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Editorial

Rhythm and synchrony in animal movement and communication

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Introduction

Animal communication and motoric behavior develop over time. Often, this temporal dimension has communicative relevance and is organized according to structural patterns. In other words, time is a crucial dimension for rhythm and synchrony in animal movement and communication. Rhythm is defined as temporal structure at a second-millisecond time scale (Kotz et al. 2018). Synchrony is defined as precise co-occurrence of 2 behaviors in time (Ravignani 2017).

Rhythm, synchrony, and other forms of temporal interaction are taking center stage in animal behavior and communication. Several critical questions include, among others: what species show which rhythmic predispositions? How does a species' sensitivity for, or proclivity towards, rhythm arise? What are the species-specific functions of rhythm and synchrony, and are there functional trends across species? How did similar or different rhythmic behaviors evolved in different species? This Special Column aims at collecting and contrasting research from different species, perceptual modalities, and empirical methods. The focus is on timing, rhythm and synchrony in the second-millisecond range.

Three main approaches are commonly adopted to study animal rhythms, with a focus on: 1) spontaneous individual rhythm production, 2) group rhythms, or 3) synchronization experiments. I concisely introduce them below (see also Kotz et al. 2018; Ravignani et al. 2018).

Spontaneous Individual Rhythm Production

Spontaneous individual rhythms deal with the temporal structure of individual behaviors, mostly in a non-interactive context. The adjective "spontaneous" here denotes a general methodological trend in observing or recording how an animal behaves spontaneously rather than in response to experimental manipulations. These individual rhythms have been studied in several taxonomic groups. African apes and songbirds are good examples of this (e.g., Arcadi et al. 2004; Trejos-Araya and Barrantes 2018).

Both chimpanzees and bonobos show forms of individual rhythmic behaviors. Bonobos perform "staccato hooting" displays, consisting of series of vocalizations which seem to repeat metronomically twice a second (de Waal 1988; Bermejo and Omedes 1999). In chimpanzees, instead, rhythmic sound production is mostly non-vocal, consisting of sequences of percussive sounds. This so-called "buttress drumming" can be observed in wild chimpanzees, who drum on hollow trees (Arcadi et al. 2004), and their captive conspecifics, who will employ any resonant object to produce loud sequences of sounds (Dufour et al. 2015; Ravignani et al. 2013a, 2013b).

Zebra finches are songbirds whose songs have been thoroughly studied. Classical work on zebra finches has explored the complex ways in which syllables (i.e., elements of a song) are organized, learnt, and reused to produce complex vocal displays (Scharff and Nottebohm 1991; Feher et al. 2009; Lipkind et al. 2013). Recent work, however, has also explored the rhythmic dimension of zebra finches' songs (Saar and Mitra 2008; Benichov et al. 2016; Norton and Scharff 2016; Spierings and ten Cate 2016). For instance, when metronomically-occurring (i.e. isochronous) sounds are overlaid to recordings of zebra finch songs, the syllables' onsets occur—more often than not—on the metronome clicks (Norton and Scharff 2016). Hence, these songbirds' songs appear rhythmically structured so that syllables occur at specific points in time.

Group Rhythms

Beyond individual rhythms, animals can produce vocal or behavioral rhythms in an interactive, coordinated manner (e.g., Couzin 2018). The classical framework of chorusing traditionally studies this kind of phenomena, even in non-auditory modalities (Ravignani et al. 2014). Duets are the simplest form of group chorusing, at least in terms of participants. Examples of duetting include those performed by birds, gibbons, lemurs and anurans. In the study of the precise rhythmic structure of duetting, mammals seem to be historically neglected. For instance, mated gibbons have been reported to sing in pairs, to enhance pair-bonding and defend a territory

(Geissmann 2002). From an observational perspective, these duets show good temporal coordination, with gibbon pairs alternating synchronous and antiphonal parts. Quantitative studies, comparable to those in other taxonomic groups, to test the precise mechanisms of vocal rhythmicity in gibbons have only recently appeared (Terleph et al. 2018a, 2018b)

From duets, when we increase the number of participants in a group rhythm, we find for instance "quartets." Neotropical plain-tailed wrens *Thryothorus euophrys* are known for their 4-parts choruses (Mann et al. 2006). Males and females alternate in their performance of complementary parts, whereas birds of the same sex synchronize.

