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Perspective

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Musical neurodynamics

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Abstract

A great deal of research in the neuroscience of music suggests that neural oscillations synchronize with musical stimuli. Although neural synchronization is a well-studied mechanism underpinning expectation, it has even more far-reaching implications for music. In this Perspective, we survey the literature on the neuroscience of music, including pitch, harmony, melody, tonality, rhythm, metre, groove and affect. We describe how fundamental dynamical principles based on known neural mechanisms can explain basic aspects of music perception and performance, as summarized in neural resonance theory. Building on principles such as resonance, stability, attunement and strong anticipation, we propose that people anticipate musical events not through predictive neural models, but because brain–body dynamics physically embody musical structure. The interaction of certain kinds of sounds with ongoing pattern-forming dynamics results in patterns of perception, action and coordination that we collectively experience as music. Statistically universal structures may have arisen in music because they correspond to stable states of complex, pattern-forming dynamical systems. This analysis of empirical findings from the perspective of neurodynamic principles sheds new light on the neuroscience of music and what makes music powerful.

Sections

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Introduction

Successions of tones are motions ... in respect to an order based on forces in tones... Musical tones point to one another, attract and are attracted ... The dynamical quality of musical tones makes melodies out of successions of tones, and music out of acoustical phenomena.
– V. Zuckerkandl[1]

Music has the power to evoke strong emotions, to inspire feelings of awe, and to create a profound sense of connection with others across cultures, borders and belief systems. Such observations have inspired systematic searches for 'universals' of musical structure and behaviour around the world[2,3]. For example, much music features a pulse that enables listeners and participants to synchronize rhythmic behaviour such as dancing at slower timescales, and pitches organized in a tonal system that are sung or played with musical instruments at faster timescales (Fig. 1). Yet despite such commonly observed features, ethnographic studies reveal profound rhythmic and tonal differences between cultures, emphasizing that learning and enculturation are important determinants of musical experience. These sorts of contrasting observations motivate the more fundamental question: how do humans, consistently across cultures, experience music as more than a sequence of isolated sounds?

Cognitive neuroscience has reached a consensus approach to this question that focuses on listeners' expectations about musical patterns. Embodied musical experiences, including felt physical experiences of groove and affective responses of chills, depend upon expectancies about what will happen next and when[4–6]. But where do such expectancies come from? This Perspective describes how both musical expectancy and musical structure depend on the dynamics of fundamental neural mechanisms, formulated in neural resonance theory (NRT). In NRT, expectations are the consequences of physiological oscillations that synchronize with music (Fig. 1) and resonate with one another to create stable patterns. NRT asserts that music cognition is the actual embodiment of these resonance relationships, physical states of the brain that have lawful relationships to external events (for example, sounds) that are determined by physical principles. Crucially, these physical principles generate predictions at both the neural and behavioural levels that can be tested empirically.

The following sections provide an overview of music based on the dynamics of fundamental neural mechanisms. First, the central principles of the NRT model are contextualized within earlier embodied and dynamic approaches. Subsequently, the main body of the paper focuses on core structures in musical perception, action and cognition, first at the slower timescales of rhythm and temporal structure, and then at the faster timescales of pitch and tonal structure. NRT analyses suggest that similar mechanisms are at play at both timescales, that these mechanisms create constraints on pattern learnability and that the relative prevalence of musical structures may be explained by the relative stability of embodied dynamic patterns. At a few key points, we highlight differences between NRT and the recent predictive coding of music (PCM) approach[7]. Finally, we speculate about future research lines to expand the dynamical neuroscience approach, and directly compare NRT with other current approaches such as PCM and statistical learning theories.

NRT

The study of neuronal oscillations is not new. However, in recent years, it has become an extremely productive area of neuroscientific enquiry that has established links between cellular function, network dynamics, perception–cognition and overt behaviour[8,9]. Nonlinear dynamics provides a theoretical language to integrate information from neural and behavioural levels based on a set of dynamical primitives obeying general laws and constraints, providing novel predictions and testable hypotheses[10]. NRT focuses on canonical models, which capture common dynamical properties of a family of neural models[11–13]. Under certain assumptions, a rigorous canonical model can be derived even if the anatomy and physiology of the neural circuits are only partially known. Thus, NRT generates robust, formal hypotheses about the neuroscience of music using sometimes only general information about neurophysiology and behaviour. Building on previous embodied and dynamical systems approaches[11,14–17], NRT combines physical principles that govern music cognition: neural oscillation, nonlinear resonance, stability and attraction, attunement and strong anticipation. These principles, along with advances in mathematical models[12,18,19], are described below.

In NRT, neural resonance refers broadly to the synchronization, or entrainment, of neural oscillations with themselves and with external stimuli[20]. The term oscillation includes any dynamical system with a well-defined frequency; thus it includes dynamical systems that display self-sustained oscillations (stable limit cycles), damped oscillations (stable fixed points) and systems that display both (bistable systems)[21].

An important property of neural resonance is that it is nonlinear. Unlike their linear counterparts (Fig. 2a), nonlinearities enable neural oscillators to generate frequencies that are not present in the input, but are related to frequencies in the input (Fig. 2b). Nonlinear resonance is observed biologically, in critical oscillations of cochlear outer hair cells[22], auditory brainstem neurons[23], nonlinear responses to tones[23], and entrainment of cortical auditory and motor populations to rhythmic sequences[24,25]. One important type of nonlinear resonance is mode-locking (n:m synchronization). Two neural oscillations with different natural frequencies can mode-lock when the frequencies are near an integer ratio. Stability increases with the simplicity of the frequency ratio and the strength of the coupling[18] (Fig. 3).

Mode-locking is an example of a stability and attraction relationship that is important for explaining musical structure. Dynamical systems in less stable states are attracted to and gravitate towards more stable states[26]. NRT asserts that stability of neural resonances leads to perception of musical structure, and musical expectancy is the feeling of a less stable state being attracted towards a more stable one. NRT suggests that stability also constrains music performance. For example, bimanual coordination during drumming is harder when left- and right-hand frequencies create a complex rather than a simple rhythm[27].

Attunement in NRT is the process whereby resonating neural circuits can tune themselves, adapting and learning through interacting with the environment[14]. Attunement unfolds over multiple timescales, increasing the stability of patterns that are experienced more often, so the system responds more quickly and flexibly[28]. Attunement occurs via two primary mechanisms: Hebbian learning via synaptic plasticity[19] (Fig. 2c) and adaptation of individual oscillator parameters, such as natural frequency[29]. Attunement processes[30] continuously learn and adapt in an unsupervised manner, to form neural circuits that embody learned musical patterns. As reviewed below, NRT models use attunement to explain developmental processes as well as the effect of enculturation and training on musical behaviour.

Strong anticipation[31] explains how the production of a 'response' can occur before the 'stimulus'[32–34], which happens naturally during music performance between musicians[35]. The tendency to anticipate is often interpreted as evidence of temporal prediction based on an internal model[7,36]. From the dynamical systems perspective, time delays reflect the system's memory of an earlier state, which in turn can cause a driven system to anticipate its driver[37] (Fig. 2d). For example, a driven oscillatory system with a time delay may be ahead of the driver system[35,38], as when finger taps precede metronome sounds during synchronization[39]. Thus, in NRT, anticipation can arise from neural transmission delays inherent in the system.

On the basis of the dynamical properties of fundamental neural mechanisms, NRT provides a unified framework that can address both natural constraints and cultural variations in music perception, cognition and performance. In contrast to their linear counterparts, nonlinear dynamical systems feature pattern-forming properties, found in many different types of oscillation, which can account for both rhythmic and tonal structure, two widely separated timescales. The tools of dynamical systems allow us to identify and study generic properties of oscillatory dynamics, Hebbian plasticity and neural time delays, which are found in cortical and subcortical circuits. The following section addresses earlier work on expectation, coordination and anticipation that informed NRT.

Foundational work

Dynamic attending theory was an early approach that linked neural oscillations with temporal expectancy, providing a conceptual framework and a set of dynamical models[16,40]. It proposed that neural oscillations synchronize with the temporal structure of the sensory environment – in music, speech and other time-varying events – to direct attention to highly expected points in time[16] (Fig. 4a). Evidence has shown that both acoustic and visual stimuli are better perceived when they occur at an expected, rhythmic position[25,41–44], and targets at expected temporal locations elicit larger attention-dependent event-related potential responses[45]. Evidence from electroencephalography (EEG) and magnetoencephalography (MEG) studies shows that the phase of neural oscillations predicts the perception of rhythmic stimuli[46] and steady-state evoked potentials (SS-EPs) suggest that delta and theta neural rhythms synchronize to environmental rhythms[47–52]. Moreover, fluctuations in beta and gamma amplitudes align to rhythmic environmental stimuli[24,53], owing to phase–amplitude coupling of slower delta and theta rhythms with beta and gamma. Broad-spectrum phase–amplitude coupling may be attributed to mode-locking in harmonic ratios[54]. Thus, oscillations appear to be fundamental building blocks of attentional processes.

