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Review

Playing music to animals: an interdisciplinary approach to improving our understanding of animals' responses to music

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Humans have profoundly changed the global soundscape. Studying how nonhuman animals respond to music can contribute to a better understanding of the effect of sound on animals. Animals are frequently exposed to human music, whether intentionally (for example, in laboratory settings), or unintentionally (for example, when animals live in close proximity to humans). Although several papers examine animals' responses to music, these typically do so from a purely animal behavioural perspective, sometimes missing relevant details about salient features of the music being played. An interdisciplinary approach that places musical and scientific knowledge on equal footing can improve our understanding of how animals respond to music and music-like sounds, in new and exciting ways. Here, we show with a systematic review that crucial factors (intrinsic music properties, listener properties, playback context and producer properties and contexts; ILPP) are not being adequately considered or reported in recently published scientific articles on the effects of music on animals, which hinders scientific reproducibility within this area of study. These problems are caused by improper referencing of music sources, misunderstanding of music and unexamined assumptions about individual variation and preferences between individuals of the same or different species. We then suggest that Berlyne's psychobiological theory might provide a useful framework for studying how animals respond to human-generated sounds.

As humans alter the landscape to meet our ever-increasing demands for space and resources, we are profoundly changing the global soundscape (Fritschi et al., 2011). This means a large and growing number of free-living and managed nonhuman animals (hereafter, animals) are surrounded by acoustic environments high in anthrophony (i.e. human-generated sound, Krause, 2008; Pijanowski et al., 2011), because they share the same habitat with humans (Applebaum et al., 2023; Eurostat, 2023; Spotswood et al., 2021). For most animals, sound is a vital source of information about their environment and about conspecifics and/or heterospecifics. Anthropogenic sound clearly affects animals' behaviour and physiology (Kunc & Schmidt, 2019). A general understanding of why and what aspects of sounds are salient and meaningful for animals could improve knowledge of how they respond to anthrophony, leading to better management practices that reduce the potentially detrimental effects of anthrophony on wild and captive animals (Elmer et al., 2021).

Some animals actively avoid areas with high levels of anthropogenic sound because anthropogenic noise itself can have negative and costly effects on their behaviour, cognition, immune and other health status indicators (Kleist et al., 2018; Masud et al., 2020; Slabbekoorn & Den Boer-Visser, 2006). In some cases, however, animals may approach human-generated sounds which differ from those of the natural soundscape. For instance, black-chinned hummingbirds, *Archilochus alexandri*, prefer to nest near natural gas wells with noise-producing compressors (Francis et al., 2009). Utilizing animals' attraction to certain sound sources or soundscapes has real conservation potential, as research demonstrates that animals settle into degraded habitats that are made to sound like healthy, thriving habitats (Gordon et al., 2019) and are more

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likely to use passageways with conspecific calls present (Testud et al., 2020). Outside of certain contexts, such as intraspecific communication, prey and predator detection (e.g. Ryan et al., 1993; Ryan & Tuttle, 1983), however, the difference between sounds that animals are attracted to or avoid is not well understood.

MUSIC AND ITS RELEVANCE TO ECOLOGY AND CONSERVATION

Human music (hereafter, music), an instance of anthropogenic sound, is only rarely considered as relevant for ecology or conservation research (e.g. Hooker et al., 2023; Leduc, Nunes et al., 2021). Yet music is present almost everywhere humans are, can intentionally mimic biophony (Doolittle, 2008) and is currently used in animal management practices (e.g. for increasing milk production, Lemcke et al., 2021; reducing anxiety, Kinnaird & Wells, 2022). Thus, music, whether live or recorded, pervades soundscapes in areas where humans spend their time (i.e. live, work and participate in recreation) and could impact the animals that also spend time in those areas.

Understanding how animals respond to music may contribute valuable insights into how animals respond to sound in general. This is because we can vary and test parameters in music, using those known to be important for human perception and response as a starting point. Music can be characterized at different levels: physical acoustic features (e.g. Wiener entropy, amplitude, peak frequency); psychoacoustic features (e.g. timbre, pitch, loudness), which vary across species depending on auditory perceptual systems; and/or musical features (e.g. rhythm, melody, harmony), which emerge due to interactions between perceptual and cognitive systems. Many species of animals show remarkable music perception abilities, which could have arisen homologously or convergently to human faculties for music perception (Hoeschele et al., 2018), and sometimes these abilities are similar to our own (Panksepp & Bernatzky, 2002). This similarity generates predictions about what aspects of sounds might be perceptually salient to animals. For example, some species can recognize particular frequencies ('perfect pitch'; Hoeschele, 2017) and can discriminate between consonant and dissonant intervals, a component of many human musical systems (Izumi, 2000; Watanabe et al., 2005), and a few species can coordinate their vocalizations or movements with an external beat (Cook et al., 2013; Patel, 2021). A better understanding of the saliency of different sound aspects to animals will help to predict their response to music in particular and to anthropogenic sound in general.

Contributions of Musicology to Studies of Animals' Responses to Music

Musicology is a broad, multidisciplinary field in which methodologies from the humanities, arts, social and/or natural sciences are applied to the study of music and its production, perception and appreciation (Parncutt, 2007). Although musicology's focus is on human music, recent decades have seen increasing numbers of cross-species studies. On the one hand, these have come from the natural scientific perspective of evolutionary musicology, or biomusicology (Fitch, 2006; Honing, 2018; Wallin et al., 2000), which aims to illuminate human capacities 'to perceive, appreciate and produce music' and its variation across other animals (Hoeschele et al., 2018, p. 149). On the other hand, zoömusicology has turned musicological expertise and methods from the humanities, arts and social sciences, as well as from ethology and bioacoustics, towards animal sounds (e.g. Doolittle, 2020; Doolittle & Gingras, 2015; Martinelli, 2009; Rothenberg, 2008; Taylor, 2017). Further musicological disciplines relevant to understanding how animals respond to music include acoustics (the physical properties of sound), psychoacoustics (the correlation of sound with psychological sensations and perceptions), music cognition (how music is perceived and cognitively assessed, and the connection between perception and affective and bodily responses) and music information retrieval (the extraction of computational measures of acoustic and musical features from audio).

Rather than review all the effects of music on animals (which has been covered elsewhere: e.g. Alworth & Buerkle, 2013; Kriengwatana et al., 2022; Kühlmann et al., 2018; Wells, 2009), this review highlights important gaps in how animals' perception of music is considered and how this limits our understanding of the diverse effects of music that have been reported. This paper describes features important for music perception in humans and argues that many of these also apply to animals. It subsequently uses a systematic review of studies on the effects of music on animals to evaluate how musical knowledge is critically needed to: (1) improve stimulus choice through a better understanding and characterization of music; (2) ensure sufficient reporting of music sources and description of music stimuli to increase scientific reproducibility; (3) elucidate how animals' perception and response to music are affected by the interaction between music's acoustic features, listener characteristics, playback conditions and producer characteristics and contexts; (4) explore how assumptions of individualism and agency influence the kind of research being conducted on how animals respond to human-generated sound. Finally, we describe how Berlyne's (1971) psychobiological theory may help to understand variable responses and generate novel predictions about how animals might respond to human-generated sound.

