Spectral Percepts: Cognition, Biology and the Origins of Musicality

What are the core spectral percepts of musicality? This workshop aims to clarify the role of spectral percepts—including pitch, timbre, and consonance—in the evolution of musicality and will be organized at the Lorentz center in Leiden, The Netherlands in April 2026.

Co-Organizers
Prof. Dr. Henkjan Honing, University of Amsterdam, NL
Dr. Bas Cornelissen, University of Amsterdam, NL
Prof. Dr. W. Tecumseh Fitch, University of Vienna, AT
Prof. Dr. Laurel J. Trainor, McMaster University, CA
Prof. Dr. Robert J. Zatorre, McGill University, CA

The scientific program of this meeting will be coordinated by the co-organizers. The Lorentz Center will handle all logistical arrangements, including travel and accommodation (log-in w/ password).

Date and venue
20–24 April 2026 at @lambda, Lorentz Center, Leiden, The Netherlands.

Contents

Abstract

In The Descent of Man (1871), Charles Darwin famously speculated that "the perception, if not the enjoyment, of musical cadences and of rhythm is probably common to all animals and no doubt depends on the common physiological nature of their nervous systems" — a "taste for the beautiful" he explained by sexual selection. Recent years have seen a development of alternative explanations, but most share his view that music has biological roots. With this statement, Darwin anticipated key elements of today's perspectives on musicality: the perception of rhythm and melody (cadence), their neural mechanisms and evolutionary origins — and indeed the pleasure they evoke.

Rhythm cognition has received increasing attention over the past decade, with major advances in comparative studies, developmental research, and neural modeling (Greenfield et al., 2021). In contrast, other dimensions of musicality—particularly timbre and pitch—have yet to be fully integrated into a theory of musicality. While comparative research in melodic and harmonic perception has a long history, it has often relied on simplified stimuli and assumptions that may fail to capture the full range of animals' perceptual abilities. Additionally, recent studies suggest that perceptual categories like pitch and timbre do not map cleanly across species, calling for a re-evaluation of the relevant 'spectral percepts'.

The proposed workshop aims to clarify the role of spectral percepts—including pitch, timbre, and consonance—in the evolution of musicality. Building on insights from neurobiology, psychology, (ethno)musicology, and evolutionary biology, it seeks to characterize these percepts and explore their variation across species and cultures. Taking a broadly Tinbergian perspective, the workshop will integrate questions of mechanism, ontogeny, phylogeny, function (Tinbergen, 1963), and cultural evolution (Fitch, 2018)—to include topics such as scale systems and tonality. A secondary emphasis will be placed on pleasure (reward and enjoyment), both as a potential driver of musical evolution and its role in the neural underpinnings of melody and harmony perception.

This intensive, small-scale workshop will consider empirical and theoretical work from leading researchers, such as Zatorre, Trainor, Patel, McDermott, and others (McDermott et al., 2016; Patel, 2017; Trainor & Unrau, 2012; Zatorre, 2024). Unlike prior meetings on musicality—including those held at the Lorentz Center (Greenfield et al., 2021; Honing et al., 2015)—this workshop deliberately shifts focus away from rhythm and production, toward the perceptual and affective dimensions of melody, harmony and timbre. Complementing recent advances in rhythmic cognition, it revisits Darwin's assumption that animals not only perceive melodies but also take pleasure in them.

Goals

The workshop aims to realize the following goals:

- Foster new interdisciplinary research on how timbre, pitch, and reward/pleasure mechanisms might have shaped the evolution of musicality.
- Pinpoint and prioritize outstanding controversies that merit deeper investigation, paving the way for a dedicated special issue currently being discussed with Philosophical Transactions of the Royal Society B.
- Draft a collaborative research agenda—grounded in cross-species and cross-cultural research—that, following Tinbergen (1963; cf. Fitch, 2018), integrates work on the mechanism, ontogeny, phylogeny, function and cultural evolution of musicality
- Identify additional initiatives and publication opportunities that advance the broader research agenda on the Origins of Musicality.