Auditory and motor synchronization have both been successfully described in terms of coupled oscillation[15,55,56], and the motor system facilitates the generation of temporal expectancies, especially in music with a strong beat[57–59]. Thus, the study of motor coordination is also relevant to temporal expectation[60,61]. The coordination dynamics approach has combined theory, experiment and dynamical modelling to describe motor coordination, auditory–motor coordination and social coordination, among others. It has demonstrated, for example, that in-phase and antiphase coordination between two fingers are stable at a slow frequency (bistability), but that an increase in frequency (the control parameter) drives the system through a bifurcation in which the antiphase mode loses stability[15]. Similarly, antiphase synchronization with a metronome is possible at slower tempos, but as the tempo increases, even trained musicians exhibit a decrease in the stability of antiphase synchronization or naturally transition to in-phase coordination[62].

The tools of coordination dynamics have also been used to study polyrhythmic motor coordination and auditory–motor

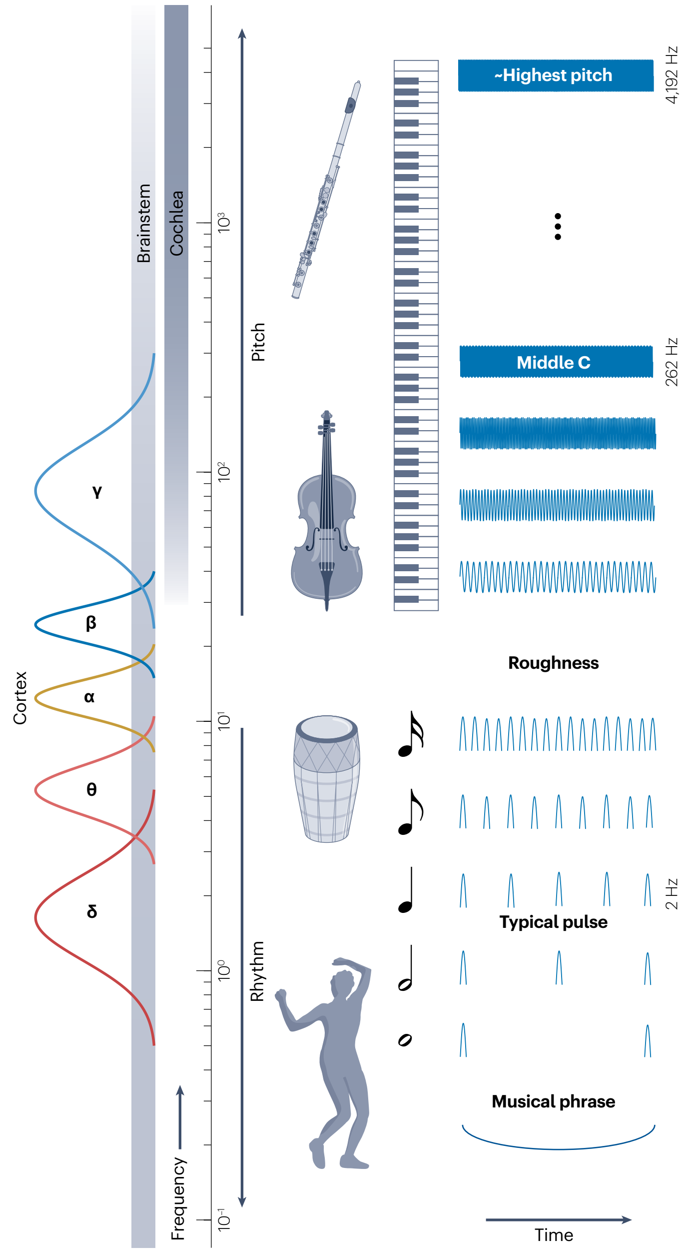

Fig. 1 | Timescales of neural oscillations and music. Neural oscillations synchronize with musical events across multiple timescales. For example, at slower timescales musical rhythms are made up of periodic events that can be as slow as fractions of 1 Hz, where movement coordination happens during dancing, and as fast as 10–12 Hz, such as found in a fast drumbeat. Correspondingly in the cortex, delta (~0.5–4 Hz) and theta (~4–8 Hz) frequency bands phase-lock to rhythmic frequencies, and bursts of alpha (~8–12 Hz), beta (~13–30 Hz) and gamma (>30 Hz) frequencies also lock to rhythmic stimulation by modulating oscillation power in time (phase–amplitude coupling). At faster timescales, musical pitches correspond to periodic waveforms, which consist of a fundamental frequency, measured in Hertz, and a set of additional frequencies called overtones (or harmonics). The corresponding brain and physiology is such that the cochlea resonates nonlinearly to frequencies from about 30 Hz up to about 20,000 Hz. The auditory nerve and brainstem phase- and mode-lock up to about 4,000 Hz, the upper limit of pitch perception. Frequencies falling between the ranges of rhythm and pitch perception are perceived as roughness (for example, buzzing sounds).

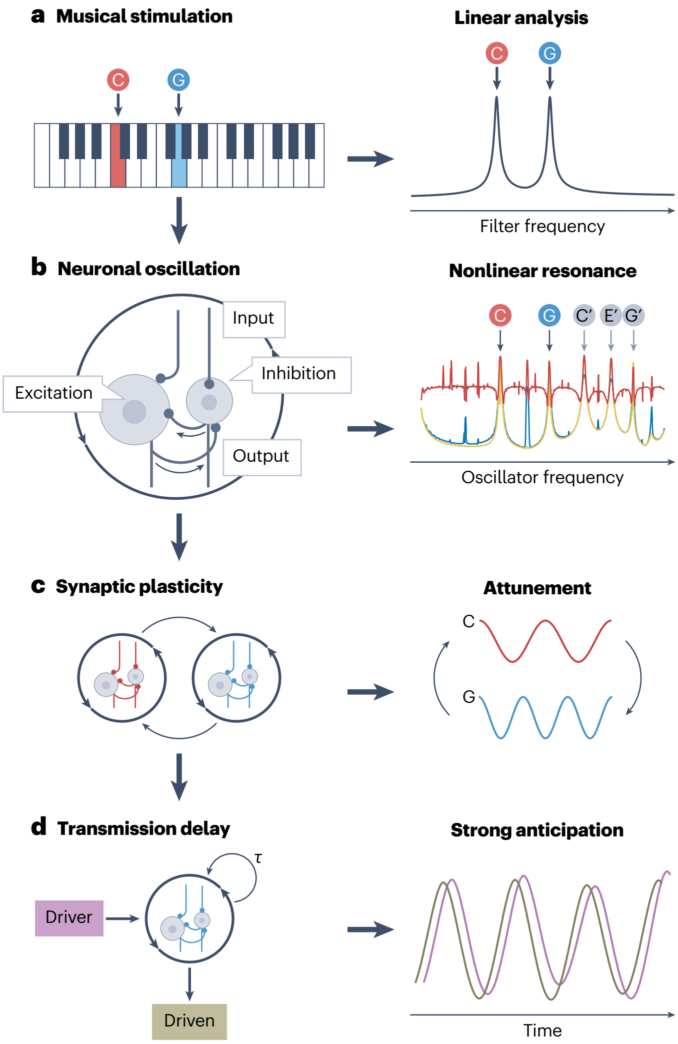

Fig. 2 | The predictions of neural resonance theory. a, Musical stimulation consisting of two pure tones at the frequencies C and G (left). Linear resonators used in traditional auditory models produce linear analyses containing peaks at stimulus frequencies only (right). **b**, When the same musical sounds stimulate neuronal oscillations (left), nonlinear resonance produces responses at summations, differences and integer ratios of stimulus frequencies (right). The responses of three different types of oscillator, critical (blue), limit cycle (red) and bistable (yellow), are shown. All oscillators respond at octaves ($2 \times f1 = C'$ and $2 \times f2 = G'$) and at the summation frequency ($f1 + f2 = E'$), some respond at additional frequencies. The right-hand images in **a** and **b** were generated from the canonical model in ref. 13 using the following parameters: linear $\alpha = -0.1, \beta_1 = 0, \beta_2 = 0$; critical $\alpha = 0, \beta_1 = -0.1, \beta_2 = -0.1$; limit cycle $\alpha = 0.01, \beta_1 = -0.02, \beta_2 = -0.02$; bistable $\alpha = -0.1, \beta_1 = 0.3, \beta_2 = -0.1$. For all types: $\varepsilon = 1$. **c**, Plastic synapses couple neuronal oscillations together via Hebbian learning (left) when they synchronize at stable frequency ratios (here, C and G, 2:3). Plastic connections can learn both amplitude and phase relations[11,19]. This results in attunement (right), strengthened responses to structured temporal patterns that are experienced in the environment[13]. **d**, Transmission delays in synaptic coupling have important implications for how an oscillation responds to an input signal (left). Delays can give rise to strong anticipation (right), where the behaviour of the oscillator precedes the behaviour of the driver. This may explain, for example, negative mean asynchrony (see the main text).

