The major-minor mode dichotomy in music perception: A systematic review on its behavioural, physiological, and clinical correlates

Giulio Carraturo[1,2,3*], Victor Pando-Naude[2], Marco Costa[3], Peter Vuust[2], Leonardo Bonetti[2,3,4,5], Elvira Brattico[1,2]

[1]Department of Education, Psychology, Communication, University of Bari Aldo Moro, Italy

[2]Center for Music in the Brain, Department of Clinical Medicine, Aarhus University and The Royal Academy of Music, Aarhus/Aalborg, Aarhus, Denmark

[3]Department of Psychology, University of Bologna, Italy

[4]Center for Eudaimonia and Human Flourishing, Linacre College, University of Oxford, United Kingdom

[5]Department of Psychiatry, University of Oxford, Oxford, United Kingdom

*Corresponding author:
Giulio Carraturo
Department of Education, Psychology, Communication
University of Bari Aldo Moro, Bari, Italy
e-mail: giulio.carraturo@studio.unibo.it

ABSTRACT

Since ancient Greece, major and minor modes in Western tonal music have been identified as the primary responsible musical feature for eliciting emotional states. The underlying correlates of the major-minor mode dichotomy in music perception have been extensively investigated through decades of psychological and neuroscientific research. This comprehensive systematic review aims to synthesise the literature on musical mode perception and its behavioural and physiological correlates. The qualitative synthesis resulted in 70 studies, showing great diversity in how the major-minor dichotomy has been empirically approached. Most studies were conducted on adults, considered participants' expertise, employed real-life musical stimuli, performed behavioural evaluations, and were published from 2010 onwards. Based on our findings, a framework to describe a *Major-Minor Mode(l)* of music perception and its behavioural and physiological correlates is proposed, incorporating individual factors such as age, expertise, cultural background, and emotional disorders. Limitations, implications, and suggestions for future research are discussed, including putative clinical applications of major-minor perception and best practices regarding stimulation paradigms for musical mode investigation.

KEYWORDS: musical mode, music perception, emotions, individual differences, expertise, emotional disorders, systematic review

HIGHLIGHTS

- Major-minor dichotomy represents the primary emotional feature in Western music
- Major mode is associated with positive emotions, minor mode with negative emotions
- Perception of major-minor mode is influenced by age, culture, personality, and health
- Neurophysiology correlates with basic emotions, pleasantness, not musical mode itself
- Major-minor dichotomy may represent a potential clinical tool for emotional disorders

1. Introduction

A fundamental dichotomy in Western tonal music, linked to the expression of emotional valence in music, is that between major and minor modes. Musical mode is determined by the pattern of tones and semitones in its scales, and the difference between major and minor modes is rooted in the interval between the tonic note and the third degree of the scale. For instance, in C major, the third degree is an E, whereas in C minor the third degree is one semitone lower, i.e., an E flat. Minor mode is expressed with three different scales: natural minor, melodic minor, and harmonic minor. In addition, the modern Dorian mode is often used as a minor mode (**Figure 1**).

Major keys are generally considered to sound bright, happy, and uplifting, while minor keys are associated with sombre, melancholy, or dramatic emotion. However, it is important to note that these associations are not always straightforward or universal, and composers have used both major and minor modes to convey a wide range of emotions and affective states [1,2].

Regarding the different types of minor modes in Western tonal music, each has its own unique characteristics and are often used in different contexts. For example, the natural minor scale is the most basic form of minor scale, and it is simply a minor scale with no alterations to any of the scale degrees. The melodic minor scale, on the other hand, raises the sixth and seventh scale degrees when ascending, but reverts to the natural minor scale when descending. This creates a slightly different sound and allows for more flexibility in melodic writing. The harmonic minor scale, meanwhile, raises the seventh scale degree by a semitone, which creates a strong pullback to the tonic note and is often used in harmonic progression. Finally, the Dorian mode is a minor mode that is based on the second degree of the major scale, and it has a unique sound that is often used in jazz and other styles of music [3].