A particularly fruitful strand of research over the last century has examined chorusing in orthopterans (crickets, bush crickets, etc.) and anurans (Ravignani et al. 2014). One orthopteran species, *Neoconocephalus spiza*, displays group choruses of hundreds of insects (Greenfield and Roizen 1993). All insects stridulate isochronously (i.e., metronomically) with a constant and small delay between pairs of individuals. More elaborate group rhythms can be seen in the Indo-Malayan katydid of the genus *Mecopoda*. As in *Neoconocephalus*, all *Mecopoda* individuals produce isochronous sounds, with potentially individual-specific periods (Sismondo 1990). When neighbors have similar sound production periods, synchrony, or antiphony ensues. When neighbors have different sound production periods, they slightly adapt to each other and end up being related by small integer ratios (e.g., 2:3). Finally, other species perform rhythmic group displays in non-auditory modalities. Fireflies (e.g., *Pteroptyx malaccae*) perform visual displays, competing to be the most conspicuous signaler (i.e., the first one to signal) and hence to attract potential mates (Greenfield 2005). This competition for conspicuousness, however, leads to the opposite of individual conspicuousness (as in the *Neoconocephalus spiza* example above), with hundreds of animals all flashing in perfect synchrony.

Synchronization experiments

A third strand of animal rhythm research stems more from comparative psychology, rather than zoology and bioacoustics. Focusing on the concept of synchrony and prediction, synchronization experiments somehow combine the 2 categories above. In other words, the capacities to partake in group rhythms are tested in isolation. In synchronization experiments, isolated individuals are usually exposed to sounds (or visual stimuli, Takeya et al. 2017; Takeya et al. 2018), which can be as simple as metronomic clicks or much more structured (Patel et al. 2009a; Cook et al. 2013). The typical task consists in 1) extracting a periodic structure from the sound stream, 2) building expectations about future incoming events, and 3) adjusting future behaviors predictively so that they occur in synchrony with the external periodicity extracted from the sound stream (Kotz et al. 2018). This work has been extensively reviewed elsewhere (Ravignani et al. 2013b; Patel 2014; Ravignani and Cook 2016; Wilson and Cook 2016; Kotz et al. 2018). However, it is important to notice that a trademark of synchronization experiments is cross-modality. In other words, the modality involved in perceiving a rhythmic stimulus is often (required to be) different from the modality used to produce a synchronous rhythmic behavior (Patel et al. 2009a, 2009b).

Contributions to This Special Column

Each paper in this Special Column belongs to one of the 3 macro-areas described above, or their intersection. Contributed papers are

beautifully diverse along several dimensions. Here, instead of rehashing the abstract of each individual paper, I will attempt to point out similarities and differences across papers along a few key dimensions.

Animals discussed include fiddler crabs (Backwell 2019), lemurs (De Gregorio et al. 2019), macaques (Katsu et al. 2019), seals (Ravignani et al. 2019), parrots, and humans (Seki and Tomyta 2019). This is a diverse group of animals, and species' diversity was one of the aims of this Special Column. This diversity is needed if one wishes to understand why animals have rhythm, especially the phylogeny and function of rhythmic behaviors.

