Interactive rhythms in the wild, in the brain, and in silico

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Abstract. There are some historical divisions in methods, rationales, and purposes between studies on comparative cognition and behavioural ecology. In turn, the interaction between these two branches and studies from mathematics, computation and neuroscience is not usual. In this short piece, we attempt to build bridges among these disciplines. We present a series of interconnected vignettes meant to illustrate how a more interdisciplinary approach looks like when successful, and its advantages. Concretely, we focus on a recent topic, namely animal rhythms in interaction, studied under different approaches. We showcase 5 research efforts, which we believe successfully link 5 particular *Scientific areas* of rhythm research conceptualized as: *Social neuroscience*, *Detailed rhythmic quantification*, *Ontogeny*, *Computational approaches* and *Spontaneous interactions*. Our suggestions will hopefully spur a 'Comparative rhythms in interaction' field, which can integrate and capitalize on knowledge from zoology, comparative psychology, neuroscience, and computation.

Keywords: communicative rhythms in behaviour; brain rhythms; comparative cognition; rhythm ontogeny; agent-based models.

Introduction

The last decade has seen an explosion of comparative research on the cognitive and communicative roots of animal rhythmic behaviour. Emphasis has been laid on rhythms in vocal communication and motoric rhythms in response to sound.

There is a clear tendency to increase interdisciplinary research, but still sometimes current work in e.g. behavioural ecology or cognitive neuroscience forgets related studies from the comparative cognition tradition, and vice versa. In particular, the comparative study of interactive rhythms is an area gaining increasing attention. As it happens for most new research topics, it suffers from a disconnection among several methodological approaches and theoretical traditions. Of course exceptions exist, such as the legendary biologist William Hamilton, who enjoyed and performed mathematical modeling of biological processes as much as pure fieldwork (Herbers, 2013).

In this opinion piece, we focus on interactive rhythms, particularly in the vocal domain: How individuals adjust the timing of their communicative acts in an interactive, social context. We aim firstly to show how interactive vocal rhythm research is rich and diverse, but still relatively sparse; secondly, by focussing on key concepts from a few papers, to highlight fruitful cases of connection between strands; thirdly to imply how, at least in this subarea, comparative cognition and behavioural ecology can smoothly blend into each other.

To achieve these aims we discuss and try to connect 5 *Scientific areas*, focusing on: *Social neuroscience*, with emphasis on how social context affects brain rhythms, and how different functional areas of the brain are connected, comparing connectivity patterns across species; *Detailed rhythmic quantification*, used to detect regularities in rhythm and to compare these across species; *Ontogeny* of vocal rhythms, based on speech development work; *Computational approaches*, using agent-based modeling to compare animal behaviours with these simulated by a computer model under a set of known assumptions; *Spontaneous interactions* in ecological contexts, relating environmental stimuli, sensory biases, and underlying brain mechanisms.

Our goal is to sketch the interdisciplinary synergy between these 5 *Scientific areas*, by focusing on 5 Research efforts. Each of these efforts connects two of the areas above, hence illustrating a potential practical link (Figure 1).
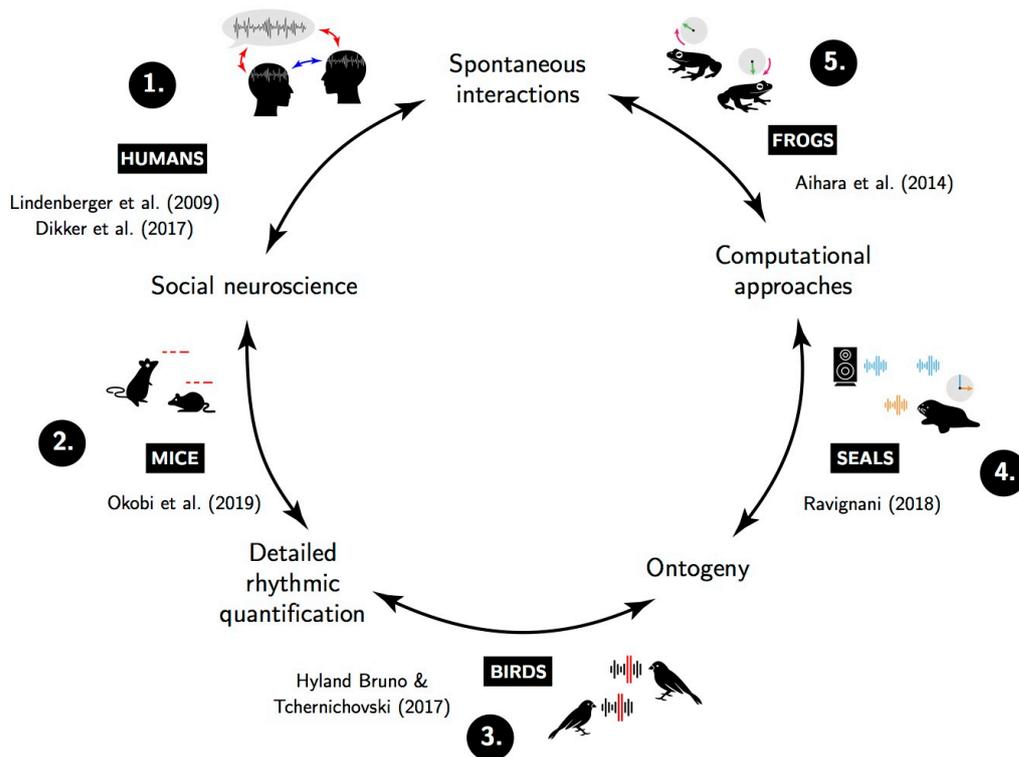
Figure 1. Pairwise links between two of the *5 scientific areas* of interest via the key *5 research* efforts and species discussed here.

