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ABSTRACT

Studies of rhythm processing and of reward have progressed separately, with little connection between the two. However, consistent links between rhythm and reward are beginning to surface, with research suggesting that synchronization to rhythm is rewarding, and that this rewarding element may in turn also boost this synchronization. The current mini review shows that the combined study of rhythm and reward can be beneficial to better understand their independent and combined roles across two central aspects of cognition: 1) learning and memory, and 2) social connection and interpersonal synchronization; which have so far been studied largely independently. From this basis, it is discussed how connections between rhythm and reward can be applied to learning and memory and social connection across different populations, taking into account individual differences, clinical populations, human development, and animal research. Future research will need to consider the rewarding nature of rhythm, and that rhythm can in turn boost reward, potentially enhancing other cognitive and social processes.

1. Introduction

Most people find music rewarding, and music has been shown to activate the brain's reward system (Zatorre, 2015). Music reward can be defined as the pleasurable (i.e., hedonic) and motivational response to music, associated with the activity of the dopaminergic reward circuitry in the brain (Ferreri et al., 2019; Mas-Herrero et al., 2021; Salimpoor et al., 2011, 2013; Zatorre, 2015). Although music reward is a crucial aspect of musical emotion (Goupil and Aucouturier, 2019), and emotion in music is intimately related to its rhythmic component (Trost et al., 2017), the discussion about the relationship between rhythm, music, and reward is quite recent in the scientific literature (e.g., Matthews et al., 2020; Stupacher et al., 2022; Witek, 2017). The latest review focusing on some aspects of this connection (i.e., music and reward) was by Zatorre (2015). Here, we propose to review the research on rhythm, on reward, and the link between the two in relation to learning and memory, and social connection/interaction. Our rationale is based on the observation that research has investigated a) links between *rhythm* and learning and memory (via temporal regularities) as well as *rhythm* and social connection (via interpersonal synchronization), and b) links between *reward* and learning and memory as well as *reward* and social connection. However, there is little research investigating connections

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between *rhythm and reward*, and how their combination might provide greater insights into learning and memory and social connection. Our aim is to bring these separate domains together, and then discuss fruitful avenues for future research across different populations in a perspectives section that addresses how these insights can inform 1) individual differences research, 2) clinical applications, 3) developmental research, and 4) links with animal research. An overview of the territory covered is given in Fig. 1. Before moving onto the learning and memory section and the social connection section, we will first briefly outline what we mean by rhythm and how individuals interact with rhythmic information, then discuss links between rhythm and reward, followed by the potential cognitive and neural mechanisms underlying rhythm and reward. Note that this review is not intended to be systematic, but rather, combines samples of relevant research across multiple areas to allow us to draw connections between them.

2. An overview on rhythm and reward

2.1. Rhythm and listeners' interaction with rhythmic information

The auditory world around us contains sounds with repeating and temporally regular patterns. Humans easily process the rhythmic information coming from different kinds of auditory stimuli with varying levels of rhythmicity. Rhythm refers to the patterns and organization of durations and inter-onset-intervals of sounds and silences over time. In music, these patterns allow for the abstraction of an underlying beat (where listeners might naturally move or clap their hands), as well as hierarchical structures of timing within a metrical organization, creating the largely cognitive construct of meter (London, 2012; McAuley, 2010). When exposed to music, listeners process several types of rhythmic information, including its structured timing patterns, meters, and tempi (Bouwer et al., 2021; Honing and Bouwer, 2019; London, 2012). Throughout the paper, we refer to music rhythm as rhythmic patterns that are constructed in such a way as to allow for the extraction of underlying temporal regularities, such as beat and meter.

The rhythmic information extracted from the external musical signal interacts with the internal states of the listener, thus promoting the temporal coordination of movements with external rhythmic events (i.e., sensorimotor synchronization). One of the most prominent interactions between the listener and external rhythmic information occurs via synchronization/entrainment (we will not go into this distinction here, but see Obleser and Kayser, 2019 for discussion of the differences in terminology, and note that we are discussing entrainment in the broad sense). This process can be conceptualized as the coupling of internal oscillations (or other forms of endogenous timekeeper mechanism) with the periodicity perceived in the external rhythm, such as the musical beat or meter. Rhythmic entrainment is pervasive, and can be observed at physiological, behavioral, and neural levels (Fujioka et al., 2012; Large, 2008; Trost and Vuilleumier, 2013). At the physiological level, beat regularity can, via different tempi, modulate cardiovascular and respiratory patterns (e.g., Khalfa et al., 2008), and even pupillary responses (Fink et al., 2018; Marimon et al., 2022). At the behavioral level, entrainment is apparent from listeners being able to perceive a musical beat, benefit from events occurring on the beat (e.g., faster processing), and also move their body in time with this beat (Damm et al., 2020; Nozaradan et al., 2015). At the neural level, the phase of oscillatory brain activity adapts to the external rhythmic signal (Haegens and Zion Golumbic, 2018; Obleser and Kayser, 2019), likely creating in the listener perceptual expectations about *when* a given event will occur (Henry and Herrmann, 2014; Jones, 1987; Lakatos et al., 2008; Large and Jones, 1999). Note that throughout this review, we will use the words expectation and prediction interchangeably; however, we are aware of discussions making distinctions between the two terms (e.g., see Rohrmeier and Koelsch, 2012).

Temporal expectations are a hallmark of musical rhythm perception, affect our perception and attention, and are necessary to entrain movement to rhythm, as they allow for the anticipation of when to start a movement to be exactly synchronized with the music (e.g., Van Der Steen and Keller, 2013). Rhythmic entrainment at the neural level has a strong link with the motor system (see also Todd and Lee, 2015), with the presence of regular beats in rhythm activating motor circuits (Grahn and Brett, 2007), and motor activity appearing intrinsically related to entrainment and temporal expectations in sensory and motor areas of the brain (Merchant et al., 2015; Morillon and Baillet, 2017). Entrainment, both behaviorally and neurally, can be observed at multiple hierarchical levels (Juslin et al., 2010; Nozaradan et al., 2011), reflecting the hierarchical metric nature of musical rhythm. For example, when moving to music, it is possible to move along with every beat of the music, every two beats, every four beats, etc. Neural responses at each of these levels are also observed, suggesting that the brain is coding this hierarchy in a nested way, leading to advantages via metric binding (Jones, 2016, 2018; Nozaradan et al., 2011).

It should be noted that for purposes of the current discussion, we are focusing on regular and metric rhythms, allowing for prediction and entrainment of movement. Most of the research has investigated rhythms with even meters (e.g., duple or triple meters), from which both beat and metrical hierarchy are relatively easy to extract for Western tonal listeners (see, for example, Hannon et al., 2012, for the influence of cultural music background), but it would be interesting in future work to further investigate more complex rhythms with uneven, asymmetric meters (e.g., London, 1995; Misgeld et al., 2022; Moelants, 2006; Repp et al., 2005), as well as non-isochronous rhythmic patterns (e.g., see Jacoby et al., 2021; London et al., 2017); and rhythmic patterns that are predictable based on memory traces, but not on recurring predictable beats (Bouwer, Fahrenfort et al., 2020; Bouwer, Honing et al., 2020). In this case, it would be important to clarify whether such rhythms with a non-isochronous underlying beat engage the same mechanisms as rhythms with a regular, isochronous beat, though perhaps to a lesser extent, or different mechanisms.

