The Evolution of Rhythmic Cognition: New Perspectives and Technologies in Comparative Research

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Abstract

Music is a pervasive phenomenon in human culture, and musical rhythm is virtually present in all musical traditions. Research on its evolution and cognitive underpinnings can benefit from a number of approaches. We outline key concepts and definitions, enabling more fine-grained analysis of rhythmic cognition in experimental studies. We advocate comparative animal research as a useful approach to answer questions about human music cognition and review experimental evidence from different species. Finally, we suggest future directions for research on the cognition of rhythm. Apart from research in semi-natural setups, possibly allowed by "drum set for chimpanzees" prototypes presented here for the first time, mathematical modeling and systematic use of circular statistics can be promising approaches.

Keywords: The evolution of music; primate cognition; animal-machine interaction; chimpanzee drum set; vocal learning; rhythm; entrainment; beat; synchronization; social cognition; comparative cognition.

Introduction

The Origins of Music

Music as a cognitive system is one of the most prominent and distinctive human features. Since Darwin, the putative direct role of natural selection in the emergence of human music has been a topic of great debate. Numerous hypotheses, which attribute an adaptive value to music, have been proposed, all featuring a social component. Music has been suggested to be, among others, a substitute for social grooming, a "training field" for social development, a filial bonding tool, and a mechanism of sexual selection (Patel, 2008). While hypotheses on music origins are difficult to test directly, the comparative method in cognition enables us to investigate the purported specificity and uniqueness of human musical abilities (Fitch, 2006). In this paper we focus on one aspect of music, rhythmic cognition, and propose new perspectives and technologies for investigating the evolution of music.

Rhythm and Cognition

Rhythm, characterized as a pattern of temporal change, plays a central role in music. The basic elements of musical rhythm are the *beats*, defined as points in time occurring in a perceptually periodic way (Patel, 2008). *Grouping* and *meter* are subsystems of musical rhythmic organization and are considered the basic structural components of rhythmic patterns (Lerdahl & Jackendoff, 1983). *Grouping* refers to the organization of the musical stream into motives, phrases, and sections. *Meter* corresponds to a regular pattern of strong and weak beats. In metrical structures, beats are organized hierarchically according to their relative strength. Moreover, the impression of the speed of the performed pattern, the *tempo*, influences the interpretation and perception of rhythmic structures. According to the tempo humans may assign different organizations to grouping and metrical hierarchy. Hence, the cognition of musical rhythm should not be investigated holistically, but in terms of *beat*, *grouping*, *meter*, and *tempo*. These, together, yield the flexibility of human rhythmic cognition: humans are able to extract structural properties from music and interpret them in several contexts. What are the basic capacities allowing this cognitive flexibility?

Beat Perception and Synchronization

The metrical hierarchy mentioned above contains a particular hierarchical level called *tactus*, which listeners perceive as 'the (primary) beat' (Lerdahl & Jackendoff, 1983), whose perception is robust to moderate tempo fluctuations (Patel, 2008). It seems that our internal processes underlying rhythm perception can be spontaneously synchronized, *entrained*, to external regular, periodic sensory cues (Grahn, 2012). In this *entrainment* model, the relative timing of events is processed by expecting their periods or phase and adjusting the expectations to actual occurrences (Grahn, 2012). This flexible beat processing mechanism is also the basis for synchronizing motor actions to musical stimuli, requiring (i) beat extraction, (ii) synchronization of an internal motor pulse to the inferred auditory beat (*beat entrainment*), and (iii) a motor pattern generation on the basis of the internal pulse (Fitch, 2012). A fundamental requirement of synchronization is hence the capacity to extract the beat, already active in newborns and infants, though not conclusively innate because of possible prenatal learning (Grahn, 2012). The capacity for beat perception and synchronization could be shared with other animals as an analogous or homologous evolutionary trait. In order to understand the nature and evolution of human rhythmic cognition, different species must be tested on tasks requiring the three aforementioned skills.