Which aspects of temporal structure are tackled in each paper? Two papers investigate the classical issue of synchrony (Backwell 2019; Seki and Tomyta 2019), each however with a fresh spin. Backwell (2019) notices how, across species, synchrony is the norm in the auditory modality, but quite an exception in the visual modality. In addition, by investigating different species of fiddler crabs, one could aim at reconstructing "rhythmic phylogenies." Seki and Tomyta (2019) also focus on synchrony, but do so using a paradigm uncommon in primate and bird experiments. Instead of reinforcing the animals to synchronize, they show how an isochronous metronome sound pushes bird pecking and human tapping behavior to be more synchronous with the metronome. Two more papers tackle the reciprocal influence of individual timing in primate duets (Katsu et al. 2019) and choruses (De Gregorio et al. 2019). Even the one paper where rhythm is studied at the within-individual level and in isolation shows some signatures of interactivity (Ravignani et al. 2019). In fact, harbor seal pups, even when vocalizing in isolation, produce call sequences with a rhythmic structure quantitatively closer to non-isochronous, interactive behaviors than to monologue-like "solo" sequences (Falk and Kello 2017; Kello et al. 2017; Ravignani et al. 2019).

Pitting the papers against Tinbergen's 4 questions (Table 1), we also see quite a diverse array of approaches to the question of why animals have rhythm. Behavioral *mechanisms* are, to a different extent, investigated in all contributed papers (Backwell 2019; De Gregorio et al. 2019; Katsu et al. 2019; Ravignani et al. 2019; Seki and Tomyta 2019). The contributions by Backwell (2019), De Gregorio et al. (2019) and Ravignani et al. (2019) also explore the biological *function* of rhythmic behaviors. Ravignani et al. (2019) covers the *ontogeny* of vocal rhythms, which is the least studied aspect of rhythmic behaviors from a comparative perspective. Finally, *phylogenies* are discussed in Backwell (2019) and Katsu et al. (2019).

Methodologically, several papers employed empirical, though not necessarily experimental, methods. Data were obtained in the field (Backwell 2019; De Gregorio et al. 2019; Katsu et al. 2019), or in captive conditions (Ravignani et al. 2019). Alternatively, behavioral experiments were performed in parrots and humans (Seki and Tomyta 2019), minimizing the verbal instructions given to human participants to enhance cross-species comparability. Relatedly, Backwell (2019) shows how playback experiments do not need to be limited to the auditory modality: visual playback experiments can elicit rhythmic behaviors in fiddler crabs (Reaney et al. 2008).

Statistical methods used to infer rhythmic patterns were also quite diverse. Classical, linear statistical methods are of course a first, necessary approach when probing temporal structure in animal interactions (De Gregorio et al. 2019; Ravignani et al. 2019). Phase response curves (Greenfield and Roizen 1993) are quite effective in predicting how the behavior of an individual will be shifted in time depending on the exact time of occurrence of a conspecific behavior (Backwell 2019; Katsu et al. 2019). Circular statistics (Fisher 1995; Berens 2009; Zar 2010) are also increasingly used in animal rhythm research (Backwell 2019; Seki and Tomyta 2019). Ideally, circular

Table 1. Tinbergen's 4 questions applied to rhythm

Question	Description	Example
Ontogeny	Rhythm *ontogeny* concerns the lifespan development of rhythmic behaviors, with emphasis on the first part of life.	The song repertoire of some songbird species goes through different developmental phases of exposure, learning, rehearsal, etc. Although songs have been mostly studied from a spectral and combinatorial perspective, also their rhythmic properties should vary and consolidate as individuals grow (Feher et al. 2009; Norton and Scharff 2016).
Mechanism	Rhythm *mechanisms* concern the neural and biological predispositions underlying rhythmic, synchronous or coordinated behavior.	The midbrain structures underpinning the metronomic, isochronous tail-wagging of dogs (Ravignani et al. 2018).
Function	Rhythm *function* concerns the evolutionary pressures that made a particular rhythmic behavior arise in a species.	Rhythmic behavior in some insect species may have evolved as response to pressures for mate attraction, whereas in some primates might have evolved for pair bonding and territorial advertisement (Ravignani et al. 2014).
Phylogeny	Rhythm *phylogeny* concerns the evolutionary tree of specific rhythmic behaviors, and whether similar behaviors are present in closely related species.	Most Otariid pinnipeds have a very isochronous vocal rhythm (the typical sea lion barking) and similar across Otariid species. Phocid species have quite diverse vocal rhythms. It appears that phylogeny may play a stronger role in Otarid rather than Phocid pinnipeds (Schusterman 1977; Ravignani 2018a; Terhune 2018).
Glossogeny	Rhythm *glossogeny* concerns the cultural transmission and change (often termed "cultural evolution") of rhythmic behaviors, as opposed to the biological predispositions underlying these behaviors.	Although still unclear to which features of animal rhythmic behaviors glossogeny may apply, songs of birds, cetaceans, and pinnipeds are promising candidates (Feher et al. 2009; Rogers 2017; Ravignani 2018a; Schneider and Mercado 2018)

