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Music for animal welfare: A critical review & conceptual framework

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ABSTRACT

Music can have powerful effects on human health and wellbeing. These findings have inspired an emerging field of research that focuses on the potential of music for animal welfare, with most studies investigating whether music can enhance overall wellbeing. However, this sole focus on discovering what effects music have on animals is insufficient for advancing scientific and practical understanding of how music can be used as an enrichment tool and can also lead to problems in experimental design and interpretation. This paper argues for a different approach to the study of music for welfare, where music is used to address specific welfare goals, taking account what animals hear in music and selecting or creating 'musical' compositions that test current hypotheses about how music is able to influence animal behaviour and physiology. Within this conceptual framework, we outline the process through which perceptual abilities influence welfare outcomes and suggest reframing music for welfare research as *Auditory Enrichment Research* which adopts a targeted approach that does not purpose music as an all-round welfare enhancer but rather investigates whether auditory enrichment can ameliorate specific welfare problems based on species-specific perceptual abilities, needs, and welfare goals. Ultimately, we hope that these discussions will help to bring greater unification, vision, and directionality in the field.

1. Introduction

Interest in therapeutic applications of music in humans has grown over the past 50 years. Some of these studies involve patients being actively involved in the production of music, however many studies involve passive listening, otherwise known as music medicine interventions (Bradt and Teague, 2018). Many clinical studies into the efficacy of music medicine interventions on conditions such as Alzheimer's disease (Fang et al., 2017) and acute pain (Lee, 2016) have demonstrated positive effects on various outcome measurements.

Because of such effects in humans, it has been hypothesised that passive exposure to music might have similar effects on non-human animals (hereafter animals). There is growing attention being paid to the utility of passive music exposure for improving animal welfare or productivity in a broad range of captive environments (Campbell et al., 2019; Hoy et al., 2010; Krohn et al., 2011; Wells et al., 2002) because it is cost-effective, instantaneous, and easy to implement. Consequently, the number of studies that examine the impact of passive music exposure on animals is increasing by the year, leading to a common view that music is likely good for animal welfare.

However, a critical evaluation of how music produces effects on animals is missing. We believe that it is imperative to understand how music affects animals because whether music is "good for welfare" depends on the specific welfare aims and goals for the target animal, the characteristics of the species concerned, as well as the environment that it inhabits. For instance, music can be used to decrease the arousal of stressed and anxious dogs in animal shelters as well as to increase arousal and sensory stimulation in laboratory-housed rats. Mechanistically, these two examples aim at inducing opposite effects on arousal. This shows that, the way music affects animals – both in terms of the mechanism and observed outcome – is not straightforward, and thus a deeper understanding of how music works is needed to help decipher how, and maybe more importantly, what type of music can be used to optimise animal welfare.

Our aim is to change how researchers study the impact of music on animal welfare by challenging the underlying assumption that music can ameliorate an animal welfare problem because it can improve wellbeing in humans. Instead, we encourage an approach from a different

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Table 1
Examples of goals that music could be used to address.

Context	Animal	Goals
Farm	Chicken Pig Fish	- Reduce pecking (aggression) - Increase meat production - Enhance growth - Reduce stress
Animal Shelter	Dog	- Reduce barking/vocalisations (anxiety) - Increase resting & other calm behaviours
Zoo	Elephant	- Reduce aggressive behaviours - Increase affiliative and sexual reproductive behaviours
Laboratory	Rat	- Increase activity - Reduce boredom

direction: Can music ameliorate a specific welfare problem based on what we know about how music produces effects on animals? We believe that the almost exclusive focus on the question of "What effect does music have on animals?" without complementary investigations into questions such as "How does music produce effects on animals?" is insufficient to advance the scientific or practical understanding of the utility of music as an enrichment tool. We focus on first exposing some methodological issues of experimental design and data interpretation and argue that these issues impede a clear grasp of whether and how music is affecting animal wellbeing. Next, we review leading hypotheses about the mechanisms through which music affects animals and suggest that considering animals' perceptual abilities will yield invaluable insights into understanding the how music works and how we can use it to improve welfare. Finally, we introduce a conceptual framework for *Auditory Enrichment Research,* which underlines that music is not necessarily special and should be treated as any other auditory stimulus, and argue that the specific welfare goals, animals' perceptual abilities, and musical features must all be considered when studying how music or other sounds can be used to improve animal welfare.