Rhythm and Beat Evidence in Non-human Animals

Vocal Learning and *Dissociation* Hypotheses

Some non-human animal species have a particularly good control over their vocal tract. Among these, humans, ele-

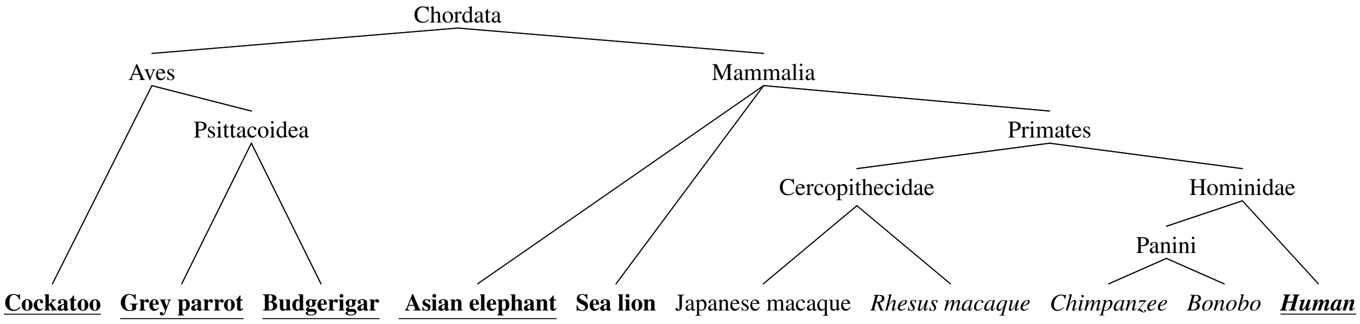

Figure 1: Phylogenetic tree of species showing: vocal learnering skills (underlined), ability to synchronize to a beat (**bold**) and spontaneous drumming behavior (*italics*). Notice how, while showing no evidence of vocal mimicry, Sea lions are capable of synchronization and several primates exhibit natural percussive behavior.

phants, some bird species and marine mammals are capable of spontaneously imitating sounds they hear without these necessarily belonging to their natural communication system. A promising hypothesis has been put forward connecting vocal learning and rhythmic abilities across species (Patel, 2008): as both sorts of tasks are better performed with a tight connection between motor and auditory brain areas, which is found in some vocal learning species including humans, the skill of vocal mimicry would be a necessary prerequisite for beat perception and synchronization. Most of the experimental evidence currently available would support this hypothesis.

As humans seem to be the only vocal learners among primates, the key question is whether the ability to perceive and produce musical rhythm is unique to humans among primates. Recent evidence (Honing et al., 2012) suggests that rhesus macaques (*Macaca mulatta*) can detect rhythmic grouping but not the downbeat in music. The authors formulate an "auditory timing dissociation hypothesis": Some cognitive skills allowing grouping are expected to exist in several primates due to common ancestry, while some others related to beat induction should be present in humans and other vocal learners due to convergent evolution. In fact, a generalized failure to produce rhythmic patterns in non-human primates would support the hypothesis of convergent evolution of vocal learning and rhythmic abilities.

Evidence from Vocal Learners

Schachner, Brady, Pepperberg and Hauser (2009) searched videos of putative animal entrainment to music using the global database YouTube. 1019 videos of non-human animals, half of which vocal mimicking species, were analyzed both for frequency and phase synchronization. Strikingly, all 33 videos showing evidence of entrainment featured a vocal learning species. Among the species considered unable to learn new vocalizations, there was no evidence of synchronization ability. Within vocal mimics, all animals examined belonged to bird species, except for the Asian elephant (*Elephas maximus*). Schachner et al. (2009) also analyzed videos of sea lions (subfamily: *Otariinae*) which showed no evidence of entrainment.

This general result on synchronization abilities in vocal learning species is backed up by experimental evidence in three different avian species. Patel, Iversen, Bregman and Schulz (2009) analyzed the head bob movements of a sulphur-crested cockatoo (*Cacatua galerita eleonora*) in response to a familiar song under unfamiliar tempo manipulations. In the absence of any training, the animal showed periods of entrainment matching phase and frequency of the musical beat. Schachner et al. (2009) provided additional evidence for entrainment in the same individual and a language-trained, African grey parrot (*Psittacus erithacus*).