Tinbergen's approach (1963) can help answering whether and why a given species "has rhythm" (Ravignani et al. 2018). At least 4 types of questions can be asked about a particular behavior (Tinbergen 1963); this behavior is, in our case, rhythm (Ravignani et al. 2018). The so-called "proximate causes" are ontogeny and mechanism. The "ultimate causes" are phylogeny and function, which may be more difficult to tackle empirically for the case of rhythm. Tinbergen's (1963) 4 questions can be enriched by Fitch's (2008; 2015) "fifth question": glossogeny (last row).

statistics can and should be used when 1) two series of temporally-structured behaviors co-occur, 2) one of which is isochronous. If these conditions hold, circular statistics enable testing the relative phase delay of an individual behavior with respect to the constant period length of another individual's behavior (see e.g., Cook et al. 2013; Ravignani and de Reus in press). A possible visual counterpart of circular statistics is the rose plot (e.g., Cook et al. 2013; Ravignani and de Reus in press): a clock-like histogram showing how often an individual phase delay occurs relative to another individual or a metronomic stimulus. Finally, a few techniques from physics, such as the Allan Factor and burstiness, appear quite promising for quantifying rhythmicity and interactivity of behaviors in time (Goh and Barabási 2008; Kello et al. 2017; Ravignani et al. 2019).

Insights can be gained by comparing the interpretation of results across contributed papers, focusing on 2 in particular. From several perspectives, the indri (De Gregorio et al. 2019) and macaque (Katsu et al. 2019) work are quite similar, both investigating the temporal dynamics of interactive calling. However, while the coordinated vocal behavior in indri is termed "chorusing" (De Gregorio et al. 2019), a similar behavior in macaques is called "turn-taking" (Katsu et al. 2019). Is the difference between chorusing and turn-taking substantial, or does it stem from naming conventions used in different research traditions (Kotz et al. 2018; Ruch et al. 2018)? In particular, similar behaviors consisting of rhythmic vocal interactions are labeled as chorusing by some (e.g., Kotz et al. 2018; Ravignani et al. 2014; Greenfield and Roizen 1993) while as turn-taking by others (e.g., Demartsev et al. 2018; Pika et al. 2018; Takahashi et al. 2013).

Going Forward: What's Next?

All contributions exemplify, in one way or another, some of the current and possibly future trends in this field.

First of all, we see the importance of species' diversity. The study of animal rhythm and synchrony has historically focused on 6 taxonomic groups: primates, birds, anurans, crabs, orthopterans, and fireflies. Primate focus has historically been on Simiiformes (or Anthropoidea), leaving out tarsiers, lorises and lemurs. Likewise, the rhythmicity of songbirds has been mostly investigated, leaving out a large amount of interesting avian species. Beyond the groups discussed here, many other species perform group displays which may have a precise temporal structure and be worth exploring rhythmically. Domestic dogs and wolves howl in groups. These animals are quite common in several parts of the world, so it is surprising that the precise timing of their choruses remains unexplored. Within mammals, rhythm in marsupials and monotremes remains completely unexplored; studying rhythm in these 2 clades would be particularly intriguing, especially considering how different their brains are from those of placental mammals (Suárez et al. 2018). In particular, work targeting complex, bilateral rhythmic coordination (Sternad et al. 2007) would be particularly interesting due to the acallosal brains of marsupials and monotremes.