The way listeners predict upcoming rhythmic events has been interpreted largely within two frameworks: dynamic attending, with resulting temporal predictions (Jones, 1976, 2018; Large and Jones, 1999) and predictive coding (Friston, 2005, 2010; Koelsch et al., 2018; Vuust et al., 2009, 2022). Note that these frameworks are not mutually

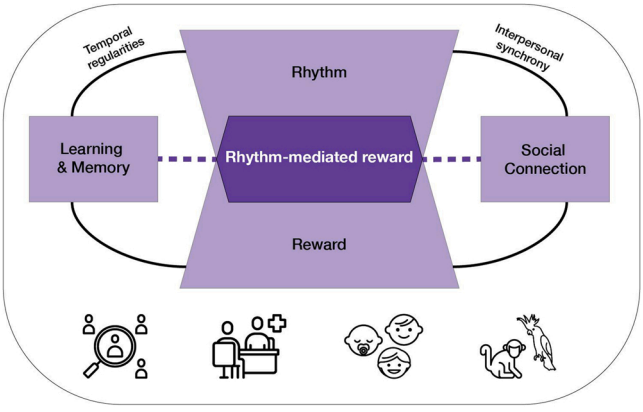

Fig. 1. An overview of the research presented in the current manuscript. Rhythm and reward and their separate connections with learning and memory (via temporal regularities) and social connection (via interpersonal synchrony promoted by temporal regularities) provide the background to the current perspective paper focusing on rhythm-mediated reward (dark purple). The dotted lines show the to-be-developed links between rhythm-mediated reward and learning and memory, as well as social connection, and are developed in the current paper. The four icons at the bottom of the graph represent the perspectives across different research fields and populations where rhythm-mediated reward could be further developed, from left to right: individual differences, clinical applications, human neurodevelopment, and links with animal research.

exclusive (e.g., Palmer and Demos, 2022). Both dynamic attending and predictive coding models suggest synchrony of internal states to the external input, either by (a) the synchronization of endogenous neural oscillations to the external rhythm, allowing directed attention to anticipated (expected, predicted) points in time (dynamic attending), or (b) the generation of predictions based on learning and the comparison of a learned representation of the world with bottom-up input (predictive coding). For the purposes of this paper, we will remain agnostic as to the theoretical framework underlying prediction in the brain, as we believe that both frameworks are valuable (and likely complementary) in explaining the links we aim to develop in the following: notably, those between temporal expectations, rhythm, and reward.

2.2. The link(s) between rhythm and reward

Rhythm (and the potentially resulting rhythmic entrainment, depending on the rhythmic pattern) appears to play a major role in music-driven affect, and has been shown to increase arousal as well as feelings of communion (Juslin, 2013; Juslin et al., 2010; Trost et al., 2017), which are strongly linked to reward processes (Zatorre, 2015). Temporal structures of music have been proposed to causally induce musical emotion by modulating physiological entrainment processes related to heart rate and respiration rate (Juslin, 2013; Trost and Vuilleumier, 2013). Subjective emotional ratings, such as on valence, arousal, and enjoyment, have also been shown to be modulated by rhythmic properties of the stimulus, such as the perceived complexity or syncopation of the rhythm (Gabrielsson and Lindström, 2010; Gundlach, 1935; Keller and Schubert, 2011). Further, the emotional properties evoked by rhythm appear to influence entrainment: for example, pleasant music produces entrainment at a finer-grained rhythmical level than does unpleasant music (Trost et al., 2014). Such links suggest a tight relationship between the cognitive and affective components of rhythm.

Crucially, in addition to influencing affect responses, such as valence and arousal, musical rhythm can specifically modulate reward responses. Whereas emotional-affective responses to rhythm have typically been studied in experiments focusing on perception (Gabrielsson and Lindström, 2010; Gundlach, 1935; Keller and Schubert, 2011), reward responses have a strong link to movement, through sensorimotor synchronization, bodily entrainment, and groove. Accordingly, research conducted on groove experience shows a tight link between rhythm, movement, prediction, and pleasure (Janata et al., 2012; Matthews et al., 2020; Vuust and Witek, 2014; Witek et al., 2014). Indeed, groove sensation, defined as the pleasurable desire to move to music, is modulated by rhythmic complexity and follows the so-called inverted U shape (Stupacher et al., 2022). In particular, and in line with theories on pleasure and expectations, it has been shown that medium complexity rhythms (compared to low and high complexity ones), lead to higher pleasure and wanting to move by providing a balance between predictability and uncertainty (Vuust and Witek, 2014; Witek et al., 2014; see also Berlyne, 1970 and Leder et al., 2004 for the relationship between complexity and liking in the visual domain). Thus, listening and moving to rhythm can lead to a range of positive responses, both in terms of affect and in terms of pleasure, and these responses typically depend on the complexity of the rhythm (see Stupacher et al., 2022 for a discussion about rhythmic complexity, groove and reward). The fact that rhythms with intermediate complexity are perceived as more pleasurable (Kraus and Hesselmann, 2021; Vuust and Witek, 2014) could reflect a domain-general feature of statistical inference learning: optimal learning rates are obtained for intermediate stimulus complexity, which are therefore more valued (Erle et al., 2017). This suggests that the hedonic nature of music may originate from generalized mechanisms linking prediction to reward.

The link between rhythm and reward through its strong movement-inducing component is further confirmed by psychometric tools aiming to measure individual differences in reward sensitivity. One way to reliably measure musical reward is with the Barcelona Music Reward Questionnaire (BMRQ, Mas-Herrero et al., 2013) which is associated with both psychophysiological and neural responses related to music reward (Ferreri et al., 2019; Martínez-Molina et al., 2016; Mas-Herrero et al., 2014). The BMRQ measures individuals' sensitivity to music reward (i.e., musical hedonia), by assessing different facets of the musical experience. The sensory-motor subscale strongly correlates with the other subscales related to musical pleasure (i.e., emotion evocation, mood regulation, musical seeking, and social reward experience) and deeply contributes to defining the complex reward experience during music listening. In particular, the sensory-motor subscale reflects the capacity to spontaneously and intuitively synchronize body movements to a rhythmic beat using simple or complex movements (e.g., from toe tapping to dancing), thus requiring the coordination of somatosensory-motor brain networks with auditory processing networks (Mas-Herrero et al., 2013). Further studies will be necessary to confirm whether higher individual sensitivity to music reward, especially in the sensory-motor subscale, is also associated with higher rhythm-driven pleasurable responses.