Hasegawa, Okanoya, Hasegawa and Seki (2011) trained budgerigars (*Melopsittacus undulates*) to peck according to the beat of an audio-visual metronome. This study is particularly relevant as (i) it extends the sample size of the previous studies to 8 birds; (ii) it makes use of powerful analytical techniques from circular statistics and (iii) it compares actual performances to those of simulated birds in order to test the hypothesis that experimental subjects use "behavioral shortcuts" which could give the illusion of beat synchronization. Overall, Hasegawa et al. (2011) provide *decisive evidence of trained synchronization ability in a vocal-mimicking species*.

A Crucial Outlier

In a recent study, Cook, Rouse, Wilson and Reichmuth (2013), investigated beat synchronization abilities in a pinniped, the California Sea Lion (*Zalophus californianus*). Crucially, sea lions, unlike seals and other marine mammals, seem to have a *low degree of vocal flexibility* (Schusterman, 2008) and are usually grouped with non-vocal learners. Cook et al. (2013) trained the animal to bob its head in synchrony with different auditory stimuli at different tempi. This ability, trained first with metronome-like stimuli at different tempi, was easily transferred to novel tempi. Similarly, once trained with actual songs, the Sea Lion was able to transfer the synchronous head bobbing to new tempi and songs with no additional training.

This exciting finding opens new lines of research (see Figure 1). On the one hand, conclusive evidence on vocal mimicking abilities in sea lions is indispensable to contrast this finding with, and eventually update, the vocal learning hypothesis. On the other hand, Cook et al.'s (2013) discovery increases the likelihood of finding beat and rhythmic abilities in some vocal non-mimics. In particular apes and marine mammals, heterogeneous in vocal learning and advanced cognitive skills, offer a promising "testing field". Unfortunately, the evidence for apes and monkeys is either observational or, coming from studies focusing on a related topic, not conclusive to prove or disprove beat entrainment.

Evidence from Great Apes

Drumming by Wild Chimpanzees Chimpanzees (*Pan troglodytes*) can be observed hitting objects in order to produce loud sounds, especially during dominance displays. Arcadi, Robert and Boesch (1998), analyzed their spontaneous drumming behavior on tree buttresses. Among other measures, Arcadi et al. (1998) report an interbeat interval distribution ranging up to 1.4 s, with a mean of 0.30s and "most interbeat intervals" less than 0.4s. Transposing this into musical terms, the drumming behavior has a mean of 200 BPM (beats per minute) and is above 43 BPM, with most recorded patterns exceeding 150 BPM.[1] Arcadi et al. (1998) found a number of individual differences in drumming behavior, notably in the interbeat interval duration, the number of beats per "drumming session" and the length of sessions. Finally, the authors tested for statistical dependence between contiguous, non-adjacent beat patterns. One of the chimpanzees produced series of four beats, where a short interval between two beats statistically predicted another short interval between two following beats. This can be interpreted as showing a weak form of regularity in natural beat production and a sporadic, local steadiness in tempo. This study shows that percussive behaviors are naturally present in primates not capable of vocal mimicry. Together with Honing et al.'s (2012) findings, this implies that rhythmic abilities across species might be graded, rather than dichotomous, suggesting that the evolution of musical rhythm be better investigated in a fine-grained manner.

Human-Bonobo Musical Interactions In the context of human-ape interaction, Large, Velasco and Gray (2008) report an occurrence of entrainment. MIDI recordings from musical interactions between a human and three bonobos *Pan paniscus* were analyzed for evidence of synchronization. The authors claim that, after having identified "37 episodes of rhythmic interaction, [...] in just under half of these episodes, statistical evidence of phase entrainment was found" (Large et al., 2008). The interactive nature of this study and the little published information leaves unclear the relative contribution of human and bonobo participants to rhythmic synchronization (Patel et al., 2009). Considering the lack of evidence for entrainment in non-human primates, this result is, in principle, promising and worth further exploration.