2. Problems in music welfare research

2.1. Lack of control sounds

The absence of a control group exposed to non-musical sounds, such as white noise (or other) is a problem that permeates the music welfare literature and makes it difficult to discern whether it is really music that is impacting animals. Without such a control group we cannot conclude that it is music, rather than any arbitrary sound being present that has given rise to the observed effect. The prevalence of studies lacking such a non-musical sound control group is not trivial. As an example, in Alworth and Buerkle's (2013) review, only 11 out of the 36 experimental papers on animals (31%) evaluated the effects of music exposure in relation to a non-musical control condition (or non-musical sound exposure period in the case of within-individual designs; Supplementary Data Table 1). In a more recent systematic review on the effect of music in rodents by Kühlmann et al. (2018), 19 out of 38 studies (50%) also did not include a non-musical or noise control.[2] If the data from these reviews are also representative for other studies on the effects of music, then we surely cannot be confident about attributing the observed effects on welfare to music per se. The positive effect of music may be obtained because adding any sounds to the environment improves welfare, a view that is supported by studies showing that even white noise can positively impact welfare measures, for example, attenuating behavioural stress responses and improving short-term memory in non-human primates (Carlson et al., 1997; Kawakami et al., 2002).

[2] Kühlmann et al. (2018) originally included 42 studies, with a total of 23 studies not including a nonmusical or noise control. However, 4 of these records were also cited in Alworth & Buekle 2013 so we did not count these four in the total or the number of studies without a nonmusical/noise control.

Careful consideration of what stimuli are appropriate controls is necessary and such controls should be specific to the hypothesis that is being tested. Depending on the feature of music that is hypothesised to have an effect, control stimuli should match as closely as possible the music stimulus, except from the feature of interest, including its loudness.

2.2. Biased stimulus selection and over-generalisation of results

Studies vary in the extent to which they justify the motivation for choosing a particular piece or type of music, with choices often being seemingly arbitrary. For instance, Western classical music serves as a stimulus in 62% of studies reviewed by Snowdon (2021) with almost half of those studies using compositions by Mozart, and a noticeable number of those using a particular composition, Mozart K.448. This focus on Mozart may be driven by Rauscher and colleague's reports of the "Mozart effect" (Rauscher et al., 1998, 1993), which was an increase in spatial abilities in humans and rats after listening to Mozart K.448. Since then, replicating the effect has been difficult (Steele et al., 1995) and a meta-analysis has suggested that the Mozart effect is negligible in humans (Pietschnig et al., 2010), but this has not deterred researchers from using Mozart K.448 in music welfare research (Li et al., 2021; Saghari et al., 2021).

Choosing experimental stimuli based solely on what has been used in the past risks pseudoreplication and limits generalization of results. Selecting short musical segments such as a segment of Mozart K.448 increases the chances that effects are caused by something that is incidental and specific to that segment and therefore not applicable to other musical stimuli or even to other segments of the same composition. Moreover, if we do not understand why and how Mozart K.448 facilitates cognitive performance, then there is little reason to believe that all compositions by Mozart or classical music as a genre would produce the same facilitative effects. Researchers have cautioned against over-generalisation of results in terms of genre (Snowdon, 2021); nevertheless, the notion that "classical music" is beneficial persists. Musical genre is a subjective human definition and a highly heterogenous category and almost always based on Western music traditions. Without considering the question whether 'genre' has any meaning to an animal, the idea that specific genres of music can be good or not good has no clear scientific foundation. The difficulty of generalising results of exposure to a single fragment or piece of music to a whole category of musical genre is further compounded by potential individual differences in response to music, the small scale of many studies (e.g. a few primates in a zoo; Wells et al., 2006) resulting in small effect sizes and lack of power calculations. As a result, the claimed effects of many studies are substantially under-powered.

In sum, in most studies, the trial-and-error method of stimulus selection has been useful for exploration of the effects of music but we believe it is now necessary to move beyond this stage. Stimulus choice must be based on explicit hypotheses about the features of music that could affect welfare-related variables of interest.

2.3. Inadequate information about music stimuli

Descriptions of music is sometimes a general label (e.g. "radio music", Brent and Weaver, 1996; "harp music", Hinds et al., 2007) or genre name such as "classical music" (Wells et al., 2006) without further details about which specific piece or even how loudly the music is being played. We believe it is important to report as much information about the music or acoustic stimulus as possible, whether it is an unmodified commercial recording or a synthesised soundtrack. These details will facilitate comparison of results across studies and expose potential confounding factors that would otherwise go unnoticed. For example, reducing the dynamic range (the difference between the loudest and quietest passages within a piece) can make all sounds in the passage equally loud and cause the impression that the music overall sounds louder (Deruty and Tardieu, 2014). Dynamic range can differ between types of music, with classical genres (e.g. chamber, choir, opera) showing a larger dynamic range than more modern genres such as rock or rap (Kirchberger and Russo, 2016). Although it is not clear whether a reduced dynamic range in music produces the same perceptual effects in animals, or whether dynamic range is an acoustic property that is even important to animals, there is a chance that the enhanced effects of classical music is due to differences in dynamic range, rather than other features.