Intrinsic and Extrinsic Features in Music Perception

In this section, we describe the contributions of key factors that affect human responses to music. In humans, the perception of music depends not only on (1) its intrinsic properties (e.g. acoustics) but also on extrinsic features; that is, (2) listener properties, (3) playback contexts and (4) producer context and properties (we will collectively refer to these as ILPP). Here, we use the term 'producer' to refer to human composers and performers. We use the term 'listener' to refer to humans or animals that are close enough to the source of music playback to hear it. Fig. 1 visually summarizes the interaction of intrinsic and extrinsic features that influence responses to music in listeners and Table 1 lists examples of each ILPP factor. First, we discuss features known to affect music perception in humans.

Intrinsic features

Intrinsic features refer broadly to time-varying acoustic, psychoacoustic or musical features that can be reproduced from recorded audio. No two recordings of the same piece of music will have identical intrinsic features, due to variation in producer properties and context (see below). The faithfulness of this reproduction will depend on the quality of the playback technology. At the lowest level, the acoustic features of sound waves are typically represented in time and frequency domains, or as spectrograms. Independent of a listener, they include the duration, energy and peak frequency of a sound. Psychoacoustic features, including pitch, timbre, consonance and loudness (Schneider, 2018), arise from the interaction of sound waves with the perceptual system of the listener. Recognition of musical features, such as rhythm, melody and harmony, requires higher-level perceptual and cognitive abilities. The perception of both psychoacoustic and musical features hence depends on the interaction between acoustic features, listener properties and playback context. If music is altered to test

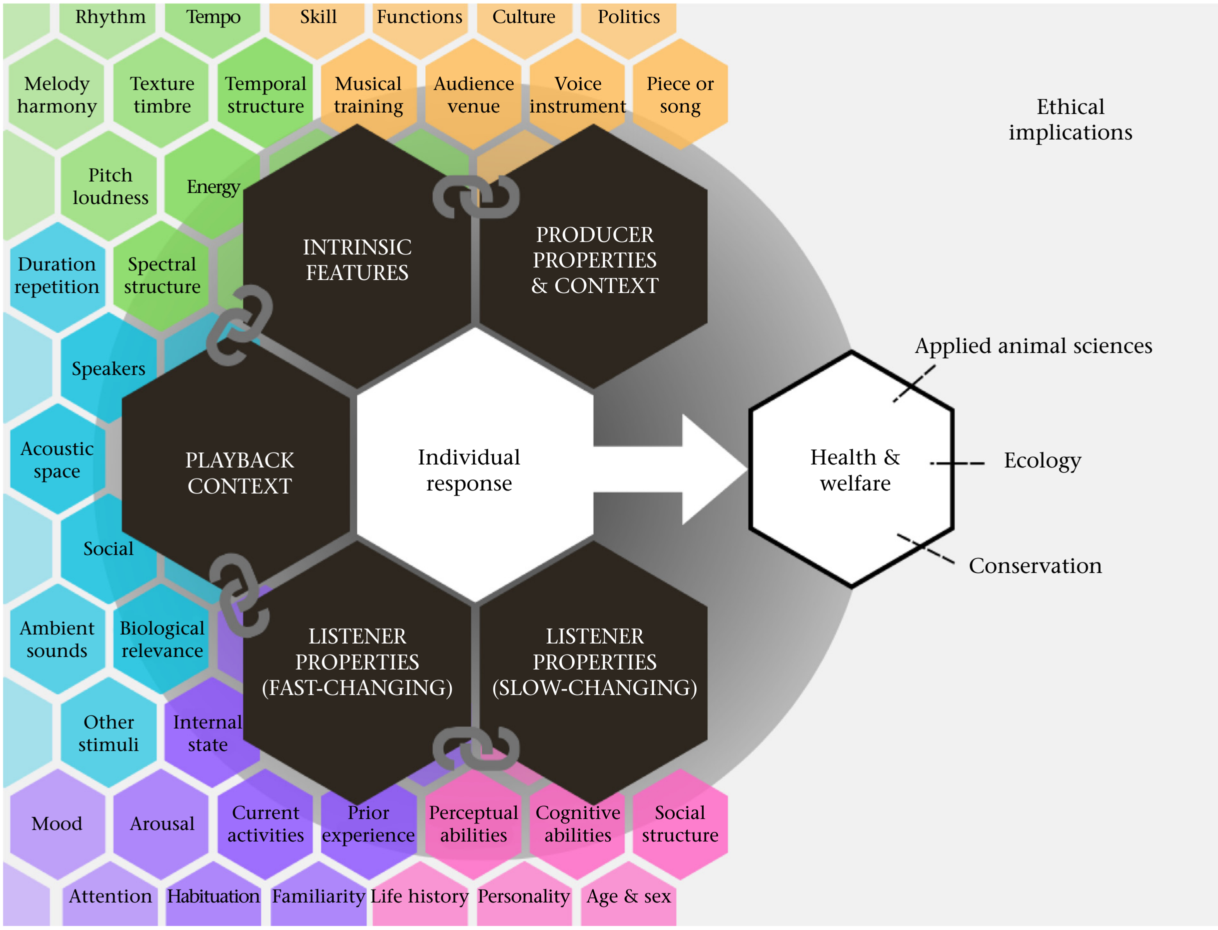

Figure 1. Individual responses to music playback (whether physiological, affective, behavioural or cognitive) may be influenced not only by intrinsic features of audio recordings used as music stimuli, but also by the properties of producers and listeners, and by physical and social aspects of the playback context. In animal studies, experimental designs (represented by the dark grey circle) should take into account all these factors when assessing the impact of music on animals. Ethical implications (represented by the light grey background) should also be considered when designing experiments interpreting the results of animals' responses to music (e.g. related to agency and individualism).

the effect of certain parameters on perception and behaviour, details of any deliberate manipulation made by experimenters to alter how the music sounds (e.g. shifting pitch) should be reported so that music-intrinsic features can be accurately reproduced in future studies.

Listener properties

Listener properties constrain what a listener can perceive, how they will interpret what they perceive and consequently how they will respond behaviourally, physiologically or affectively to music (Kriengwatana et al., 2022). In humans, the effects of music can be influenced by slow-changing (or permanent) and fast-changing listener characteristics. Slow-changing characteristics may include age (Nieminen et al., 2011), sex (Nieminen et al., 2012), perceptual abilities (e.g. assessed through the frequency dependence of audibility thresholds), learning (Krumhansl, 2000), musical training (Broughton et al., 2021), history of musical exposure (Lahdelma et al., 2021), familiarity (Lahdelma & Eerola, 2020; Senn et al., 2021) and preferences (Bodner & Bensimon, 2016). Faster-changing properties include fluctuating internal physical and psychological states, such as mood (Xue et al., 2018) and attention (Koehler & Broughton, 2017; Loui & Wessel, 2007), which are partly determined by activities before or during music exposure. Some of these characteristics can be either slow or fast changing, such as when learning might affect how the person perceives the next sound they hear, or when sudden hearing loss alters what was previously a constant perceptual ability.

