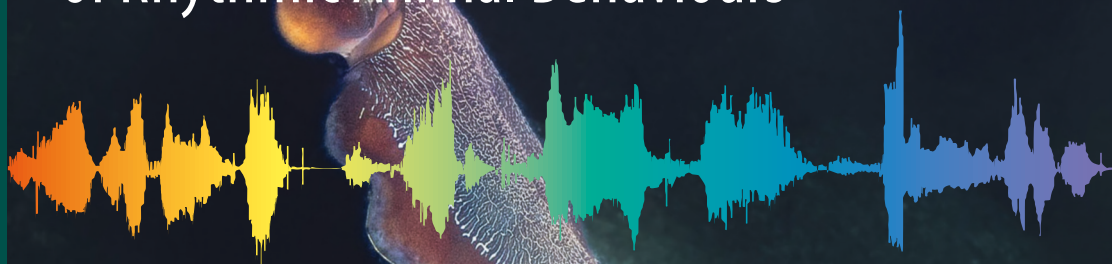


Fascinating Life Sciences

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The What, How and Why
of Rhythmic Animal Behaviours



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The Next Frontier in Research on Rhythm Cognition and Rhythmic Communication

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Abstract

In this concluding chapter, we focus on outlining the next frontier in research on rhythm cognition and rhythmic communication (RCC), synthesising conceptual, methodological, comparative, and applied directions, as they emerge from the

Disclaimer. This chapter does not represent a unified position or consensus among the contributing authors. Rather, it provides a brief overview of the current state of the field and outlines possible directions for future research. The field remains fragmented, with differing perspectives on what should be studied and how. The chapter is intended to be inclusive of the diverse frameworks, hypotheses, and viewpoints represented in this volume.

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contributions to the *Nature Beats volume*. While consensus has grown regarding the composite nature of rhythmic competence and the need for integrated quantitative approaches, the field remains marked by conceptual heterogeneity and

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inconsistent operational criteria. To advance RCC research, the chapter identifies pressing needs for conceptual clarity, methodological standardisation, and ecologically grounded definitions of rhythmic phenomena across modalities and species. We also highlight future research trajectories for major theoretical

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frameworks, including the Vocal Learning–Beat Perception and Synchronisation hypothesis, Gradual Audiomotor Evolution hypothesis, Neural Resonance Theory, socio-ecological hypotheses of synchrony, and evolutionary accounts linking rhythm to social bonding and stress regulation. A bottom-up, species-specific, and comparative approach is advocated to capture the full structural and functional diversity of RCC and to evaluate mechanisms spanning neural oscillations and functional connectivity, biomechanics, development, reward systems, and environmental constraints. Finally, the chapter emphasises the translational value of RCC research. Rhythm-based interventions hold promise for educational, clinical, welfare, conservation, and human-animal interaction contexts. By integrating mechanistic, evolutionary, and applied perspectives, future research can uncover the biological principles underlying rhythmic behaviour and its central role in communication, cognition, and sociality across the animal kingdom.

15.1 Introduction

Rhythm cognition and rhythmic communication (RCC) have become an effervescent area of research. Research on these topics has gained significant momentum as a way of tracking the evolutionary roots of human musicality, following the discovery that some nonhuman mammals and birds are capable of synchronising movements with an external rhythm. Recently, however, research on RCC has branched out to also include other aspects of RCC, besides rhythmic synchronisation.

The aim of this book was to capture the full span of this expanding area of research, starting with its conceptual, terminological, and methodological debates (Chap. 1 [1]), and continuing with forms of RCC in humans and the rest of the animal kingdom (Chaps. 2 [2], 3 [3], 4 [4], 5 [5], 6 [6], 10 [7], 12 [8], 13 [9], Chap. 14 [10] and peer commentaries therein), as well as underlying and modulating mechanisms (Chaps. 1 [1], 2 [2], 5 [5], 6 [6], 7 [11], 8 [12], 9 [13], 10 [7], 11 [14], 13 [9], and 14 [10]). On the backdrop of this broad thematic span, we sought to emphasise both the intrinsic and the translational value of comparative research, while also highlighting a comprehensive need for both meticulous analyses with a narrow focus and increasingly integrative approaches.

We dedicate this last chapter to summarising current gaps in RCC research to set a—hopefully collaborative—research agenda for the next two decades, starting with demands for conceptual and methodological development (Sect. 15.2). We then refine and further expand on this agenda in sections that contemplate the next frontier in RCC for the theories represented in the book (Sect. 15.3), as well as in terms of exploratory (Sect. 15.4) and applied work (Sect. 15.5).

15.2 Conceptual and Methodological Development

Currently, there is a broad consensus regarding the composite nature of rhythmic competence, where RCC can be studied from multiple perspectives reflecting increasingly complex rhythmic abilities, from the physical level of the signal to music and group interactions (Chap. 1 [1]). Even within each of these perspectives,

the complexity of the analysed phenomenon can vary. For example, from the physical signal perspective, structural complexity can vary from metronomic isochrony to hierarchically stratified rhythms. On the methodological front, there is emerging consensus that studies of RCC should report durational, density, and variance measures and that RCC requires combined approaches integrating local and global metrics.

Beyond such points of convergence, however, there is a comprehensive need to work towards increased conceptual consistency, methodological development, and standardisation. Conceptual stances diverge even for well-researched topics such as isochrony or synchronisation, where we lack accepted operational criteria such as thresholds for minimal sequence duration or maximal variance.

This ambiguity is also reflected in debates regarding adequate quantification tools or the very topics that should constitute the field and be worthy of scientific investment. In a human-centric perspective, studies of nonhuman RCC are framed as having scientific value as a way of gaining insight into the evolution of human musicality and/or speech. Within this perspective, however, opinions vary as to whether only sustained rhythmic synchronisation (Chaps. 5 [5] and 14 [10]) is relevant to this goal or RCC more broadly, i.e. also encompassing the production and perception of solo rhythms (Chaps. 3 [3], 4 [4], 6 [6], 7 [11], 8 [12], 9 [13], 10 [7], 11 [14], 12 [8], and 13 [9]). An additional view that is increasingly gaining support emphasises the intrinsic value of investigating the temporal organisation of animal communication and behaviour regardless of what we can learn about the evolution of musicality (see also Sect. 15.5). Ultimately, these perspectives form a continuum, with findings from humans guiding research towards new insight about RCC in other species and findings from nonhuman animals inspiring new directions of research in humans.