Scientific case

What are the core spectral percepts of musicality?

Despite significant progress in music cognition research (Margulis, 2019; Rentfrow & Levitin, 2019), the cognitive basis of our capacity for music remains poorly understood. A productive strategy has been to decompose this capacity into its constituent components (Fitch, 2018; ten Cate & Honing, 2025). Two strong candidates have emerged: relative pitch, the ability to recognize a musical interval or melody regardless of its exact pitch or tempo, and beat perception, the ability to extract a regular beat from a varying rhythm. Both capacities are widespread in humans, already observed in infancy (Háden et al., 2024; Trehub et al., 2019) and appear to be foundational to perceiving, making and enjoying music (Honing, 2021a).

To match recent progress in rhythmic cognition, this workshop shifts attention to melodic cognition. The central question (cf. Patel, 2017) is simple but elusive: what makes two melodies similar (i.e., perceptually invariant) across cultures and across species? Focusing on melodic and timbral aspects, what are the core spectral percepts of musicality? What roles do relative pitch, absolute pitch, spectral shape, or contour play? How central are consonance and tonality, topics of ongoing debate (Mehr et al., 2019; Zatorre, 2016)? And what about timbre, a dimension whose role in melodic perception may well be underestimated?

At the most basic level, periodicity in sound, the acoustic correlate of pitch, is neurally encoded in many species, independently of its use as a communication signal. For example, marmosets possess neurons sensitive to pitch (Bendor & Wang, 2005), located in a region of auditory cortex, similar to that in humans. Likewise, the frequency-following response, an evoked electrical potential which represents the fundamental frequency of a periodic sound, is found in subcortical and cortical areas of various species. But encoding frequency is only the first step in building musical structures — and this is where the current debate lies.

In particular, there is no consensus on the melodic representations that humans — let alone non-human animals — use to recognize melodies. Obvious candidates include the intervallic structure of the melody (e.g., the sequence of musical intervals) and the melodic contour (i.e., the overall direction of movement, cf. Dowling 1978). However, at least one perceptual study (McDermott et al., 2008) has shown that timbral contours such as loudness and brightness contours are nearly as useful as pitch contours for recognizing familiar melodies. Other species may rely on altogether different cues, such as spectral shape (Bregman et al., 2016). And since most classic studies have relied on pure tones or synthetic sounds with no timbral variation (Dowling, 1978; Schellenberg & Trehub, 1994), the spectral percepts most salient for other species, may simply have gone unnoticed.

Indeed, timbre has often been considered secondary in music research (McAdams & Siedenburg, 2019). Timbre will receive special attention in this workshop, as timbral perception may hide more flexible 'relative listening' than previously thought. Moreover, it is primarily in the timbral domain that one may expect other species to rely on aspects of the musical signal that are not yet understood (Hoeschele, 2017; ten Cate & Honing, 2025; Wagner & Hoeschele, 2022). Allowing the possibility of fundamentally different spectral percepts — from spatial hearing in bats to extremely fast temporal processing in zebra finches — will be crucial for understanding the evolution of the spectral percepts that underly music in our own species.

Synthesis

We aim to develop a cognitively and biologically informed theory of the origins of the spectral percepts that underlie musicality. Achieving such a broad synthesis requires integrating implications of both existing and novel findings across a range of disciplines including neurobiology, psychology, (ethno)musicology, and evolutionary biology. Central to this effort is the inclusion of findings from other taxa that have become key models in the biological study of musicality—most notably primates, pinnipeds, and birds. Cross-species comparisons can reveal which aspects of musicality are unique to humans (or to other species), which are shared, and how these capacities may have evolved (Honing, 2021b).

