Isochrony, vocal learning and the acquisition of rhythm and melody

Andrea Ravignani

Comparative Bioacoustics Group, Max Planck Institute for Psycholinguistics, Nijmegen, NL
andrea.ravignani@mpi.nl

ABSTRACT

A cross-species perspective can extend and provide testable predictions for Savage et al.'s framework. Rhythm and melody, I argue, could bootstrap each other in the evolution of musicality. Isochrony may function as a temporal grid to support rehearsing and learning modulated, pitched vocalizations. Once this melodic plasticity is acquired, focus can shift back to refining rhythm processing and beat induction.

Musicality consists of the (neuro)biological underpinnings to perceive and produce music. Research in the evolution of musicality needs cross-species evidence. As a parallel, to understand the evolution of bat wings, one asks why all other mammals lack wings and why other flying animals have evolved them. Likewise, our species only constitutes one datapoint to construct evolutionary hypotheses on musicality. Comparisons with other species are necessary to avoid post-hoc explanations of evolutionary traits.

Four concepts discussed in Savage et al. are key for understanding musicality, both in humans and other animals (Figure 1). *Isochrony* describes metronomic temporal regularity, like the ticking of a clock (Merker et al., 2009; Ravignani & Madison, 2017). *Synchrony* is the perfect co-occurrence in time of two series of events, with no strong teleological or mechanistic focus (Kotz et al., 2018; Ravignani, 2017). *Vocal learning* is the ability to learn and modify non-innate vocalizations, including melodies (Lattenkamp & Vernes, 2018). *Beat induction* denotes a top-down capacity to induce a regular pulse from music and move in synchrony to it (Grahn & Brett, 2007; Honing, 2012).

Do other animals have these capacities supporting musicality? Isochrony appears in many species' communication (e.g. from lobster rattles to sea lion barks: Patek & Caldwell, 2006; Schusterman, 1977), autonomously-regulated behavior or (neuro)physiology. Synchrony is widespread but scattered across taxonomic groups (Ravignani et al., 2014; Wilson & Cook, 2016). Vocal learning is rare but potentially arose multiple times in evolution due to different pressures across species (Nowicki & Searcy, 2014; Garcia & Ravignani, 2020; Martins & Boeckx, 2020). Beat induction has only been found in a few animals, as acknowledged by Savage and colleagues (Kotz et al., 2018; cf. Mehr et al., claiming its presence in many species).

Savage and colleagues briefly characterize these four abilities; this invites discussion of cross-species implications and predictions as to how they evolved to support musicality. I add a fifth, still largely unexplored capacity: vocal rhythms, which consist in producing, perceiving, learning, or imitating signals with accuracy in the temporal - as opposed to the spectral - domain. While this capacity to precisely time one's vocalizations is related to its spectral counterpart, vocal rhythms also have their own mechanistic and communicative value (Wirthlin et al., 2019). I argue that, across species, these five capacities are linked, mapping them to Savage et al.'s framework.
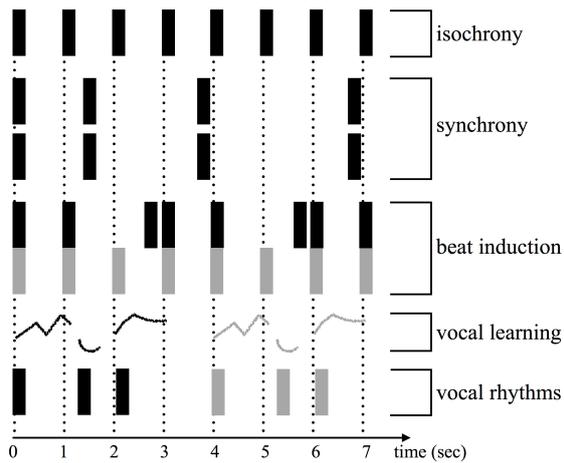
Figure 1. Conceptualization of the four abilities partly explored in the target articles plus a fifth one, vocal rhythms, which deserves entering the discussion. Isochrony, when present in acoustic or motoric behaviors, may provide a clear, extremely predictable temporal grid, similar to squared notebooks guiding children who learn how to write. An isochronous pattern is, per se, neither musical nor demanding to produce or perceive. Isochrony has low entropy, definitely lower than expected for 'musical' patterns (Milne & Herff, 2020; Ravignani & Madison, 2017). Production of isochrony can result from a motoric behavior entraining to a neural oscillator. Perception of isochrony requires, at least, comparing pairs of temporal intervals, an ability found in several species (e.g. Church & Lacourse, 1998; Heinrich et al., 2020; Ng et al., 2020). While isochrony is characterized by equal timing in a series of events, synchrony requires pairwise coincidence of events from two series, neither of which needs to be isochronous (Ravignani, 2017). Given an acoustic sequence (black), beat induction consists in inferring an isochronous pulse (grey), which need not physically exist in the sequence (Kotz et al., 2018; Honing, 2012). Synchronization differs from beat induction in being independent from isochrony, relatively inflexible, achievable for a narrow range of tempi and unimodal (Patel et al., 2009). Vocal learning - here with emphasis in its spectral domain - includes, among other things, the capacity to copy (grey) a vocal signal (black)(Lattenkamp & Vernes, 2018; Wirthlin et al., 2019). A vocal rhythm (black) is a temporal pattern of events, which conveys most information in the temporal domain (Ravignani et al., 2019) and could also be learnt or imitated (grey).