On a conceptual level, there is a need to acknowledge—and indeed discover—additional components of rhythmic competence beyond commonly studied notions such as beat perception and motor entrainment. For example, rhythm cognition also involves interval estimation, tempo perception, pattern recognition, statistical learning, chunking, categorical perception, a preference for integer ratios and more (a point to which we return in Sect. 15.4.1). Rhythmic complexity itself remains poorly conceptualised, and current data highlight both the promise and the gaps in current understanding (Sect. 15.4.1).

Methodologically, there is a growing need to refine experimental and observational paradigms to better study rhythm perception, including its automatic versus intentional dimensions and potential biological significance across species. This requires accounting for neuromuscular constraints and socio-cognitive influences to avoid confounds in cross-species comparisons (as detailed in Sects. 15.3 and 15.4).

15.3 The Next Frontier for Current RCC Theories

Having identified the key coordinates of conceptual and methodological needs (Sect. 15.2), we turn to the Next Frontier for the key theories and hypotheses that have been represented in the contributions to this book, focusing on empirical research designed to test and further develop them. Rather than revisiting these

frameworks in detail (for which we refer to the relevant chapters), our goal here is to suggest concrete avenues for future studies that can help validate or expand current theoretical proposals.

15.3.1 The Vocal Learning-Beat Perception and Synchronisation Hypothesis

One of the most influential frameworks in the study of RCC is Aniruddh Patel's Vocal Learning Hypothesis, which posits a close connection between *advanced* vocal learning (VL) capacities and beat perception and synchronisation (BPS) (for reviews and critical discussions, see Chaps. 7 [11] and 14 [10]). According to the VL-BPS hypothesis, the strong auditory-motor connections required for VL also support the neural architecture necessary for BPS. The dorsal auditory pathways are central to this framework, with VL-BPS emphasising their role in auditory-motor integration.

As an adaptation, vocal learning is likely reinforced by reward mechanisms. Thus, a corollary of VL-BPS is that vocal learning species exhibit enhanced motivation to attend to complex auditory structure and spontaneously synchronise with external rhythms (Chap. 7 [11]). The VL-BPS hypothesis has inspired a wave of comparative studies in both vocal learning species—such as parrots, songbirds, and seals—and vocal non-learning species, including sea lions and primates (Chaps. 3 [3], 7 [11], and 14 [10]), in particular, the peer commentaries by Cook and Reichmuth (Sect. 14.2.1) and Okanoya (Sect. 14.2.4).

The next frontier for research driven by the VL-BPS hypothesis spans several objectives. In humans, it involves deepening our understanding of the cognitive and neural relationships between beat-based rhythmic processing and aspects of language in both adult and developmental populations. In nonhuman species, the next frontier involves continued exploration of the neural mechanisms of temporal prediction in beat-based auditory rhythms and investigating how these mechanisms compare to those used by humans. A particularly intriguing question is whether any animals besides parrots can spontaneously develop predictive and tempo-flexible synchronisation to musical beats through social interaction with humans, without formal training. Horses, for example, could be a promising candidate species for such investigations. Finally, another important future direction involves understanding the developmental and neurobiological factors that explain why some pet parrots develop dancing behaviour in response to musical rhythms while others do not.

15.3.2 The Gradual Audiomotor Evolution Hypothesis

The Gradual Audiomotor Evolution (GAE) hypothesis proposes that the neural and behavioural capacities for beat perception and synchronisation (BPS) evolved incrementally within primates rather than emerging suddenly in humans (Chap. 7 [11]). GAE views human rhythmic and musical behaviour as the outcome of a stepwise

strengthening of audiomotor connectivity—linking auditory cortices, motor planning circuits, and subcortical timing structures. This contrasts with the VL-BPS hypothesis (Sect. 15.3.1), which ties rhythmic synchronisation more tightly to the evolution of complex vocal learning. Although early studies suggested that only vocal-learning species could synchronise predictively to a beat, recent behavioural and neural evidence has reshaped this view.

Rhesus macaques (*Macaca mulatta*), for example, can synchronise predictively to auditory and visual metronomes when motivated by reward, showing tempo flexibility, error correction, and continuation tapping (Chap. 7 [11]). Neural recordings reveal cyclical population dynamics in the medial premotor cortex that encode tempo and beat timing—evidence for an internal rhythmic clock. These findings suggest that primate brains already possess the computational substrate for beat-based timing, even if rhythmic behaviour is not intrinsically rewarding as it is for humans.

Recent extensions of GAE, such as the BPS Components Continuum (Chap. 7 [11]), frame rhythmic ability as a graded spectrum from basic interval timing to predictive beat entrainment. Future work should test this continuum using comparative behavioural paradigms and multimodal neuroimaging to quantify how cortical–subcortical connectivity, particularly within the medial cortical–basal ganglia–thalamo (mCBGT) circuit, scales with rhythmic proficiency. Another key question concerns the evolution of intrinsic reward: while macaques rely on external reinforcement, humans find synchronisation pleasurable, perhaps due to dopaminergic coupling between motor and auditory systems.

Expanding research to lemurs, gibbons, and chimpanzees—species showing proto-rhythmic behaviours such as duetting, drumming, swaying, etc.—will further test GAE. Integrating field data, rhythm analytics, and cross-species training will help link neural circuitry, motivation, and ecology in the evolution of rhythmic behaviour.

15.3.3 The Neural Resonance Hypothesis

The Neural Resonance Theory (NRT) proposed by Ed Large (Chap. 8 [12]) posits that rhythmic perception and synchronisation emerge from oscillatory neural dynamics that may be conserved across species. According to NRT, intrinsic neural oscillations entrain to external rhythmic stimuli, forming the foundation for beat perception and temporal prediction.