2.3. Potential cognitive and neural correlates underlying rhythm and reward

Theoretical approaches and experimental evidence suggest that perceptual expectations and predictions created during music listening lie at the core of musical affect (Huron, 2008; Meyer, 1956). Reward responses to rhythm may therefore be linked to the strong temporal expectations that can be induced by musical rhythm. While extracting musical regularities across both pitch and time dimensions, listeners' brains create expectations about future events, notably which events are likely to occur and when (Jones and Boltz, 1989; Koelsch et al., 2019). The feelings of pleasure associated with music and musical emotions could be driven by the intrinsic value of successfully anticipating musical events or encountering expectancy violations or surprise, and from the tension and resolution/relaxation patterns created by prediction error and fulfillment (e.g., Meyer, 1956). Until now, the link between musical pleasure and expectations has mainly been tested by manipulating the melodic and harmonic components in music (e.g., Cheung et al., 2019; Gold et al., 2019; Lehne et al., 2014; Steinbeis et al., 2005; Tillmann et al., 2006). As rhythmic patterns (and the potentially underlying beat) play a crucial role in creating temporal expectations (e.g., Jones and Boltz, 1989; Lerdahl and Jackendoff, 1983; see also Trost et al., 2017), these may underlie the elicitation of pleasurable responses, as has been observed for expectations on the pitch dimension, whether melodic or harmonic (Cheung et al., 2019; Gold et al., 2019; Steinbeis et al., 2005). These findings would be in line with research on groove suggesting that musical rhythm exploits the brain's principles of prediction, which promote pleasurable responses and desire for sensorimotor synchronization from musical rhythm (Vuust and Witek, 2014).

At the neural level, rhythm processing has been associated with a widespread network of brain areas, including the basal ganglia, cerebellum, premotor cortex, and supplementary motor area (Grahn, 2012, see also Schwartze et al., 2012 for cortical and subcortical contributions). Among these activations, the basal ganglia, and especially the dorsal structures of the striatum (i.e., the putamen and the caudate nucleus) arise as central regions and main neural correlates of beat perception (Grahn, 2009; Nozaradan et al., 2017; Teki et al., 2011; Thaut et al., 2008) and interval timing (together with the cerebellum). Critically, these regions also show strong links to the reward system (e.g., see the striatal-beat model, linking the reward system and interval timing, Buhusi and Meck, 2005). Music reward responses activate an extensive neural network of subcortical and cortical regions involving the basal ganglia (especially the ventral striatum, containing the nucleus accumbens, but also its dorsal part comprising the putamen and the caudate nucleus; see e.g., Zatorre, 2015), the insula, the superior and inferior temporal gyri, the anterior and the ventromedial prefrontal

cortices (Mas-Herrero et al., 2021). More specifically, the caudate nucleus and putamen have been shown to play a role not only in musical structure processing and beat perception and generation, but also in the anticipation of musical pleasure, sensation of groove, and chill responses during music listening (see Janacsek et al., 2022 for a review; see also Stockert et al., 2021 for the role of temporo-cerebellar connectivity in the temporal processing of sound).

Neuroimaging findings from groove research suggest a complex picture in which both the ventral and dorsal striatal systems and their interaction within the reward circuitry generate positive affective responses supporting the pleasurable sensory-motor response to music (Matthews et al., 2020). In line with this evidence, computational models and electrophysiological recordings of human and non-human primate basal ganglia show intrinsic low-frequency neural oscillatory activity in the 1–8 Hz range (Marceglia et al., 2007; Terman et al., 2001; Wichmann and DeLong, 1999). Therefore, their activity naturally fluctuates at frequencies that match with the dynamics of musical beat and meter structure and could potentially entrain to music rhythms. On a cautionary note, although these recordings provide interesting insights on basal ganglia's dynamics in a pathological state (in Parkinson's Disease specifically), they may not necessarily reflect the neural dynamics of the basal ganglia in a healthy state. However, it appears that basal ganglia could take part in both the processing of temporal expectations (as theorized by the dynamic attending and predictive coding frameworks) and the encoding of the associated reward value. Finally, at a neurochemical level, dopaminergic transmission has been shown to causally induce music reward hedonic and motivational responses (Ferreri et al., 2019). Importantly, research on patients with Parkinson's Disease suggests a crucial role played by dopaminergic availability in successful rhythmic processing (i.e., beat perception; Cameron et al., 2016; see also Cannon and Patel, 2021). A recent study by Pando-Naude et al. (2023) showed that the inverted U shape reflecting groove responses was not observed in participants with Parkinson's Disease. The link between reward and rhythmic processes might therefore be supported, at a neural level, by the engagement of the same dopamine-dependent brain regions.

By investigating whether music pleasantness influences rhythmic entrainment, Trost and colleagues (2014) showed that more pleasant music (here implemented as consonant music), as compared to less pleasant (i.e., here dissonant) excerpts, facilitated rhythmic processing and increased caudate nucleus activity. Relatedly, Matthews et al. (2020) reported that pleasant-medium complexity rhythms modulated both motor and reward brain networks, with nucleus accumbens, caudate and putamen being associated with ratings of pleasure and wanting to move (see also Stupacher et al., 2022). Note also that links between the basal ganglia, cerebellum, and cerebral cortex have been postulated to show a tight connection between cognitive, motor, and affective areas in the brain also outside of the music cognition literature (Bostan and Strick, 2018).

Taken together, the evidence reviewed so far suggests a strong link between rhythmic expectation and music reward, which seems to be supported neurally by dopaminergic reward-motor pathways. The current opinion paper will consider such pervasive links with the aim to identify research domains and topics, notably focusing on cognitive, sensory-motor, and social mechanisms that could benefit from a better understanding of the relation between rhythm and reward processes. Our aim is therefore twofold: first, questioning whether and how observed results in the music cognition field and beyond could be read and interpreted in light of the rhythm-reward connection; second, to propose and discuss experimental lines likely to promote and stimulate further research in the field across different domains. To this aim, we will first focus on two main topics: (1) learning and memory, and (2) social interaction and connection. In particular, we will consider whether and how synchronization to a rhythmic stimulus can improve learning and memory performance via reward mechanisms. Next, we will discuss how rhythm and reward can influence social connections and social bonding, related to the interplay between self, other, and joint action in interpersonal synchronization. Based on this overview, we will then discuss implications of the rhythm-reward link for the investigation of individual differences, clinical applications, developmental research, as well as for animal research. Outlining the importance of rhythm and reward across these diverse areas aims to propel future research to further investigate this complex, yet fruitful topic.

3. Learning and memory

3.1. Rhythm, learning and memory

Learning and memory processes can be boosted by auditory stimuli presenting temporal regularities over time, such as isochronous rhythms and rhythmic sequences with an underlying metric structure. For example, Selchenkova et al. (2014) showed that learning of an artificial pitch grammar is enhanced when the grammar sequences are presented with a regular (rather than irregular) presentation of the material. Such facilitation appears also when a hierarchical metrical structure (e.g., repeating elements at multiple levels) is present in comparison to an isochronous presentation (Selchenkova et al., 2014). The benefits of temporal regularities have been further shown in the working memory domain. Regularly presented material is better memorized than irregularly presented material, for both tone sequences (e.g., Povel and Essens, 1985) as well as spoken text (e.g., Purnell-Webb and Speelman, 2008). Further, the temporal regularities do not need to be implemented into the to-be-encoded material. Isochronous auditory sequences (in comparison to non-isochronous sequences or silence) presented during the *delay* between encoding and recall in a verbal span task promote the rehearsal of memory traces, in turn enhancing information maintenance and retrieval (Fanuel et al., 2018; Plancher et al., 2018).