Playback context

Playback context refers to the physical and social environment where music is perceived (e.g. concert hall, at home, during a commute), as well as the playback equipment used to deliver music stimuli. The physical space and playback equipment control acoustic and psychoacoustic features of the sounds (e.g. through reverberation and the loudspeaker frequency bandwidth), and can directly influence the emotional excitation of human listeners (Pätynen & Lokki, 2016). In humans, affective responses to music are also modulated by social aspects, such as social feedback (Koehler & Broughton, 2017).

Producer properties and context

Whether precomposed, or produced spontaneously (improvization), the acoustic features of recorded musical performances are only partly determined by properties of their composers and performers (such as voice and/or instruments used). They also depend on the context; that is, the physical, social and cultural-historical setting in which the music is created, performed and/or recorded, as well as on the recording technologies used.

Table 1
Examples of intrinsic, listener, playback and producer (ILPP) features

Intrinsic features	Duration of the piece of music
	Average sound pressure level (SPL)
	SPL range
	Frequency range
Listener properties	Species
	Music experience (fast changing)
	Age (slow changing)
	Sex
Playback context	Ambient sound levels
	Deliberate manipulations by experimenters
	Room acoustics
	Playback equipment
	Presence of humans
	Presence of other conspecifics
	Pauses between pieces within a playback session
	Pauses between playback sessions
	Number of repetitions
	Section of the piece of music
	Total duration of playback
Producer properties and context	Piece of music
	Composer(s)
	Performer(s)
	Live or studio recording
	Release date
	Sampling rate

Producer properties and context refer to aspects of the composition, performance and recording of the piece of music. The resulting recording (audio), when played back, has intrinsic features (acoustic, psychoacoustic, musical) of which some can be measured objectively and described with summary statistics. The responses of animals are further determined by the playback context (including controlled aspects of experimental design), and slow- and fast-changing listener properties.

Research in animal communication suggests that ILPP factors also have potent effects on some species other than humans. Specifically, animals communicate with each other to inform about their internal states, the presence of ecologically relevant events in their environment (Seyfarth et al., 2010) or to manipulate or manage the behaviour of recipients (Rendall et al., 2009). The acoustic structure of a signal is related to the communicative purpose of that signal (form—function relationship) and is evolutionarily conserved over many taxa (Briefer, 2012; Bryant, 2013). We would therefore expect that intrinsic acoustic properties, the listener and the playback context can play a role in influencing animals' responses. In Table 2, we give examples and evidence of why these factors should be considered and reported in animal studies. If there is evidence that animals respond to a feature, we suggest that this must be reported. If evidence is limited to humans, we suggest that it could be reported.

DO ANIMAL STUDIES CONSIDER INTRINSIC AND EXTRINSIC FEATURES OF MUSIC PERCEPTION?

We have made the case that animals not only respond to intrinsic music features, but they may also have the capacity to be influenced by extrinsic features. To determine whether animal studies are considering the whole range of ILPP factors, we conducted a systematic review of original, peer-reviewed research articles in Web of Science published over the last 3 years (between 2021 and 2024) that tested animal responses to music. This is not intended to be an exhaustive review of all studies but to provide a representative insight into the current state of research on effects of music on animals. The search terms we used are listed in full in the Supplementary Material. We chose a range of animal terms to ensure a broad survey of different species while also targeting species that we know have been the focus of research on animal responses to music (e.g. laboratory rodents, Kühlmann et al., 2018; farm animals, Ciborowska et al., 2021; zoo-housed nonhuman primates, Robbins & Margulis, 2014; Wallace et al., 2017; companion animals, Lindig et al., 2020).

We included articles that met the following criteria: (1) animals were passively or actively exposed to music, and their behavioural, physiological, affective or neural responses were measured; (2) the authors described the stimuli as ‘music’ or ‘music-like’. We excluded articles that were: (1) not original, peer-reviewed research articles (e.g. review articles or commentaries); (2) articles that analysed song or music production by animals; (3) articles where neither human experimenters nor animal subjects had control over music stimulus exposure; (4) articles that examined music perception and/or discrimination abilities. For each included article ($N = 76$), we noted if 24 parameters pertaining to ILPP were reported (see Table 1). We additionally noted whether music stimuli were chosen based on genre labels and whether animals had the choice of turning music on or off (i.e. control; total 26 parameters extracted). Full details of our search strategy, PRISMA flowchart and list of included articles are available in the Supplementary Material.

A visual summary of the results is given in Fig. 2. Most studies (97.4%) were on captive animals (74 out of 76 studies). We discuss findings related to each ILPP feature and genre.

Intrinsic Features

Duration of each music stimulus (e.g. song) was reported in 22.7% of studies, which did not include the study using a single frequency (dos Santos et al., 2023). Range of sound pressure levels (SPL) was reported in 46.8% and average SPL was reported in 33.8% of studies.

Listener Properties

Although there is good evidence that both sex and age of an animal can affect its response to sound (Table 1), sex of the study animals was reported in only 77.3% and age was reported in 73.7% of the studies. Some studies reported only the life history stage (e.g. ‘pregnant’, ‘lactating’ or ‘adult’) rather than the chronological age of the animal (e.g. Kamar & Yusof, 2023; Kochewad et al., 2022). Whether animals had prior music exposure was explicitly reported in only 12.2% of studies performed on captive animals, even though captive animals could have experienced music at some stage.

Playback Context

Playback equipment was specified in 36.4% of studies. Room acoustics (room size, enclosure size, soundproofing or building materials used) was reported in 29.7% of studies that were conducted indoors. Ambient sound levels were reported in 20.8% of studies. Social housing conditions (whether animals were housed alone or with other conspecifics) was reported in 67.6% of studies that used captive animals. Human presence during music playback was rarely reported (14.5%).