Western listeners are generally familiar with the major-minor tonal system due to its prevalence in everyday music [4]. Major and minor are indeed the most used modes in Western music, and their structural difference produces prominent distinct emotional responses. Therefore, mode is considered, together with tempo, a strong determinant of musical-emotional responses [5]. Notably, the explicit emotional recognition of music mode develops later in life than the recognition of tempo, and appears to depend on both individual characteristics and cultural factors, especially in the first years of life [6,7]. Previous studies have suggested that musical training and age can further modify major-minor perception and its affective processing [1,8], even though no explicit knowledge of major-minor mode structures is needed in order to produce the related emotional responses [9]. However, there is evidence of large and systematic inter-individual differences, since several factors such as expertise, mood, and personality may affect major-minor perception [2,10–13].

Neural and physiological studies have revealed that major and minor modes of music activate distinct brain regions, with a significantly stronger involvement of limbic structures and reward circuits in response to minor mode [14,15]. However, the findings of these studies are heterogeneous, likely due to differences in methodology and type of stimulation. Interestingly, specific neural activity in response to music mode can be detected already in the very first years of life, as indexed by electroencephalography (EEG) measures studies [16], whereas divergent results have been observed among older children without music training [17]. Additionally, several studies report biased emotional processing of musical features (including musical mode) in both clinical and subclinical conditions [18–21].

There is a vast literature on the behavioural, brain, and physiological correlates of the major-minor dichotomy in music perception. However, the variety of methodological approaches used has hindered a

unifying view and has led to contradictory results. Moreover, previous reviews have explored the behavioural and physiological correlates of other musical features such as rhythm, tempo, pitch, timbre, melody, harmony, and syntax [22,23]. In terms of musical mode, Virtala & Tervaniemi (2017)[1] summarised evidence on the perception of musical mode focusing mainly on the neurocognitive basis of this dichotomy, and suggested that major-minor and consonance/dissonance processing are present early in development and have partly universal, biologically hardwired origins, likely related to human vocalisations [24]. However, brain maturation, musical enculturation, and music training significantly modulate sensory and affective processing. More recently, Asano et al. (2022)[25] conducted a meta-analysis of neuroimaging studies focusing on tonal cognition, with an emphasis on harmony processing, and identified specific brain areas in the right frontal lobe that are similar to those involved in affective speech prosody.

Here, we conducted a systematic review to comprehensively summarise and organise the literature on major-minor mode perception and its behavioural and physiological correlates. Specifically, we aimed to answer several questions: what factors influence individual sensitivity and affective perception of major-minor dichotomy? What types of methods and paradigms are used to investigate it? Can musical mode be seen as a clinical stimulation paradigm? What are the implications of the findings for future research?