Temporal regularities are a critical component also for long-term memory processes. Stimuli presented isochronously or with a temporally regular structure during encoding facilitates the sensory processes at a neural level, thus increasing recognition performance (Hickey et al., 2020; Jones and Ward, 2019; Thavabalasingam et al., 2016; see also Trapp et al., 2018 for sustained benefits of rhythmic stimulus alignment). This facilitation observed on learning and memory can be interpreted within a dynamic attending framework, whereby the entrainment of internal neural oscillations to the temporal regularities of an external regular rhythm can guide attention over time (Jones, 1976, 2016, 2018; Large and Jones, 1999). Consequently, listeners can develop predictions about the temporal occurrence of a future event and allocate more attentional resources to expected temporal moments, thus resulting in enhanced cognitive processing for events occurring at these moments (Jones et al., 2002; see also Escoffier et al., 2010).

3.2. Reward, learning and memory

Learning and memory processes are also intimately related to reward. Indeed, together with the hedonic and motivational components, learning constitutes a crucial component of reward (Berridge et al., 2009). Reward learning is a process by which organisms acquire information about stimuli, actions, and contexts that predict positive outcomes, and by which behavior is modified when a novel reward occurs, or outcomes are better than expected (National Institute of Mental Health, 2022).

At a neural level, the link between time, reward and learning is supported by both animal and human studies suggesting that reward learning is promoted by the predictive or anticipatory nature of mesolimbic dopaminergic activity (Schultz, 1997). In particular, dopamine cells in the vertebrate midbrain can report errors in the prediction of reward, crucially involved in the main forms of learning (such as reinforcement learning; see Glimcher, 2011; Schultz, 2016). More specifically, dopamine neurons are able to anticipate future rewards based on previously learned experience, and update predictions and behavior,

thus resulting in new learning (Schultz, 2016). Furthermore, it has been proposed that the dopaminergic release in the reward system is able to boost long term-potentiation in the mesolimbic-hippocampal loop (involving the ventral tegmental area and hippocampus), in turn facilitating long-term memory consolidation. According to the neo-Hebbian theoretical framework for episodic memory (Lisman et al., 2011), any rewarding stimuli promoting dopaminergic release could boost memory formation and consolidation processing, thus resulting in long-term memory improvement. Accordingly, several studies have shown that secondary reward, such as money (Adcock et al., 2006), but also more abstract rewards, such as curiosity states (Gruber et al., 2014) and intrinsic reward coming from learning itself (Ripollés et al., 2016, 2018) can increase memory performance not only for the rewarding stimulus, but also for the associated, non-rewarding information (e.g., pictures or faces). Crucially, this effect is neurally supported by an increased activation in reward dopaminergic regions and hippocampal formation crucial for memory consolidation (e.g., Gruber and Ranganath, 2019). Along these lines, studies have confirmed a direct implication of music reward in memory formation by showing that the pleasure felt during music listening can improve the retrieval of both musical material (Ferreri and Rodriguez-Fornells, 2017) and non-musical (i.e., verbal) associated information (Cardona et al., 2020). Importantly, there is evidence that the link between musical pleasure and memory is modulated by synaptic dopaminergic availability (Ferreri et al., 2021) and individual differences in music reward sensitivity (Ferreri and Rodriguez-Fornells, 2022).

3.3. Rhythm, reward, learning and memory

As the rhythmic component of music is related to both attentional and reward mechanisms, it can be hypothesized that attentional-predictive mechanisms and reward processes both play a role in the rhythm-facilitating effects for learning and memory performances. It could be, indeed, that the temporal regularities facilitate predictions, thus not only increasing attentional processes, but also promoting the dopaminergic release crucial for learning and memory formation. However, the relationship between rhythm, reward, and learning/memory (through predictions), remains almost unexplored. Therefore, it will be profitable to investigate whether rhythm benefits on learning and memory are, at least in part, mediated by the rewarding nature of auditory rhythmic stimulation.

A way to test this link would be to employ classical paradigms using isochronous auditory stimulation and comparing this to rhythmic stimuli where the degree of rhythmic complexity is manipulated. Medium-complexity rhythms (i.e., showing a medium level of syncopation) promote, as compared to low- and high- complexity rhythms, pleasurable feelings and wanting to move, and recruit the dopaminergic reward network (Matthews et al., 2020; Witek et al., 2014). According to Koelsch et al. (2019), this is due to the fact that, at intermediate levels of syncopation, the system experiences an optimal level of precision-weighted prediction error (i.e., where the prediction itself and the precision of that prediction are moderately accurate). Movement to the rhythm is suggested to enhance the predictability of the rhythm, allowing for more precise predictions (Koelsch et al., 2019; Vuust and Witek, 2014). A natural next step of investigation could therefore be to test whether medium-complexity rhythmic stimulation could result in better learning and memory performance. If dopaminergic-dependent reward responses are at least one of the underlying mechanisms of rhythmic benefits on learning processes, then intermediate levels of syncopation, associated to higher reward responses, should lead to higher learning performance (e.g., artificial grammar learning), improved working-memory maintenance and better long-term retrieval than low- or high- complexity rhythmic auditory stimulation. Please see Fig. 2A for a schematic of these connections.

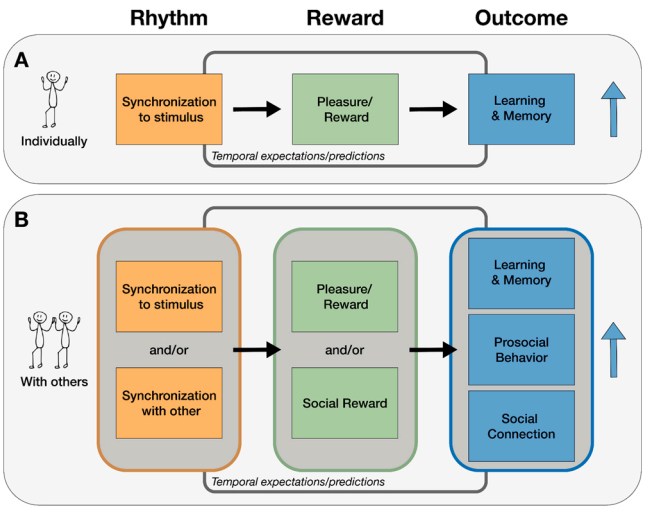

Fig. 2. Schematic presentation of the links between rhythm and reward proposed in this paper, and how these links could lead to enhanced outcomes in relation to learning and memory, prosocial behavior, and social connection. In A) we outline this process at the individual level. Synchronization to a stimulus leads to temporal expectations/predictions, which can directly benefit learning and memory. Adding the reward component could enhance the reward related to synchronization, and boost even further the effect on learning and memory. In B) we show the same individual synchronization pattern, but in a more complex setting, namely with the additional element of synchronization with another person/group. In addition to the reward from this synchronization, there is a social reward component, which can further benefit learning and memory, as well as prosocial behavior and social connection. In both A and B, we suggest that combining rhythm and reward explicitly, for example, by introducing groove music or interesting tension/resolution patterns, can enhance learning and memory, social connection, and prosocial behavior, to a greater extent than through temporal prediction alone.

