The evolution of rhythm from neurons to ecology

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Introduction and aims

Why are animal rhythms important? Cross-species work can help isolate what is unique in the human capacity for rhythm. In addition, cross-species work can provide inference on the origins and evolution of human rhythmic capacities. Neural tissue and cognitive capacities do not fossilize: by pinpointing shared biological mechanisms between humans and other animals, cross-species research can help reconstruct the evolution of rhythmic capacities in humans. This symposium will unify multiple comparative approaches to the evolution of musical rhythm. Specifically, we aim at (1) providing a platform for multiple fields to compare theoretical frameworks and methodologies across species, (2) integrating findings from behaviour, neuroscience, modelling, and cognition, (3) actively spurring cross-fertilization between musical rhythm and animal timing research, (4) drawing inferences on the evolution of human rhythm.

Researchers from disciplines directly relevant to rhythm, such as music cognition, comparative psychology, biology, mammalian development, and neurobiology, will tackle several questions, within and across contributions: How do animals perceive, remember and generalize rhythmic patterns? Which biological predispositions affect processing of rhythmic structure? How do rhythmic abilities change over development? Which species can process isochronous patterns? Do neural circuits for isochrony and beat perception differ in non-human animals? Do other species show unimodal vs. multimodal rhythms and dance-like behaviour? Which basic principles of rhythm processing can be captured by mathematical models?

The four symposium contributions addressing these questions are quite diverse, featuring several species (crucially those with some rhythmic flexibility hence most relevant to human rhythm), paradigms and scientific backgrounds. In brief, this symposium will investigate rhythm evolution all the way from single-neuron recordings to behavioral ecology.

Vocal learning as a preadaptation for the evolution of human beat perception and synchronization (Aniruddh D. Patel)

The capacity to synchronize movements to an auditory beat is central to musical behavior. What are the evolutionary foundations of this ability? The vocal learning and rhythmic synchronization hypothesis proposes that our ability to move in time with an auditory beat in a precise, predictive, and tempo-flexible manner originated in the neural circuitry for complex vocal learning. A variety of studies have supported the hypothesis, but one study has significantly challenged it. Furthermore, it is increasingly clear that vocal learning is not a binary trait, but a trait that varies more continuously across species. In light of these developments and of recent progress in the neurobiology of beat processing and vocal learning, the vocal learning hypothesis is revised. It now proposes that an advanced form of vocal learning acts as a preadaptation for sporadic beat perception and synchronization, and provides intrinsic rewards for predicting the temporal structure of complex acoustic sequences. It further proposes that in humans, mechanisms of gene-culture coevolution transformed this preadaptation into a genuine neural adaptation for sustained beat perception and synchronization. l will describe this new proposal and the predictions that it makes for neuroscience, cross-species studies, and genetics.

Evolution of dancing communication in songbirds (Nao Ota & Masayo Soma)

Courtship display of birds shows a remarkable similarity with human communication and music. In a variety of avian species, males are known to show ritualized mating dance while singing to impress females. These behaviors raise questions of how and why they achieve the fine temporal coordination between dancing and singing. Interestingly, such multimodal courtship signals are produced not only by males but also by females in some socially monogamous species, such as estrildid finches (family estrildidae). The phylogenetic comparative study on estrildid finches has revealed that dancing and singing evolved independently in this clade, which implies that neural mechanisms responsible for singing has little to do with the ability to dance. To further elucidate the functions of multimodal courtship, we also conducted behavioral analyses targeting multimodal courtship display of cordon-bleus. The patterns of singing and dancing interacted with each other so as to enhance the efficacy of both audio and visual signals. We also found social effects on the courtship display. Namely, males and females perform multimodal display frequently when presented with audience birds, suggesting that simultaneous song-dance communication functions for advertising their current mating status to other birds, in addition to attracting a mate.

Brain dynamics in the primate audiomotor circuit during isochronous beat perception and entrainment (Hugo Merchant)

The ability to extract the regular pulse in music and to respond in synchrony to this pulse is called beat synchronization and is a natural human behavior exhibited during dancing and musical ensemble playing. Previously, we showed that macaques can predictively entrain to isochronous metronomes, although they have a bias towards visual rather than auditory rhythmic stimuli. In this study we recorded the simultaneous activity of hundreds of cells in the core (A1) and belt (A2) areas of the auditory cortex as well as in the medial premotor areas (SMA) when monkeys performed both a task that included beat perception (BP) and tapping synchronization (TS) epochs and during passive listening of the metronome. Notably, we found that both A1 and A2 not only showed responses associated with auditory sensation in all tasks, but also neural signals related with active sensing. The latter showed activity that increased during BP and TS with a switch in response phase from sensory driven, tens of ms after the stimulus in the passive condition, to a predictive sensory response during BP and TS. In addition, some A2 neurons showed neural responses aligned to the tapping movements, suggesting that the auditory cortex has access to an internal beat prediction signal, probably coming from the cortical premotor system. Indeed, in SMA we found time-varying single-cell responses which, when projected into a low dimensional space, formed rotatory population neural trajectories that showed two main properties. First, a complete circular loop was formed for each produced interval, converging to a similar state-space location close to the tapping time. The convergence to this neural attractor state could be the internal representation of the pulse that is transmitted as a phasic top-down signal to the auditory areas before each tap. Second, these oscillatory trajectories did not overlap across durations, a signature of temporal scaling; instead, they showed a linear increase in their radius as a function of the target interval. These preliminary results give experimental support to the notion of the dynamic interplay between the active sensing signals of the auditory areas and the internal beat representation of medial premotor system during rhythmic perception and entrainment.

Interactive vocal rhythms in seal pups and in silico (Andrea Ravignani)

The temporal and rhythmic structure of animal vocalizations can shed light on the evolution of musical rhythm. Understanding vocal timing and rhythm in a few specific mammals (e.g. pinnipeds, elephants, bats) drives a cross-species hypothesis in evolutionary neuroscience: vocal learning and rhythm perception and synchronization may be causally related. Seals are among these mammals, and their puppyhood is the most active vocal period in their lives. Building on both comparative psychology and animal behavior, this work attempts an alternative approach to animal rhythms by asking questions relevant to musical rhythm while piggybacking on the species ecological relevance and adaptive function of timing and rhythm. We present data from two species of seal pups in three different setups: 1) recordings of natural vocal rhythms, 2) playback experiments to elicit vocal responses and 3) perceptual listening experiments to measure behavioral responses. We complement empirical data with mathematical and agent-based computational modeling. Our data suggest that seal pups can produce and perceive rhythmic sequences. They can discriminate between isochronous and non-isochronous rhythms. Seals vocal exchanges show rhythmic interactivity and antisynchronous coordination, quantitatively similar to the turn-taking in jazz improvisation. Evidence for antisynchrony, rather than synchrony, in seals has several implications. In particular, it suggests that the rhythm-vocal learning link across species may be more complex than previously surmised.