3. Mechanisms: what produces the observed effects?

In this section we describe three potential mechanisms that are often put forward to explain the observed effects in music welfare studies (but rarely directly tested). We will discuss evidence supporting and challenging these hypotheses with the aim of identifying gaps in our knowledge and the types of questions that need to be answered to arrive at a clearer picture of how music may be affecting animals. These mechanisms are not mutually exclusive and may be operating simultaneously.

3.1. Masking of aversive or stressful sounds

In captive settings, noise arising from ventilation, human activity, construction, building maintenance, etc. is often unavoidable. As these sounds maybe stressful for animals, music could improve welfare by masking these undesirable ambient sounds (*acoustic masking hypothesis*). This hypothesis implies that animals do not need to perceive music in ways similar to humans at all, as music may simply be another form of noise that is less stressful and/or more tolerable. If music is just noise to animals, then non-musical sounds or different types of music should all produce similar behavioural and physiological effects. In fact, non-musical sounds can have beneficial effects on animals. For example, white noise appeared to render macaques calmer during blood collection (Kawakami et al., 2002) and improve their cognitive performance (Carlson et al., 1997). However, there is some indication that music may have effects beyond just masking noise. Out of the 11 papers that included a non-musical sound control in Alworth and Buerkle's (2013) review, 10 reported that music produced stronger effects than the non-musical control (Supplementary Data Table 1). Different types or pieces of music also seem to differentially affect behaviour and physiology in some animals (Alworth and Buerkle, 2013; Wells, 2009), which further suggests that the impacts of music on welfare are not only due to acoustic masking.

However, two issues of concern arise from using music to mask background noise. First, in many studies, music is played between 60 and 75 dB, which is at least 10 dB louder than ambient background noise that ranged from 35 to 65 dB. This suggests that music might not only mask unwanted background noise but also meaningful communication sounds. In wild animals, acoustic masking of meaningful sounds is thought to be one of the primary reasons why anthropogenic noise is harmful (Slabbekoorn et al., 2010). Second, direct evidence to support the acoustic masking hypothesis is rather limited, as studies do not set out to explicitly test it (it is more often invoked as a post hoc explanation of results). Moreover, studies showing that music is just as effective (or more effective) at decreasing behavioural and physiological indicators of stress as playback of any masking noise are scarce.

3.2. Sensory stimulation

Music's ability to act as a form of sensory or cognitive enrichment is another widely used explanation of why music is beneficial for animals (*sensory stimulation hypothesis*; Wells, 2009). According to this view, the amount and variety of sensory cues that animals are exposed to are reduced in captive settings. Music enhances welfare by increasing the complexity of environments ("richness") that animals can sense, perceive, and respond to, which may stimulate brain development and expression of diverse behaviours. Mechanistically, this hypothesis is feasible because the auditory system is remarkably plastic, with research in birds and mammals showing that the cortical representation of sounds changes depending on acoustic environment in adult and especially in developing individuals (Chang and Merzenich, 2003; Keuroghlian and Knudsen, 2007; Prather et al., 2010). A study by Noreña et al. (2006) used what they termed an enhanced acoustic environment (EAE), which was an artificial sound spectrum of tone pips in different frequencies that was narrower than broadband noise but broader than pure tones. The auditory neurons in juvenile cats exposed to the EAE actually became less responsive to the frequencies in the EAE, but neurons that were originally tuned to the EAE frequencies became more sensitive to frequencies neighbouring the EAE spectrum. This indicates that conceptualizing the relationship between variety and amount of auditory input and brain as "more is better" is oversimplistic and that adding sounds to the environment may have unexpected consequences in the brain, at least for tonotopic organisation. The concept of "more is better" may also not apply if animals are passively exposed to sounds and cannot control the timing and degree of exposure. Even in humans, passive exposure to music also seems to have no long-term beneficial effects on the brain (Eggermont, 2014).

Importantly, the sensory stimulation hypothesis does not specify *how* increased auditory stimulation through music would improve welfare, i.e. it does not define what aspects of music are enriching, and why. Thus, it is unclear whether music should be perceived as such or as a random sound for effects to be obtained. This makes it difficult to properly falsify the sensory stimulation hypothesis. For example, if music is found to improve spatial memory in adult laboratory rats (Rauscher et al., 1998), could it be because the rich sensory experiences afforded by music increased neural activation and/or growth or because hearing sounds in the environment increased arousal and attention which benefited learning of the task? These explanations suggest that music does not need to be perceived as musical to have effects. Moreover, if rats perceive music as random and unstructured noise, then music could have influenced behaviour via stochastic resonance, a phenomenon found in physical and biological systems (reviewed in Douglass et al., 1993; Hänggi, 2002) whereby random noise in a nonlinear system enhances the detection of weak signals (also cross-modally, see Wisenfeld and Moss, 1995). In this case, white noise could be defined as sensory stimulation since it contains high variation in spectral as well as temporal content. Clearly, development of this hypothesis and formulation of explicit predictions is much needed to test and validate how music could improve welfare through sensory stimulation.