The broad synthesis we envision will address questions like: How widespread (evolutionary ancient) is the use of pitch to recognize tone sequences? Is spectral contour an evolutionary older, more stable alternative? Why do humans gravitate to pitch for melody recognition? Is using pitch to recognize melodies in part a cultural phenomenon? Which aspects of melodic perception are shared across species and what is the link to other aspects of their cognition (such as vocal learning)? In the end, we aim to address the questions: How can the constituent components of musicality best be combined in a cognitive and biologically informed theory? And how does this theory further constrain evolutionary theories of musicality?

Controversies

To clarify the spectral percepts that underlie human musicality, this workshop will address some of the key controversies surrounding the perception of pitch and timbre. Most disagreements center on (1) the role of learning, (2) the influence of culture, (3) cross-species comparisons, and (4) possible evolutionary scenarios. Below, we highlight several controversies that exemplify these broader issues and frame the workshop's agenda.

Following these discussions, the workshop explores current debates related to musical pleasure, enjoyment, and reward, addressing how aesthetic and affective responses to music may differ across individuals, species, and contexts.

Pitch versus timbre perception

Pitch is a percept. So is timbre. Both have been studied extensively in humans, birds and some other taxa. In human music, melodic sequences typically consist of complex harmonic tones—sounds containing a fundamental frequency and harmonics that are integer multiples of it.

While melodies can vary in timbre, duration, and loudness, humans predominantly rely on pitch patterns to recognize melodies, perceiving sequences with identical pitch contours as the "same melody" despite differences in timbre. This reflects a core feature of human music cognition named relative pitch. But is this reliance on pitch a uniquely human trait, or a broader feature of auditory processing? It has long been assumed that, like humans, songbirds use pitch (typically absolute pitch) for recognizing tone sequences.

Yet, recent findings challenge this assumption. Bregman et al. (2016) showed that European starlings do not rely on pitch to identify sequences of complex harmonic tones (cf. Patel, 2017). Instead, they appear to use spectral shape (or spectral envelope) as the primary cue. However, the signal processing technique central to that study (contour-preserving noise vocoding) also allows for alternative interpretations: neither pitch, nor spectral envelope, but fine spectral temporal modulation (i.e. spectral contour) being what songbirds attend to.

Consonance controversy

Why certain tone combinations sound 'consonant', while others sound 'dissonant', is one of the oldest problems in the natural sciences. Even seemingly innocent characterizations of the phenomenon — is a consonance pleasant? — spark controversy, yet the significance of consonance and dissonance is evident both in the cross-cultural use of consonant intervals in musical scales and in the expressive use of dissonance in specific traditions. Dissonance should be distinguished from roughness, a more physiological phenomenon related to interactions within the basilar membrane. Recent research suggests that consonance is a complex cognitive construct influenced by both acoustic properties such as roughness and harmonicity and cultural familiarity (e.g. Lahdelma & Eerola, 2020).

However, a twofold controversy remains (Harrison, 2021): (1) whether humans have an inherent preference for consonance over dissonance, and (2) if so, how such a preference can be accounted for in evolutionary terms. McDermott et al. (2016) challenged the idea of universal consonance preference in a study of the Tsimane', an indigenous Amazonian group with minimal exposure to Western music. They found no evidence of a preference for consonant over dissonant intervals (even if roughness was unpleasant) and argued that such preferences are shaped primarily by cultural experience. This conclusion was contested by Bowling et al. (2017) who pointed to evidence from non-human animals (Chiandetti & Vallortigara, 2011) and human infants (Trainor et al., 2002), suggesting that consonance perception is not solely dependent on cultural learning.