A central challenge for future NRT research is to uncover the evolutionary origins of these resonance mechanisms through cross-species, comparative work. Key milestones include determining whether nonhuman species capable of rhythmic synchronisation can also perceive complex rhythmic structures such as pulse and meter, including “missing pulse” rhythm. To address these questions, experimental tasks involving tempo perturbations and syncopated rhythms will be essential. Additionally, invasive neural recordings in animal models, combined with dynamical systems modelling, will permit identifying conserved oscillatory mechanisms.

Developmental studies comparing human infants and trained animals may illuminate how rhythmic attunement emerges and unfolds over time. Understanding how intrinsic frequencies adapt and stabilise through Hebbian learning could clarify the role of plasticity in rhythm acquisition. Moreover, examining integer-ratio preferences in human development and across cultures and by comparison with animal vocalisations may reveal evolutionary constraints on rhythm production.

Taken together, cross-species and developmental comparisons of rhythmic learning and synchronisation driven by NRT could help distinguish between convergent evolution and shared ancestry. Ultimately, integrating behavioural, neural, and computational approaches will be essential to trace the evolutionary trajectory of musical rhythm cognition.

15.3.4 Rhythmic Synchronisation as a Beacon Display Evolved in the Context of Male Territoriality and Female Exogamy

In a provocative hypothesis (Chap. 14 [10] but see also Chap [5]) based on striking examples of precise inter-individual group synchrony in arthropods and anurans, Björn Merker has conjectured that human rhythmic synchronisation evolved in ancestral socio-ecological conditions characterised by male territoriality and female exogamy. Analogous to the socio-ecology of clumped males and migrating females that is the setting for precise synchrony in the animal examples, such circumstances create a selection pressure for conspicuous, long-range signalling aimed at attracting dispersing females. In such a setting, rhythmic synchronisation of, say, sound signals would amplify their environmental reach by superposition of their discrete elements, allowing the signal to reach more female ears compared to unsynchronised signalling.

Looking ahead to research challenges posed by this hypothesis, three principal issues may prove fruitful. Not all species that feature clumped males and migrating females exhibit group synchrony in their signalling. That is, in fact, what is expected if signal synchrony happens to be a factor in a speciation event: the non-synchronising subpopulation remains behind a reproductive isolating barrier relative to the synchronising subpopulation, and the two subpopulations split into separate evolutionary lineages. Since both humans and chimpanzees exhibit male territoriality and female exogamy, while only humans synchronise their signalling, Merker has suggested that signal synchrony played a role in the human-chimpanzee split. Close scrutiny of related species that share similar ecological circumstances but differ in signal synchrony may disclose the more particular factors at play in such splits.

A further New Frontier issue concerns the fact that in arthropods and anurans, only males engage in synchronous chorusing, while in humans, both sexes are enthusiastic synchronisers (as noted by the peer commentary of Popescu and Fitch in Chap. 14 [10]). As suggested in Merker's response, genome-based studies that target components of human musicality may eventually be able to tell us whether genetic constraints on the human capacity for inter-individual synchrony promote female synchrony as a correlated genetic response to selection on males. And finally,

do bonobos in the wild exhibit the vocal behaviour which has been named “staccato hooting” in captive bonobos (as described in Chap. 14 [10])? It is said to exhibit inter-individual synchrony and needs to be confirmed as more than a chance occurrence. Should it occur with synchrony in the wild, this might mean that the conjectural scenario for a human–chimpanzee split was repeated in a subsequent bonobo–chimpanzee split.

15.3.5 The Social Bonding Hypothesis of Music Evolution

The social bonding hypothesis proposes that music evolved primarily to strengthen social cohesion. Among others, this proposal is based on data showing that joint music-making—even just joint listening—promotes group unity, effectively acting as a powerful social glue. For instance, group singing has been shown to promote interpersonal closeness, cooperation, and a rapid sense of group identity (as discussed in Chap. 11 [14]). One particularly important mechanism enabling this effect is rhythm. By getting people to anticipate one another’s actions and synchronising them in time, shared rhythm and coordinated movement are also in a position to align emotional states, in turn enhancing trust and affiliation within the group (Chap. 11 [14]).

To further elucidate the validity of the social bonding hypothesis of music evolution, future research should continue on its way to a more fine-grained comparative approach. Such data has indeed already provided a rich source of insights that have led to the initial formulation of this hypothesis. In particular, more systematic work is needed on nonhuman primates and other (vertebrate and nonvertebrate) species that engage in coordinated vocal behaviour, such as duetting and chorusing (Chaps. 3 [3], 5 [5], 10 [7], 12 [8], and 14 [10]). These natural phenomena offer a unique opportunity to test whether rhythmic coordination serves similar affiliative functions outside our species. Empirical efforts should prioritise field-based observations complemented by controlled experiments to evaluate how rhythmic synchrony influences cooperation, tolerance, and behavioural alignment among individuals. Developing quantitative approaches to examine the relationship between rhythmic regularity and behavioural coordination in animal communication will be key to understanding how the temporal structure of calls supports social functions.

Ultimately, investigating the role of rhythm in nonhuman vocal interactions may clarify whether the mechanisms that support musical bonding in humans are unique evolutionary innovations or reflect continuities in primate social behaviour, or even more deeply rooted traces of convergent evolution.

15.3.6 The Stress Relief and Social Bonding Hypothesis of Dance Evolution

Tandem-walking or “conga-line” behaviour in traumatised great apes—first documented in chimpanzees and later confirmed independently in multiple sanctuary populations (Lameira, personal observations)—appears to function as a rhythmic

co-stereotyping that stabilises dysregulated autonomic systems. Through synchronous, full-body entrainment, individuals may achieve stress relief and regain the social buffering lost through maternal or early-life deprivation (discussed in Chap. 12 [8] and Chap. 13 [9]). In this form, tandem-walking offers a plausible precursory mechanism for the stress-modulating and bond-reinforcing functions that many theories attribute to early human dance.