Duration of total music exposure was reported in 86.5% of studies (this did not include two studies where animals could control how much music they heard; Hirskyj-Douglas & Kankaanpää, 2022, pp. 1497—1511; Truax & Vonk, 2023). Intervals between music playback sessions (when no music was presented) was reported in 78.6% of studies. Intervals were not reported in the two studies where animals could control music presentation and in four studies with only one playback session. Intervals between playback of each music stimulus within a playback session (e.g. transition between songs) was reported in 18.9% of studies not including the two studies where animals controlled music presentation. Repetition (i.e. how many times a music stimulus was

Table 2
Suggested features of stimuli and playback conditions to report (analogous to ARRIVE guidelines, Percie du Sert et al., 2020)

Feature	Must-have (M) or Could-have (C)	Rationale for inclusion with supporting evidence that animals respond to this feature
Species	M	Listener properties that are relevant for music perception and response at the level of species include the species' cognitive ability, hearing ability and social structure/organization. Although listener properties have not yet been systematically evaluated, some of their influences have been noticed. A few studies on music for animal welfare paid attention to animals' perceptual capacities, such as hearing range (e.g. Hampton et al., 2020; Snowdon et al., 2015; Zapata Cardona et al., 2023) or properties of conspecific vocalizations, in predicting how animals will respond (Snowdon et al., 2015; Snowdon & Teie, 2010). Attention is needed to ensure that a stimulus is within the hearing capacity of the species and is not close to sounds that are aversive to that species. There is also an as yet underappreciated relationship between animal communication and social behaviour (Briefer et al., 2024) and it is possible that responses to acoustic stimuli may vary with social organization of a species. There are also listener attributes that vary within species. The most important, and those that can readily be assigned, are discussed in the following rows.
Sex	M	Sex can affect the response to music. For example, in budgerigars, *Melopsittacus undulatus*, males preferred arrythmic stimuli whereas females preferred rhythmic stimuli (Hoeschele & Bowling, 2016). Sex differences may be due to differences in sex-specific behaviours or due to differences in hormonal state. Within a sex, variation in hormone levels associated with different reproductive stages may also affect the response to music; e.g. the probability of response of female túngara frogs, *Physalaemus pustulosus*, to male calls increased with increased gonadotropin levels (Lynch et al., 2006). If the sex of the animals used in a study was not known or not possible to distinguish, then this should be explicitly stated.
Age	M	Sensory ability to perceive stimulus and cognitive capacity to discriminate can vary with age of the animal (Frisina, 2009). There are also other interindividual variation in traits that may influence how an animal responds to music that are less readily identified. Individual responses to acoustic stimuli can vary according to 'temperament' of individuals (e.g. shyer eastern chipmunks, *Tamias striatus*, reacted more strongly to alarm calls; Couchoux et al., 2018) or according to the 'current state and perceived threat' (e.g. at higher ambient temperatures, great tits, *Parus major*, responded in more risk-aversive ways to conspecific mobbing calls; Cordonnier et al., 2023). Animals in different 'affective welfare states' can also respond differently to the same sound in judgement bias tests (Mendl et al., 2009).
Prior experience with music	M	An animal's prior experience with the same or similar stimulus, and experience associated with that, can influence subsequent responses. An animal's response to species-specific sounds can depend on prior experience; e.g. in zebra finches, *Taeniopygia guttata*, females showed a preference for a previously experienced male song (Riebel et al., 2009). We have not found studies testing the effect of prior experience to artificial sounds but, for instance, prior experience of consecutive, repeated exposure to a music stimulus caused habituation in dogs (Bowman et al., 2015).
Piece of music (composer, performer, release date, section)	M	Providing information that pinpoints the music stimulus used is crucial for understanding what animals respond to and for reproducibility. Citation of music sources according to academic conventions can solve this problem, but if this is not possible then specifying performance and release date (in addition to composer) and exact section of music used (if applicable) can help remedy this problem as well. Animals can discriminate between different pieces of music (e.g. Porter & Neuringer, 1984). However, variability among recorded performances, whether by the same or different performers (e.g. differences in expressive style, tempo, vocal timbre and instrumentation) means that specifying the music stimuli by name of the piece or song and the recording artist (or composer, for classical music) does not adequately specify the acoustic, psychoacoustic or musical features of the music stimulus. The release date can specify the exact performance used. Animals such as songbirds can discriminate between birdsong from different populations and individuals (Nelson & Poesel, 2007) and rats, *Rattus norvegicus*, can discriminate between the same piece or song performed by different artists (Okaichi & Okaichi, 2001). Pieces of music usually contain contrasting sections (resulting in 'intraperformance variability'). This means if only part of a larger piece of music is used, the section that has been used should be specified (e.g. track number, movement title, timing) as different sections within a piece of music can be very different.
Duration, pauses and repetition	M	Animals can habituate to a stimulus and stop responding to it, or respond to it negatively, if it is presented often and/or repetitively (Bowman et al., 2017; Sierro et al., 2023). Pauses between music stimuli are also important to report, as animals behave differently towards intermittent versus continuous sounds (Neo et al., 2014) and sometimes prefer silence over sound (McDermott & Hauser, 2007; Truax & Vonk, 2023).
Frequency range and sound pressure level (SPL)	M	Pieces of music will range both in amplitude and frequency. Animals vary in their sensitivity to different frequencies, thus knowing what parts of a stimulus can be heard is important. Loud sounds can be stressful (Kight & Swaddle, 2011) and sounds with higher or lower pitches can induce different behavioural responses from listeners (Morton, 1977). Reporting whether sound meters used to measure SPL are set for human hearing (i.e. 'A' filter or not) may also enable knowledge of what animals are hearing.
Details of deliberate manipulation of stimuli by experimenters	M	During playback of a piece of music its exact attributes can be deliberately manipulated (e.g. sped up, slowed down, played backwards and/or had the tuning altered). Songbirds, for example, have extraordinary temporal discrimination abilities (Dooling & Prior, 2017) and may perceive manipulations not detected by a human listener. Animals can distinguish between variation in sounds produced by humans or conspecifics (Nelson & Poesel, 2007; Okaichi & Okaichi, 2001). Researchers should also report, to the best of their ability, if the music has been compressed and/or equalized, as this will affect the frequencies heard and the variability between loud and quiet sounds. This is required to understand the animal's listening experience and for stimulus replicability.
Ambient sound levels	M	The stimulus of interest may be at least partially masked by background sounds (e.g. machinery in animal rooms, vocalization of other animals present). For a listener to perceive a stimulus, it requires that the ratio of the signal to the background noise (i.e. signal-to-noise ratio, SNR: The difference between signal and noise amplitudes measured in decibels) within a frequency band exceeds a critical detection threshold (e.g. for birds this can range from 18 dB to 37 dB depending on the frequency), and discrimination of the signal from other signals (e.g. perceiving certain attributes of the music as threatening or reassuring) requires an even higher SNR than

(*continued on next page*)

Table 2 (*continued*)