synchronization. Polyrhythms are two-part rhythms in which rhythmic frequencies are related by integer ratios[63,64] (Fig. 3). In dynamical systems, mode-locking predicts that synchronization in simple integer ratios (for example, 1:1 and 2:1) is more stable than in more complex ratios (for example, 4:3 and 5:4; Fig. 3). This aligns with evidence that people can coordinate lower-order polyrhythmic relationships more stably, in both bimanual rhythm performance and auditory–motor synchronization[63,64], than higher-order integer ratios. Notably, although drummers learn to stabilize more complex polyrhythms (for example, 4:3 and 3:5), even highly skilled musicians are generally less stable in producing higher-order ratios[27].

One striking feature of auditory–motor synchronization is that motor responses tend to precede stimulus onsets, known as the negative mean asynchrony (NMA). Although the NMA has resisted various attempts at simple explanation[39,65], a combination of dynamical modelling and empirical experimentation has demonstrated that anticipation may emerge simply from delayed self-feedback within dynamical systems[31,32]. This so-called strong anticipation arises from inherent regularities in system functioning[37] and can result in the driven system anticipating the driver's chaotic and neural spiking dynamics[31,33,34].

In summary, previous research has shown how dynamical principles explain mechanisms of expectation, coordination and anticipation, supported by both behavioural and neural data. Specifically, synchronization of neural oscillations to environmental rhythms provides an explanation of temporal attention and expectation, dynamical principles explain the relative stability of coordination at different frequency ratios and phases, and delay-coupled oscillations predict anticipation in sensorimotor coordination. NRT embraces these tools and concepts and expands upon them, positing neural oscillator networks and learning dynamics to handle the complex and varied structures of music. The next sections focus more specifically on music, with applications first to the slower timescale of rhythm and then the faster timescale of pitch.

Rhythmic timescales

The temporal structure of real music is far more intricate than the periodic ticks of a metronome (Fig. 4a). Musical rhythms display complex patterns of timing and accentuation[66] (Fig. 4b), but they are easiest to perceive, remember and reproduce when their inter-onset intervals reflect simple integer ratios (for example, 2:1:3)[67–69]. This may be because people tend to perceive a pulse underlying these rhythms. Pulse is a perceived – but not necessarily sounded – periodicity with a frequency around 1.5–2.5 Hz (refs. 47,59). Most adults spontaneously tap, clap or move to music at this frequency. However, the ability to synchronize to the pulse has a long developmental trajectory[70], and some adults cannot perceive pulse in complex rhythms at all, despite being able to reproduce the complex rhythm itself[71].

Pulse

NRT hypothesizes that pulse is a delta band oscillation whose frequency can be different from – but is related to – frequencies in the musical rhythm. This oscillation is a mechanism of event expectation, as in dynamic attending theory[16] (Fig. 4a). When events fail to occur at expected times, but instead occur between pulses, this is called syncopation, and syncopation provides a good opportunity to test the hypothesis of nonlinear resonance. Syncopations can be so strong, such as in Brazilian samba[72], that there may be little physical energy at the pulse frequency. It is possible to construct rhythms that are so syncopated that there is no physical energy at the pulse frequency, called 'missing pulse' rhythms[73] (Fig. 4b). In the case of a missing pulse rhythm, the brain would have to create the pulse frequency via nonlinear resonance.

In one NRT model, an auditory–motor network was stimulated with note onsets, and pulse frequency oscillations arose in the motor planning network, demonstrating that nonlinear resonance is sufficient to explain this phenomenon[73]. Moreover, behavioural studies with missing pulse rhythms showed that people perceive the pulse at the frequencies predicted by nonlinear resonance[51,73]. EEG and MEG SS-EPs revealed the predicted missing frequency, and its amplitude correlates with perception[50–52].

As linear models such as filter banks[74,75] respond only at frequencies present in the input (Fig. 2a), they cannot explain this percept. Moreover, the SS-EP at the pulse frequency cannot reflect a sequence of evoked potentials (passive neural responses to events) because frequency analysis of such a response would not include this missing frequency[51,76]. Although functional MRI studies have produced a number of candidate brain regions[57,58], as yet it is not known where the pulse periodicity originates. Transcranial magnetic stimulation (continuous theta burst stimulation) that attempted to downregulate cortical activity in candidate areas only moderately affected pulse perception[77]. As the NRT model makes quantitative predictions about pulse frequency amplitude in auditory versus motor areas, experiments with missing pulse rhythms could help to identify the anatomical substrate of pulse perception, and further test the model.

Groove

Recurring syncopated rhythms can produce an urge to move and a positive affective state of seemingly effortless perception–action coupling called groove[74]. Too little syncopation leads to low groove ratings, but moderate syncopation leads to high groove ratings. Interestingly, too much syncopation also leads to low groove ratings[78], producing an inverted U-shaped relationship between syncopation and groove[79]. The PCM model explains this effect based on prediction. Participants perceive a pulse and compare pulse-based temporal expectations with event onset times. In very high complexity rhythms, the combination of large deviations from pulse-based predictions and low precision of predictions produces low groove ratings[7,80] (Fig. 4c). However, when the pulse perception NRT model[73] described above was applied in an MEG groove experiment[81], it predicted that people generally do not perceive pulse in the very high syncopation rhythms (Fig. 4d).

In the MEG study, the NRT model predicted both groove ratings and pulse frequency amplitude in auditory and motor cortices, supporting the notion that groove arises owing to oscillatory motor activations[81]. In addition, neural resonance predicts groove perception in terms of the amplitude of oscillatory activity in auditory and motor cortices. Studies show poorer neural resonance (intertrial phase coherence), worsening pupillary entrainment and poorer tap synchronization for high rhythmic complexity, low groove rhythms[82,83], although musicians may be an exception[84]. Interestingly, in idiomatic pop music, drumming complexity does not seem to reach levels that lead to low groove ratings[85]. Thus, whereas some research supports the predictions