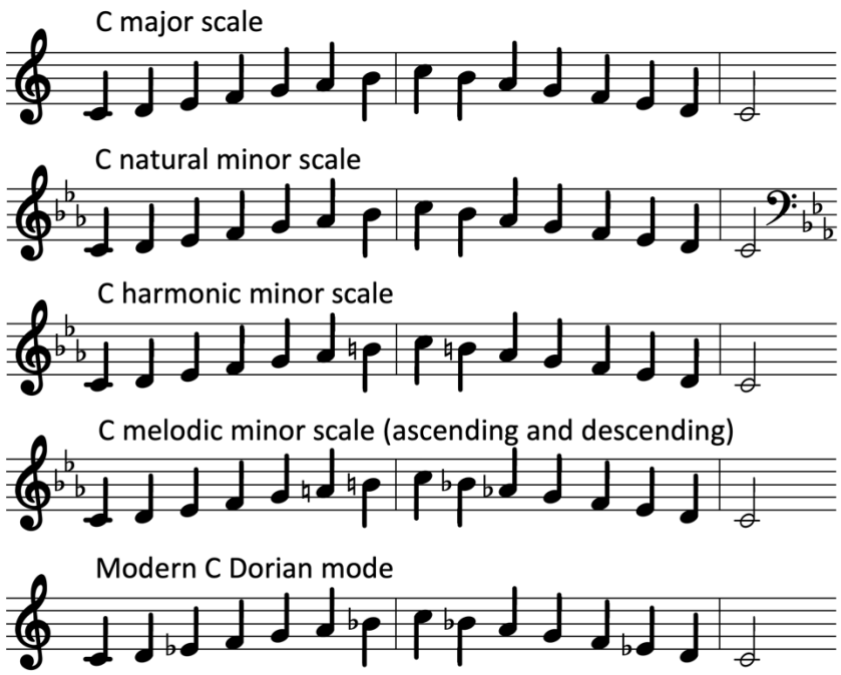

Figure 1. The major and minor modes in Western tonal music. The difference between major and minor modes is rooted in the interval between the tonic note and the third degree of the scale. Major keys are generally considered to sound bright, happy, and uplifting, while minor keys are associated with sombre, melancholy, or dramatic emotion. The natural minor scale has no alterations to any of the scale degrees, while the melodic minor scale raises the sixth and seventh scale degrees when ascending but reverts to the natural minor scale when descending. The harmonic minor scale raises the seventh scale degree by a semitone, and the Dorian mode is a minor mode based on the second degree of the major scale, and it has a unique sound that is often used in jazz. These scales have different unique characteristics and are often used in different contexts in Western music.

2. Methods

2.1. Search Strategy

This systematic review followed procedures form the Cochrane Handbook for Systematic Reviews [26] and from the Centre for Reviews and Dissemination [27]. The review protocol was registered in the International Prospective Register of Systematic Reviews (PROSPERO: CRD 42018090462). The systematic approach was carried in accordance with the PRISMA statement [28]. Three authors (GC, MC, and VPN) each performed a search in the electronic databases Scopus, PubMed and PsycInfo by combining the following keywords and MeSH terms opportunely adapted to each database: music, musician, musical mode, music perception, music performance, music playing, music composition, major mode, minor mode, musical training, expertise, behavioural correlates, individual differences, cognition, emotion, happiness, sadness, valence, arousal, mood disorders, depression, neural correlates, auditory stimulation, magnetic resonance imaging, magnetoencephalography, electroencephalography, evoked potentials, transcranial magnetic stimulation, electrocorticography (details in **Supplementary Information**). The reference lists of the included articles were scrutinised manually for additional publications. The search results were imported to Covidence [29], in RIS or XML format, for screening.

2.2. Study Selection

Three authors (GC, MC, and VPN) independently and systematically screened the literature by titles and abstracts and then read the full texts to identify their eligibility using the Covidence tool. Studies investigating musical mode perception, including all ages and levels of musical expertise, in English, and published in refereed journals were selected. Also, studies in which musical mode was not the main aim of investigation but that offered relevant results to our purpose were included, as well as studies exploring musical mode perception in light of clinical conditions. Studies not in English, not showing relevant outcomes of interest, single cases, reviews, and dissertations were excluded. No years or places of publication were imposed. Any disagreements in the literature search and data extraction were resolved by a fourth author (LB).

2.3. Data Extraction

Data extraction was performed by GC and cross-checked by MC and VPN. The following information was extracted from each study: year of publication, geographical location, number of participants, age group (adults, children, both), musical expertise (musicians, non-musicians, undefined), type of stimulation (chords, excerpts, musical pieces, or tone scrambles), centrality of musical mode in the research questions of each study, and type of method (behavioural, physiological, both). The great variety of stimuli used among the studies was extracted and labelled for each study as “chords” when the stimulation was a single or a short sound (maximum 2s duration), “excerpts” with musical stimuli ranging from 2.5s to 29.5s, or “musical pieces” for all those of 30s or more. Finally, the fourth category of stimuli consists of “tone scrambles”: rapid, randomly ordered sequences of pure tones.

As for the methods used in the reviewed studies, “physiological” refers to methods of brain imaging and brain neurophysiology, as well as psychophysiological measurements such as heart rate and skin conductance; “behavioural” refers to tasks usually involving the affective evaluation of musical stimuli.