We start with two papers, by Lindenberger and colleagues (2009) and Dikker and colleagues (2017), studying *Spontaneous interactions* within the context of human *Social neuroscience*, investigating the brain rhythms underlying socio-ecological interactions. This research effort is included in the first section titled: "Humans: Social neuroscience of spontaneous interactions". We then move to the research effort of Okobi and colleagues (2019), titled: "Mice: Detailed quantification of social rhythm". This research probes the neural underpinnings of natural vocal rhythms in singing mice, and connects the *Social neuroscience* and *Detailed rhythmic quantification* areas. Afterwards, the third effort is included in the section named: "Birds: Measuring rhythmic ontogeny". In this section, we present works by Hyland-Bruno (2017) and Hyland-Bruno & Tchernichovski (2017) regarding the development and learning processes underlying rhythm in bird songs, which connects *Detailed rhythmic quantification* with *Ontogeny*. The fourth link, presented in the section "Agent-based models of rhythm development", is between *Ontogeny* and *Agent-based modeling* of interacting agents illustrated through a paper on rhythmic capacities of a seal pup (Ravignani, 2018). The last research effort is titled: "Tree frogs: Agent-based modelling of spontaneous interactions". Specifically, it describes the work done by Aihara

and colleagues (2014). This last paper 'closes the circle' (Figure 1) connecting the *Agent-based modeling* with the social *Spontaneous interactions* scientific areas.

1 - Humans: Social neuroscience of spontaneous interactions

In research on cognitive functioning, in both human and non-human animals, neuroimaging studies have traditionally tested single individuals in highly controlled lab environments. However, calls for more interactive experimental settings (Schilbach et al., 2013) as well as more ecologically relevant behavioural tasks (Krakauer et al., 2017) are spurring these strands of research to analyze neural data through a more ethological lens. Although the structural neurobiology needed for vocal communication is under investigation in many species (Kelley & Bass, 2010) and the neural activity underlying naturalistic social interactions has long been studied in some (e.g. Hopkins, 1988), cognitive neuroscience can still bring valuable insights to the table on interpersonal neural synchronization in human temporal coordination and social interactions.

Electroencephalography (EEG) hyperscanning techniques, in which neural electric signals are recorded from multiple participants simultaneously, have been employed for studying the neuroscience of human social interactions (Liu et al., 2018; Babiloni & Astolfi, 2014). Given their high temporal resolution, EEG hyperscanning measurements seem particularly suited for studying interactive rhythmicity.

In the musical domain, Lindenberger, Li, Gruber & Müller (2009) used EEG hyperscanning to measure synchronized neural activity between pairs of participants playing the guitar. They found that phase synchronization increased significantly in both setting the metronome tempo and in coordinating play onset, and argue that between-brain oscillatory couplings reflect between-participant similarities in the temporal properties of their percepts and actions.