Building from this hypothesis, a central priority for future research is to expand the empirical record across species and populations. Although the initial evidence emerged from a single chimpanzee dyad, subsequent reports from American zoos and African sanctuaries, suggest that the phenomenon arises repeatedly and convergently. Systematic data mining of online video repositories (e.g. YouTube) could identify additional occurrences in chimpanzees, gorillas, bonobos, and orangutans. Ideally, these efforts should be complemented by direct, high-frame-rate recordings in sanctuaries and rehabilitation centres where orphaned or socially deprived apes are housed. Such work would allow the collection of standardised data on bout duration, tempo, phase-locking accuracy, initiation cues, tactile dynamics, and social context, ultimately clarifying whether tandem-walking reflects a generalised great-ape stress-coping strategy or a phenomenon tied to specific ontogenetic conditions.

Current advances in AI-based pose-estimation technology make this expansion especially timely. Next-generation primate-specific models—such as OpenMonkeyStudio, PrimatePose, LeapTrack, or dedicated DeepLabCut models fine-tuned for bipedal synchrony—can now extract highly precise pose and gait metrics even from low-quality footage. Transformer-based pose-time-series architectures can detect micro-lags, leader-follower reversals, and continuous mutual adjustments between partners. Likewise, graph neural network motion encoders are well suited to modelling synchrony as a multi-body coupling system rather than as two independent trajectories. When combined with 3D reconstructions (or monocular depth inference), these tools can quantify interpersonal distance regulation, hand placement, and the geometry of tactile coupling, thus revealing the underlying sensorimotor mechanisms that maintain synchrony.

Future research should also integrate behavioural analyses with physiological, affective, and social data. Non-invasive endocrine sampling or monitoring (e.g. using cine-infrared-thermography) could test whether tandem-walking aligns with known biological markers of stress relief and social bonding. Where possible, lightweight sensors or video-based techniques (e.g. remote photoplethysmography) could capture heart rate and HRV changes during synchrony, while sociometric mapping could assess whether tandem-walking alters affiliation networks or reduces aggression. Together, these measures would help determine whether the behaviour primarily functions for autonomic regulation, social cohesion, or both.

To move beyond correlation, carefully designed semi-experimental paradigms will be needed. Mild environmental manipulations—such as temporary separation, the introduction of new individuals, or controlled interruptions of ongoing bouts—could reveal the triggers and reinstatement dynamics of tandem-walking. Rhythmic versus arrhythmic auditory cues could test whether external beats influence

synchrony stability. Observations of whether apes spontaneously resume phase-locked motion after pauses would clarify whether they maintain an internal representation of a joint rhythm. Comparisons between strongly bonded and weakly bonded dyads, or across different ages and developmental backgrounds, may illuminate how social and affective factors shape the behaviour.

Finally, comparative work across species remains essential. If tandem-walking consistently emerges in chimpanzees, gorillas, bonobos, and possibly orangutans under similar developmental conditions—especially in populations of orphans or socially disrupted individuals—this would point to a shared hominid predisposition for using rhythmic synchrony as a means of stress regulation and affiliative repair. Such evidence would strengthen the argument that early human dance could have originated as a small-scale, dyadic mechanism for co-regulation, later elaborated culturally into collective ritual and aesthetic expression. Expanding the search for this behaviour to new populations, both through digital repositories and direct field-work, will be critical for understanding how rhythmic synchrony functions in great apes today and how it may have shaped the earliest stages of dance evolution in our own lineage.

15.4 Exploring Evolutionary Trends with Bottom-Up Research

Scientific interest in rhythm as a dimension of animal communication has been mainly driven by human-centric models, using musicality and speech as benchmarks. Such top-down approaches may obscure the broader evolutionary and biological significance of RCC, which, as demonstrated by this book, is widespread across the animal kingdom. In light of the research presented in previous chapters, there is a pressing need to embrace bottom-up approaches that prioritise species-specific multidisciplinary investigations. Such research could account for ecological, bio-cognitive, and developmental constraints, offering a more nuanced and inclusive framework for rhythm science. This reframing also challenges the notion of rhythm as primarily a cognitive and/or cultural construct, instead positioning it as a biological phenomenon deeply embedded in the neuromechanical and ecological realities of diverse species, humans included.

By focusing on how RCC is shaped by organism–environment interactions, bottom-up research can uncover the evolutionary logic behind rhythmic behaviours and their communicative functions. It can also help identify which traits—e.g. vocal learning, signal complexity, audiomotor coupling, group living, imitation, bipedal locomotion, and more—predict which rhythmic capacities. Moreover, bottom-up research is essential to address the field’s empirical fragmentation, conceptual heterogeneity, and lack of methodological standardisation. To systematically explore the milestones of this new frontier, we examine research gaps through the lens of the book’s guiding questions: *What* should be studied as part of RCC research? *How* is RCC generated and modulated? *Why* is rhythm pervasive in communication?

15.4.1 The WHAT Question

To be able to uncover evolutionary trends in RCC, the scope of inquiry has to be broadened in terms of *species*, *modalities* of production and perception, aspects of *rhythmic structure*, and the range of *rhythmic abilities*. Regarding species, an obvious focus of expansion is the primate lineage, given its shared ancestry with humans (Chaps. 3 [3], 7 [11], 10 [7], 12 [8], and 14 [10], in particular Sects. 14.2.3 and 14.2.5). This will enable a *homology*-based perspective on rhythmic communication broadly, and on the evolution of human speech, music, and dance in particular. The (socio)-cognitive complexity of primates, along with neuroanatomical and functional homologies relevant to rhythm perception and motor control, further strengthen the case for a systematic investigation of RCC in primates.

Beyond our closest relatives, this expansion could follow a taxonomic approach: building outward from species that have been heavily studied—e.g. laboratory model organisms—to gradually incorporate more species within the same order, and eventually more orders within the same family (Chaps. 3 [3] and 14 [10]). This strategy would support comparative rigor while avoiding overgeneralisations and would help establish a broader, ecologically valid understanding of RCC across taxa.

It is important to note that some of these model species (e.g. insects, anurans, zebra finches, budgerigars, bats, singing mice) have attracted the interest of RCC researchers due to exhibiting RCC-relevant traits, such as vocal learning, the capacity to produce complex vocalisations, rhythmic synchronisation, etc. (Chaps. 3 [3], 5 [5], 7 [11], 9 [13], 10 [7], and 14 [10]). Thus, for such cases, a *convergent evolution* perspective may offer insights that complement (or even surpass) those gained from homology. In other words, the RCC traits that these taxa share with humans may reflect shared mechanistic affordances and/or socio-ecological selective pressures that in our species have favoured the evolutionary emergence of musicality (including dance) and speech. This is one reason why songbirds have been extensively studied, but there is a strong case for expanding research to other groups that share relevant abilities yet remain underexplored.