Feature	Must-have (M) or Could-have (C)	Rationale for inclusion with supporting evidence that animals respond to this feature
		detection (de Kort et al., 2024; Lohr et al., 2003). Ambient sounds before and during music playback could be provided as supplementary information.
Social environment	C	The disruption of customary social relationships by the music stimulus may cause stress and change an animal's response to music (Hawkins et al., 2024). Presence of a familiar or unfamiliar human may also affect stress and hence an animal's response to music.
Room acoustics	C	The capacity of a listener to perceive a signal depends on the distance between source and listener and the signal's frequency (as sounds of different frequencies carryover different distances), and this also depends on the environment in which the stimulus is broadcast. So, the distance between sound source and listener as well as room acoustics (size of room, size of enclosure, hard vs soft surfaces) may play a role in how the listener perceives a stimulus. Size of the enclosure will affect whether animals are able to vary their perception (proximity, volume) of the sound stimulus. Audio recordings of the space where animals are exposed to music before and after music playback may be needed to better understand what features of music become more or less salient and/or distorted.
Recording conditions	C	Original recording conditions of a music stimulus should be reported (e.g. studio/live, close-up) to account for the existence of sounds that may change the effect of the stimulus. Some recordings may also contain sounds that are not part of the musical work but may potentially affect the listener (e.g. crowd sounds in live recordings, or Glenn Gould's audible singing in his piano recordings). Acoustic features of live recordings will vary from performance to performance, as performers are influenced by audience presence and feedback, and intentionally or incidentally alter their performance in subtle or obvious ways (LeBlanc et al., 1997; Moelants et al., 2012).
Playback equipment	C	Loudspeaker make and model are important to know, because they affect the frequency distribution and bandwidth that can be produced (for example, bass frequencies are not produced in small speakers). Equipment, therefore, might affect animal responses. All the studies in our literature survey used digital recordings but if a different recording medium or format is used (e.g. analogue tapes) then it should be mentioned.

Most of this information will be captured by appropriately referencing the music stimuli.

repeated) was reported in 9.6% of studies, and did not include the two studies where animals controlled music presentation and the study where a single frequency was used.

Most studies did not intentionally manipulate or alter music stimuli (67.5% of studies). However, out of the 24 studies that did manipulate music stimuli, only six studies (25%) reported sufficient information to replicate the manipulation. In at least one case, the researchers were unaware that the music they played had been lowered in pitch from the original ('"The Division Bell" (pitch at 432 Hz) by Pink Floyd was selected'; Russo et al., 2021), potentially leading to problems should anyone try to replicate the experiment.

Producer Properties and Contexts

Relevant information was extracted from 75 studies (excluding one study that used a single frequency; dos Santos et al., 2023). Sampling rate was reported in 7.8% of studies. Composer information was given in 58.7% of studies. Information about composers as for example 'French classical piano' and 'flute music' (Kamar & Yusof, 2023) refers to a style as determined by region and era, and a broad instrumental category that could include music from many contrasting genres; neither is sufficiently specific. In two cases the music was described as using a particular Indian raga (Kochewad et al., 2022; Rathod & Vaidya, 2024), which refers to a set of melodic patterns and pitch relationships (Kaufmann, 1968). Although naming the composer is not standard for a raga, naming the performer or improvisor and recording would be essential for replicability, as interpretation varies widely, not only between performers but between different performances by the same performer. Several studies used one or more pieces from the same composer. Mozart's compositions were the stimulus in 36.8% of the studies: out of those, 71.4% used Mozart's 'Sonata for Two Pianos in D Major', K.448 and 14.3% used Mozart's string quartets K.428, K.525, K.458. Different pieces by Bach were also used in four studies (dos Santos Lemes Lechuga et al., 2023; Lippi et al., 2022, 2023; Palermo Mendes et al., 2023).

Performer information was reported in only 14.7% of studies, but the same piece of music may differ between performers and animals have been shown to distinguish between vocalizations from different individuals (reviewed in Carlson et al., 2020). Release date (needed to distinguish between multiple recordings made by the same performer that may be different) was reported in only 5.3% of studies. Similarly, live or studio recordings were reported in 5.3% of studies, but live recordings may contain sounds from the audience that animals may respond to. The musical work was named in 58.7% of studies but the specific section(s) of the work the animals were exposed to were named in only 13.7% of studies. Hence, only a minority of studies provided sufficient information on the music stimulus to allow replicability of the study.

Genre

Music stimuli were grouped according to genre in 24 out of 70 studies (34.3%). Six studies did not report sufficient information to deduce whether genres were used (Dong et al., 2024; Epstein et al., 2021; Liu et al., 2022; Mao et al., 2022; Wang et al., 2022; Xu et al., 2022). For example, Mao et al. (2022) and Dong et al. (2024) described their stimuli as 'soothing music' and 'background music', respectively, without further explanation or examples.

WHERE CAN MUSICOLOGY HELP TO IMPROVE STUDY DESIGNS?

Our results show that recent studies on how animals respond to music do not sufficiently consider, control for or report many ILPP factors. As a result, music recordings were generally not described in sufficient detail to pin down specifically which sounds were experienced by an animal. This raises the issue of scientific replicability and confuses any attempts to identify the salient features of the sound environment that animals respond to. It potentially marks an underlying assumption that certain differences that are important to human listeners are not important to other animals (e.g. the performers of a piece of music, even though this factor leads to considerable differences in the audio). We further identified problems related to assumptions about music categories (according to composer or genre), misinformation about music and