2.5. Quality assessment

As there is no universally accepted and evidence-based tool available to evaluate the quality of studies across

different research designs, the task of quality assessment becomes challenging. To comprehensively assess the quality of the included studies in this systematic review, the QualSyst tool [30] was used. This tool offers a comprehensive and quantitative approach to evaluate the quality of research, covering a diverse range of study designs, in a systematic and reproducible manner. A summary score is calculated for each paper by summing the total score obtained across relevant items and dividing by the total possible score (i.e.: 28 – (number of “n/a” x 2)). A score higher than 0.75 suggests high quality, between 0.55 and 0.75 suggests moderate quality, and lower than 0.55 suggests low quality in the study.

3. Results

3.1. Characteristics of included studies

The PRISMA flowchart for systematic reviews (**Figure S1**) and the PRISMA checklist (**Table S1**) provide a thorough overview of the identification, screening, eligibility, and inclusion procedure of studies. A total of 2,406 records were identified through manual and database searching. After removing duplicates, 1,858 articles were initially screened by title and abstract. Next, 386 records were screened by full-text review. Finally, 70 publications were included in the qualitative synthesis, with a total of 4,449 subjects.

Table 1 lists all the studies included in our systematic review and their characteristics. The geographical distribution of the studies is: USA (12), Canada (9), Finland (9), Japan (8), Denmark (6), UK (6), Italy (5), China (3), Australia (2), Russia (2), France (2), Netherlands (1), Portugal (1), Croatia (1), Switzerland (1), Taiwan (1), and Germany (1). This information highlights how studies investigating musical mode perception have been carried out mainly among Western listeners. All in all, most studies (63%) have been published from 2010 onwards. Thirty-eight articles specifically aimed at major-minor mode investigation, whereas in the remaining 32 studies this dichotomy is included but is not the specific focus.

Table 2, which contains a cross-tabulation of the studies as a function of the method and the sample, points out the larger body of research investigating the major-minor dichotomy in the adult population (59) compared to children (6), 5 studies included both groups. Most of the studies (52 out of 70) reported participants' level of musical expertise, although the years of musical training were indicated only in 24 articles (including 4 papers also reporting training time per day/week). Participants' level of education in years was described in very few articles (7 out of 70). Behavioural studies represent most articles reviewed here (33), whereas a few applied exclusively physiological measures (10). The remaining 27 papers applied both physiological and behavioural methods. Studies considering clinical samples are 8, including one study on subclinical population. Finally, we summarised all the main findings relevant to the questions addressed in **Table S2**.

3.2. Types of Stimulation used in Research

In **Table 1**, we indicated the type of stimulation as "chords", "excerpts", "musical pieces" or "tone scrambles". This distinction was necessary considering the variety of stimuli and their durations used in the studies. For instance, some of the studies reviewed employed musical stimuli with a duration of less than 1s [17,31–33], whereas among other investigations, the eliciting stimuli were longer than 5 minutes [34,35], or composed of "non-musical" tone sequences [2,36]. Such methodological differences needed to be identified and considered in the evaluation of the elicited responses. Included in this review are 18 studies using musical chords as stimuli, 32 studies employing musical excerpts, 16 with longer-lasting musical stimuli/musical pieces, 2 including both chords and excerpts, and 2 employing tone scrambles. Arguably, the behavioural and physiological responses elicited by chords or short fragments of music are more likely to be a direct consequence of major-minor dichotomy. Longer real-life music pieces in turn are more ecologically valid since they are more similar to the type of music to which we are exposed every day. However, in the latter, mode may be confounded with other aspects of musical structure conveying emotions.

3.3. Centrality of Musical Mode in the Studies

Most of the papers reviewed consist of investigations specifically aimed at major-minor mode (54%). However, we decided to also include studies not aimed exclusively at investigating this dichotomy since it is

quite common that more than one feature is simultaneously investigated within the same study (such as mode, timbre, and tempo); yet we considered the role of our keyword (musical mode) significant for our questions. The "indirect" role of the keyword could be explained considering that several studies mainly focused on investigating emotional responses to music rather than major-minor dichotomy per se. In this perspective, the distinct affective connotation associated with major-minor mode was often exploited as an inducer of happy/sad emotional responses. Thus, in these studies musical mode was the independent variable, and the emotional response was the dependent variable.