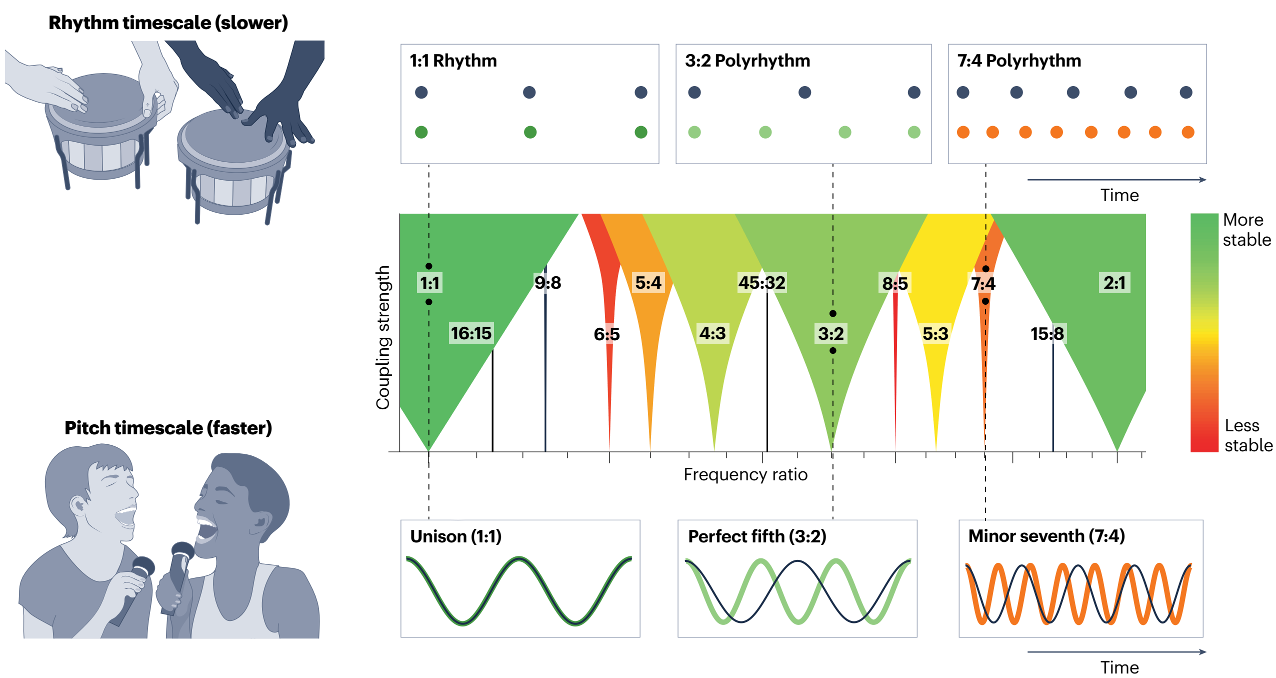

Fig. 3 | Stability predictions across timescales. Stability predictions hold at both the slower timescales of rhythm and the faster timescales of pitch. Middle: two nonlinear oscillators at different frequencies can synchronize (or mode-lock) to each other when the frequency ratio is close to an integer ratio and the coupling is strong. Mathematical analysis, published in ref. 18, shows that mode-locking is more stable for a simple ratio (for example, 1:1 and 2:1) than a complex ratio (for example, 7:4 and 45:32). Here, we plot together the analyses for multiple frequency ratios using the parameters $\alpha = 0.05$, $\beta_1 = -0.05$, $\beta_2 = -0.05$ and $\varepsilon = 1$. The coloured regions (called resonance regions) show the frequency range and coupling strength for which mode-locking is stable. Frequency ratios are based on just intonation. The resonance regions are wider for simple integer ratios than complex ratios, indicating more stable mode-locking at simple ratios under perturbation and noise. Predictions of stability may explain many aspects of perception and performance, including both rhythmic patterns (polyrhythms) at a slow timescale (top) and pitch patterns (harmonies) at a faster timescale (bottom).

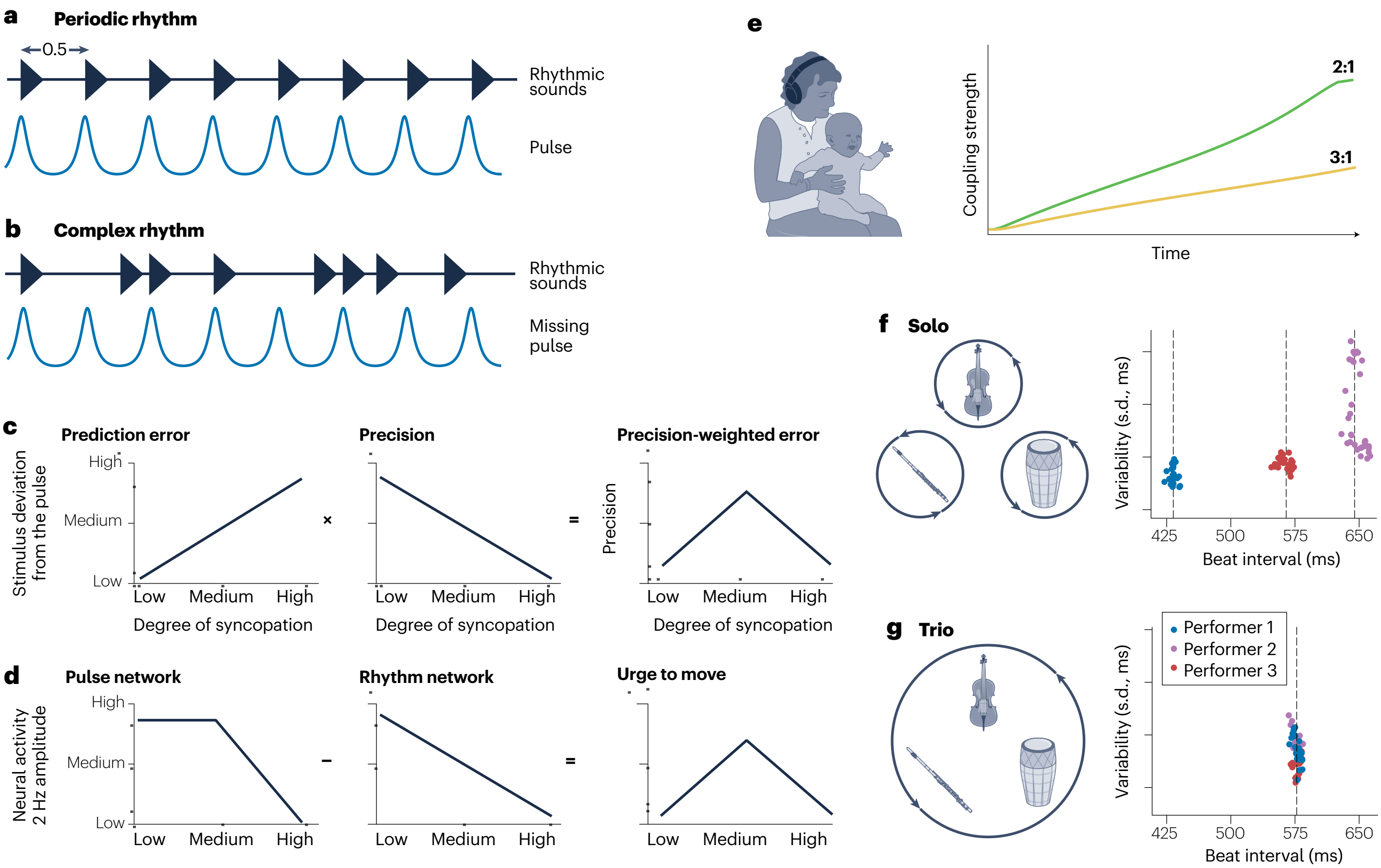

Fig. 4 | Rhythm and temporal structure. a, Temporal expectation: a simple, predictable rhythm leads to the formation of strong temporal expectancies, as described in dynamic attending theory. Temporal expectancies are modelled as attending rhythms (bottom), where the higher the peak, the greater the expectancy for an event. **b**, Pulse: a complex rhythm has varied inter-onset intervals that form integer ratios. Pulse is a perceived periodicity thought to embody temporal expectancy, even in highly syncopated rhythms (bottom). Tone onsets in weak metrical positions creates syncopation. Here, half of the events occur at unexpected timepoints, creating a 'missing pulse' rhythm. **c**, Groove: predictive coding of music predicts that people must first hear the pulse to compute deviations from predictions. **d**, Neural resonance theory predicts that the urge to move is low in the most highly syncopated rhythms because people cannot perceive a pulse. **e**, Development and enculturation: infants' perception of rhythm and metre can be shaped by passive exposure or by cross-modal interactions[91] such as bouncing to a musical stimulus. Neural resonance theory models predict that infants learn simple rhythmic relationships (2:1) more quickly than complex relationships (3:1)[28], reflected in the coupling strength of oscillator connections. **f**, Solo music performance: in solo performance, spontaneous tempo (in the absence of cues, top) is governed by each performer's intrinsic dynamics. **g**, The trio performance (bottom) shows performers' aligned timing (beat interval and variability), reflecting coupling between the ensemble performers[172]. Panel **c** adapted from ref. 7, Springer Nature Limited; panel **e** adapted with permission from ref. 28, Wiley (data for appended 3:1 curve also from ref. 28); and data plotted in **g** and **h** are from ref. 172.

of NRT, additional research will be required to fully distinguish between the predictions of NRT and PCM.

Metre and attunement

In addition to pulse, listeners may perceive metre in complex rhythms, periodicities faster and slower than the pulse, and related to the pulse and to one another by simple integer ratios, such as 2's and 3's (refs. 66,86). Metre provides structured patterns within which musical rhythms are perceived and produced throughout the world[3,87]. Both pulse and metre have long developmental trajectories, and they can vary depending on musical tradition[88,89]. Thus, explanation of pulse and metre requires a theoretical framework that includes learning and enculturation. For example, some non-Western musics[86,90] feature 'unequal' metres, in which the pulse is a non-periodic pattern, such as 3–2–2 (long–short–short)[28,87,88]. Recent NRT research has begun to ask whether Hebbian learning in oscillatory networks can result in attunement to both equal and unequal metres and explain how connections between auditory and motor networks develop.