Contrasting Evidence from Macaques

Communicative and Social Function of Drumming Similarly to chimpanzees, naturally occurring drumming behavior can be observed in macaques. Remedios, Logothetis and Kayser (2009) remark that "rhesus macaques produce loud, stretched and repetitive sounds by using artificial objects, such as cage doors, in their environment." The authors report a series of behavioral observations and playback experiments aimed at uncovering the perception and function of drumming behavior in three rhesus macaques (*Macaca mulatta*). Observations of macaque drumming in Remedios et al. (2009) provide a mean of 294 BPM, with a standard deviation of 174 BPM. Playback experiments (Remedios et al., 2009) show that the animals orient more often to drumming sounds than any other natural sound. The authors conclude that drumming serves social functions in rhesus monkeys and is likely to constitute a support or extension to other means of species-specific communication.

Interval Timing Abilities Zarco, Merchant, Prado and Mendez (2009) compare the ability of 20 human subjects and 3 rhesus macaques to synchronize to visual and auditory metronomes and to project this interval timing ability once the metric cue has been removed. They conclude that these monkeys are "not able to synchronize their tapping behavior to the sensory metronome as human subjects do" (Zarco et al., 2009). It is essential to notice that the authors base their conclusion on a linear test of "phase matching" (Patel et al., 2009). Zarco et al. calculate the average time difference between metronome cues and tap onset and compare this between species using a repeated measures ANOVA. As monkeys tap, on average, 300 ms after the metronome and the ANOVA gives a significant difference only for species, Zarco et al. (2009) conclude this is evidence that monkeys do "not synchronize their tapping to the sensory metronome". Further analyses suggest that the monkeys have, however, some form of timing prediction abilities, having shorter reaction times to stimuli with constant, rather than unpredictable, inter-onset intervals. Zarco et al. (2009) is a crucial contribution to the field, providing the first experimental paradigm for testing one component of rhythm in non-human primates. However one cannot be sure that more specific tests from circular statistics would have led to the same conclusions in terms of phase or tempo synchronization.

Subsecond Beat Prediction Konoike, Mikami and Miyachi (2012) conducted a similar experiment with two Japanese macaques (*Macaca fuscata*, closely related to rhesus macaques). The monkeys were reinforced for pushing a button in response to an audiovisual metronome. Crucially for our purposes, a synchronization threshold was set a priori: if a metronome beat was not matched with a tap within

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[1] These purported tempi only partially overlap with those commonly used in human music. The slowest recorded value would correspond to a Lento, while the majority of chimpanzee interbeat intervals would translate to tempi such as Allegrissimo or Prestissimo.

350-400 ms, the entire trial would be aborted. Reaction times were shorter with regularly-spaced beats when compared to an "unpredictable" inter-beat interval condition, as long as inter-beat intervals did not exceed 1 second. However, comparing the synchronization thresholds imposed by the authors to the reaction times, there could be a differential effect of the thresholds in shaping reaction times between subjects. As in the previous case, this study contributes to understand what is unique about human rhythmic abilities. A suggestive hypothesis put forward by Konoike et al. (2012) is that their subjects' rhythmic control could depend on an automatic timing system rather than higher cognitive mechanisms. The a priori synchronization threshold and the lack of a statistical test on tempo matching prevent us from drawing conclusions about music-specific rhythmic abilities in these primates.

Synchronization of Arm Motion Nagasaka et al. (2013) report mutual synchronization between pairs of Japanese macaques in a laboratory setup. Interestingly, in each interaction, the ratios of BPM of the two subjects were small integers, suggesting periodical occurrence of synchronized taps. However it seems that visual, rather than auditory, information had a decisive role in macaques' synchronization accuracy when moving in response to a video of a conspecific.

The *Social Convergence* Hypothesis

Recent findings (Large et al., 2008; Nagasaka et al., 2013) point towards the importance of social context in obtaining positive results when testing for rhythmic and music-related abilities. Children can already entrain to a pulse from 2.5 years of age, being particularly accurate when drumming along with a human partner, rather than an artificial one (Kirschner & Tomasello, 2009); rhythmic abilities, coordination and cooperation could be partially connected within hominid evolutionary history. The recent "*Social Convergence* hypothesis" puts forward the importance of human social instincts in the development of rhythmic abilities: isochrony would be an easy way of achieving synchrony, which in turn is a form of coordinate, cooperative auditory signal generation (Fitch, 2012).