4. Social connection

4.1. Rhythm and social connection

The regularity and predictability of musical rhythm provides a strong basis to coordinate joint action and facilitate interpersonal synchrony and prediction, both in smaller and larger groups. For example, when dancing with a partner, performing music in an orchestra, or listening to a live musical performance, individuals synchronize both with the rhythm and with each other, providing a social context in addition to the rhythmic information. Importantly, regularities in musical rhythm provide a temporal reference to coordinate large groups of people, even when they are not in direct physical contact (Launay et al., 2016). Such interpersonal movement synchrony, which has been causally linked to synchrony of brain oscillations (Novembre et al., 2017), is a key component of social behavior and interpersonal bonding across different stages of human development (Cirelli et al., 2014; Hove and Risen, 2009; Miles et al., 2009; Rennung and Göritz, 2016; Trainor and Cirelli, 2015), and is seen across all cultures, often related to rituals (Clayton et al., 2020; Dissanayake, 2006; Merker et al., 2009; Rubin, 1995; Turner, 2015).

Interpersonal synchronization, while often appearing effortless, involves highly precise predictive and coordination mechanisms to integrate movements of the self, other, and the collective joint action (Keller et al., 2016; Pecenka and Keller, 2011). Individuals also modify their movements to facilitate interpersonal synchronization and joint action. For example, Vesper et al. (2011) found that participant pairs reduced their temporal variability when pressing keys together compared to individually, and that this lower variability was linked to enhanced interpersonal coordination. This phenomenon has also been shown in musical ensemble performance (Bishop et al., 2019; Glowinski et al.,

2013; Novembre et al., 2019), and research has shown adaptation to a partner's movements at the millisecond timescale (Heggli et al., 2021; Konvalinka et al., 2010; Nowicki et al., 2013). Furthermore, it has recently been shown that the simple presence of another person, without any auditory stimulation, can spontaneously lead to interpersonal motor synchrony (Koul et al., 2023). This adaptation perhaps underlies studies showing that adding a social element can improve synchronization to a beat in children when they are drumming with a partner compared to drumming alone or with a machine (Kirschner and Tomasello, 2009). Adding a social context, including additional elements of adaptation, motivation, attention, and perceived intentionality (see Michael et al., 2020; Mills et al., 2019; Novembre et al., 2012), may aid predictive processing. However, individual differences are relevant, as the benefit of the social context depends on individuals' predictive abilities (Pecenka and Keller, 2011) as well as social competence and personality dimensions (Fairhurst et al., 2014; Keller et al., 2014). Globally, it appears that the additional social context and interpersonal interaction can enhance prediction and decrease temporal variability of synchronization, while also facilitating social connection (see Michael et al., 2020 for a discussion of potential mechanisms involved). Thus, the link between social connection and rhythm processing appears to be mediated by interpersonal synchronization.

4.2. Reward and social connection

Social experiences and social connection are typically rewarding, and have been shown to activate similar dopaminergic reward networks in the brain as nonsocial rewards, such as money and food (Bhanji and Delgado, 2014; Krach et al., 2010). For example, activation of the reward system has been shown when receiving social rewards such as reports that you have a good social reputation (Izuma et al., 2008; Wake and Izuma, 2017) or being liked (Davey et al., 2010). Interestingly, engaging in social activity *without* an extrinsic social reward also activates the reward network, suggesting that social interaction may be intrinsically rewarding. For example, greater activation in social and reward networks (including the ventral striatum) was shown when participants played interactive games with a person through a live video compared to a pre-recorded video (Redcay et al., 2010), or when pairs of friends were sharing an emotional experience (Wagner et al., 2015). Similarly, manipulating eye-gaze of a virtual agent to be more "human-like" resulted in increased activation in the ventral striatum and other reward areas compared to eye-gaze that was computer-directed (Pfeiffer et al., 2014). These studies show that the very act of sharing experiences with another person activates reward areas in the brain, appears to be intrinsically rewarding (Tamir and Mitchell, 2012), and enhances emotional experience compared to having those same experiences alone (Wagner et al., 2015). Further, research has suggested that it may be the *anticipation* of a reward (social or monetary) that activates the ventral striatum and reward network (Rademacher et al., 2010). The importance of social interaction to reward processes has led researchers to suggest that social interactions should be included within experimental studies to form a better picture of these links (Redcay and Warnell, 2018), as social connection and social interaction are strongly linked to reward.

4.3. Rhythm, reward, interpersonal synchronization, and social connection

Music is an ideal stimulus to study rhythm, reward, and social connection simultaneously, as musical rhythm is typically regular (underlying beat), temporally predictable (Koelsch et al., 2018), rewarding (Matthews et al., 2020), and can provide the scaffolding for interpersonal synchronization. Interpersonal synchronization (e.g., dancing together, drumming together) is a pleasurable experience that also facilitates social commitment, possibly through activation of the reward system (Kokal et al., 2011). There appears to be a strong link between synchronization with another person (either listening to the same music or creating music through joint action), social reward, and pro-social behavior (Keller et al., 2014; Rabinowitch and Meltzoff, 2017a, 2017b; Savage et al., 2021; Trost et al., 2017, see also Kirschner and Tomasello, 2010 for children). For example, synchronization with a partner has been shown to increase pain thresholds and result in higher ratings of social bonding (Tarr et al., 2016); increase likeability of the synchronization partner (Launay et al., 2014); and increase social cooperation (Wiltermuth and Heath, 2009), especially in participants with higher empathy (Stupacher et al., 2021). Further, coupling of body sway direction during a speed dating experiment also predicted whether participants were interested in pursuing a long-term relationship (Chang et al., 2021). It has been suggested that these links between rhythm, pro-social behavior, and social bonding may be related to activation of the reward system and release of certain endorphins and chemicals (Savage et al., 2021). For example, increased pain thresholds while engaging in interpersonal synchronization (compared to passive music listening) are suggested to occur due to the release of endorphins (Dunbar et al., 2012; Tarr et al., 2014, 2016). Further, administering oxytocin to participants (compared to a placebo) enhanced their ability to predict a partner's tap timing, resulting in enhanced synchronization and lower temporal variability (Gebauer et al., 2016). Based on this evidence, reward might be a critical element in the link between rhythmic synchronization and social bonding, and could possibly even drive these effects. Please see an outline of this idea in Fig. 2B.

In particular, prediction might be the mechanism by which the dopaminergic reward system is involved in the link between social bonding and music, as suggested by the *music as social bonding* hypothesis (Savage et al., 2021). This hypothesis proposes that specific musical features allowing for temporal regularities (such as discrete pitches generating an isochronous beat or repetitive rhythmic patterns) enhance predictability via the reward system, thus promoting synchronization among individuals (e.g., when dancing), and resulting in positive feelings of predictions with affiliative emotional and rewarding effects (Savage et al., 2021). The strong rhythmicity and predictability of music therefore makes it a crucial facet of this link, which could facilitate interpersonal synchronization and reward. There also appears to be a link between caudate activity during joint synchronization and future prosocial behavior, making interpersonal synchronization socially adaptive (Kokal et al., 2011). It has been suggested that links between social bonding, rhythmic synchronization, and reward may have evolved to allow for social bonding on a large scale as social group sizes increased (Launay et al., 2016; Savage et al., 2021). The capacity of musical rhythm to elicit strong predictive processes can therefore engage the reward system and facilitate interpersonal communication across groups or individuals (Savage et al., 2021).