Additionally, rhythm must be studied as a multimodal phenomenon. Acoustic rhythms dominate current research (Chap. 3 [3]). Yet, visual, tactile, and vibrational modalities may be equally widespread and important (Chaps. 2 [2], 3 [3], 4 [4], 5 [5], 6 [6], 11 [14], 12 [8], and 13 [9]), especially in species with limited auditory capabilities (Chap. 3 [3]) or in environments where sound transmission is compromised (Chap. 6 [6]). These alternative rhythmic channels represent an area of study that is not only empirically underrepresented but also methodologically underdeveloped. A key target for future research is to investigate the interplay of different modalities in RCC, and how this interplay contributes to communicative effectiveness (Chaps. 2 [2], 3 [3], and 9 [13]).

With respect to rhythmic structure and rhythmic abilities, isochrony production and synchronisation have dominated both human and comparative research, while isochrony perception and beat perception have been mainly studied in humans. Hence, most conceptual and methodological developments have been tailored to

these topics, although even in this case, the progress of comparative research is hampered by a lack of consensus (discussed in Sect. 15.2).

An important aspect in these debates is the need for defining and operationalising rhythmic phenomena from a functional—rather than formal—perspective. Such a shift is essential to the reliability of comparative research, in particular to the comparison of rhythmic signals that unfold at considerably different timescales across species. For example, fruit flies and many fish species produce acoustic signals that are tens of times faster than human music, dance, or speech (Chaps. 3 [3] and 9 [13]). Even the rhythmic signals of other mammalian species (e.g. singing mice, bats, canids, felids, fossorial rodents, and insectivores) can be several times faster than those of humans (Chaps. 3 [3], 4 [4], and 9 [13]). Conversely, perceptual capacities in these taxa are optimised for species-relevant rhythmic properties (Chaps. 3 [3] and 9 [13]). These examples highlight the inadequacy of applying human-centric operational criteria - i.e. derived from human research and, thus, constrained by human-specific neurophysiology and anatomy - and the need for developing ecologically valid measures (Chaps. 9 [13] and 14 [10], in particular, the commentary of Cook and Reichmuth in Sect. 14.2.1). In turn, this exposes the need for research aimed at evaluating RCC in terms of flexibility, motivation, and naturalistic timing ranges in order to permit a more accurate and inclusive understanding of rhythmic abilities across species.

Besides addressing these inconsistencies, another milestone for future research is to develop conceptual and methodological approaches for studying non-isochronous and complex rhythms in a comparative perspective, including turn-taking and antiphonal calling, that is, a phase-shifted synchronisation (as detailed in the commentaries of Okanoya in Chap. 14, Sect. 14.2.4 and Popescu and Fitch in Sect. 14.2.6). To advance this frontier, inspiration can be drawn from musicological and speech analysis, and from recent efforts to deal with this topic in nonhuman communication (Chaps. 3 [3], 9 [13], 10 [7], and 12 [8]). Given the vast diversity of rhythmic signals and our limited understanding regarding their possible patterns, exploratory, bottom-up research—inspired by the actual signals—will be needed for methodological development.

Research on the developmental precursors of human rhythmic synchronisation offers valuable insights (Chaps. 10 [7] and 14 [10], in particular, the peer commentaries of Cook and Reichmuth and Patel), providing a more adequate framework for interpreting findings in nonhuman species. From this perspective, future research should address forms of rhythmic engagement and temporal alignment, along with other insights provided by data on the maturational curves of rhythm perception and spontaneous rhythm production in human infants (Chaps. 10 [7] and 14 [10], in particular, Sects. 14.2.1 and 14.2.5).

On the cognitive front, the next research frontier lies in developing a holistic understanding of rhythm cognition, extending beyond commonly studied aspects like predictive timing and beat perception. Rhythm cognition also encompasses temporal interval estimation, tempo perception, pattern recognition, sequence learning, chunking, categorical perception, preference for integer ratios, and recursion, among others (Chaps. 7 [11], 8 [12], 9 [13], 11 [14], 12 [8], and 14 [10], in

particular Sects. 14.2.4 and 14.2.6). In animals, even the more familiar components of rhythm cognition remain minimally explored, highlighting a clear need for empirical expansion.

15.4.2 The HOW Question: Mechanisms and Constraints

The chapters of this book reveal a myriad of pieces in the complex mechanistic puzzle that underlies RCC, yet only a few are captured by current hypotheses (Sect. 15.3). Indeed, research on the role these play in RCC is still in an early phase, highlighting a comprehensive need for scientific exploration. While our understanding of the neurobiology and biomechanics of non-communicative rhythms (e.g. locomotion, breathing) has advanced considerably over the past decades, progress in the study of RCC has been limited. In this domain, thus, there is a pressing need to deepen our understanding of how low- and high-level mechanisms—from the muscles to motoneurons to central pattern generators to subcortico-cortical circuits—contribute to the production of communicative rhythms and how they enable or constrain rhythm perception (Chaps. 7 [11], 8 [12], 9 [13], 11 [14], 13 [9], and 14 [10], in particular Sects. 14.2.3, 14.2.4, and 14.2.5).

Given the overlapping substrates of communicative and non-communicative rhythms (Chaps. 2 [2] and 9 [13]), a first step in this direction could be to compare these two categories of rhythmic output to identify similarities and differences. Another promising research avenue is to examine the coupling and decoupling between physiological (breathing, locomotion) and communicative rhythms (percussion, stridulation, vocalisation, etc., Chap. 9 [13]). However, such advances will not be possible without detailed examination of the individual components, and a deeper understanding of how variations in circuitry or organ function—across species or between different organs within the same species—constrain RCC (Chap. 9 [13]).

