rhythms is believed to increase colony productivity, but the contributions of the endogenous clock, environmental entrainment and mutual entrainment among workers remained unknown. Testing individuals that had differing levels of contact with fellow workers and sophisticated analysis of colony activity showed that indirect contact—which 'coupled' individuals by allowing them to sense odour and vibration cues of their neighbours—significantly enhanced synchrony.

Over very long time periods—one year and beyond—rhythms can arise that are properties of a population or species rather than an individual. These rhythms are typically fluctuations in abundance or biomass, and the rhythms of several species comprising a biological community may interact with each other. In many cases, such rhythm interactions take the form of anti-synchrony between species occupying different trophic levels, e.g. predator and prey. Cases of synchrony also occur and probably arise when the several species have common behavioural or ecological responses to a recurring environmental variable, e.g. abundance or rarity of a nutrient or a physical condition such as temperature or pH. Ecologists are interested in such interspecific synchrony because it may de-stabilize a community by making extremely low populations and extinctions more likely. Ghosh *et al.* [22] pursue this issue, focusing on the statistical indices used to measure community synchrony, and the inability of traditional indices to contend with the different ways in which a given degree of synchrony can be achieved. In particular, they show that a situation in which several species are highly synchronous only when rare will exert a different influence on stability than a situation where several species are synchronous when common, and they introduce modified indices to accommodate these distinctions.

## 6. Connecting the sections and beyond

This theme issue covers the way that animals, including humans, express overt behaviour rhythmically over repeated cycles, how the rhythms of multiple individuals, or multiple rhythms within a given individual [14], interact with one another, and how the rhythm interactions are perceived by the interactants themselves and by outside parties in the same or different populations or even in other species [19]. Assembling the 16 articles side by side reveals parallels that might not otherwise be evident. Synchrony and anti-synchrony—alternation at an approximately 180° phase angle—are the rule across species. These interactions appear to result from a small number of sensorimotor mechanisms by which a rhythm's free-running repetition rate or its relative phase is adjusted [23]. The several mechanisms occur among organisms—chordates and arthropods [15,23]—whose most recent common ancestors lived at least 600 Ma and most likely had rudimentary nervous systems at best. Thus, the shared mechanisms probably reflect evolutionary convergence: confronted by common selection pressures to communicate clearly and persuasively, to cooperate, to compete effectively with other groups or within one's own group, or to evade natural enemies, the number of solutions could be quite limited. Such restriction may function at both the level of neural mechanism and of temporal format in which the rhythm interaction is broadcast.

At first glance, long-term circadian rhythms and their interactions appear to differ fundamentally from the ultradian rhythms that prevail in human and non-human animal communication. Circadian rhythms originate in intra-cellular molecular clocks—the so-called biological clock—not regulatory pacemaker neurons in the central nervous system. But circadian activity does entail many prominent displays of synchrony, and individuals entrain to one another's activity. What sets circadian activity, and synchrony, apart is entrainment to environmental *zeitgebers*, which would not be possible for ultradian rhythms. Responses to a *zeitgeber* allow widely dispersed individuals lacking any contact to synchronize their circadian rhythms with precision, a process that cannot occur in ultradian rhythm. Biologists have modelled both ultradian and circadian synchrony as a coupled oscillator [21,24], and they have found that adaptations of the classical Kuramoto model offer a reasonable description in both synchrony categories. Importantly, Yoshiki Kuramoto developed the model for describing chemical oscillations [25], and neuroscientists have applied it widely, including at the neuronal level. The synchrony covered in this theme issue clearly has parallels well beyond behaviour.

Long-term synchrony that occurs between species is yet more distinct, but again basic correspondences with ultradian synchrony exist. In both categories synchrony—between individuals or species—may sometimes emerge as an incidental by-product whose consequences for the parties concerned are unclear and might even be absent. Moreover, synchrony is often imperfect under such circumstances, e.g. leaders and followers in animal choruses [19,20], and it is the asynchronous imperfection that can have profound consequences for the individuals or species. Ghosh *et al.* [22] point out how asynchrony in the temporal alignment of species forming a biological community bears resemblance to events in the business cycle, highlighting further external connections, in this case to the field of human economic affairs.