Melodic organization: scales and tonality

Much recent work on the origins of musicality has focused on foundational components. A critical next step is to also account for higher-level aspects of music, such as musical scales. Across cultures, scales exhibit striking regularities that may reflect cognitive constraints. For instance, the use of unequal step sizes (non-equidistance) has been suggested to provide processing benefits (Pelofi & Farbood, 2021). Much of the discussion focusses on explaining the actual pitches. Many scales contain pitch classes that overlap with the overtone series (i.e., pitches related by simple integer ratios), a phenomenon also observed in the song of the hermit-thrush (cf. ten Cate & Honing, 2025). Theories explaining scale structure differ widely: some stress alignment with the overtone series (Gill & Purves, 2009), others point to interactions of both pitch and timbral perception (Marjieh et al., 2024) or constraints on vocal production (Vernes et al., 2021).

More controversial yet is the question of tonality. The term has a specific meaning in Western common-practice harmony, but more broadly refers to the perception of certain pitches being more stable than others. This perceptual hierarchy was first studied using a probe tone paradigm, where listeners rate the stability of a probe tone relative to a melodic context (Krumhansl & Shepard, 1979). While some suggest that tonal hierarchies appear cross-culturally (Mehr et al., 2019), others argue this is a culture-specific phenomenon. Closely related, but less explored, is the question of modality, a term to describe forms of melodic organization in traditions from Turkish maqam to Indian raga and how these may relate to the learning of sequential patterns in music through processes like statistical learning.

Pleasure: its mechanism and function

Darwin spoke of the "enjoyment" of melodies in the context of sexual selection. Could certain melodic patterns—say, in a songbird—signal desirable biological qualities? And if so, might pleasure underpin that "taste for the beautiful"? It has, in any case, become clear that music can induce pleasure in humans. Across species, reward is encoded using reward prediction errors: it is the difference between the expected and obtained reward value that modules activity in reward-related regions such as the striatum using a mechanism mediated by dopamine. Music engages with this reward system, but does so via interactions with sensory, cognitive and mnemonic processes that may not have direct counterparts in other species. This points a key comparative question: to what extent do the function and connectivity (i.e., inputs and outputs) of the reward system vary across species, especially in relation to music-induced reward?

These considerations bear on a long-standing evolutionary debate: is music-induced pleasure an adaptive trait with functional significance, or merely an evolutionary byproduct (Mehr et al., 2020; Savage et al., 2021)? Curiously, neurobiological evidence, including work by Zatorre and others, has been interpreted in support of both views. Another further challenge is how to quantify pleasure across species. Current methods range from counting aesthetic chills and collecting self-report ratings to measuring physiological responses or neuroimaging markers (Zatorre & Salimpoor, 2013). Yet each approach has limitations: chills are culturally variable and, it seems, infrequent; BOLD responses reflect vascular rather than purely neural activity, and no universally accepted metric for pleasure currently exists. These and related controversies underscore the need for methodological innovation, integrative frameworks and critical interdisciplinary dialogue — precisely what this workshop aims to facilitate.

Credits

Henkjan Honing and Bas Cornelissen wrote the initial draft and final version of this proposal; Tecumseh Fitch, Laurel Trainor, Robert Zatorre, Carel ten Cate and Ani Patel commented on and contributed to earlier drafts.

References

Bendor, D. & Wang, X. Q. (2005). The neuronal representation of pitch in primate auditory cortex.Nature, 436(7054), 1161–1165.

Bowling, D. L., Hoeschele, M., Gill, K. Z. & Fitch, W. T. (2017). The nature and nurture of musical consonance. Music Perception, 335(1), 118–121.

Bregman, M. R., Patel, A. D. & Gentner, T. Q. (2016). Songbirds use spectral shape, not pitch, for sound pattern recognition. Proceedings of the National Academy of Sciences, 113(6), 1666–1671. https://doi.org/10.1073/pnas.1515380113

Chiandetti, C. & Vallortigara, G. (2011). Chicks like consonant music. Psychological Science, 22(10), 1270–1273. https://doi.org/10.1177/0956797611418244

Darwin, C. (1871). The descent of man, and selection in relation to sex. John Murray.

Dowling, W. J. (1978). Scale and contour: Two components of a theory of memory for melodies. Psychological Review, 85, 341–354.