Taken together, the data generated from these research directions will deepen our understanding of species-specific optimisation across the mechanisms that underpin RCC. This, in turn, will enable better-tailored experimental tasks and more accurate interpretations of cross-species performance differences, clarifying whether these stem from cognitive or other mechanistic factors (as argued in Chap. 9 [13] and the commentary of Cook and Reichmuth in Chap. 14 [10]). This will allow the field to grapple with the diversity of motor behaviours used in entrainment studies. The intrinsic frequency and volitional control of different effectors—from head bobs to foot taps—vary across species and must be accounted for in experimental design. Additionally, such mechanistic data will provide empirical foundations for advancing our understanding of ritualisation, a process widely regarded as a driving force in the evolution of communication.

Understanding RCC in a comparative framework also requires close attention to its developmental trajectories, both in humans and in nonhuman species. Human data show that rhythm cognition and rhythmic communication develop at the

cross-roads between bio-cognitive abilities that follow certain maturational curves and environmental influences. Different components of RCC follow distinct ontogenetic trajectories, with early-emerging abilities scaffolding later ones. These insights could inform research with nonhuman species, where developmental studies remain scarce (for some exceptions, see Chaps. 3 [3] and 10 [7]).

While existing data demonstrate the plasticity of rhythmic abilities, research on the socio-ecological scaffolding of RCC during development remains limited—both in humans and nonhuman species. Socio-cognitive modulators, such as social motivation for synchronised behaviour, appear to play a crucial role (Chaps. 7 [11], 11 [14], and 14 [10], in particular, the peer commentary of Cook and Reichmuth), yet they are still underexplored. Understanding how social rewards influence rhythmic learning, how caregivers scaffold rhythmic development, and how early exposure shapes rhythmic competence is essential for tracing the ontogeny of rhythm. Expanding research to include non-Western musical stimuli and contexts, as well as ethological data from diverse species, will further contextualise rhythm within broader cultural and ecological frameworks.

Overall, there is a pressing need for longitudinal studies to track how RCC components emerge, stabilise, and diversify over time. Such studies can identify critical periods for rhythmic learning and clarify how social contexts influence development—insights essential for reconstructing the evolutionary pathways of RCC and for refining our methods.

Finally, another underdeveloped but promising area for understanding evolutionary trends in RCC is the role of environmental constraints. As discussed in Chap. 6, factors such as habitat acoustics, population density, and substrate properties can shape the structure and efficacy of rhythmic signals. Over evolutionary timescales, these constraints may drive signal divergence and even speciation. Additionally, anthropogenic changes are altering the ecological contexts in which RCC occurs, impacting signal transmission, timing, and reception. These disruptions can have serious consequences for reproductive success and species survival, making rhythm increasingly relevant to conservation biology (see Chap. 6 [6] and Sect. 15.5.3). Despite its significance, research on this broad set of mechanisms remains limited and fragmented.

15.4.3 The WHY Question

While more traditional functional hypotheses (discussed in Sect. 15.3) focus on rhythmic synchronisation, this volume expands the scope of RCC, offering several additional hypotheses. First, rhythmic patterning—through its inherent repetitiveness—may provide a robust structural solution to communicative challenges across diverse ecological contexts (Chaps. 3 [3] and 6 [6]). Additionally, the flexibility of rhythmic patterning may also support speciation by catering to demands for species recognition, as well as individual recognition (Chap. 3 [3]). Moreover, because RCC is tightly constrained by neuromuscular substrates (Chaps. 2 [2] and 9 [13]),

rhythmic patterning can convey individual fitness. Differences in rhythmic stability, pattern accuracy, and frequency rate may reflect motor precision, stamina, and cognitive control, which would align with theories of sexual selection and social signalling (Chaps. 3 [3] and 9 [13]). The intimate link between rhythm and emotion (Chap. 11 [14]) further suggests the role of RCC in managing social interactions, by conveying arousal and valence and influencing emotional states in both conspecifics and allo-specifics.

To test some of these functional hypotheses about RCC, research must address within-species and within-individual variability in rhythmic competence. Systematic studies of rhythmic stability, pattern accuracy, and perceptual acuity could uncover neurobiological, developmental, social, and ecological influences—thereby illuminating the selective pressures that have shaped rhythm as an adaptive communicative strategy. Complementary studies could assess signal transmission in noisy environments or evaluate cross-habitat resilience of rhythmic versus arrhythmic sequences.

However, to validate functional hypotheses about RCC, perception studies are a necessary complement to the meticulous analyses mentioned above. This remains a major gap in RCC, and we still know very little about the biological significance of the pervasive rhythmicity that patterns animal communication. It is, for example, unclear whether animals use rhythmic patterning, rather than other cues, for conspecific recognition, individual identification, or when reacting to signals in context-adaptive ways. Without an ability for perceiving rhythm, the rhythmic sequences produced by individuals may not necessarily be meaningful (Chaps. 1 [1], 3 [3], 9 [13], and 14 [10]). They may simply reflect mechanistic constraints rather than functional communicative roles. Clarifying this distinction is crucial for understanding the evolutionary and biological relevance of rhythmicity in animal signalling.

For complex rhythms with hierarchical organisation, it is important to assess whether animals perceive these stratified structures or focus on specific levels. A related question is whether particular levels—or the entire hierarchical arrangement—convey biologically significant information (Chap. 3 [3]). Understanding which aspects of rhythm animals attend to, and how these influence behaviour, is essential.

Historically, it has been difficult to demonstrate that nonhuman species—even those with advanced vocal abilities like songbirds—attend to rhythm rather than single intervals. Recent studies (Chaps. 1 [1], 7 [11], 9 [13], and 14 [10], in particular, the commentaries of Cook and Reichmuth in Sect. 14.2.1, Patel in Sect. 14.2.5, and Okanoya in Sect. 14.2.4) have begun to provide positive evidence, but this gap must be narrowed to validate functional hypotheses about the evolution of rhythmic communication. To increase the efficacy of experimental tasks, the field will have to acknowledge—and capitalise on—the species-specific mechanistic peculiarities that shape RCC at all levels of the neuroethological architecture (see Chap. 9 [13]) and the peer commentary of Cook and Reichmuth in Chap. 14 [10] and Sect. 15.4.2.