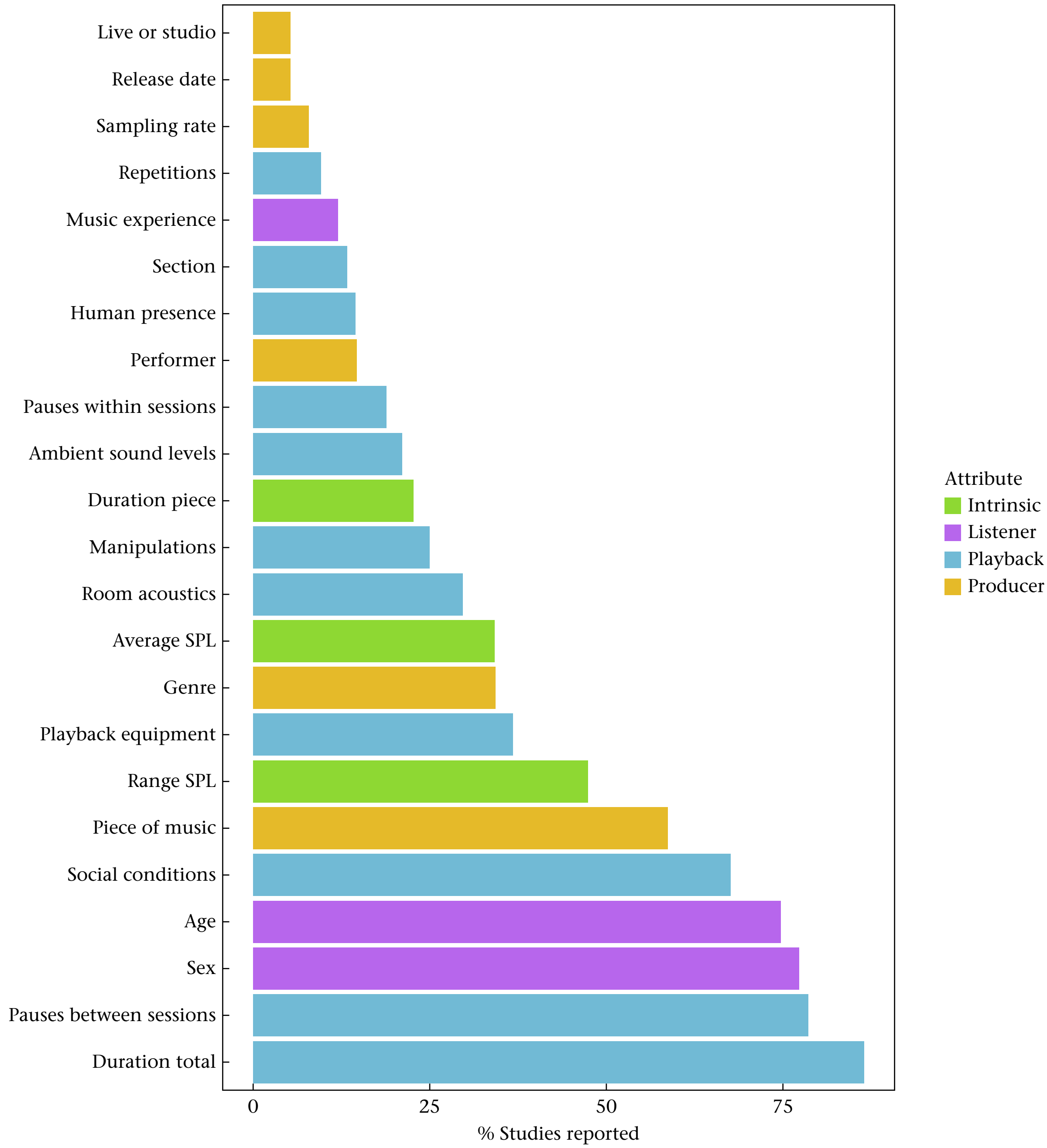

Figure 2. Results of systematic review showing percentage of studies within the last 3 years that report features listed in Table 1.

views of individualism and animal agency that not only have ethical implications but can implicitly/unconsciously shape experimental designs and questions.

Referencing and Citation of Music

Music stimuli should be cited in research papers according to standard scholarly practices used in human music research, giving sufficient information to identify the precise recording(s) used: for example, 'Collins, J. (1970) "Farewell to Tarwathie", Whales and Nightingales [Vinyl]. New York: Elektra Records'. In the case of hard-to-find recordings, citations could be usefully supplemented by providing audio stimuli in digital repositories, or as journal supplementary information. If copyright issues prevent this, recording metadata such as the International Standard Recording Code (https://isrc.ifpi.org/en/) could be provided for each digital track. Table 2 lists and describes the most important aspects of stimuli and playback conditions that animal studies should report to allow understanding of what was played and achieve replicability and reproducibility.

Assumption of Homogeneity for Music From the Same Composer and Genre

Over 30% of studies in the past 3 years continue to simply use genre to characterize the music stimulus. A smaller, but related assumption seems to be that music from the same composer will either sound the same or have similar effects on animals.

Musicological research into automated music genre recognition shows that musical genre categories are not objectively defined nor stable, and that there is considerable variability within genres and overlap between them.

Subjectivity in construction of genre taxonomies and human classification

Music genre recognition (MGR) is used by digital music services to classify music and make recommendations to its users. Within MGR it is widely acknowledged that genre taxonomies (usually conceived hierarchically) are subjective because different taxonomies, whether used for commercial systems (e.g. Spotify) or for research, rarely agree on the names of taxons (e.g. 'classical', 'hard rock') or their location within the hierarchy. Moreover, taxonomies depend on both intrinsic (acoustic, psychoacoustic, musical) and extrinsic (artist, album, country, period) features (Aucouturier & Pachet, 2003; Ramírez & Flores, 2020). This is one reason why individual items may be located in multiple genres (McKay & Fujinaga, 2006; Ramírez & Flores, 2020). Even when categorizations are based on intrinsic features only, these almost inevitably include some features that are predicated on perceptual features of the human auditory system (e.g. Mel Frequency Cepstral Coefficients; Fu et al., 2011) or on human biological responses, and may be inapplicable to other animals. For example, subgenres of electronic dance music are defined in part by the tempo, which is determined in relation to typical human heart rates and/or movement (Burger & Toiviainen, 2020; Chen et al., 2021; Leimeister et al., 2014). There is also disagreement in allocation of musical items within taxonomies between human classifiers, with each other and with commercial systems (Ramírez & Flores, 2020; Schedl et al., 2014).

Change and instability of genre classifications

Rather than taxonomies describing a stable 'order of things', any system of classification depends on who is doing the classifying, what they are doing it for and the methods employed (Sturm, 2014). As tastes and technologies change, genres evolve, spawn new genres and disappear (Aucouturier & Pachet, 2003; Nie, 2022). We note that the number of named genres identified by Spotify using a blend of machine learning and human curation, expanded from 1742 in 2018 (Johnston, 2018) to almost 6000 in 2023 (Krogh, 2023). Furthermore, even the most standard genre labels may refer to categorizations of vastly different bin sizes. For example the word 'classical' is commonly used to refer to enormously varied styles of Western classical music composed throughout Europe and countries influenced by European music since the 9th century, and typically performed in more formal contexts (although it may also be used more narrowly to describe music written in Europe and European-influenced countries during the Classical era, 1750–1820), while 'country' refers to a less diverse grouping of music written and performed primarily (although not exclusively) in the U.S.A. over the past 100 years. Therefore, rather than relying on genres, it may be more fruitful to test how specific ILPP factors and their interactions affect animals.

Misinformation About Music

Because so much musical knowledge is practice based (experiential) rather than traditionally academic, it can be hard for nonmusicians to recognize which sources of musical information are reliable, and which are popular oversimplifications, misconceptions or even conspiracy theories. While most papers in our systematic review avoided perpetuating outright musical falsehoods, some showed the influence of popular music misconceptions, such as belief in the now-largely-debunked 'Mozart effect' (previously discussed in Kriengwatana et al., 2022). While scientists may choose to continue to use Mozart K.448 to maintain consistency across studies, it is important to recognize that Mozart K.448 is not in itself unique, nor does it have a specific 'function in stimulating brain activity' (Luo et al., 2021), and that most of its positive effects could probably be replicated with other pieces of music with similar qualities (such as other piano pieces, other Classical-era compositions, other pieces with a steady rhythm, other pieces in a similar frequency range, etc.), or with nonmusical forms of cognitive stimulation.