Using low-cost portable EEG systems, hyperscanning techniques can also be brought to the 'field', allowing testing for interbrain coupling in a broader number of situations. Dikker and colleagues (2017) investigate spontaneous neural synchronization to environmental input under radically naturalistic circumstances compared to usual neuroscientific approaches: they simultaneously recorded a group of high school students during regular class activity. Measuring brain-to-brain synchronization across the entire group, the authors found that the degree of neural synchronization between students could predict both social dynamics (group affinity and empathy) and class engagement (self-reported focus and teaching style appreciation). Dikker and colleagues (2017) argue that between-brain synchronization here is driven by shared attention mechanisms: neural

oscillations become more similar between students when they are paying attention, because they entrain to the same external stimulus (e.g. the teacher who is lecturing).

These studies highlight promising ways to investigate the neural underpinnings of human real-world musical and vocal interaction. Both studies demonstrate that interacting neural rhythms can be used as physiological markers of real-world social interaction on a behavioural level. Lindenberger and colleagues (2009) show that coordinated rhythmic behaviour is associated with interpersonal synchronization on the neural level, and Dikker and collaborators (2017) reveal that such synchronized neural rhythms also predict more complex human social dynamics in truly naturalistic settings.

Other work, on spontaneous brain-to-stimulus synchronization, indicates that this mechanism correlates both with neuroanatomical connectivity patterns and performance on ecologically relevant tasks like word-learning (Assaneo et al., 2019).

Carefully designed studies like these showcase opportunities for the interpretation of human neural data in behaviourally relevant contexts. Taken together, these methods provide encouraging steps towards a better understanding of the brain mechanisms behind real-world human vocal rhythms.

2 - Mice: Detailed quantification of social rhythm

Social interactions, including human music making and conversation, involve the dynamic modulation of actions based on cues picked up in the behaviour of others. In the study of vocal rhythms, acoustic exchanges between conspecifics are ideal test cases to probe such sensorimotor transformations. Despite the ubiquity of timed acoustic interactions, well-described across taxa in behavioural ecology (Schwartz & Freeberg, 2008; Bee & Micheyl, 2008; Pika, Wilkinson, Kendrick, & Vernes, 2018; Ravignani, Verga, & Greenfield, 2019), few animal models have been examined neuroscientifically.

Okobi and colleagues (2019) introduce Alston's singing mice (*Scotinomys teguina*) as a new mammal model exhibiting turn-taking behaviour. To inspect the causal dynamics behind these precisely timed vocal interactions, they use an innovative combination of behavioural measures and neural techniques. Comparing isolated singing to countersinging in duets, Okobi and colleagues (2019) found that individual vocal productions were more stereotyped in isolation, and showed more variation in duetting. Specific brain centres were mapped to jaw movements during song production by measuring muscle cell electricity (electromyography) and electrically stimulating neural populations (intracortical microstimulation), leading to the orofacial motor cortex (OMC) as a crucial centre controlling song-related musculature. Subsequent perturbation and focal cooling

experiments targeted at the OMC during isolated singing showed that disrupting the OMC alters song progression without influencing individual note structure. Finally, the causal role of the OMC in social vocalizations was corroborated in a playback experiment: countersinging responses to playback songs were absent in mice where the OMC was pharmacologically deactivated, while they were successfully elicited in a control group.

Okobi and colleagues conclude that a hierarchical mechanism underlies countersinging in Alston's singing mice, with distinct functional regions controlling vocal production and coordination: the OMC influences the pacing of songs, without altering the structure of individual notes. The distinction between temporal structure on the level of the song and the level of individual notes is well characterized through the authors' measure of the 'song trajectory slope': plotting note duration against note onset time, it becomes obvious that these slopes for individual mice are much more variable in social than in isolated settings.

This study convincingly shows that, for Alston's singing mice, involvement of the motor cortex is necessary for successful vocal interaction, whereas previous mammalian models have assumed that subcortical structures alone are sufficient for vocal timing (see e.g. Jürgens, 2009). The clever design of behavioural measures (e.g. the song trajectory slope) was essential for this finding: these detailed measures accurately captured differences in subcomponents of vocal rhythmicity between social contexts, which could then be causally linked to neural dynamics.

3 - Birds: Measuring rhythmic ontogeny

In many vertebrates, precisely timed sequences of behaviour are not innate but are acquired by juvenile animals (Aronov et al., 2011). In songbirds, for instance, mature song emerges gradually from an unstructured immature subsong, until it matches the internal template of the adult song (Konishi, 1965). Still, little is known about how the rhythmic components of songs are learned in order to answer questions like "how do song rhythms become consolidated?" and "how do different timescales of song rhythm relate to one another?".