15.5 The Applied Relevance of RCC Research in Humans and Nonhuman Species

15.5.1 The Relevance of RCC to Clinical and Educational Contexts in Humans

Rhythm-based interventions hold significant promise across clinical and educational contexts throughout the human lifespan. The mechanisms underlying rhythmic communication and coordination (RCC) are closely linked to a wide range of cognitive and socio-emotional processes, including attention, working memory, impulse control, temporal sequencing, arousal regulation, and social bonding (Chaps. 7 [11], 8 [12], 9 [13], and 11 [14]). In educational settings, knowledge about the role of rhythm in these processes can be exploited to inform curriculum design, teaching methods and after-school activities. Preliminary work substantiates this applied potential, showing that music-based interventions improve reading fluency, executive function, classroom engagement, and cooperation.

In early development, rhythm plays a foundational role. One of the factors that puts prematurely born infants at risk for developmental delays and deficits regarding sensorimotor, respiratory, and cognitive capacities is the abrupt interruption of the multi-layered rhythmic stimulation experienced in the womb (Chap. 10 [7]). At later developmental stages, deficits of rhythm perception and motor control have been linked to disorders that affect (socio-) cognitive abilities implicated in communication, cooperation, executive control, and emotion regulation. Virtually, all the major developmental disorders are in this list: dyslexia, stuttering, developmental coordination disorder, self-regulation disorder, ADHD, and autism (Chap. 10 [7]).

Rhythm-based interventions capitalising on these insights have recently begun to emerge. For example, interventions leveraging rhythmic stimulation in the tactile, vestibular, and auditory modalities—stroking, carrying, water mattresses, rockers, maternal heartbeat, and music—have been devised and implemented in the preterm neonatal care with positive outcomes regarding emotion regulation, motor and respiratory development (Chap. 10 [7]).

In older children, different forms of music-based interventions have been found to enhance communicative skills, emotional regulation, and executive control across several disorders. For children with developmental language problems, the efficiency of music-based interventions could be anchored in the link between vocal learning and rhythmic competence theorised by the VL-BPS (see Chap. 7 [11] and the commentary of Patel in Chap. 14 [10]), the timing mechanisms emphasised by GAE (Chap. 7 [11]) and/or the neural resonance mechanisms posited by NRT (Chap. 8 [12]). If so, designing further interventions inspired by these frameworks could be beneficial. In this domain, rhythm-based approaches may improve verbal abilities by enhancing audiomotor integration, the brain's sensitivity to temporal patterns, and phonological awareness.

For children with autism spectrum diagnoses, rhythm-based interventions could improve social and communicative skills. Rhythmic movement provides

predictable sensory input, which can help regulate the nervous system by reducing sensory overload. This is known to be an issue in these populations, which pushes individuals towards avoidance, withdrawal, and stimming behaviours, which are essentially rhythmic. Hence, dance routines, which involve repetition and structure, are comforting and engaging for autistic individuals.

In ADHD conditions, rhythm-based procedures have been explored both as diagnostic and therapeutic tools. ADHD is characterised by underactive dopaminergic (DA) pathways, which affect timing, working memory, and sequencing capacities. Thus, in line with mechanisms of rhythm genesis and rhythm tracking discussed in (Chaps. 7 [11], 8 [12], 9 [13], and 11 [14]), rhythm-based interventions have the potential to ameliorate ADHD deficits through DA upregulation. In turn, this could boost temporal and sequence processing, as well as executive control. In concert with effects exerted on other neurochemical mechanisms, rhythmic movement could also contribute to regulating arousal, impulsivity, and hyperactivity.

RCC research is also increasingly relevant for conditions diagnosed later in life, including neurodegenerative diseases and psychiatric disorders (as mentioned in Chaps. 7 [11], 9 [13], 11 [14], and 13 [9]). In Parkinson's disease, rhythmic stimulation can bypass impaired basal ganglia circuits to improve motor control (Chaps. 7 [11] and 9 [13]), capitalising, for example, on neural resonance mechanisms (Chap. 8 [12]). In Alzheimer's disease and other forms of dementia, rhythmic stimulation may have beneficial effects by inducing neural entrainment and engaging biochemical pathways that support the brain's natural clearance of harmful agents. The same mechanisms may also contribute to improving emotional, attention, and memory.

Cognitive timing is impaired in schizophrenia and other psychotic disorders. This also affects the processing of event sequencing and duration, making it difficult to align behaviour to external timing cues. This type of impairment has been linked to altered coupling of neural oscillations between slow and fast bands—a mechanism that is crucial for coordinating brain activity across regions (as discussed in Chaps. 8 [12], 9 [13], and 13 [9]). In this context, rhythmic interventions could help restore timing mechanisms and improve attention, memory, and executive function by resynchronising relevant brain networks and boosting predictive timing.

Finally, rhythmic stimulation—in the form of controlled breathing, exposure to rhythmic music, chanting, music-making, or rhythmic movement—is increasingly used in the management of personality and mood disorders (Chaps. 11 [14] and 13 [9]). In these contexts, the benefits of rhythmic engagement are likely mediated by neurophysiological and neurochemical mechanisms of emotion regulation, self-awareness, and interpersonal skills that are activated by rhythmic stimuli. For example, rhythmic activities can engage mechanisms of emotion regulation to balance arousal, facilitate emotional release, or promote relaxation (Chaps. 11 [14] and 13 [9]). In addition, rhythmic stimulation is known to foster social engagement and social bonding, which provides another psychobiological path towards enhanced well-being (Chap. 11 [14]).

While rhythmic practices are increasingly adopted to manage neurodegenerative and psychiatric disorders, systematic basic RCC research is required in order to tailor these practices to the treatment needs of the specific syndrome and the sensitivities of the individual. Research that improves our understanding of why, how, and when rhythmic intervention helps will pave the way towards evidence-based guidelines and practices.

15.5.2 The Applied Relevance of RCC Research to Animal Welfare

Studying rhythmic patterns in animal communicative signals can be a valuable tool for understanding emotional and social states (Chaps. 3 [3], 12 [7], and 11 [14]). In turn, this has direct applications for animal welfare assessment and husbandry practices in all managed care environments, from pet animals to zoos, sanctuaries, farms, and laboratories.