Together, this research suggests that engaging in synchronous movement with others can facilitate predictive mechanisms (also based on predictive abilities of each individual), activate the reward system, and increase social connection/prosocial behavior. Therefore, it should be fruitful for future research to investigate not only the facilitating link of prediction (and predictive abilities) on interpersonal synchrony, but to further investigate whether the effect of interpersonal synchrony on social connection and social bonding can be modulated by rhythm, and in particular its rewarding nature. For example, highly rewarding music that promotes the experience of groove (Matthews et al., 2020) might act to enhance the social connection between two or more people synchronizing. Groove-inducing music provides the ideal level of complexity in relation to predictive mechanisms and the metrical hierarchy, as it is not perceived as too simple nor too complex by the listener (Vuust and Witek, 2014). It is further possible that adding a social context to synchronization tasks might also improve performance on learning and memory tasks, as there is the added element of social reward. For example, two people synchronizing together with groovy music might perform better on a current or subsequent task than if they synchronized with the music alone (or if they are unsynchronized). In

support of this suggestion, research has shown that participants in a silent-disco paradigm were more likely to remember person-related memory targets of the people they were dancing in synchrony with, compared to those they were dancing out of synchrony with (Woolhouse et al., 2016). Following such studies, it could be hypothesized that interpersonal synchronization to rewarding music should influence not only predictive mechanisms, but also foster social connection and prosocial behavior.

5. Perspectives and new research approaches based on the rhythm-reward connection

5.1. Individual differences

Related to rhythmic reward, the question arises whether the framework outlined above could also be applicable across individual differences research. For example, individual differences in rhythmic abilities and reward sensitivity, together with social behavior traits (e.g., empathy, locus of control), may affect the relationship between rhythm, reward, memory, and social behavior in multiple ways. Even though basic beat perception and synchronization skills appear to arise spontaneously without musical training in humans (Cirelli et al., 2018; Fiveash et al., 2022; Zentner and Eerola, 2010), music training does enhance these skills (Rammsayer et al., 2012), and there are large individual differences in the ability to perceive and produce rhythm, both throughout development, and amongst healthy adults (Bonacina et al., 2019; Fiveash et al., 2022; Grahn and McAuley, 2009; Grahn and Schuit, 2012; Mills et al., 2015; Thompson et al., 2015; Tierney et al., 2017). Such differences can be assessed by dedicated test instruments (e.g., Dalla Bella, Farrugia et al., 2017; Fujii and Schlaug, 2013; Law and Zentner, 2012; Müllensiefen et al., 2014) that typically measure multiple aspects of rhythm processing (Fiveash et al., 2022; Tierney and Kraus, 2015). Some of this individual variation may be due to differences in musical experience or training, and some may be due to genetic factors that influence the development of brain structures and functions that underpin rhythmic abilities (Niarchou et al., 2022). For example, individual differences related to synchronization have been shown for a speech rhythm synchronization task both for behavioral and neural measurements (Lizcano-Cortés et al., 2022). Participants who readily entrained to regular speech and participants who did not entrain were shown to have distinct white matter architecture connecting frontal and auditory regions (Assaneo et al., 2019). Potential other neural correlates related to sources of variation in rhythmic skills include neural responses at early levels of auditory processing (e.g., brainstem responses) and the degree of connectivity between higher-level auditory and motor cortical regions, as well as regions supporting higher-level cognitive and social processes (Chen et al., 2006, 2008; Heggli et al., 2021; Tierney et al., 2017).

Individual differences in rhythmic abilities could affect the reward experience in different ways. First, differences in rhythmic abilities may affect an individual's ability to connect socially to others through interpersonal synchronization, and hence, the reward that could be the result of social behavior. Studies of sensorimotor synchronization have found that inter-individual variations in temporal adaptation and anticipation skills are associated with distinct neural signatures as well as different dimensions of personality, such as empathic perspective taking and locus of control (Fairhurst et al., 2014; Novembre et al., 2019; Nozaradan et al., 2016). These associations might influence the dynamics of social interaction, including leader-follower roles, and the degree to which it is socially rewarding to synchronize with particular individuals. Links between temporal prediction abilities and how well people can synchronize with each other (Pecenka and Keller, 2011) may thus influence the impact of social connection through rhythm on reward. Second, differences in rhythmic abilities may affect the extent to which people experience pleasure in response to music. At the neural level, the extent to which reward networks are activated during synchronization behavior depends on rhythmic abilities of the participants (Kokal et al., 2011). It has also been shown that functional connectivity between auditory and reward regions in general may depend on musical experience, with greater connectivity when people listen to music they are culturally familiar with (Guo et al., 2021). Interestingly, recent findings showed that individuals' *perceived* synchrony with a beat is more associated with groove ratings than the measured synchrony and syncopation (Matthews et al., 2022). This finding shapes an even more complex picture, in which individual differences not only in rhythmic abilities, but also in the subjectively perceived rhythmic skills may drive the pleasurable response to music.

In addition to rhythmic abilities, individuals differ in their sensitivity to reward in general, and music reward in particular. Sensitivity to music reward has been shown to vary in the population (Mas-Herrero et al., 2013), and is at least partly independent from general reward circuitry, as evident from a subgroup of people with musical anhedonia (Belfi and Loui, 2020). To benefit from the potential advantages that the rhythm-reward link affords for memory and social connection, it is likely necessary that in addition to the ability to engage in rhythmic behavior, the sensitivity to (musical) reward should be developed to a sufficient extent in an individual. Recent work has indeed shown that not everyone benefits equally from musical reward in terms of learning and social behavior. First, while pleasure in response to music can increase memory for both the music itself and unrelated information, this benefit depends on individual differences in reward sensitivity, with higher reward sensitivity linked with increased memory (Ferreri and Rodriguez-Fornells, 2022). Second, the extent to which rhythmically synchronous behavior is socially beneficial depends on how much people enjoy the music that the behavior is synchronized to (Stupacher et al., 2020). Thus, individual differences in rhythmic reward sensitivity may influence potential benefits of rhythmic reward both for memory and social bonding. Such findings could be because of lower rhythmic abilities, lower sensitivity to reward, or lower enjoyment of a given musical piece. To fully benefit from the link between rhythm and reward, future research may focus on predicting for whom rhythm may be most beneficial for enhancing learning or promoting social connection. It would also be interesting to investigate whether and how sensitivity to music reward could be trained, with the aim to enhance benefits of the rhythm-reward link on learning and memory and social connection, especially when considering clinical populations (Cochen De Cock et al., 2018).