Fitch, W. T. (2018). Four Principles of Biomusicology. In H. Honing (Ed.), The Origins of Musicality (pp. 23–48). MIT Press.

Gill, K. K. Z. & Purves, D. (2009). A biological rationale for musical scales. PLoS ONE, 4(12), e8144. https://doi.org/10.1371/journal.pone.0008144

Greenfield, M. D., Honing, H., Kotz, S. A. & Ravignani, A. (2021). Synchrony and rhythm interaction: From the brain to behavioural ecology. In Philosophical Transactions of the Royal Society B: Biological Sciences (Vol. 376, Issue 1835). Royal Society Publishing. https://doi.org/10.1098/rstb.2020.0324

Háden, G. P., Bouwer, F. L., Honing, H. & Winkler, I. (2024). Beat processing in newborn infants cannot be explained by statistical learning based on transition probabilities. Cognition, 243. https://doi.org/10.1016/j.cognition.2023.105670

Harrison, P. M. C. (2021). Three Questions concerning Consonance Perception. In Music Perception (Vol. 38, Issue 3, pp. 337–339). University of California Press. https://doi.org/10.1525/MP.2021.38.3.337

Hoeschele, M. (2017). Animal Pitch Perception: Melodies and Harmonies. Comparative Cognition and Behavior Reviews, 12(1), 5–18. https://doi.org/10.3819/CCBR.2017.120002

Honing, H. (2021a). Music Cognition : The Basics. Routledge.

Honing, H. (2021b). Unravelling the origins of musicality: Beyond music as an epiphenomenon of language. Behavioral and Brain Sciences, 44(E78), 66–69. https://doi.org/10.1017/S0140525X20001211

Honing, H., ten Cate, C., Peretz, I. & Trehub, S. E. (2015). Without it no music: Cognition, biology and evolution of musicality. In Philosophical Transactions of the Royal Society B: Biological Sciences (Vol. 370, Issue 1664). Royal Society of London. https://doi.org/10.1098/rstb.2014.0088

Krumhansl, C. L. & Shepard, R. N. (1979). Quantification of the Hierarchy of Tonal Functions Within a Diatonic Context. In Journal of Experimental Psychology: Human Perception and Performance: Vol. S (Issue 4).

Lahdelma, I. & Eerola, T. (2020). Cultural familiarity and musical expertise impact the pleasantness of consonance/dissonance but not its perceived tension. Scientific Reports, 10(1), 8693. https://doi.org/10.1038/s41598-020-65615-8

Margulis, E. H. (2019). The Psychology of Music: A Very Short Introduction. Oxford University Press.

Marjieh, R., Harrison, P. M. C., Lee, H., Deligiannaki, F. & Jacoby, N. (2024). Timbral effects on consonance disentangle psychoacoustic mechanisms and suggest perceptual origins for musical scales. Nature Communications, 15(1). https://doi.org/10.1038/s41467-024-45812-z

McAdams, S. & Siedenburg, K. (2019). Perception and cognition of musical timbre. In P. Rentfrow & D.J. Levitin (Eds.), Foundations of Music Psychology: Theory and Research (pp. 71–120). MIT Press. https://www.mcgill.ca/mpcl/files/mpcl/mcadams_2019_foundmuspsychol.pdf

McDermott, J. H., Lehr, A. J. & Oxenham, A. J. (2008). Is relative pitch specific to pitch? Psychological Science, 19(12), 1263–1271.