3.3. Arousal modulation

We use the umbrella term *arousal modulation hypotheses* to refer to hypotheses stating that music benefits animals by altering arousal. In humans, music has strong effects on physiological measures of arousal (which are suggested to underlie the benefits of music exposure) such as blood pressure, heart rate, respiration rate, and body temperature (Bernardi et al., 2006; Dillman Carpentier and Potter, 2007).

The ability of certain sound features to modify arousal and behaviour in animals was noted by McConnell (1991), who found that across different cultures and species, animal trainers tended to use sounds that were shorter and repetitive to signal animals to initiate movement, and to use sounds that were longer and continuous to signal to animals to cease or stop behaviour. This suggests that some sounds may be connected with specific arousal states and are thus easier to learn to associate with behaviours involving these states. Furthermore, she provided experimental evidence that dogs were more likely to learned to move towards experimenters if the acoustic commands were short, repetitive notes with a rising fundamental frequency as compared to a single long, continuous note with a descending fundamental frequency. Later studies using more complex music stimuli and measuring more complex behaviours, however, show mixed results, with music generally reducing anxiety behaviours in dogs (reviewed in McDonald and Zaki (2020), increasing play in piglets in Zhao et al. (2021) but not in Li et al. (2019), and increasing stress-related behaviours in chickens (Campo et al., 2005). Similarly, the effects of music on physiological arousal such as heart rate, blood pressure, and heart rate variability in different animals do not always find an arousal modulation effect (Bowman et al., 2017; Brent and Weaver, 1996; Hinds et al., 2007; Sutoo and Akiyama, 2004). Thus, music appears to be able to modulate both behavioural and physiological arousal, although inconsistencies between studies may be caused by interspecific differences and studies not testing for effects of specific acoustic features on components of behaviours as McConnell (, 1990, 1991) did.

Besides having an impact on physiological parameters of arousal, music also has powerful effects on emotional arousal in humans (Blood and Zatorre, 2001) and this has also been hypothesised for animals. Based on primate research, Owren and Rendall (2001) suggested that vocalisations can be construed as signals that manipulate receiver behaviour in a predictable manner because they exhibit acoustic features that trigger low-level mechanisms of arousal, attention, and emotion in receivers, or are consistently paired with behaviours (from the sender) that induce emotions in receivers (termed "learned affect"). Thus, human music with acoustic features that tap into sensitivities of a species' perceptual system or have been associated with particular outcomes might be able to induce emotions in other species. Features of music may also coincide with features of animal vocalisation that are cues of an individual's emotional state and induce the same state in other conspecifics through emotional contagion (Snowdon, 2018). Thus, according to emotional arousal modulation hypotheses, music must have properties that are perceptually salient and meaningful to animals to have an effect (Snowdon, 2021). One difficulty with falsifying this hypothesis is the problem of quantifying animal emotions. Physiological arousal is easier to objectively measure than valence but potentially less informative of how musical stimuli are interpreted. It is therefore important to be explicit about the desired effect of a musical intervention and any putative assumptions about emotion, mood, or affect drawn from measures of physiological arousal. Incorporation of behavioural assessments can provide useful insights into valence attributed to music (Zepata Cardona et al., 2022), although there is still no gold-standard measure of emotional states in animals.

4. Relating music perception to the effects of music on welfare

It is clear from the previous section that the hypotheses about the mechanisms through which music affects animals need to be developed further. We believe that this can be aided by knowledge of similarities and differences between human and animal music perception. When humans listen to music we hear a composition, a tonal arrangement, melody, and rhythm. Our ability to perceive these features as a unified whole rather than a collection of arbitrary non-connected dimensions allows us to recognize musical melodies even when aspects of the melody such as tempo and pitch are shifted, which aids our ability to group music into various genres. But do animals perceive music the way we do? Do they also group compositions in a similar manner? At first sight, several experiments suggest this may be so. For instance, carp learned to discriminate blues from classical music and were able to classify novel stimuli from these genres to the correct category (Chase, 2001). Similarly, pigeons trained to discriminate several Bach organ pieces from Stravinky's *Rite of Spring*' generalised this discrimination to novel parts of these compositions or another piece from these composers (Porter and Neuringer, 1984). However, when Bach was exchanged for Vivaldi the pigeons suddenly started generalizing Vivaldi to Stravinsky rather than to Bach. This example illustrates that the feature pigeons apparently attended to was different from what humans attend to. What exactly this was is not clear, as this requires a more systematic and detailed analysis of the perceptual and cognitive processing of the sounds by pigeons. However, we need to be aware that animals might use low-level or local auditory features, such as presence of particular frequency ranges, amplitude variation, tempos or some other feature to discriminate the musical pieces (Hoeschele et al., 2018).