5.2. Clinical applications

Understanding how rhythm and reward processing interact may be beneficial to further investigate and improve potential music-based therapeutic tools in clinical populations. One clinical example combining rhythm and reward with basal ganglia implication is Parkinson's disease (PD) for which rhythmic auditory stimulation (RAS) has been reported as a promising therapeutic tool (Dalla Bella, 2020; Ghai et al., 2018; Koshimori and Thaut, 2018; Wang et al., 2022; Ye et al., 2022), despite patients' temporal processing impairments (e.g., Dalla Bella, Benoit et al., 2017; Hove and Keller, 2015). Motor symptoms in PD, specifically gait dysfunctions, can be alleviated by presenting patients with rhythmic cues. When a rhythmic cue is present, patients typically show improvements in gait, such as longer stride length and faster walking speed (Dalla Bella, 2020; Ghai et al., 2018; Ye et al., 2022). Although different types of rhythmic cues can be used, music, with its inherent rhythmicity and rewarding nature, may be ideally suited as a cue. The mechanisms underlying the beneficial effects of rhythm for PD patients are still debated. Two hypotheses have been suggested in the literature, involving (a) the residual activation of the basal ganglia by auditory rhythm processing, or, alternatively, (b) compensation of the impaired basal ganglia by activation of a network including the cerebellum (Dalla Bella, 2020; Damm et al., 2020; Naro et al., 2022; Ricciardi et al., 2016). A third hypothesis is that music in

general, and rhythm in particular, leads to a reward response, which could enhance basal ganglia activity and improve gait (Damm et al., 2020). Concerning the latter, one study reported that patients who scored high on the mood regulation and emotion evocation subscales of the BMRQ benefited more from RAS than patients with lower scores, suggesting that sensitivity to musical reward in general (which may include reward related to rhythm) may play a role in the beneficial effects of rhythm on movement (Park, 2022; see also Grau-Sánchez et al., 2018 for similar outcomes in stroke patients). Rhythm seems to have a specific contribution in music with its effects on gait, in contrast to music enjoyment in general, which did not influence gait in healthy adults (Roberts et al., 2021). Future research should now further investigate whether the rewarding aspect of music and rhythm may either in itself lead to motor benefits, or may enhance the effects of rhythmic cues. This may also help us better understand the neural mechanisms underlying rhythmic-based therapies, and how to improve them (e.g., by further exploiting groove, making the connection between rhythm and reward; Hove and Keller, 2015).

Rhythm-based interventions also provide promising tools for improvement in language perception and production skills, both in the normal population and for patients with aphasia, developmental language disorders (DLD) and stuttering (see Fiveash et al., 2021; Ladányi et al., 2020). Rhythmic pacing, auditory-motor combinations and singing help speech production in aphasic patients (Stahl et al., 2011; Stahl and Kotz, 2014), and similar approaches have been proposed for children with Autism Spectrum Disorder (e.g., Wan et al., 2011). Benefits from short-term rhythmic stimulation and long-term rhythmic training have also been reported for children with developmental language disorders who have been shown to have rhythm processing deficits even for non-verbal materials (e.g., Colling et al., 2017; Cumming et al., 2015; Muneaux et al., 2004). Short-term stimulation, such as regular rhythmic music-like excerpts that are presented before naturally spoken speech, has been shown to improve grammatical processing of spoken sentences (Bedoin et al., 2016; Fiveash et al., in press; Ladányi et al., 2021; Przybylski et al., 2013). Long-term stimulation, such as musical training focused on rhythmic processing, has been shown to improve phonological awareness and reading performance in dyslexic children (e.g., Flaugnacco et al., 2015).

Interestingly, for patients with aphasia, rhythmic-based therapy seems to specifically target neural activity in the basal ganglia, with basal ganglia lesions accounting for more than 50% of the variance related to rhythmicity improvements of speech production (Stahl et al., 2011). The role of basal ganglia circuits have been reported also for DLD, together with the frontal cortex in a procedural deficit hypothesis (Ullman and Pierpont, 2005), as well as for stuttering (Alm, 2004; Chang et al., 2016). Patients who stutter also show rhythm processing deficits (e.g., Falk et al., 2015; Sares et al., 2019; Wieland et al., 2015) as well as benefits from external auditory rhythmic stimulation (Toyomura et al., 2011). Taken together, it remains to be tested how the impact of rhythm-based therapies may be related to – and potentially even further boosted by – not only rhythm processing, but also rhythm-related reward.

5.3. Human neurodevelopment

The processing of auditory rhythmic cues develops early in the human brain, even prior to birth. As early as 25 weeks gestational age hearing is functional (Eggermont and Moore, 2012), and structural components of the auditory system allow the fetus to hear the omnipresent rhythmic sounds of the maternal heartbeat and respiration as well environmental rhythms (Parncutt, 2016). The prenatal experience with different forms of rhythmic stimulation (both intra- and extra-uterine) influences the maturation of neural circuits that later support rhythm development (Webb et al., 2015), and hence later rhythmic capacities. Neural evidence suggests late premature and full-term newborns are already sensitive to rhythmic temporal patterns (Edalati et al., 2022; Háden et al., 2015; Winkler et al., 2009), and behavioral evidence suggests that newborns use rhythm to discriminate between language categories (Nazzi et al., 1998; Ramus et al., 2000). Later on and during the first year of life, behavioral and EEG studies show that infants are sensitive to beat and metrical rhythmic cues (Cirelli et al., 2016; Flaten et al., 2022; Hannon and Johnson, 2005; Hannon and Trehub, 2005; Phillips-Silver and Trainor, 2005). These early capacities are impacted by musical/rhythmic experience (Cirelli et al., 2016; Flaten et al., 2022; Zhao and Kuhl, 2016), suggesting high experience-dependent plasticity for rhythm development. Around 5 months, infants begin to move spontaneously to music and adjust their rate of movement to track changes in musical tempo (Rocha and Mareschal, 2017; Zentner and Eerola, 2010). However, generally these movements are not synchronized to the auditory stimuli (Tichko et al., 2022), and it takes years for children to become adept at synchronizing movements. Sensitivity to rhythm and development of rhythm-related capacities continues during older childhood, adolescence, and even into adulthood (Nave-Blodgett et al., 2021; Thompson et al., 2015; Tichko et al., 2022). Exposure to rhythmic auditory signals during infancy and childhood has been associated with improved development of cognitive abilities both in the short- and long-term, in particular those related to language (e.g., Chern et al., 2018; Fiveash et al., 2020; François et al., 2013; Woodruff Carr et al., 2014).

During early development, the rhythmic content of music plays an important role in social bonding and prosocial behavior (a common experience in an infant's social world) (Cirelli et al., 2014). Singing and musical interactions directly improve parent–infant attachment via synchronization (Cirelli and Trehub, 2020; Corbeil et al., 2016; Nakata and Trehub, 2004; Trehub, 2015; Trehub et al., 2015; Vlismas et al., 2013). For example, infant-directed singing has been shown to entrain the social behavior of infants at 2 months and 6 months, and visual cues of the caregiver are also entrained to the rhythm and response of the infant (Lense et al., 2022). These studies suggest early interactions between rhythmicity and cognitive functions (e.g., learning and social bonding), and attest to the positive impact of rhythmic stimulation on cognitive and social mechanisms during early development.