Pulse and metre are learned during development[88], and modelling suggests that neuronal oscillation and Hebbian learning are sufficient to explain infants' perceptual attunement to the rhythm structures of their cultures[19,30,91]. Beginning in prenatal development[91,92], the human fetus becomes sensitive to rhythmic inputs from the ambient environment. This initial sensitivity becomes attuned (Fig. 2c) to culture-specific rhythmic structures during postnatal development, producing perception–action biases for rhythm called perceptual narrowing[88]. In one study, an auditory network with frequencies spanning the delta and theta range was stimulated with Western and non-Western rhythms. During training, connections between network oscillators emerged, reflecting the structure of the Western or non-Western rhythm[30]. Importantly, attunement occurred without an error signal, suggesting that nonlinear resonance and Hebbian plasticity are sufficient to bootstrap learning. After training, oscillatory networks exhibit biases towards certain auditory rhythms, similar to perceptual biases for culture-specific rhythms in late infancy and childhood. Better neural tracking of rhythm in adults with more musical training[48,93] may also be accounted for by increased coupling strength via attunement[19].

Human perceptual systems also attune to motor–vestibular rhythms. Bodily movement to music activates the human vestibular system, affecting rhythm perception[94]. Bouncing infants or adults moving to a metrically bistable rhythm produce preferences for accented rhythms that match the rate of bouncing or movement[95,96], and oscillatory networks explain motor–vestibular effects as a consequence of multistability and short-term attunement. In an auditory–motor network, inclusion of vestibular input induced one of two modes of metre perception — either a duple or triple metre — in response to a metrically bistable rhythm, and the simpler relationship (2:1) was learned more quickly[28] (Figs. 3 and 4e). Indeed, it is a generic prediction of NRT that small-integer ratio connections develop more quickly and that given the same amount of exposure they become stronger[19]. Thus, in this network, simple rhythms (for example, 2:1) were learned more rapidly relative to complex rhythms (for example, 3:1), consistent with NRT's predictions that as the complexity of rhythmic patterns between neural oscillators and external rhythms grows, stability declines[18,19]. Moreover, Hebbian plasticity in oscillator networks can enable continual learning of complex, rhythmic patterns with or without a teaching signal.

Performance and expertise

Music performance typically involves precise synchronization of events by multiple performers. It is often studied by asking people to produce musical sequences at their own pace and in the absence of a stimulus tempo. Individuals show large differences in spontaneous production rates[97,98], and these spontaneous rates have systematic effects on their performance in groups (Fig. 4f,g). Empirical findings of spontaneous rates are consistent with NRT predictions of the way in which natural frequency influences coordination stability.

Spontaneous tempo. The effects of spontaneous tempo and tempo adaptation in music performance can be well described by neural oscillators with adaptable frequency and return to natural frequency[29]. In this NRT model, the natural frequency is an attractor, but the frequency of another oscillator to which it is coupled is also an attractor. Frequency undergoes short-term attunement, allowing it to adapt to the tempo of other performers, but synchronization is better when oscillators operate closer to their natural frequencies. Several studies have provided support for such a model. Musicians show the greatest synchrony when they produce rhythmic patterns close to their spontaneous rate, and the synchrony decreases as they move further from the produced spontaneous rate[99]. Spontaneous production rates optimize the temporal consistency of performance[100]. Musicians also show tempo drift towards their spontaneous rate[99], suggesting that intrinsic frequencies serve as attractors[29]. Musically untrained individuals show larger constraints of natural frequencies than do trained individuals[99], suggesting that increased musical experience, including exposure to a wide variety of rhythms, yields increased neural flexibility and stability. Natural frequencies are important for musical ensembles as well. Both musicians and non-musicians exhibit better musical synchrony with a partner when their spontaneous rates are similar[97,98]. In addition, duet partners show enhanced EEG power at their unique spontaneous performance rates during solo music performance, relative to other frequencies[101], and power spectral density increases as the duets' asynchrony decreases[102].

Strong anticipation. Anticipatory synchronization is a necessary component for music performance as musicians must adapt and anticipate each other's actions[99,103]. Delay-coupled feedback in a driven oscillator provides parsimonious explanations for NMA in synchronization with a periodic metronome as well as asynchronies in music performance. Delay-coupled feedback in a driven oscillator (Fig. 2d) that is sensitive to feedback amplitude accurately predicts how the size of NMA is related to tempo, and how it can be smaller for musicians than for non-musicians[38]. As with NMA, delay-coupled systems provide a way to understand anticipation that happens naturally between musicians during music performance[38] (Fig. 4g). Delay coupling has successfully predicted partners' anticipatory synchronization in duet piano performance[35]. Each partner was modelled as a phase oscillator that compared its phase at a time delay with the present phase of its partner. The model successfully predicted behaviour in various coupling conditions, depending on whether one partner heard feedback (unidirectional), both partners heard feedback (bidirectional) or neither partner heard feedback[34]. Thus, delay coupling is sufficient to account for anticipation without internal projections of the partner's actions, as suggested by predictive coding models. Although predictive coding emphasizes the influence of external and experiential factors, mechanisms inherent in time-delayed feedback allow for the emergence of anticipation. This makes strong anticipation a robust explanation for a wide range of anticipatory behaviours without the need to posit more complex interactions between top-down and bottom-up predictive processes[103].

Tonal timescales

The same dynamical principles that are useful in understanding the slower cortical timescales are also useful for understanding nonlinear resonance at faster cellular timescales[11,21,22] (Fig. 3). Oscillations and phase-locking have been studied in the auditory periphery and central auditory pathway (Fig. 5a) for decades. For example, critical oscillations of cochlear outer hair cells phase-lock to sound[104], and resonance-based models parsimoniously explain both physiological and perceptual consequences of active cochlear processing[22,105–107]. Action potentials in the auditory nerve and brainstem phase-lock at frequencies up to thousands of Hz, and chopper and onset cells in auditory nuclei mode-lock to sounds[23,108]. In humans, time-locked neural responses can be recorded non-invasively from the scalp using the EEG frequency-following response (FFR). Tonotopically organized networks of nonlinear oscillators capture nonlinear responses observed in the FFR[109], and are generalizations of linear resonators (that is, bandpass filters), which have been traditionally used in models of the cochlea and brainstem[110].

Pitch

A fundamental role of the central auditory system is to determine the pitch of sounds, allowing us to categorize and order notes in a musical scale. Early models of pitch perception, based on autocorrelation, hypothesized the existence of synaptic delays to carry out the requisite temporal computations[111]. However, the lack of physiological evidence for time delays has dampened interest in this theoretical approach[112]. Alternatively, pitch perception and related perceptual phenomena