McDermott, J. H., Schultz, A. F., Undurraga, E. A. & Godoy, R. A. (2016). Indifference to dissonance in native Amazonians reveals cultural variation in music perception. Nature, 25, 21–25. https://doi.org/10.1038/nature18635

Mehr, S. A., Singh, M., Knox, D., Ketter, D. M., Pickens-Jones, D., Atwood, S., Lucas, C., Jacoby, N., Egner, A. A., Hopkins, E. J., Howard, R. M., Hartshorne, J. K., Jennings, M. V, Simson, J., Bainbridge, C. M., Pinker, S., O, T. J., Krasnow, M. M. & Glowacki, L. (2019). Universality and diversity in human song. Science, 366(November), 1–17. https://doi.org/10.1126/science.aax0868

Niarchou, M., Gustavson, D. E., Sathirapongsasuti, J. F., Anglada-Tort, M., Eising, E., Bell, E., McArthur, E., Straub, P., Aslibekyan, S., Auton, A., Bell, R. K., Bryc, K., Clark, S. K., Elson, S. L., Fletez-Brant, K., Fontanillas, P., Furlotte, N. A., Gandhi, P. M., Heilbron, K., … Gordon, R. L. (2022). Genome- wide association study of musical beat synchronization demonstrates high polygenicity. Nature Human Behaviour. https://doi.org/10.1038/s41562-022-01359-x

Patel, A. D. (2017). Why Doesn't a Songbird (the European Starling) Use Pitch to Recognize Tone Sequences? The Informational Independence Hypothesis. Comparative Cognition & Behavior Reviews, 12, 19–32. https://doi.org/10.3819/CCBR.2017.120003

Pelofi, C. & Farbood, M. M. (2021). Asymmetry in scales enhances learning of new musical structures. Proceedings of the National Academy of Sciences of the United States of America, 118(31). https://doi.org/10.1073/pnas.2014725118

Rentfrow, P. J. & Levitin, D. J. (Eds.). (2019). Foundations in Music Psychology: Theory and Research. The MIT Press.

Schellenberg, E. G. & Trehub, S. E. (1994). Frequency ratios and the discrimination of pure tone sequences. Perception & Psychophysics, 56(4), 472–478. http://www.ncbi.nlm.nih.gov/pubmed/7984402

ten Cate, C. & Honing, H. (2025). Precursors of music and language in animals. In D. Sammler (Ed.), The Oxford Handbook of Language and Music. Oxford University Press. https://doi.org/10.1093/oxfordhb/9780192894700.001.0001

Tinbergen, N. (1963). On aims and methods of ethology. Zeitschrift Für Tierpsychologie, 410–433. http://onlinelibrary.wiley.com/doi/10.1111/j.1439-0310.1963.tb01161.x/abstract

Trainor, L. J., Tsang, C. D. & Cheung, V. H. W. (2002). Preference for Sensory Consonance in 2- and 4- Month-Old Infants. Music Perception, 20(2), 187–194. https://doi.org/10.1525/mp.2002.20.2.187

Trainor, L. J. & Unrau, A. (2012). Development of Pitch and Music Perception. In Human Auditory Development (pp. 223–254). Springer. https://doi.org/10.1007/978-1-4614-1421-6_8

Trehub, S. E., Weiss, M. W. & Cirelli, L. K. (2019). Musicality across the lifespan. In P. J. Rentfrow & D. J. Levitin (Eds.), Foundations in Music Psychology: Theory and Research (pp. 265–303). The MIT Press.

Vernes, S. C., Kriengwatana, B. P., Beeck, V. C., Fischer, J., Tyack, P. L., ten Cate, C. & Janik, V. M. (2021). The multi-dimensional nature of vocal learning. In Philosophical Transactions of the Royal Society B: Biological Sciences (Vol. 376, pp. 1–15). https://doi.org/10.1098/rstb.2020.0236

Wagner, B. & Hoeschele, M. (2022). The Links Between Pitch, Timbre, Musicality, and Social Bonding From Cross-Species Research. Comparative Cognition and Behavior Reviews, 17, 13–32. https://doi.org/10.3819/CCBR.2022.170002

Zatorre, R. J. (2016). Amazon Music. Nature, 535, 496–497.

Zatorre, R. J. (2024). From perception to pleasure: The neuroscience of music and why we love it. Oxford University Press.