Even more troubling is when scientific researchers fall prey to popular music conspiracy theories, including those about the note A being tuned to 432 Hz, and 'solfeggio frequencies'. Substantiable statements, such as 'Evidence supports that music can modulate many physiological roles, exerting clear effects on the central nervous system' (Bidari et al., 2023) become intertwined with conspiracy theories, e.g. 'For this effect to be positive, music should be tuned at a frequency of 432 Hz'; Bidari et al., 2023), and false histories, e.g. 'in the past, musical instruments were tuned to 432 Hz' (Bidari et al., 2023; Russo et al., 2021). In fact, $A = 432$ Hz has never been a widespread or universally agreed upon tuning (Haynes, 2002; Rosenberg, 2021), and according 432 Hz any special significance has to do with numerology based on the scales used in Western classical music and the (arbitrary) length of seconds, rather than any intrinsic characteristics of the frequency itself or its 'resonance' with human or nonhuman bodies or the universe. One study also conflated a legitimate music pedagogical technique (the use of solfège syllables, solfeggio in Italian, to sing the notes of a scale) with a similar-sounding fabrication popularized by New Age entrepreneur David Hulse (2009), 'solfeggio frequencies', citing papers about the pedagogical value of solfège in support of their choice to play 'solfeggio frequencies' to zebrafish (dos Santos et al., 2023). These misconceptions about music hamper a thorough exploration of the effect of music on animals but can be prevented through interdisciplinary collaborations.

Individualism, Agency and Ethical Implications

Among the 76 studies that we reviewed, only two (2.6%), both conducted on captive zoo-housed animals (Hirskyj-Douglas & Kankaanpää, 2022, pp. 1497–1511; Wu et al., 2021), give animals control over their music listening experiences. In the majority of studies we reviewed, animals exposed to music were confined to a small space (cage or stall) and were unable to remove themselves from the music. Human audiences in most cases deliberately choose to listen to music (or are at least free to stop listening). Donaldson and Kymlicka (2011) differentiate between domesticated animals living in close proximity and mutual dependence with humans ('citizens'), liminal animals living in proximity to humans but independent of them ('denizens') and animals who live independently from humans in their own environment ('sovereigns'). This threefold concept helps situate our results in a broader context. Playing music to animals living in mutual dependence with humans ('citizens') on the one hand means that these animals are often habituated to human-generated sounds and might even have been exposed regularly to music, with which they may have positive, negative or neutral associations. On the other hand, they may live in a confined situation that makes it difficult or even impossible for them to choose to avoid music exposure. Free-living, wild animals can have more control over their interaction with human music than domesticated or liminal animals, by adjusting their behaviour (Francis & Barber, 2013). So, the scientific need for a controlled environment for the collection of musical and behavioural data can exist in tension with the ethical need of providing animal participants the choice between listening and not listening.

We would argue that in cases where animals do have control over their sound environment, many species will willingly exert it. The ability to control sound exposure (e.g. by moving away or towards sounds) may contribute to animals' sense of agency, defined as 'the capacity of animals to engage in voluntary, self-generated and goal-directed behaviour that they are motivated to perform' (Littlewood et al., 2023). Increasing sonic agency could lead to immediate and/or delayed impacts on behaviour, physiology and welfare beyond the effects of the sound stimulus itself. Being able to control the sound environment may also affect animals' behaviours towards music and other human-generated sounds in the future. Overall, the present and past choices that animals have had to influence their sound environments, combined with their proximity, experiences and relationships with humans, will probably affect their responses towards music and other human-generated sounds. These ideas are partially supported by Kleinberger et al. (2020), who created a system for a zoo-housed parrot to turn music on or off. The animal subsequently used this to control when they wanted to interact with visitors, as more visitors assembled and interacted with them when they turned the music on, and left when they turned the music off.

Moreover, patterns of sound preference (when and how much sound) exhibited by animals may not match what animals are typically exposed to in passive listening studies. Zoo-housed lemurs that were able to enter or exit a device to trigger or terminate sound playback showed a strong preference for very short durations of sound exposure (order of seconds) and usage peaked during specific hours of the day (Hirskyj-Douglas & Kankaanpää, 2022, pp. 1497−1511). This preference contrasts with the majority of the passive exposure studies, where animals are exposed to music (sometimes the same piece repeated, e.g. 19 out of 76 studies played only Mozart K.448) over and over for hours at a time and at times chosen by experimenters. Although preferences undoubtedly vary between species and are influenced by feeding and husbandry schedules, Hirskyj-Douglas and Kankaanpää's results suggest that there is a good chance that the duration and timing of music exposure used in passive exposure studies may not be what (most) animals want, but the impact of self-chosen short exposure of music on the animals' behaviour and physiology still needs to be studied. In human contexts, the positive or negative effects of music can vary greatly according to when and how the music is played, even if the musical stimulus itself remains the same. Listening to a song once, voluntarily, could be a source of pleasure, while being forced to listen to that same song repeatedly for many hours a day can be unpleasant, or even a form of torture (Grüny, 2020). Other species of animals may well be similar.

While research on music for animals has often been species-oriented, it might be fruitful to consider a broad spectrum of musical interest and receptivity within a species. Animal individualism views that even within a species, each animal is a unique individual, with specific needs, desires, habits, preferences and experiences. It places critical importance on the presence of individual variation: animals in a group or population are not equivalent nor homogeneous. The study of animal personality aligns to a degree with the concept of individualism, in that it recognizes that there is between-individual variation in behavioural responses and that this variation is adaptive (Dall et al., 2004; Dingemanse & Wolf, 2010). While the existence of individual variation in response and preference is not contested and has been reported in music studies (Hirskyj-Douglas & Kankaanpää, 2022, pp. 1497−1511; Truax & Vonk, 2023; Watanabe & Nemoto, 1998), we believe it needs to be emphasized more strongly in studies of animal responses to music (and perhaps to human-generated sounds in general).

Only 12% of studies in our literature search explicitly reported whether animals had prior experience with music and several studies only specify animal age as 'adult'. Here, the assumption may be that responses to sounds do not change with experience and will remain stable and unchanging once animals reach adulthood (perhaps with exceptions during life history stages such as reproduction), which fails to recognize the dynamicity and adaptability of animals.

Lestel (2004) has philosophically conceptualized the 'singular animal', thus hinting at the possibility that in some species of animals, a high degree of musicality and interest in music may be found only in certain individuals. For example, composer and environmentalist Jim Nollman writes of his experience playing music with orcas: 'I next discovered it was not "the orcas" playing with me, but two whales in particular that gravitated to the boat whenever we transmitted.' (Nollman, 2008). Furthermore, whether an individual animal demonstrates a particular response or behaviour or not may be partially context specific. Evidence for highly individualized drumming skills by a single chimpanzee (Dufour et al., 2015, 2017) speaks for the transferability of Lestel's concept to the musical domain. Thus, captive environments require a high degree of awareness for individual and even context-dependent variations in musical preferences and responses, and future studies could pay more attention to individual variation in the response of animals to music and possible factors that may explain between-individual variation.