To understand what animals can perceive in music, we thus need to follow an experimental approach in which music is deconstructed into its constituents, such as spectral features (e.g. frequency, spectral envelope, consonance), melody and rhythm, for which the sensitivity is examined. Hoeschele et al. (2018) provide a recent overview of what is known about these abilities, and below we present a brief summary of the findings from this work. Note, however, that animals' abilities to discriminate different sound parameters reveal nothing about their preference for certain sound features, nor tells anything about potential welfare applications.

4.1. Perception of spectral features

The spectral features present in many animal vocalisations often contain biologically relevant information. For example, pitch can convey information about the signaller's quality (Christie et al., 2004) or exaggerate cues of body size (Charlton and Reby, 2016). Different species appear to be differentially sensitive to absolute versus relative pitch. Compared to humans and rats, birds are superior at discriminating pure tones from different frequency ranges (Weisman et al., 2012). But while humans can easily recognize a melody that has been transposed a few semi-tones as the same melody (which relies on relative pitch perception), zebra finches did not recognise songs when the frequencies were shifted up or down by 8% or more ((Nagel et al., 2010 but see Bregman et al., 2012 for better performance in starlings). Animals also differ from humans in perception of timbre (with black-capped chickadees showing poor generalization to novel timbres; Hoeschele et al., 2012), octave equivalence (being absent in chickadees and budgerigars; Hoeschele et al., 2013; Wagner et al., 2019), and consonance (showing mixed results; Hulse et al., 1995; Izumi, 2000; McDermott and Hauser, 2004; Wagner et al., 2020). Thus, the perception of different spectral features of complex sounds involves various types of mechanisms, showing both differences and similarities among various species (e.g. Dooling and Prior, 2017; Hoeschele, 2017).

4.2. Rhythm perception

Animals may show rhythmic elements in their natural behaviour, but this does not reveal whether or what they perceive about rhythmic structures as present in music or other artificial sounds (Bouwer et al., 2021). Several animals can discriminate between regular (isochronous) and irregular (non-isochronous) sequences constructed from identical sound pulses (e.g. (Celma-Miralles and Toro, 2020; Humpal and Cynx, 1984)), but some show poor or inability to discriminate between these sequences (Hagmann and Cook, 2010), or to generalise the discrimination to sequences in which the intervals are shortened or lengthened (van der Aa et al., 2015 but see Rouse et al., 2021), possibly due to their use of local cues (e.g. absolute duration of specific intervals) rather than to the global pattern (ten Cate et al., 2016). Perception of beat and meter are fundamental to human musicality but found in only a few species (Honing, 2018). The ability to perceive beat and synchronise movements to a beat across different tempi (entrainment) was initially thought to be limited to vocal learning species such as parrots (Patel et al., 2009; Schachner et al., 2009). However, the finding of beat perception in a Californian sea lion (that does not vocally imitate sounds), indicates that the ability to entrain to a beat might be more widespread than previously thought (Cook et al., 2013). Nevertheless, similar to spectral features, the perception of rhythmic features also shows substantial variation among species.

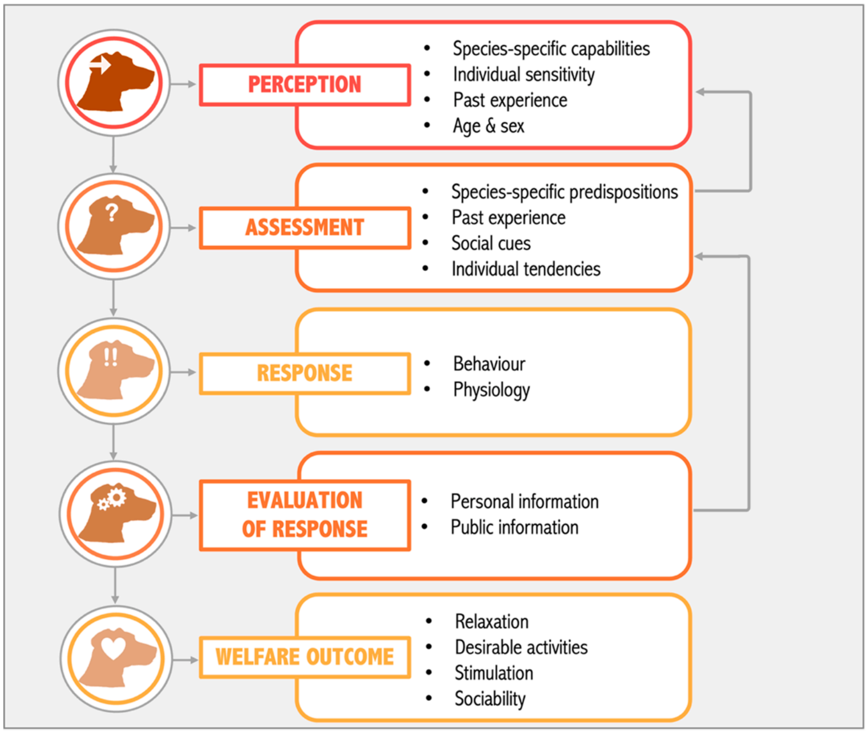

Fig. 1. Process through which perceptual abilities influence welfare outcomes.