Future Directions

If research on rhythmic cognition aims to advance and make groundbreaking discoveries, there are some directions we propose it should take. First, a broader range of animal species should be tested: apes, marine mammals and non-avian vocal learners are key groups whose success or failure in beat and other rhythmic production tasks will arbitrate between a number of proposed hypotheses. We stress that such testing should happen as much as possible in an experimentally-controlled, though ecologically valid environment. Below we propose a viable approach for chimpanzees, using musical instruments explicitly built with those constraints in mind. Second, statistical techniques used to analyze entrainment data should be adequate to the purpose. If we think about statistics as a tool for getting closer to scientific facts, statistical techniques whose assumptions better fit the object under investigation will lead us closer to solid science. Inference drawn from a statistical test resting on inadequate assumptions will lead to less robust conclusions. Third, mathematical modeling of the emergence of beat and rhythm is an important complement to experiments. Analytical models and agent-based simulations can help sharpen hypotheses about which cultural, social and biological evolutionary processes endowed different species with different cognitive skills in terms of rhythm and music.

Circular Statistics

Most data coming from beat and rhythm experiments involve a *periodic time* component. Before applying a statistical test, it is essential to think about the nature and dimensionality of the data. As a parallel, if we wanted to compare the amount of rain falling on Britain over time, we should conceptualize rain as falling onto a 2-dimensional space, rather than the real number line, $\mathbb{R}$. As the classical t-test for paired samples is defined on $\mathbb{R}$, it would not be appropriate to use it on geographical data. The fact that rhythmic data are originally associated with time makes time series analysis a possible approach to test a range of hypotheses.

The best option is to use, when possible, circular statistics (Fisher, 1995). Its key feature consists in supposing that data is distributed on a circle, rather than the usual real number line. This grants ideal analytical tools for data sets with a periodic time component, such as those deriving from beat and rhythm experiments. Several researchers in the field have successfully used these techniques on human (Kirschner and Tomasello, 2009) and animal data (Hasegawa et al., 2011).

Towards Rhythmic Production in Chimpanzees

Above we hinted at a viable methodological approach for testing beat and rhythm production abilities in higher primates. Chimpanzees already exhibit drumming behavior in the wild. A first step towards testing rhythm hypothesis in a semi-natural context could be to endow chimpanzees with a device they can use to play and which produces sounds when manipulated. At the same time, such a "music making device" should be particularly well adapted to the rigor of scientific experiments. No musical instrument or device, specifically designed for chimpanzees, sensing movements and feed-backing sounds, is currently available for purchase. Such device should: (i) be resistant to chimpanzees' strength, (ii) enable them to produce sound through object manipulation, (iii) systematically record data sensed from these movements, (iv) scientists to experimentally vary the sound properties of the object, without having to physically modify or replace it. We describe two prototypes specifically adapted to chimpanzees, which allow to map sounds to physical movements and satisfy the requirements above. These prototypes constitute, to our knowledge, the first attempt at animal-computer cognitive interaction. Here we outline their general features. For a thorough technical description and calibration data, see Ravignani et al. (in preparation).

Two Chimpanzee Drum-Set Prototypes

Desiderata and General Features The prototypes were built with a main idea in mind: spurring the chimpanzee to spontaneous interaction and play. To maximize the chances of interaction, they were constructed and calibrated after scrutinizing videos of chimpanzees playing with objects, including the gum toy used in one of the prototypes. Each prototype consists of a sensing and a feedback unit. Sensing units feature acceleration and strain sensors embedded into manipulable objects. These units send acceleration or strain data to a computer, which converts them into sound and plays it in real time. The drum sets satisfy a number of logistic and technical desiderata. The sensing part is resistant, modular, low-voltage, inexpensive, interesting for the primate and easy to connect and configure. The software grants fast elaboration of data by performing few, simple operations, so as to limit the computational load.[2]

Prototype A: Wired The *wired prototype* is a parallelepiped containing piezoelectric sensors and connected to a Mac computer via an Arduino[3] board. A dedicated Python[4] script is in charge of the auditory feedback. It can be mounted vertically on a wall or on the wire-mesh of chimpanzees' enclosures. This prototype has several advantages:(i) it is built with cheap and easy to find components, (ii) it entails no risk of electrocution and (iii) its ricochet property naturally suits the animal's tendency to hit and push objects.