Rhythmicity—whether expressed through sound, substrate-borne vibrations, movement, or interactive behaviours—is a fundamental component of animal communication. As shown in Chaps. 3 [3], 9 [13], and 11 [14], variations in the rhythmic properties of communicative signals may convey information regarding fitness, sex, age, readiness to mate, arousal, etc., providing cues about the physiological and emotional states of the individuals. In addition, these can modulate the emotional states of receivers (Chap. 11 [14]). Basic research focused on systematically mapping animal RCC will deepen our understanding of the emotion–rhythm link in animal communication, having tremendous applied potential to inform behavioural indicators of well-being. In managed care settings, rhythmic behaviours can be systematically observed and analysed to assess welfare, helping to identify signs of boredom, anxiety, or social isolation. This research will also have the potential to support the development of evidence-based enrichment programs that align with species-specific needs. To design such interventions, however, we first need to understand the species’ capacities for rhythm perception and production, and how these are linked to social communication, emotional regulation, and behavioural expression.

15.5.3 The Applied Relevance of RCC Research to Conservation Efforts

As shown in Chap. 6, basic research on RCC can play a crucial role in conservation efforts, particularly when considering the anthropogenic transformation of the natural world. Ecosystems undergo rapid and profound alterations due to human activities, ranging from climate change and habitat fragmentation to noise and light pollution. These changes cause disruptions that affect whether and how animals produce and perceive rhythmic signals, since the signals are influenced by environmental rhythms and their communicative efficacy depends on adaptations moulded

by habitat properties. Because rhythmic signals are essential to multiple survival functions (Chap. 3 [3])—from mating and offspring viability, to navigation, feeding, or defence—these disruptions can have deleterious effects on the conservation status of species (Chap. 6 [6]). Understanding these disruptions can inform conservation efforts and habitat restoration.

For example, artificial light pollution interferes with natural light cycles, affecting neurochemical and endocrine processes that regulate RCC. This can lead to mistimed behaviours like premature birdsong, reducing mating success, and increasing predation risk. Climate-driven temperature changes impact rhythm-based communication in ectothermic species (e.g. frogs, fish, spiders), decoupling signal production and perception, and threatening reproductive success. Anthropogenic noise masks natural sounds, forcing animals to alter their calls. These adjustments can reduce signal clarity and attractiveness, with energetic and survival costs. Habitat changes and invasive species introduce acoustic competition, compelling native species to modify their rhythms, potentially affecting reproduction (Chap. 6 [6]).

Understanding these rhythm-related dynamics provides conservationists with tools to assess species welfare in the wild and design targeted interventions. By monitoring rhythmic behaviours and their disruptions, researchers can identify stressors, evaluate habitat quality, and implement enrichment strategies that support species-specific communication needs. Ultimately, integrating basic RCC research into conservation science enhances our ability to mitigate the impacts of environmental change and promote the resilience of animal populations in managed and wild ecosystems.

15.5.4 The Applied Relevance of RCC to Human–Animal Interaction

Rhythm plays a subtle yet powerful role in shaping human–animal interactions, influencing behaviour, emotional responses, and the quality of interspecies relationships. In everyday contexts such as training and caregiving, rhythmic cues—whether in voice, movement, or routine—can help regulate animal behaviour and foster emotional stability (Chap. 11 [14]). The predictability of human rhythmic actions may contribute to stress reduction, enhancing trust and learning outcomes.

In therapeutic settings, rhythmic synchrony between humans and animals has shown promise in enhancing bonding and therapeutic outcomes. Equine-assisted therapy, for instance, often involves coordinated movement between horse and rider, where shared rhythm may facilitate emotional attunement and physiological regulation. Similar effects have been observed in canine-assisted interventions, where rhythmic walking or breathing patterns between handler and dog appear to support emotional co-regulation.

Despite these promising observations, the mechanisms underlying rhythm in human–animal interaction remain underexplored. Future research should

investigate how different types of rhythmic signals—acoustic, tactile, visual, and movement-based—contribute to interspecies communication and emotional synchrony. Studies could examine whether rhythmic entrainment between humans and animals enhances learning, reduces anxiety, or strengthens social bonds, and how these effects vary across species and contexts.

Moreover, comparative research across domesticated and wild animals could reveal whether sensitivity to human rhythm is a product of domestication or a broader feature of animal cognition. Investigating rhythmic dynamics in animal-assisted therapy could also inform clinical practices, helping to optimise intervention protocols based on rhythmic compatibility or entrainment potential.

As rhythmic communication is increasingly recognised as a cross-species phenomenon, integrating it into the study of human–animal relationships provides a rich avenue for interdisciplinary research—bridging behavioural science, neuroscience, ethology, and therapeutic practice.

15.6 Conclusions

To truly advance rhythm science, the field must embrace conceptual clarity and methodological rigor. At present, conceptual, terminological, and methodological heterogeneity hampers data comparability and undermines the comparative project. Harmonising research protocols and developing standardised metrics for rhythmic analysis will be essential.

Future RCC research will have to expand beyond acoustic rhythms to also investigate visual, tactile, and vibrational modalities. It will also have to embrace evolutionary and mechanistic depth. Combining field observations with lab experiments will help distinguish homology from convergence and identify selective forces shaping rhythmic capacities—shedding light on the adaptive functions of rhythmicity and on the evolution of human musicality and speech. Additionally, by bridging mechanistic and functional perspectives—e.g. linking neural oscillations, motor constraints, reward systems, etc. with the ecological and social significance of RCC—will enable explanatory models connecting proximate mechanisms to ultimate causes.

Studying these interactions and dynamics demands innovative methods and cross-disciplinary input from neuroscience, ethology, musicology, and computational modelling. Only through such integrative efforts can we begin to reveal the principles that govern rhythmic behaviour across species and contexts and understand its role in the broader tapestry of communication, cognition, and evolution. Finally, RCC research has broad applications—from clinical and educational interventions to animal welfare and conservation. Thus, rhythm science occupies a unique position at the intersection of fundamental and applied research, offering insights into one of nature’s most pervasive organising principles.

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