4.3. Music may affect animals through shared principles of vocal expression and perception

The summary on animal music perception abilities could suggest that species differences in music perception may be so large that no generalisation about the effects of music on welfare can be made. However, this view might be too pessimistic because there are also some basic perceptual principles that seem to apply across species. As described above, arousal modulation hypotheses suppose that human music can alter (emotional) arousal in other animals because acoustic features that convey arousal are similar across species. These similarities stem from parallels in vertebrate vocal production systems and the effects of emotional and physiological state on these systems and hence on the sounds produced (reviewed in Briefer, 2020, 2012), which allows interspecies recognition of emotional arousal in vocalisations (Congdon et al., 2019; Filippi et al., 2017). Thus, music with characteristics comparable to emotionally charged vocalisations could affect arousal similarly across species if the vocal features that signal emotional arousal are also consistent across species.

Morton's (1977) 'motivation-structural rules' hypothesis proposes that across birds and mammals, vocalisations produced in more hostile contexts are lower frequency, broadband, and noisy compared to those produced in more fearful or friendly contexts, which are more tonal and higher frequency. His prediction about the acoustic structure of hostile vocalisations is generally supported across different birds and mammals but evidence for a consistent structure of fearful/friendly vocalisations is more mixed (August and Anderson, 1987). For instance, cotton-top tamarins vocalisations during high arousal fear and in response to threat were shorter, more frequently repeated, and more broadband and noisier than during friendly social interactions (Snowdon and Teie, 2010). Fear-induced and aggressive vocalisations may include noisy nonlinear elements that are difficult to habituate to or to ignore and that increase arousal and attention in receivers (Blumstein and Récapet, 2009). The attention-grabbing and arousal-increasing properties of these types of vocalisations may make them particularly effective at modifying receiver behaviour in specific ways (Owren and Rendall, 2001). Recently, Briefer (2020) has suggested that hostile and fearful vocalisations may share some common features because they are both characterised by negative valence and high arousal. Accordingly, the relationship between vocal structure and function may become clearer if the two dimensions of emotions (arousal and valence) are distinguished. Her review of mammalian vocalisations indicates that increased arousal is associated with louder and higher rate of vocalisations while increased positive valence is associated with longer duration vocalisations. Furthermore, frequency may communicate the social status of the signaller in relation to receiver, and noisiness may induce the receiver to approach or retreat (Briefer, 2020, 2012). Changes in vocal amplitude, tempo, and duration also support the view that prosodic patterns may be important for conveying emotions in different species (Filippi, 2019, 2016). Thus, these hypotheses provide evolutionary-based explanations for why some types of sounds present in music may induce similar emotions in humans and other animals and a basis from which we can select or create music to induce desirable behaviours and welfare outcomes (Snowdon, 2021; Snowdon and Teie, 2010).

The idea that music with features emulating emotions in vocalisations can alter arousal in animals has some support. Music composed to match the frequency range, pitch, and tempo of positive and negative vocalisations in cats and cotton-top tamarins were approached more often (Snowdon et al., 2015) or induced more anxious or calm behaviours than unmodified human music (Snowdon and Teie, 2010; Hampton et al., 2020). When hearing music with a lowered pitch, dogs increased vigilance behaviour, potentially because they perceived low pitch music as hostile (Amaya et al., 2021). Sounds created to simulate acoustic nonlinearities also increased vigilance behaviours in several animals (Blesdoe and Blumstein, 2014; Blumstein and Récapet, 2009; Slaughter et al., 2013). Additionally, piglets increased gross locomotor activity (walking, standing) to music with faster tempos (Li et al., 2019). Relationships between pitch, acoustic nonlinearities, and tempo/prosody in music and the emotions they induce in humans appear to follow similar patterns as in animals. For instance, when melodies are transposed to a lower pitch, humans perceive these as less polite, less

BOX 1
Outstanding questions.

What contributes to individual variation in response to music?