Prototype B: Wireless The *wireless prototype* consists in a hollow dog toy enclosing a Wii Remote[5]. A computer receives data (via Bluetooth), which is is processed and sonified using patches written in Max[6]. This device has several advantageous features: (i) chimpanzees generally enjoy manipulating objects, and chimpanzees have been both reported (Pruetz & Bloomsmith, 1992) and observed by us while manipulating the model of toy used here (ii) its construction requires less work than the wired prototype and its components can be easily purchased, (iii) it has a wireless communication system, particularly advantageous in some applications.

The Importance of Modeling

Above we hinted at the importance of developing mathematical models of the emergence of rhythm. The last century has seen a radical increase in the quantitative approaches used in most areas of human knowledge. In particular, mathematical models and computer simulations have proven themselves particularly useful in testing the internal consistency of hypotheses, sharpening scientific assumptions and providing new viable directions for experimental testing. Scholars interested in the evolution and emergence of structure in language, for instance, have provided quantitative accounts (Kirby, 2001), which have been later validated through cognitive experiments (Kirby, Cornish & Smith, 2008).

Similarly, recent experiments (Honing et al., 2012) have shed light on what can be accounted for by human culture or biology in rhythmic abilities. However, thorough explanations are still missing about the evolutionary forces, whether biological or cultural, which have shaped musical rhythm and the underlying human cognitive abilities. *Quantitative evolutionary thinking* can be used to study the emergence of music and rhythm, and models linking biology to culture could be an exciting second step.

While investigating what is special about musical rhythm and which species possess the cognitive abilities to process it, human and animal experimental work should be complemented by models aimed at explaining the ultimate mechanisms of what is observed in everyday musical behavior. The lack of quantitative work trying to explain the emergence, cultural dynamics and biological evolution of music is surprising when we consider its pervasiveness in human lives.

Conclusions

We suggested directions and methodologies for investigating the evolution of musical rhythm in a comparative, interdisciplinary perspective. Usage of a variety of statistical techniques on the same data set and replication are essential before conclusive claims of lack of synchronization can be made about a species or taxon. Moreover, experiments should be designed keeping in mind the critical theoretical distinctions introduced above.

Recent evidence provided by Honing et al. (2012) and Cook et al. (2013) may lead to newly redefined hypotheses, which in turn make the experimental testing of apes and marine mammals a fundamental prerequisite for a theory of human uniqueness of rhythmic abilities. The drum sets we present are intended for apes to perform acoustic non-vocal production in a captive, though not restrained context. In general, as technological tools for human-machine interaction become available, new methodological paradigms for animal-machine interaction can be developed and used to test critical species in musical tasks. Mathematical modeling and agent-based simulations can be a great complement to empirical data, hopefully generating the same productive theory-experiments interplay seen in other disciplines.

Similarly to the broad variety of reaction time distributions across species and tasks, evolution has shaped animal brains and motor skills so that different species may require different statistical null hypotheses with respect to attempted synchronized motor behavior (for instance, due to perceptual or motor lower bounds on reaction times). Circular statistics, with its variety of theoretical distributions (von Mises, cardioid, wrapped normal, etc) and time-periodic tests, is ideal for testing hypotheses about rhythmic synchronization with

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[2] The software processing part has four key tasks: data filtering, data transformation to extract meaningful parameters, logging specific variations of these parameters and play particular sounds in correspondence of these variations. Parameters and settings can be changed in order to vary the sensitivity of the device. The mapping between raw data, parameters and sound output can be altered depending on the experiment.

[3] www.arduino.cc

[4] www.python.org

[5] www.nintendo.com

[6] cycling74.com/products/max/

different underlying assumptions.

The *Vocal Learning* and *Social Convergence* hypotheses make different predictions on which species should have rhythmic abilities (Fitch, 2012). Both of them, however, are related to another uniquely human trait: language. Further development of experimental paradigms allowing social interactions under experimentally-controlled conditions will enable to contrast these hypotheses and produce evidence relevant to the evolution and cognition of both music and language.

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