**Data accessibility.** No data are included in this paper.

**Authors' contributions.** All four editors contributed to the writing and editing of this introduction.

**Competing interests.** All editors declare that they have no competing interests.

**Funding.** This theme issue was inspired by a workshop, 'Synchrony and rhythm interaction: from neurons to ecology', that was held at the Lorentz Center in Leiden, Netherlands in 2019. The workshop

was funded by the Lorentz Center, by the Institute of Logic, Language and Computation (ILLC) at the University of Amsterdam and by the Australian National University.

**Acknowledgements.** We thank the Lorentz Center for assistance in organizing the workshop that led to this theme issue. We are most grateful to the authors of the articles in this issue, to the referees who reviewed earlier versions of the articles, and to Editor Helen Eaton of the Royal Society for her guidance at every stage.

## Guest Editor biographies



**Michael Greenfield** is currently a Research Professor of Ecology & Evolutionary Biology at the University of Kansas, USA and an Invited Professor in the Équipe Neuro-Ethologie Sensorielle at the Université de Lyon/Saint-Etienne in France, after 35 years as Professor at University of California–Los Angeles, then the University of Kansas and most recently the Université de Tours/Centre National de la Recherche Scientifique in France. He is a behavioural and evolutionary biologist with broad interests in animal communication and sexual selection. His recent projects have centred on acoustic signalling and perception, with a particular focus on evolutionary genetics and chorusing phenomena. He is the author of *'Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication'* (Oxford University Press, 2002) and a Fellow of the Animal Behavior Society.



**Henkjan Honing** is a professor of Music Cognition at both the Faculty of Humanities and the Faculty of Science of the University of Amsterdam. He studies what musicality is or can be, and to what extent human beings share musicality with other animals. His aim is to define the cognitive and biological mechanisms that underpin musicality. In addition to a research agenda (*The Origins of Musicality*, 2018, MIT Press), Honing has published several books for the general public, including the English-language publications *Music Cognition: The Basics* 2021, Routledge) and *The Evolving Animal Orchestra* (2019, MIT Press). Honing's books and lectures are popular with a broad audience and are appreciated both inside and outside the scientific world. You can find more about the Music Cognition Group at [www.mcg.uva.nl](http://www.mcg.uva.nl).



**Sonja Kotz** is a translational cognitive neuroscientist, investigating temporal, rhythmic and formal predictions in audition, music and speech across the lifespan, in animal models, and patients (Parkinson's disease, stroke, tinnitus, psychosis, dyslexia). In her research, she uses a wide range of behavioural and neuroimaging methods (magnetoencephalography; electroencephalography; structural magnetic resonance imaging; functional magnetic resonance imaging; and transcranial magnetic stimulation). She heads the Neuropsychology section at Maastricht University and holds several honorary professorships (Manchester, Leipzig and Lisbon). She is a senior/associate editor for several journals (e.g. *Neuroimage*, *Cortex*, *Plos One*). Find more about her laboratory @ [www.band-lab.com](http://www.band-lab.com).



**Andrea Ravignani** leads the Comparative Bioacoustics Group at the Max Planck Institute for Psycholinguistics. His research combines insights and knowledge from speech sciences, bioacoustics, comparative psychology, neuroscience, evolutionary biology, music cognition, artificial intelligence and mathematics. Andrea investigates the evolutionary and biological bases of rhythm cognition and flexible sound production, and the role they played in the origins of music and speech in our species. He performs sound recordings and behavioural non-invasive experiments in several animal species (mostly seals) as a comparative effort to understand the evolutionary history of human capacities. He complements animal research with human testing, neurobiological evidence, mathematical models and agent-based simulations. Andrea is a firm supporter of kindness in science and academia.

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