How the rhythm and reward systems develop conjointly is still relatively unexplored, and could provide an interesting future avenue of research to understand the impact of music training and rhythmic exposure on learning and social bonding over development. The sensitivity of the reward system seems to evolve following an inverted U shape, such that adolescents have a reward system that is more responsive, with higher dopaminergic responses to rewards as compared to children or adults (Galván, 2010). This observation raises the question whether this developmental change also impacts music-related rewards. Infants are at the early end of the inverted U shape; however, they still enjoy rhythmic activities, such as being bounced and sung to rhythmically. This, together with studies suggesting that temporal/rhythmic prediction is already functional very early in development (e.g., Edalati et al., 2022; Winkler et al., 2009), suggest that, similar to adults, infants may potentially be sensitive to anticipatory cues in rhythm, its intrinsic reward and benefit for social interaction and joint synchronization. This now opens new venues for research investigating rhythm and reward processes with stimuli like infant-directed speech or singing (e.g., nursery rhymes), which play with rhythmic structures and temporal expectations. Beyond being pleasant for infants (and caregivers), these rhythmic stimulations might be critical for shared attention, learning processes and social bonding (see e.g., Lense et al., 2022). Investigating the modulation of infants' reward responses via the manipulation of temporal expectations during infant-parent interactions (e.g., via more or less predictable turn-taking in infant-directed speech, or via the employment of more or less predictable rhythmic structures in nursery rhymes) might therefore shed new light on the role of rhythm-mediated reward on learning, memory, and social interaction for development.

5.4. Links with animal research

While there are individual differences in both the ability to perceive and produce rhythm and the sensitivity to (rhythmic) reward in humans, most humans have these traits (Mas-Herrero et al., 2013; Tranchant et al., 2016; Tranchant and Peretz, 2020). However, the link between rhythm and reward in other species is not equally clear. Reward is an old evolutionary mechanism in biological organisms, and we can expect it to be conserved in many species, including mammals. However, rhythmic abilities seem less common and developed across species than they are in humans (Bouwer et al., 2021), though this paucity of evidence may in part be due to lack of ecological testing (Henry et al., 2021). Notably, rhythm work in animals amounts to a tiny fraction of human work; to put this in perspective, it was only in 2009 that the wide-spread understanding that beat perception and synchronization was a uniquely human ability was challenged by showing at least partial capacity in some parrots (Patel et al., 2009; Schachner et al., 2009). Since 2009, some animal studies have accumulated, but the field is still far from sketching general trends (see Honing, 2019 for a collection of recent work). We know that several species can synchronize to rhythm or discriminate rhythmic patterns. Interestingly, in many cases, animals only do so if provided an extrinsic reward, such as food reinforcement (Cook et al., 2013; Rouse et al., 2021).

Of particular interest in that respect are several studies in rhesus macaques, where the monkeys were first thought to not synchronize predictively to a metronome (Zarco et al., 2009), but later found to be able to do so if given more frequent, and more targeted, rewards (Gámez et al., 2018; Takeya et al., 2017). Specifically, monkeys could predictively synchronize to auditory and visual metronomes when the reward increased in response to decreased asynchrony, and monkeys were able to generalize predictive synchronization to tempi that had not been trained before (Gámez et al., 2018; Takeya et al., 2017). This may suggest that the difference in rhythmic behavior between humans and other species may not lie in differences in inherent rhythmic abilities; instead, while humans receive intrinsic reward from rhythm, animals in many cases do not, and, like the monkeys in these studies, must be rewarded explicitly for showing predictive rhythmic behavior. However, of note, both studies only used isochronous stimuli, and monkeys required extensive training to perform the synchronization tasks (Gámez et al., 2018; Takeya et al., 2017). Moreover, the monkeys showed better performance with visual than auditory stimulation, contrary to humans, who are biased towards the auditory modality (Gámez et al., 2018). Thus, while these studies tentatively suggest that with proper reward, monkeys have more rhythmic abilities than previously thought, their behavior is still in stark contrast to humans, who can entrain to complex, non-isochronous auditory rhythms without any training. The difference in modality, and the limitation to isochronous stimulation may raise the question whether the mechanism responsible for the synchronization is in fact the same in humans and monkeys (Honing et al., 2018; Merchant and Honing, 2014; Takeya et al., 2017) and therefore, whether monkeys are a good animal model for studying how rhythm and reward are related.

An animal model that may be more informative to the study of rhythm and reward can be found for example in Snowball the cockatoo, one of the most famous examples of animal synchronization. Snowball has been shown to synchronize spontaneously to music without any food rewards (Patel et al., 2009, see also Schachner et al., 2009), and it has been suggested that Snowball may have been driven by a form of social reward (Patel, 2021; Wilson and Cook, 2016). This social reward mechanism is seen in different behaviors across animal species, such as dogs and chimpanzees (Patel, 2021), and may also explain why chimpanzees, in the absence of a sound stimulus, do show interpersonal synchrony in their movement (Lameira et al., 2019). Why then do dogs and chimpanzees not stand out for their rhythmic capacities? It could be that social reward is, in some species, a pre-adaptation for intrinsic reward which in turn is necessary but not sufficient for rhythm (Patel, 2021; see also Merker, 2005). Within and beyond this testable hypothesis, comparative animal work can offer a testbench for scenarios linking rhythm and reward in our species. In particular, one can test which behavioral, neuroendocrine and physiological prerequisites can give rise - in a range of alternative biological scenarios, namely species - to rhythmic reward in humans. However, in doing this, it is important to consider several factors which may provide explanations either alternative or complementary to the rhythm reward hypothesis. First, the species-specific preferences for, and salience of, stimulus features such as rate and modality may differ from those typically found in humans (Henry et al., 2021; Snowdon, 2021). Second, different species may vary in their capacity to process complex auditory information; for instance, olfaction and vision may be more ecologically relevant than audition in some non-human primates as opposed to in humans. Third, other animals may receive different benefits from, and have different goals for, interacting with music or music-like material (e.g., regular sequences) than humans (Kriengwatana et al., 2022). Finally, in some species, music may not be engaging at all (Mcdermott and Hauser, 2007; Ritvo and MacDonald, 2016).

6. Conclusion

In the current paper, we have outlined rhythm research, reward research, and research investigating connections between the two from cognitive and neural perspectives. Rhythm and reward appear to be intricately linked in the brain, and better understanding how rhythm can enhance reward, and how reward can boost synchronization to rhythm can open up a wide array of new research areas. We focused on two domains where both rhythm and reward have been separately shown to be beneficial: (1) learning and memory, and (2) social connection. We highlighted how rhythm and reward might work together in driving the positive effect on cognition and social interaction, and proposed how further studies combining these separate research fields could help in disentangling their interaction and/or boosting their effects. We discussed how this combination can provide important insights and a plethora of new research questions across many populations, tying into individual differences research, clinical applications, human development, and even animal research. This larger perspective shows that both rhythm and reward are integral to the human experience (observed across individuals and across cultures, for example in oral traditions and rituals). The further study of the rewarding nature of rhythm, and the role of reward during synchronization to rhythm can further our understanding across both research fields, resulting in a whole that may be greater than the sum of its parts.

Competing interests statement

The authors declare no competing financial or non-financial interests.

Data availability

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