The core of Savage et al.'s idea of melodic and rhythmic musicality features vocal learning and beat induction. These are also at the core of an influential hypothesis in evolutionary neuroscience (Patel, 2006), predicting in some cases their joint co-occurrence across species. However, a few outlier species point to a mismatch between the current data and the hypothesis' predictions (Cook et al., 2013), requiring an updated theoretical framework.

Within Savage et al.'s framework, I argue that rhythm and melody may have bootstrapped each other in humans and other species gradually, especially in social interactions, such as chorusing, turn-taking, etc. (Christophe et al., 2008; Hannon & Johnson, 2005; Höhle, 2009; Ravignani et al., 2014). An isochronous sequence, such as the repetitive bark of a sea lion, provides a temporal grid of predictable sound events. Both the producer of an isochronous rhythm and its conspecifics can rely on this periodicity to learn and experiment in the spectral, hence melodic, domain during vocal learning: vocal emissions could be anchored to the onsets of the isochronous sequence. Hence, rhythmic isochrony may function as temporal grid to rehearse learnt vocalizations (and possibly orient attention; Bolger et al., 2014; Cason et al., 2015; Jones, 2010; Norton, 2019). In turn, learnt, consolidated vocalizations may serve as a 'spectral anchor' to segment conspecifics' temporal sequences (Hyland Bruno, 2017; Lipkind et al., 2013), also generating vocal rhythms. Therefore, melodic templates acquired via vocal learning can afford increased attentional or cognitive resources spent on the rhythmic domain, including temporal segmentation and regularization. This provides a bootstrapping mechanism for Savage et al.'s co-evolutionary dynamics to work, and a test bench for some signaling hypotheses in Mehr and colleagues.

This hypothesis generates several testable predictions. First, by testing species along the vocal learning continuum (Martins & Boeckx, 2020), and extending this continuum to beat induction, species with a stronger sense of beat should be found among those with more developed vocal learning capacities. Chickens, great apes, parrots and humans are examples of

species predicted to show, in this order, increasing abilities in both domains. Second, isochrony should go hand in hand with synchrony but not with beat induction, so that species with developed isochrony should also synchronize. Third, empirical evidence for the rhythm-melody scaffolding process (Cason et al., 2012; Emmendorfer et al., 2020) could be obtained from large-scale developmental datasets, which should feature both humans and non-human animals, and contain data from as many capacities as possible from Figure 1. As ontogeny sometimes recapitulates phylogeny (e.g. Heldstab et al., 2020), one would test whether the same stepwise processes hypothesized above appear in the first years of human life (Höhle, 2009). Fourth, a partial neural dissociation between rhythm and melody may occur early in life and become less severe over development; the dynamics of this dissociation could be tested via longitudinal neuroimaging studies (Bengtsson & Ullén, 2006; Salami et al., 2016). Fifth, within Savage et al.'s framework, physiological evidence for the rhythm-melody gradual interplay could come from measurements or manipulations of the dopaminergic reward system and the endogenous opioid system, testing whether they provide complementary, alternating effects. Finally, most of these putative links can be, following Savage et al., modulated by species-specific social factors, such us group density and social networks. Likewise, their value as honest signals can be tested to provide empirical support for Mehr et al. using, among others, methods from cultural evolution research (e.g. Miton et al., 2020; Lumaca et al., this issue).

To conclude, the frameworks proposed in both target articles can benefit from a finer dissection of core abilities for musicality (Figure 1 and Honing, this issue). These must then be tested across species to infer plausible evolutionary scenarios.

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