Second, we see an increasing emphasis on cross-species comparison and methodological comparability. An example of this is the human-avian comparative experiments in Seki and Tomyta (2019), where instructions to human participants are minimized, making one step towards testing species in comparable ways. Future comparative research should strive to achieve, as much as possible, a good tradeoff among testing (1) top-down, theoretically-driven concepts (2) in an ecologically-relevant, possibly species-specific setup, (3) while achieving cross-species comparability.

Third, in contrast with research in comparative psychology, we see attempts to connect rhythmic behaviors with evolution and ecology (Backwell 2019; De Gregorio et al. 2019; Ravignani et al. 2019). As previously done with other behavioral traits, a long-term

goal of this strand would be to construct "rhythmic phylogenies" (Gingras and Fitch 2013; Gingras et al. 2013), and map their interaction with environmental constraints (Terhune 2018).

Fourth, a new strand of animal rhythm experiments seems to focus on spontaneous rhythmic interaction. Seki and Tomyta (2019), in particular, test whether synchrony can be spontaneously achieved in a species whose common behavioral repertoire does not include synchrony. Some parrots in Seki and Tomyta (2019) indeed show a tendency towards synchronizing. Compare this with a recent experiment in a harbor seal pup (Ravignani 2018b, in press), where sound playbacks of conspecific calls elicited antisynchronous (rather than synchronous) vocal responses. In addition, spontaneous rhythmic interaction connects to 2 related themes: learning and ontogeny. Future questions on rhythm learning and ontogeny will include: How much learning do specific rhythmic behaviors require (e.g., Cook et al. 2013), as opposed to mere exposure triggering behavioral predispositions (e.g., Backwell 2019)? How do (possibly learnt) rhythmic behaviors develop over the lifespan (e.g., Ravignani 2018a vs. Ravignani et al. 2019)?

Fifth, rhythmic interactivity appears to have taken center stage (see also Pika et al. 2018; Ravignani and de Reus in press; Ruch et al. 2018). All papers in this issue, together with several others which appeared over the last few years, deal with interactive rhythms. This trend mirrors what has been happening in human cognitive neuroscience, where individual-centered research has gradually left room for group experiments. If we can learn anything from past human work is that maintaining good experimental control in group experiments is hard, but achievable.

Sixth, the field of animal rhythms appears quite open to novel analytical techniques. These are often re-purposed from other fields, such as physics (e.g., Allan Factor, Kello et al. 2017), chronobiology (e.g., phase response curves, Greenfield and Roizen 1993; Sismondo 1990), and neuroscience (e.g., spiking neural trains, Kreutz et al. 2007).

Finally, 2 more trends, which are not represented here but due to be more prominent in this field, are neuroscience and genetics. Once a behavior is understood, neuroscientific methods enable a deeper understanding of its nature in light of all of Tinbergen's 4 questions. Neuroscientific approaches are, of course, particularly relevant to understand mechanisms (Kotz et al. 2018). And they also need not be invasive (e.g., Honing et al. 2018). Likewise, genetics will be helpful to map rhythmic phylogenies. Along these lines, pioneering work has already been performed in insects (e.g., Zhou et al. 2011).

In short, rhythm and synchrony in animal movement and communication is an exciting multidisciplinary field developing at a fast pace. Many questions are open, and numerous low-hanging fruits are ready for grabs to those interested in the topic. In particular, datasets to answer several questions have already been collected, but only analyzed in their spectral dimension. The field of animal rhythms is open to those who want to approach it from their own unique perspective. I am extremely curious and positive about how the field will look like in 20 years from now.

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