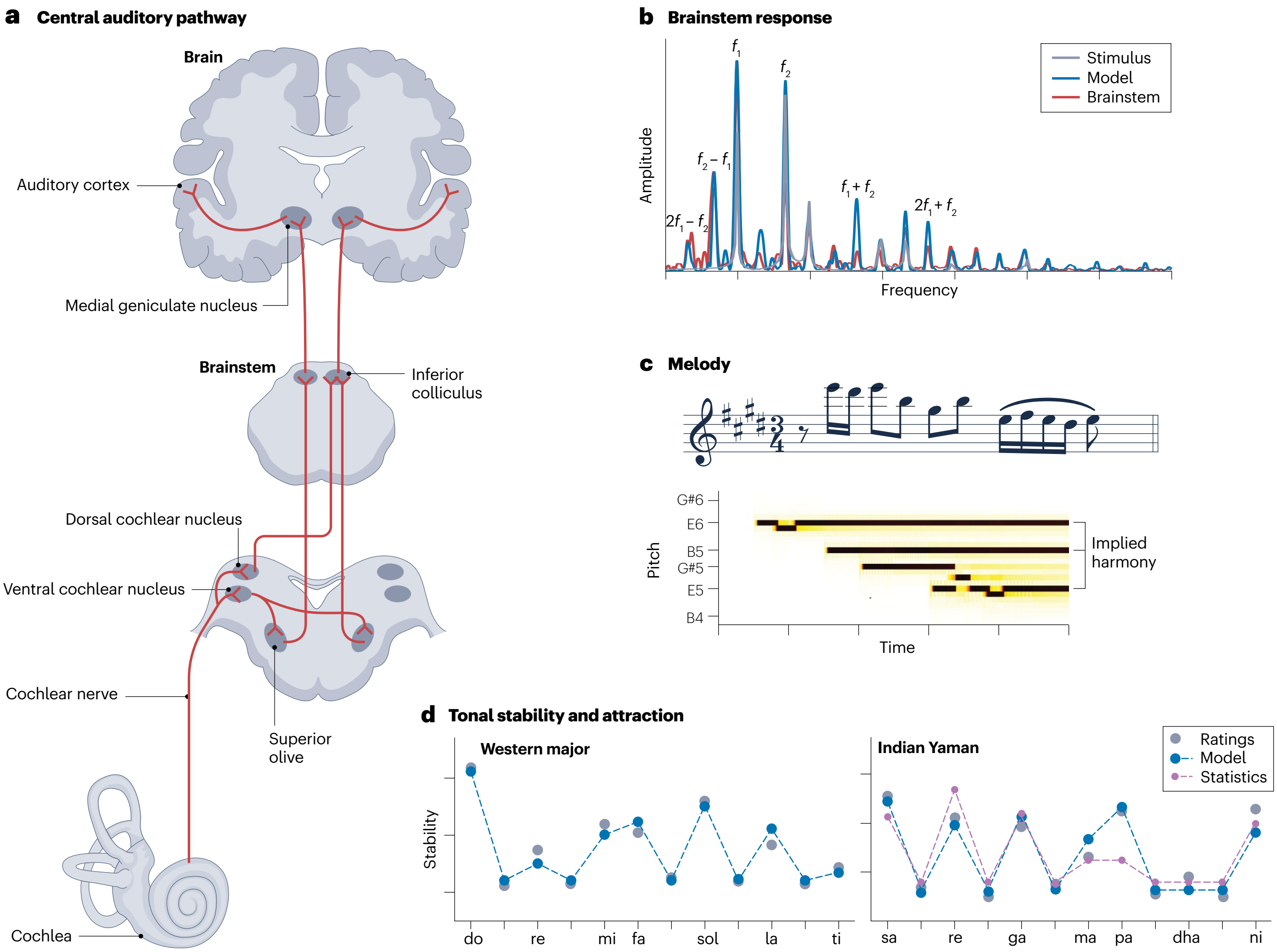

Fig. 5 | Consonance, melody and tonality. a, The mammalian central auditory pathway[173], highlighting cochlea, brainstem, thalamus and auditory cortex. **b**, The frequency-following response[122] is generated mainly in the brainstem. The brainstem frequency-following response (red) includes all frequencies in the stimulus (grey) and many other frequencies that are not present in the stimulus. The neural resonance theory (NRT) model (blue) including cochlea, cochlear nucleus and inferior colliculus predicts all of these frequencies[109]. **c**, The dynamic interactions between pitches in an oscillatory neural network model (bottom) can predict the implied harmony in a melody (top, J. S. Bach's violin partita No. 3, BWV 1006)[138]. The pitches belonging to the implied harmony (E, G# and B) persist in the model (black), whereas other pitches are quickly suppressed (yellow). **d**, NRT predicts tonal stability ratings. For Western music (C major, left) and North Indian raga (Yaman, right), the tonal stability of scale tones was predicted by an NRT model[134] (large blue dots and lines) and compared with human ratings[146] (large grey dots). The NRT predictions strongly fit both data. For raga Yaman, the NRT predictions fit the rating data better than the duration statistics (small purple dots and lines)[148]. Note that the names for respective cultures are shown. Panel **a** adapted from ref. 173, CC BY 3.0; panel **b** adapted with permission from ref. 109, Elsevier; panel **c** adapted from ref. 138, CC BY 4.0; panel **d** (left) adapted from ref. 134, Springer Nature Limited; and panel **d** (right) adapted with permission from ref. 148, University of California Press.

can be explained as nonlinear resonance in a dynamical system[113]. Specifically, nonlinear resonance explains the pitch of the missing fundamental, that is, the lowest frequency that is missing in the waveform but perceived by the listener. It also explains the shift of perceived pitch when harmonic frequencies are shifted by equal amounts[114] — another crucial aspect of pitch perception. The pitch shift matches closely with the frequency of a nonlinear oscillator that resonates to the two lowest-frequency components of the stimulus (a so-called three-frequency resonance)[113]. Furthermore, physiological models of pitch perception feature nonlinear oscillators as basic elements[115,116]. In one model, the strength of firing synchrony among chopper cells in the ventral cochlear nucleus was used to extract periodicities in frequency channels, which is physiologically plausible, and is similar in many respects to the autocorrelation operation used in earlier models[116].

Consonance

Harmonic intervals are pairs of simultaneously sounded pitches. The perceived pleasantness and unpleasantness of intervals can be referred to as consonance and dissonance, respectively[117]. Early psychoacoustic approaches explained dissonance as interference of complex tones on the cochlea[118]. However, more extensive perceptual studies linked the perception of consonance to harmonicity and to small integer ratios[119,120]. Simple integer ratios lead to consonant intervals (for example, 2:1 for the octave and 3:2 for the fifth), and complex ratios lead to dissonant intervals (9:8 for the major second and 7:4 for the minor seventh) (Fig. 3). Mode-locking stability (Fig. 3) precisely predicts the standard ordering of consonance as described in Western tonal music theory[121] and predicts consonance rating data of Western listeners[119]. Moreover, oscillators can synchronize in an integer ratio when their intrinsic frequencies deviate from the precise integer ratio, in which slight detuning from precise integer ratios (the coloured regions in Fig. 3, middle) can be tolerated in tuning systems (for example, the equal temperament). Thus, mode-locking represents a possible dynamical mechanism for consonance and dissonance.

Tonal fusion
Tonal fusion refers to how the brain binds — or fuses — harmonic features of a complex tone. Tonal fusion of sounds related by a simple integer ratio is readily explained by nonlinear resonance in the auditory system. Harmonic frequencies exhibit integer ratios, and Hebbian plasticity can bind oscillations with simple frequency relationships[19]. Moreover, frequency components not present in the acoustic signal are conspicuous in brainstem FFRs[122] (Fig. 5b), including nonlinear difference tones and their harmonics, resembling descriptions of harmonicity. The existence of nonlinear resonances in the FFR suggests that they arise, in part, from mode-locking in brainstem neurons[109]. Indeed, mode-locking accurately predicts the brainstem FFR to consonant and dissonant musical intervals[109,122]. Thus, predictions of neural resonance link consonance with harmonicity, and ultimately to tonal fusion. In other words, mode-locking (n:m) may do the work of feature binding for complex tones, much as phase-locking (1:1) does the work of feature binding in the visual system[123,124].

Attunement
Recent work on consonance perception implicates a contribution of culture and learning, suggesting a possible role for plasticity in the central auditory system. Consonance ratings of intervals vary across cultures[125,126], and evidence suggests that musical training may fine-tune the stability of musical intervals possibly via synaptic plasticity and/or cortico-fugal connectivity[109,122], and that people can learn novel tuning conventions[127,128]. In fact, subjective judgements of musical intervals reflect both intrinsic and cultural influences. When asked to rate pleasantness, Tsimane listeners in Bolivia rated all intervals as essentially equal, whereas listeners in the USA showed clear preference for consonant intervals over dissonant intervals[125]. Yet, when the question was changed to whether the two-tone interval was one sound or two (tonal fusion) the results from both Tsimane listeners and listeners in the USA followed the small-integer ratio prediction[129].

The effects of enculturation and musical training are explained in terms of attunement of the situated dynamical system to its environment. Thus, the view of NRT is that consonance and dissonance correspond to the stability of resonant patterns, which is jointly determined by intrinsic (neurodynamic) stability and attunement based on cultural exposure. Neurodynamic stability explains why small integer frequency ratios (2:1, 3:2 and 4:3) are found in musical tuning systems across history and around the world, and other, less stable ratios are more variable[127]. Attunement predicts that less intrinsically stable relationships can be strengthened with exposure, enabling people to learn novel intervals or chords based on higher-order ratios[128].

Melody and tonal structures
A melody is a sequence of tones, and the distance between two sequentially sounded pitches is called a melodic interval. When melodic intervals that vary along a continuum are categorized, identification functions show sharp and reliable category boundaries, and interval discrimination functions are non-monotonic with peaks at boundaries between adjacent interval categories[130–132]. This is called categorical perception[127] and suggests that the intervals of the scale act as attractors, such that continuously varying intervals must be differentially identified to be discriminated. Simulations show that intrinsic dynamics of nonlinear oscillators can sustain the memory of individual tones after the physical sounds end, and coupling between oscillators can then support and stabilize the combined resonant pattern if the oscillations form simple frequency relations[133,134]. This explains how intervals based on simple frequency ratios produce more stable memory traces than intervals based on complex ratios: infants, children and adults distinguished consonant melodic intervals (for example, a fifth, 3:2) from similarly sized dissonant intervals (for example, a tritone 45:32) only when the consonant interval was presented first[133,135]. This finding cannot be explained by harmonic template matching[136], which relies on simultaneously sounding frequencies, but can be explained by self-stabilizing resonance in a nonlinear oscillatory network[134].