1. Prior music experience, personality, age, sex, social tendencies
   When should music be played?
2. When, how much, how often? Examination across macro and microscales, i.e. during different life stages (e.g. development), season, or time of day.
   How loud should music be played?
3. Is there a preferred intensity and does this vary depending on life-history stage and species?
   How much variety should there be?
4. When does habituation occur and are there are acoustic features that animals find rewarding but do not easily habituate to?
   How important is agency in auditory enrichment?
5. Does having control over music enhance its effects? What are effective ways of letting animals choose and/or modify their acoustic environment?

Highlights

- There is a growing interest in using music to enhance animal welfare.
- However, studies of music for animal welfare needs to move beyond the simplistic idea that all music can be beneficial for all animals in all circumstances.
- We highlight problems with experimental design, data interpretation, and how consideration of animal's perceptual abilities can inform and advance current hypotheses on how music works as enrichment.
- We propose an *Auditory Enrichment Research* framework where welfare goals, animals' perceptual abilities, and musical features must all be considered when studying how music can be used to improve animal welfare.

submissive and more threatening and vice versa (Huron et al., 2006). Adding noise to music also increased arousal and reduced positive valence in human listeners (Blumstein et al., 2012). Finally, high arousal is induced by faster musical tempos, faster tone attacks and strong duration contrasts between strong and weak elements (Juslin and Laukka, 2003). These parallels between human and animal responses to emotion-mimicking features in music are promising and require further work to systematically explore such relationships in animals. Cross species comparisons must consider that what is slow or low pitched for one species might be fast or high pitch for another and based on characteristics of species-specific vocalisations.

In conclusion, there are features of emotions in vocalisations that generalise across different species, giving rise to specific and testable predictions about music's effects on animals. Nonetheless, a single musical piece, composer, or genre will not affect all animals in the same way because of species differences in perception which are related to the selection pressures that shaped their auditory perceptual and processing mechanisms. Hence, a knowledge of what sounds are important and meaningful for a species is crucial for finding or creating music that will have specific desired effects.

4.4. How music gets under the skin: from perception to response and wellbeing

Perception is the first step through which music can modify animal behaviour and physiology and predicts which music features are likely to have an effect ("*Perception*" in Fig. 1). As we outlined, major constraints and interspecific differences in the perceptual sensitivity to various acoustic features are likely to affect animal responses to music. What is perceived is next subjected to further cognitive processing ("*Assessment*"), which modifies arousal and assigns valence to the stimuli which affects the type and extent of behavioural and physiological responses ("*Response*"). A major influence here will be to which extent the music shares some acoustic characteristics with vocalisations of the species or with other biologically meaningful sounds. Assessment can also be influenced by prior experience, social cues (e.g. observation of others' responses), and individual tendencies (e.g. optimistic or pessimistic biases). The above factors render it highly unlikely that there is a single piece or type of music that can be universally applied and improve welfare for all animals in all situations.

After physiological and behavioural responses are executed, animals can then evaluate and learn about the effectiveness or appropriateness of their responses, especially whether to modify their assessment and response to the stimuli in the future ("*Evaluation of response*"). This feedback step involves using personal and public information (information obtained through direct experience or through observing others' experiences, respectively), and may explain behavioural habituation or sensitization to the effects of music. For welfare applications, being able to predict habituation is crucial for understanding how much variety is important or needed to maintain effects. Feedback also occurs between the levels of *Assessment* and *Perception*, where perception of certain cues can be affected by the valence assigned to the stimulus (Droit-Volet et al., 2013; Zhao and Chen, 2009). Ultimately, the entire process of perceiving, assessing, responding, and evaluating responses to music will determine whether and how music improves welfare, such as by increasing relaxation behaviours, expression of desirable activities, and experiencing adequate sensory stimulation ("*Welfare outcomes*").

There is currently little data on the how experience with music, individual tendencies (i.e. personality or temperament), age, sex, social factors, and social information use can influence an animal's perception, interpretation, and response to music. Even in humans, variation in the amount of musical experience modulates the effects of music on health and physiology (Cervellin and Lippi, 2011) and familiarity can mediate the relationship between arousal and pleasure (van den Bosch et al., 2013). These issues are not addressed in acoustic masking, sensory stimulation, or arousal modulation hypotheses, which shows that there is much room for expansion of existing hypotheses or exploration of novel ones. We summarise these and other important outstanding questions that need to be addressed in BOX 1**.** Acknowledging these questions, such as the influence of experience/familiarity on perception (and thus welfare outcomes) may also motivate researchers to consider distinguishing between the short- and long-term effects of music