Studies conducted by Hyland-Bruno and Tchernichovski investigated song-rhythm learning in songbirds (Hyland-Bruno, 2017; Hyland-Bruno & Tchernichovski, 2019). Zebra finches learn their songs by imitating an adult (Marler, 1970). Although mature songs exhibit hierarchical organization, the repetitions of motifs – the bout – are no longer stereotyped. Indeed, in a first study (Hyland-Bruno & Tchernichovski, 2019), the authors found patterns of flexibility in the rhythmic organization of song bouts, visualizing them as

sorted raster plots of acoustic features. They showed that when motifs (M) were strung together (M-M) with two or three intervening short calls, named connectors (c, leading to M-cc-M, M-ccc-M), the time interval between the motifs was highly variable, allowing a variation in timing across singing performances. Even among co-tutored birds that learned the same motif, the authors observed strong individual variability in the temporal plasticity of song bouts (Hyland-Bruno & Tchernichovski, 2019). During song development, the juvenile bird filters the influence of an external auditory model through a previously-internalized rhythm template.

Controlled song-learning experiments were further performed in a second study (Hyland-Bruno, 2017), which tested whether the song rhythm is learned, or it is instead an epiphenomenon of the learning of temporal sequences. Initially, birds were trained to learn to imitate a regularly-timed (isochronous), monosyllabic song sequence (AAAA). Afterwards, when the birds learned the song with "AAAA" sequence, a new song target "ABAB" was introduced with an additional syllable. Birds were hence divided into two experimental groups. In the first one, the tested birds heard the new syllable B congruent with the existing rhythm: the song "AAAA" had the same isochronous rhythm of "ABAB". In the second group, they were tested on a new target non-isochronous song, where the new syllable was slightly shortened in duration. Hyland-Bruno (2017) found that over ontogeny zebra finches more readily incorporated a new syllable when the tutored rhythm was unchanged, suggesting that a rhythmic pattern is established and used during song learning. An isochronous rhythm helped the birds adopt a new song sequence.

Based on these results, the authors propose an updated schema of the song imitation process, situating sequence learning within a rhythmic framework. The authors showed how juvenile birds develop their vocal learning capacity following the un-stereotyped time structure of the adult's song bouts. These studies show that rhythmic coordination can be crucial for individuals engaging in vocal communicative acts, and highlight the importance of the social context and the rhythmic environment in which song learning develops.

4 - Seals: Agent-based models of rhythm development.

The ontogenesis of vocal rhythms is only sporadically investigated. This makes the predictions based on related empirical work quite vague, as the hypothesis space has not been constrained by previous experiments. In these particular cases, agent-based modeling can be useful, as it summarily probes the space of possible outcomes as a second best option instead of relying on previous (in this case non-existent) actual experiments.

An example of combining agent-based modeling with developmental rhythm research is provided by a recent case study in a harbour seal pup. A seal pup was probed for its capacity to vocally respond to simulated playbacks of conspecifics (Ravignani, 2018). As no similar experiment was run in this or related species, mechanisms observed in other taxa provided different hypotheses on the potential rhythmic behaviours of the seal pup.

Alternative, competing hypotheses on how the seal pup would react to rhythmic playbacks included 1) an arousal mechanism, by which an individual hearing more calls responds with more calls, with no rhythmic adaptation at all: the focal animal and the playback stimulus might have the same number of calls, which, however, do not have a systematic relation between their onsets; 2) adaptive synchrony, as often seen in human movement, by which an individual modifies the rate and delay of its calls so that they occur at the same time as those of a conspecific; 3) phase delay, as attested in bush crickets, which is based on a simple internal oscillator triggering calls which gets reset every time a conspecific is heard; 4) antisynchrony, as indirectly predicted by a classical theoretical model, by which an individual will modify the rate and delay of its calls so that they occur at a fraction of the period of a conspecific (Hamilton, 1971; Merker et al. 2009; Ravignani, 2014; Ravignani & de Reus, 2019).

Before running playback experiments, agent-based simulations were performed to see how 4 hypothetical seals, each adopting one of the 4 strategies above, would react to the playbacks. Data collected from the actual experiment was analyzed with traditional statistical tools. In addition, however, comparison of the four models with the experimental data showed that the seal behaviour observed in the experiment matched one of the models (antisynchrony) and clearly differed from the others (Ravignani, 2018).