Implied harmony. The interplay of melodic steps and leaps is important in determining implied harmony in musical melodies[137]. A nonlinear oscillatory network model with short-term Hebbian plasticity captured the implied harmony arising from step and leap dynamics[138]. Simulations showed that the oscillators tuned to the chord tones resonate at high amplitudes after the corresponding stimulus tones stop, whereas the oscillators tuned to the non-chord (embellishing) tones are suppressed immediately by the subsequent tones (Fig. 5c). Resonant patterns formed in the model driven by unaccompanied melodies taken from Mozart piano sonatas matched the annotated harmony better than the statistics of tone duration.

Tonality. Tonality is the perception of stability and attraction relationships among the pitches in music. Tonality is observed in the music of documented musical systems across the world[2,3,127], and the specific relationships depend on learning and enculturation[127]. A specific tone, called the tonic in Western music theory, is the most stable and provides a focus around which other tones are organized, based on a hierarchy of stability[139]. Tonal stability can be measured empirically by asking listeners to rate how well a single tone in the scale (a 'probe tone') follows a musical context[140].

The frequency of occurrence of tones in tonal melodies correlates strongly with Western tonal hierarchies[6,140–143], whereas psychoacoustic consonance correlates weakly with tonal hierarchies[140]. However, statistical approaches take such regularities as given and cannot explain how they arise. Alternatively, stability and attraction may instead be emergent properties of auditory memory[144,145]. NRT takes this view, hypothesizing that stability and attraction relationships emerge from the intrinsic dynamics of an oscillatory neural network stimulated by musical tones. Thus, tonal stability is the dynamic stability of frequency relationships within a specific musical context. Stable tones attract less stable tones nearby, which is experienced as melodic expectancy. Indeed, it was shown that the stability of resonance between the scale tones and the tonic predict the tonal hierarchy in Western music measured using the probe tone method[134,140,146] (Fig. 5d). The relative stability of each scale tone was predicted by a simple formula derived from a dynamical analysis of coupled oscillators. It is remarkable that dynamical stability does not depend on statistical regularities, but instead predicts the tonal hierarchies, which are known to be highly correlated with the statistics. This implies that dynamical stability may give rise to statistical regularities in music, possibly by constraining musical structures that can be stably formed and learned.

Enculturation. Dynamical predictions also hold across musical cultures. One cross-cultural study measured the stability of tones in North Indian raga for Indian listeners who were familiar with the style and for North American listeners who were unfamiliar[147]. It was found that Indian and North American listeners had similar stability ratings that correlated with the durations of the tones in the context. A statistical account would suggest that Western listeners quickly internalized tone statistics. A later study showed, however, that in contrast to tone duration statistics, the dynamical prediction produces higher correlations with the tonal profiles and better predicts the ratings of both native Indian listeners and unfamiliar Western listeners[148] (Fig. 5d). This suggests that nonlinear resonance predicts cross-cultural invariances in tonality perception. An effect of enculturation was found too. Separate analyses for the Indian and the Western ratings showed that culture-specific predictors (drone and scale membership for the Indian listeners and major and minor tonal hierarchies for the Western listeners) increased the data fit on top of the contributions of dynamical stability and tone durations. In NRT, cultural effects are attributed to the attunement of a dynamical system to its environment. A future study could investigate whether Hebbian learning in oscillatory networks could replicate the commonalities and differences in the Indian and the Western rating data. Also, further research is warranted to see whether NRT can predict stability and attraction relationships in novel tonal systems[128,149].

Affect. NRT further suggests that affective musical experiences can be explained in terms of neurodynamic stability and attraction. In dynamic relationships among tones, simple integer ratios or tonal 'consonance' are more attractive and may therefore provide a sense of resolution or reward compared with the tension experienced by more dissonant, complex integer ratios. Such relationships may explain why the more-stable major mode is experienced as 'happy' and the less-stable minor mode as 'sad'[150] in Western music. The attractor landscape of an individual listener would be further influenced by the degree to which they are attuned to a specific musical culture. Attunement during musical enculturation may explain why specific valence associations are perceived by adults and older children, but not by younger children[151]. In the absence of attunement, intrinsic dynamics underlying harmonic stability could also explain how African Mafa listeners perceive emotional affect in Western classical music[152] or how Western listeners perceive affect in Indian raga music[153,154]. Such findings provide an alternative to the idea that musical affect is experienced merely due to arbitrary cultural convention[4,6,7].

Discussion

The application of dynamical systems as a tool in the cognitive neuroscience of music is still in its infancy. In fact, it is likely that NRT has not yet enumerated all relevant predictions of its current models. Dynamical models are, in part, attractive because they can be used to make specific, quantitative and even counter-intuitive predictions from general assumptions about neural mechanisms. Even simple models can behave in unexpected ways and serve as a valuable asset to generate testable hypotheses about music cognition[73,107,109,148] (to see first hand more about what NRT models predict, readers are encouraged to try the toolbox that was used to build and run many NRT models[155]). Incorporating dynamical systems modelling into hypothesis generation and conceptualization of musical structure can help to propel the field of cognitive neuroscience towards linking music cognition directly to observable neurodynamics. Below, we discuss implications and future directions for NRT and contrast NRT with other approaches.

A core characteristic of NRT is that both the slower timescale mechanisms of rhythm and the faster timescale mechanisms of pitch are predicted to operate via principles of driven and coupled dynamical systems. Although canonical modelling illustrated this point here (Fig. 3), to the best of our knowledge there is scant empirical evidence directly comparing behavioural or neural predictions across timescales. In one interesting study[156], polyrhythms were created with two pulses at different tempi, in which tempo ratios were modelled after consonant and dissonant pitch interval ratios[119]. Consonance and dissonance ratings correlated strongly across timescales, with more complex ratios – whether polyrhythms or pitch intervals – rated as more dissonant, in line with NRT. In another study, cortical responses to rhythms and pitches revealed differences that suggest different canonical oscillation types may be at play at different timescales[157]. In future research, direct comparisons at the level of behaviour and neurophysiology could inform dynamical modelling and analysis.

Attunement based on Hebbian plasticity has been used to explain certain key results in development[30]. Attunement may also be applicable to modelling the emergence of rhythmic abilities such as pulse and metre perception, which have long developmental trajectories[158]. Relatedly, some adults cannot hear pulse or metre in complex rhythms[89,159], and future work should more fully address individual variation and its dependence on simple relations such as coupling strength. At the faster timescale of pitch intervals, more stable patterns should be also learned more quickly than less stable ones and be modulated by the pre-existing plastic connections. For example, in learning artificial musical grammars based on the Bohlen–Pierce scale[149] (a tonal system based on the tritave (3:1) rather than the octave (2:1)), NRT predictions would be straightforward. Furthermore, the NRT prediction that some structures should take longer to learn than others is derived from analysis of Hebbian plasticity[19]. This prediction matches intuition and experience, but is at odds with approaches that rely strictly on internalization of statistical regularities. Thus, future work investigating the learning-related predictions of NRT should directly contrast dynamical with statistical predictions.

NRT predicts that stable musical structures (for example, smaller integer ratios) will surface more often than less stable ones. These structures should occur across musical cultures, or as statistical universals[3], because the cognition and behaviour that presumably generated the music follow dynamical principles outlined here. Notably, rhythms do not have to be perfectly periodic or intervals perfectly tuned. NRT models account for perturbations in surface musical structure, such as mistuning or phase deviations, because stable states exist within attractor basins that provide flexibility. Moreover, complex interactions of resonating neural circuits may create stable states that deviate from precise phase and frequency relationships. In line with this, comparative studies have revealed widespread use of perfect consonances and other simple integer ratios at both faster[2,127,147] and slower[3,160,161]

Glossary

Anticipation
The process by which a system responds to an expected event before the event occurs.

Attraction
The evolving state of a dynamical system towards a more stable state, such as an orbit.

Attunement
The adaptation of neural circuits to the environment, enhancing response stability and flexibility.

Beat
In Western music theory, a simple (often periodic) rhythm that can be perceived within another rhythm.

Bistable systems
Systems with two stable states.