Assuming that animals must have similar musical interests and preferences to humans would be anthropocentric, and it is necessary to take precautions against unwarranted anthropocentric biases as far as possible. At the same time, anthropomorphism is a more ambiguous concept, neither inherently helpful nor inherently harmful. A cautious, considered, 'critical' anthropomorphism that recognizes the possibility of similar responses to sounds based on shared biological or psychological traits and/or environments may lead to a more considerate use of music with animals. Prum's research on evolutionary aesthetics emphasizes that the subjective experiences and aesthetic decisions of animals have contributed to the evolution of biodiversity, and permits plausible conjectures about the evolutionary shared ancestry of aesthetic preferences and the aesthetic receptivity of different species (Prum, 2018). In this sense, a refined and cautious, animal-centric anthropomorphism (de Waal, 1999) could help us to better understand in which ways animals share human music preferences and interests.

THE PSYCHOBIOLOGICAL THEORY

Berlyne's (1971) psychobiological theory, which aims to explain human aesthetic preferences for art (not only music) by proposing that intrinsic and extrinsic ILPP features interact to affect human listener responses, may provide a suitable framework for understanding animals' responses to sounds in general; for example, music and anthropogenic noise. Even without presuming to know if or how other species of animals might distinguish between 'music' and 'noise' (something that varies even among human cultures), we can use Berlyne's theory to help guide choices about what kind of music exposure may be helpful or harmful for animals.

The theory assumes that there is an optimal level of arousal that follows an inverted U-shape function, where arousal is the physiological and psychological state of wakefulness. The hedonic value of an auditory stimulus therefore depends on how close it brings the listener to their optimal arousal level. Psychophysical properties (e.g. loudness and pitch), ecological properties associated with harmful and distressing or gratifying and beneficial outcomes, and collative properties of the stimulus (which require comparing or collating information from two or more sources, e.g. stimulus novelty, complexity, ambiguity) are presumed to increase or decrease arousal, towards or away from the optimal level.

A key strength of the psychobiological theory is that it accounts for ILPP factors by recognizing that a listener's arousal levels are not always constant, so the hedonic value of the same stimulus can change-over time and context for a single listener. Whether the stimulus is evaluated as having a positive or negative hedonic value can therefore be predicted by assessing the listener's current arousal levels and the amount of increase or decrease in arousal a stimulus is likely to induce.

As a hypothetical example, in quiet environments with minimal stimulation, music and noise (depending on their psychophysical, ecological and collative properties) could increase the animal's arousal to a moderate level, which the animal would find pleasurable. In noisy environments, however, the animal may already be in a high state of arousal and the addition of music or noise could increase it further and beyond the optimal level, which the animal would then find distressing. Berlyne (1966) describes a study where rats were housed in a noisy or quiet environment. Rats housed in the noisy environment were more motivated to hear previously presented sounds rather than a novel buzzer sound (measured as number of lever presses in a Skinner box), whereas rats housed in quiet environments showed the opposite motivation. The psychobiological theory's emphasis on arousal modification could also explain why sound playback might decrease arousal if it completely masks potentially arousing environmental sounds such as predator cues, but increase arousal if it partially masks the predator cue (due to increased ambiguity of the sound; Berlyne, 1971).

The psychobiological theory also has useful predictions for the effects of anthropogenic noise on cognitive performance. Distraction by noise while performing essential activities that require cognitive or attentional resources (e.g. foraging, assessing mates and monitoring predators) is one of the explanations as to why anthropogenic noise is harmful for animals (Chan et al., 2010; Dominoni et al., 2020; Potvin, 2017). The psychobiological theory predicts that (1) noise should affect cognition only if it substantially alters arousal and (2) as with music, how much arousal noise induces depends on the variability of sound characteristics within and among anthropogenic noise recordings used as experimental stimuli (intrinsic features determined by producer properties and context), the individual's perceptual and cognitive capacities and current arousal state, and playback context (including difficulty of the cognitive task).

Noise with very highly arousing properties would disturb performance regardless of task difficulty and the individual's cognitive capacity or current arousal state. If noise causes arousal to increase dramatically, the animal could be less motivated to perform the task and more motivated to escape the acoustic stimulation. Noise with only moderately arousing properties would disturb performance in individuals already in a moderate or higher arousal state, and be more disruptive as task difficulty increases and as individuals have fewer cognitive resources available to devote to the task.

Some of these predictions are indirectly supported by a few empirical studies, but none measures arousal. For instance, pink noise matching spectral and temporal properties of traffic noise affected cognitive performance of laboratory-raised great tits, *Parus major*, in a difficult task, but not in an easy one (Halfwerk & van Oers, 2020). The ability of wild shore crabs, *Carcinus maenas*, and the tide-pool damselfish Sergeant major, *Abudefduf saxatilis*, to find food in laboratory settings was also not affected by boat noise in relatively simple tasks (i.e. in an open arena or in a maze with only two options; Hubert et al., 2021; Leduc, Costa, et al., 2021; Wale et al., 2013). However, performance on more difficult tasks was not measured. Urban noise did not affect learning performance of free-living Australian magpies, *Gymnorhina tibicen*, or black-capped chickadees, *Poecile atricapillus*, that had daily exposure to urban noise (Connelly et al., 2022, 2024; Templeton et al., 2023), which could suggest that familiarity with the noise prevented a significant change in arousal and subsequent effects on cognition. In laboratory-raised zebra finches, *Taeniopygia guttata*, traffic noise was found to affect inhibitory control, motor learning and spatial memory in one study but not in another (Daria et al., 2023; Osbrink et al., 2021). Individual variation in noise-induced arousal might possibly explain these contradicting results.

It would be worthwhile to learn more about the properties of anthropogenic sounds, including noise and music, that increase psychophysiological arousal and by how much, and subsequently to test the relationships between sound presence and characteristics, arousal and cognition, to understand whether cognitive performance is significantly affected when the combination of task difficulty and properties of sound substantially alters arousal.

CONCLUSIONS

Currently, music stimuli are poorly characterized or improperly referenced in the literature, significantly impeding our understanding of how music affects animals' behaviour, physiology and cognition. Genre labels are not a shorthand for intrinsic features of music and do not reliably predict the acoustic, psychoacoustic or musical features of works contained within them. We strongly encourage scientists to collaborate with musicologists to prevent these and other misunderstandings about music in the future. The contributions of sound environments to animal agency remains a relatively unexplored but exciting topic of research. Research into the effect of music on animals can also benefit from the flexible and diverse concept of aesthetic preferences. Thus, we encourage critical reflection on the roles of choice and control of music exposure, and of individual and aesthetic preferences, in scientific efforts to understand how animals respond to music. Finally, viewing music and other anthropogenic sounds from the psychobiological theory's perspective generates novel ideas that can be used to help predict instances where individuals would be more strongly affected and allows for individuality in responses. Equipped with this interdisciplinary approach, we believe future research might avoid the pitfalls we have described, and significantly improve our understanding of how animals respond to music (and possibly other sounds) in new and exciting ways.

Author Contributions

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Declaration of Interest

The authors have no relevant conflict of interest to disclose.

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