One additional angle, unfortunately not probed in this experiment, could be to use agent-based models to actually model developmental processes (e.g. de Boer, 2001; de Boer & Kuhl, 2003). By collecting data over developmental stages, and running corresponding computer simulations, one could test how acoustic behaviours change over ontogeny while summarizing their fundamental mechanisms.

5 - Tree frogs: Agent-based modelling of spontaneous interactions

Antisynchrony is also at the core of another paper, this time showing how two 'strange bedfellows' can be fruitfully combined: Work with animals in the field, and simulated computer agents acting according to theoretical models.

In particular, while studying choruses of Japanese tree frogs in the field, Aihara and colleagues (2014) built simple mathematical models of the frogs' vocal behaviour. The

authors used a classical 'phase oscillator model' (Ota et al., 2019; Strogatz, 2004). The gist of the model is that every agent (e.g. every frog) can be imagined as an analogue clock. Each clock has only one clock hand, potentially moving at a different speed. Each clock's behaviour can be described by 2 main parameters: the angular velocity, namely how fast the hand runs (i.e. how fast time flows), and the phase, which is the direction the hand points to (i.e. the current time). If one hypothesizes that the two clocks can influence each other, the resulting 'clock equations' for each agent can be noted mathematically and implemented in computer code. The power of this method is that all possible interactive scenarios among agents can be simulated, and the model can be modified and expanded with additional parameters.

To summarize the modelling side, the authors used simulations providing predictions on how an actual chorus in the field would look like (see also Aihara, 2009; Aihara et al., 2011). They then went to the field and measured the signalling behaviour of the actual frogs using a novel sound-imaging method, enabling real-time visualization of each frog call (Mizumoto, et al. 2011). Analyses of the video recordings showed that that two-cluster antisynchronization was more frequent in choruses of male Japanese tree frogs. The finding qualitatively confirms what the mathematical model previously predicted: the existence of two-cluster antisynchronization in the choruses of male Japanese tree frogs. However, the authors did not detect a wavy anti-synchronization in the field experiment, although it did appear as a stable solution in the numerical simulation (though less often observed than the two-cluster antisynchronization).

Aihara and colleagues (2014) motivated this inconsistency in terms of particular field condition occurring during the recordings. The sound images device was adopted only along one edge of the field where the larger numbers of male frogs aggregated. In such a setup, a straight-line distribution of the calling male frogs was approximately realized, compromising the wavy antisynchronization of the male frogs signalling behaviour.

They suggested that male Japanese tree frogs may dynamically change their calling times even in the same chorusing session beyond the expectation of the present mathematical model. Aiming to predict as many as possible spatio-temporal structures occurring within the collective animal behaviour dynamics should be the main task of these mathematical models, which then can be tested against empirical field research.

Conclusions

The aim of this short piece was not to perform an exhaustive literature review. Instead, we intended to link a few points at the intersection of science, scientific methodology and meta-science.

Apart from the overall connection among the few papers we have chosen, each of them individually contains important lessons on the added value of combining two or more approaches. The human studies show that valuable and ecologically valid insights on interpersonal cross-brain interactions can be obtained from recording EEG in social settings. The mice study shows how combining rhythm-tailored behavioral measurements with neurobiological techniques targeting specific areas can help establish fine-grained mechanisms for precise rhythmic behaviours. The bird study shows how long-term monitoring of all vocalizations produced by birds developing in controlled environments, combined again with advanced rhythm measurements, enables to track the long-term impacts of early social experiences and identify constraints on flexibility. The seal study firstly confirms the importance of studying the vocal behaviour in the early stage of the individual's life and, secondly, suggests how agent-based modelling can both provide predictions before an experiment is run, and confirm the empirical results after the experiment. The frog study shows how even spontaneous animal interactions in the wild can be mathematically modelled, hence combining the ecological approaches with the precision of mathematics.

We realize that our usage of the term 'rhythm', as in 'vocal rhythms' and 'interactive rhythms', is quite broad, and the behaviours we focus on could also be referred to as dynamic modulation of actions. Each field studying rhythm struggles with a clear definition (just for rhythm in music, for instance, see the many definitions in Toussaint, 2019). Our aim is to have a definition which, being as broad as possible, can be applied to virtually any animal behaviour or neural process.

To conclude, we are optimistic that many subareas at the boundary of comparative cognition and behavioural ecology will reciprocally communicate and exchange theoretical and methodological approaches, as several others are already doing.

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