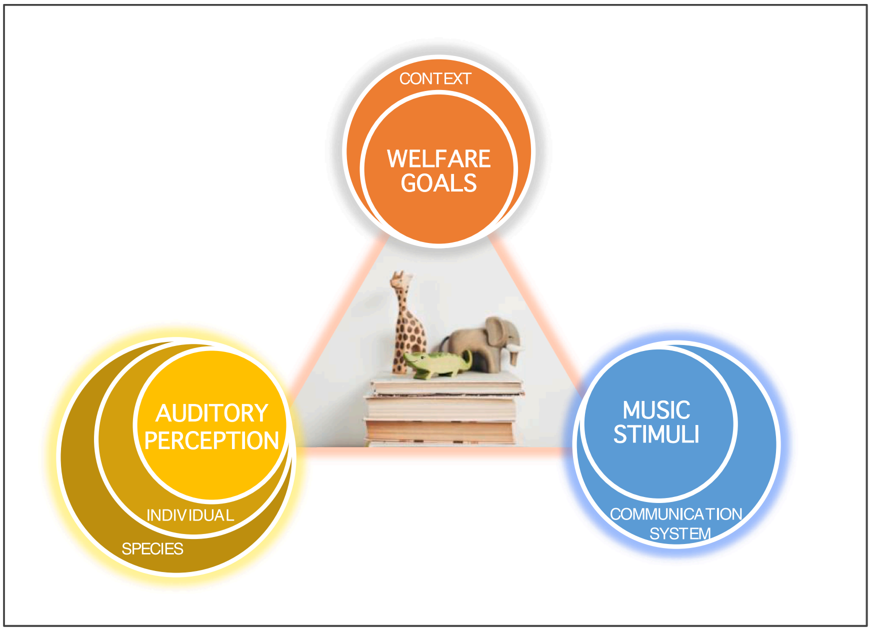

Fig. 2. Conceptual framework for Auditory Enrichment Research, which includes the study of music for animal welfare. Each of the three points in the triangle (welfare goals, auditory perception, and music stimuli) must be considered when designing experiments and interpreting data.

exposure and whether welfare benefits arising from these effects are expected to be immediate or delayed. For example, acoustic masking effects and benefits may be immediate if masking provides relief from frightening sounds. The effects of sensory stimulation on the developing brain may require much longer exposure and induce more permanent effects. Another topic that requires exploration is agency, whereby animals have the opportunity to select, control and modify their own acoustic environment, such as choosing among various sounds or adjusting characteristics of the sounds played to them (Gupfinger and Kaltenbrunner, 2017; Hanson et al., 1976).

5. A conceptual framework for acoustic enrichment research

Based on our views expressed above, we present a conceptual framework for auditory enrichment research that links specific welfare or commercial production goals with knowledge of animals' auditory perception and with the use of music stimuli with features that are perceivable (Fig. 2).

According to this framework, if we want to use music as enrichment, we should not start by assuming that music will improve general welfare, but rather must first carefully establish several points. First, what are the specific welfare goals? That is, what do we want to achieve by playing music to animals? What behaviours do we want to see increased or decreased? The answers to these questions will depend on the species as well as the context (Table 1). Once these goals have been identified, the relationship between animal's perceptual abilities and the sounds played to them must be considered: What musical features can animals perceive? Do they show preferences for some features over others? Finally, the appropriate stimuli should be selected or constructed: Do the stimuli contain features that could produce the desired behavioural or physiological responses? The effectiveness of music, or, for that matter, any other sound stimulus, in modifying responses will be based on the extent to which its features overlap with acoustic features contained in animal's communication systems and other ecologically meaningful sounds. It may be more effective to create novel artificial sound stimuli to ensure that these features are prominent, instead of presuming an existing composition will achieve the desired responses. Creating such stimuli may be guided by bioacoustics knowledge about a particular species and by cautious application of some more general principles such as the motivation-structural rules or general prosodic patterns. Thus, there is a need for systematic studies on the effects of biologically inspired 'music' that is purposed specifically for enrichment.

6. Conclusions

The use of music for animal welfare needs to move beyond the simplistic idea that music can be beneficial for all animals in all circumstances. Specifically, using music to increase animal welfare or productivity must take into consideration what features the focal animal species is able to perceive and how musical features relate to meaningful sounds in its natural auditory world. Comparative research on animal acoustic communication systems and auditory perception provides often overlooked resources that are important for developing, expanding, and testing hypotheses about how music might be used to alter behaviour towards specific welfare goals. Focusing on the relation between animals' perceptual abilities and music stimuli can also elucidate interspecific variation in response to music, and taking individual differences in sound experience and environment into account may improve tailoring the acoustic features and timing of sound stimuli to optimise their effects.

In short, when using music for acoustic enrichment, we need to ask: what acoustic features are important to animals, i.e. what do they signal? Can animals perceive these features in music? Does music with these features exploit the relevant perceptual abilities of the animal, thus leading to a predictable response that we can use to improve welfare? And last, but not least, we must be open to the possibility that further studies may demonstrate that carefully constructed sounds, tailored to a specific species and purpose may be more effective than playback of any existing music.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2022.105641.

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