Consonance
The perceived pleasantness of a musical interval.

Critical oscillation
An oscillation poised at a bifurcation point, the transition between damped and self-sustained oscillation.

Dissonance
The perceived unpleasantness of a musical interval.

Dynamic attending
Entrainment of attentional processes with external temporal signals to focus on specific events in time.

Embodiment
A state of the brain and/or body that has a lawful, physical relationship to external events (for example, sounds) determined by physical principles. This embodied representation contrasts with the notion of a symbolic representation, in which symbols have arbitrary relationships to external events.

Enculturation
The process by which individuals learn, adopt and maintain their cultural traditions. Musical enculturation occurs through exposure to the structure of music of one's native culture, including tuning, scale and metre.

Expectation
The prediction of events and event timing based on context and prior experience. Musical expectations are violated when unexpected events occur or when (expected) events occur at unexpected times.

Groove
Embodied sense of rhythmic movement or the desire to move in response to a patterned sequence of sounds such as music.

Harmonic intervals
The pitch difference between simultaneous musical tones.

Harmony
Two or more complementary notes played or sung at the same time. The chords that accompany a melody.

Hebbian learning
An increase in synaptic efficacy that arises from a presynaptic cell's repeated and persistent stimulation of a postsynaptic cell. Hebbian learning in oscillatory neural networks occurs only when the neural oscillators resonate to each other (phase- or mode-lock).

Implied harmony
The (simultaneous) harmony implied by a (sequential) melody, without being explicitly present.

Just intonation
A tuning system in which intervals are tuned to whole number frequency ratios (such as 3:2 and 4:3).

Limit cycle
A closed orbit (self-sustained oscillation) on which a dynamical system remains.

Melodic interval
The pitch difference between two tones that are sounded one after another (as in a melody).

Metre
In Western music theory, nested patterns of strong and weak beats perceived in a rhythm.

Missing fundamental
The pitch perceived as the first harmonic, when the first harmonic is absent from the waveform.

Mode-locking
Synchronization in an integer (non-1:1) ratio.

Natural frequency
The inherent rate at which a system oscillates when not subjected to external forces, which is determined by its physical characteristics.

Nonlinear oscillator
An oscillator for which nonlinear processes determine the internal states and the response to external signals.

Nonlinear resonance
Phase and amplitude response of a nonlinear oscillator to stimulation.

Oscillation
A motion characterized by a stable frequency and amplitude that repeat over time, such as a sinusoidal pattern.

Pattern forming
The orderly outcome of self-organization as observed in biology, chemistry and physics.

Phase-locking
Synchronization in 1:1 frequency ratio where the phase difference between two systems (or a system and an external stimulus) is maintained constant.

Pitch
That aspect of auditory sensation that allows us to order tones on a musical scale.

Predictive coding of music
Theory that states the brain deploys a predictive model based on prior experience to minimize prediction errors, through a recursive Bayesian process, when listening to music.

Pulse
The most perceptually salient beat; that is, the beat to which a listener would tap when synchronizing with a rhythm.

Rhythm
The complex pattern of timing and accentuation.

Stability
A state or an orbit of a dynamical system is stable if the system is attracted to it.

Strong anticipation
Anticipatory behaviour in interactions with the environment that emerges owing to transmission delays (delay coupling).

Synchronization
Phase and/or frequency locking of coupled oscillators to one another or to external stimulation. Used interchangeably with entrainment.

Syncopation
The displacement of a musical accent from strong beats to weak beats.

Tonal hierarchy
The structured organization of tones in which specific tones are perceived as more stable than others, and less stable tones are attracted towards more stable ones.

Tonality
The perception of stability and attraction relationships among the pitches in musical work.

Transmission delays
A time delay in communication between neural areas, biophysically explained by long-range axonal transmission of information.

timescales. Future dynamical systems approaches should examine cross-culture musical corpora for statistical universals, guided by dynamical predictions.

Stability of perceived musical structures and attraction to stability after a perturbation may contribute to the emotional experience of music. For example, high-arousal musical works are those that exhibit faster tempo and sudden loudness changes[162]. Entrainment to these temporal elements involves the vestibular system[94], which in turn could influence heart rate[163] and the limbic system[164], viscerally influencing the experience of emotional arousal even when spectrotemporal properties of the music are degraded[165,166]. At faster timescales, consonance and dissonance in harmonic intervals, linked to positive or negative valence in emotion and associated with pleasantness and unpleasantness[117], may similarly influence embodied musical emotion. In Western tonal music, rules of musical grammar[66,139] generally align with the notion of simple integer ratios 'anchoring' tonality in a musical passage at structurally prominent positions, whereas complex ratios serve to add dissonance or tension between those points, effectively creating a sense of closure when tension moves back to relaxation. Future investigations into the role of stability and attraction in musical emotion should also allow for cross-cultural differences between rhythmic and tonal systems, as different resonant patterns are established during attunement to different musical systems. Still, the general prediction of NRT is that the direction of dynamical stability, that is, attraction from less to more stable structures, would influence experienced musical emotion. For the remainder of the discussion, we consider NRT in light of other approaches to music cognition.

Theories of predictive processing such as PCM propose that musical expectancy is a recursive Bayesian process, in which specialized brain networks compare bottom-up sensory input with top-down predictions, and minimize prediction error through precision-weighted adjustments[7]. Like PCM, NRT explains how the brain generates musical predictions. Some PCM proposals have even incorporated oscillator models or suggested that neural dynamics be considered an implementation of predictive coding[167]. However, NRT relies on intrinsic dynamics of physiological mechanisms to explain structure and expectancy, whereas predictive coding is a very different account based fully on prior learning. Above we showed that a successful NRT model of groove does not endorse PCM's principle of precision-weighted prediction error; instead its predictions were based on the (in)ability of resonance to activate a pulse frequency oscillation. Although it seems that anticipatory actions require explicit future predictions, we showed that even anticipation may emerge from delayed self-feedback within dynamic systems[35,38]. Finally, according to NRT, musical behaviours across slower and faster timescales are governed by dynamical principles, such that the dynamics embody musical structure. This is fundamentally different from PCM, in which specialized neural circuits — only at the slower timescale — compute and update predictions influenced by top-down processes exerted onto the model. The nuances of these different perspectives have not yet been fully contrasted, but future work could help to determine which approach robustly predicts empirical data.

Theories that rely on statistical learning, including PCM, posit that the brain builds internal models based on statistical regularities in the environment to make predictions. Thus, consistent statistical structure in music — that is, patterns — can be learned and predicted by the brain. By contrast, NRT predicts that musical statistics and regularities emerge from the stable dynamics and patterns intrinsic to neural systems. As a result, NRT predicts which patterns are easier to learn than others and why some patterns are more commonly found in music around the world, whereas pure statistical learning cannot.

However, one line of work describes pulse perception as a form of Bayesian inference in a periodic frame and shows how such a model can be systematically transformed to a forced, damped oscillator[167]. This approach focuses on building a mathematical bridge between statistical learning and dynamical systems. Another recent model shows that rhythmic behaviour such as synchronized tapping is learnable by a recurrent neural network, and dynamical analysis revealed that the network learned to oscillate and synchronize through interactions between excitatory and inhibitory units[168]. The model captures neural data from rhythm learning in non-human animals[168,169], potentially explaining why non-vocal learning species[36] can learn to synchronize to a musical beat[170,171]. Future research that compares, contrasts and integrates dynamics with other approaches to learning could bridge a substantial theoretical gap. This could enhance our understanding of neural processing in music perception and performance, as well as possibly providing links from music cognition to other more global cognitive processes, such as decision-making.

To conclude, in this Perspective, we have discussed how fundamental dynamical principles based on known neural mechanisms can explain the basic features of music found across timescales. NRT can provide insights into both neuroscience and human behaviour, as well as the link between the two. Such insights can shed light on the interconnectedness of brain and body, the ability of music to communicate affect and emotion, the role of music in interpersonal bonding, and applications of music to brain health.

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Author contributions

The authors all researched data for the article, provided substantial contributions to discussion of its content, wrote the article, and reviewed and edited the manuscript before submission.

Competing interests

E.W.L. is founder of, and owns stock in, Oscilloscape, Inc. (dba Oscillo Biosciences). J.C.K. is currently a paid employee of, and owns stock in, Oscilloscape, Inc. E.W.L. and J.C.K. are authors of patents owned by Oscilloscape, Inc. The subject matter of the current paper is not directly related to the business interests of Oscilloscape, and no products of Oscilloscape are discussed in this paper.

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