3.4. Quality assessment

The quality of the included studies in this review was comprehensively assessed with the QualSyst tool following the recommendations by Kmet et al. (2004)[30]. Since we did not include any qualitative studies in this review, only the checklist for assessing the quality of quantitative studies was used. Additionally, the review only included observational studies, and no interventional studies, and therefore items 5, 6, and 7 were scored as not applicable (NA). The total scores for each study ranged from 0.32 to 1.0 with a mean of 0.9 ± 0.12. Overall, the included studies showed good practices with high scores in items related to design description and interpretation of results and conclusions; lower scores in items related to subject characteristics and controlling for confounding effects (**Table S3**).

4. Discussion

The major-minor dichotomy is a fundamental aspect of Western tonal music, and it refers to the two most commonly used modes, or scales. The major mode is characterised by a bright, happy, and uplifting sound, while the minor mode is characterised by a darker, sadder, more melancholy, and introspective sound.

In this comprehensive review, we conducted a thorough literature search and selection process that identified 70 relevant studies on the perception of musical mode (54% mode-centred) that included 4,449 participants. While most studies focused on major-minor mode, some studies investigated emotional responses to music, with musical mode being the independent variable, and the emotional response being the dependent variable. The geographical distribution of the studies was mainly in the Western hemisphere, however, the USA, Canada, Finland, and Japan had the most significant number of studies. Also, most of the research was published after 2010. Furthermore, our review shows that behavioural studies represent most articles, with a few applying exclusively physiological measures and others using both. It is also worth noting that the type of musical stimulation used in the studies varied, with some using short fragments of music while others used longer pieces. In terms of the quality assessment, 90% of the studies were scored as high-quality publications, while only one study was scored as low quality.

Overall, our review suggests that the major-minor dichotomy has been a significant focus of research in music perception, although it is often investigated alongside other features of music. It is important to consider the role of musical mode in investigations of emotional responses to music, as this dichotomy can be a powerful inducer of happy/sad emotions, and thus, has potential clinical applications for mood disorders, for example. Here, we propose a framework to describe a *Major-Minor Mode(l)* in music that can be used to provide insights into the ways in which music affects our emotions, cognition, and physiology.

4.1. Affective evaluation of the major-minor dichotomy

The affective evaluation of major and minor modes can be seen in various musical compositions. For example, many joyful and celebratory songs are written in major keys, such as "Happy Birthday" or "The Star-Spangled Banner." These songs use major chords and melodies that are uplifting and energetic, which evoke feelings of joy, excitement, optimism, and celebration [37]. On the other hand, minor keys are often used in music to express sadness, grief, or melancholy. For instance, many funeral dirges or requiems are composed in minor keys, such as the famous "Funeral March" by Chopin or Mozart's "Requiem in D Minor." These pieces use minor chords and melodies that are haunting, sorrowful, and poignant, which evoke feelings of sadness, introspection, and longing.

However, it is important to note that the affective evaluation of major and minor modes is not always straightforward. While major keys are typically associated with happiness, they can also be used to express other emotions, such as anger or sarcasm. For example, "The Entertainer" by Scott Joplin is a lively ragtime piece written in a major key that sounds cheerful and upbeat, but the composer intended it to be ironic and satirical. Similarly, while minor keys are often associated with sadness, they can also convey a sense of mystery, suspense, or even romance. For example, the "Moonlight Sonata" by Beethoven is a well-known composition written in a minor key that expresses a sense of introspection and longing, but also contains moments of beauty and tranquillity.

The valence-arousal model

Music is a complex and powerful medium that can evoke a wide range of emotions and experiences in

listeners. However, the link between music and emotions can be intricate and not always apparent. The same piece of music can elicit different emotional responses in different people, and individual differences such as personality, musical preference, and cultural background can all play a role in shaping listeners' emotional experiences, as it will be discussed later. One way that researchers have tried to understand the emotional impact of music is through the so-called valence-arousal model.

Whilst the association between musical modes and distinct emotional responses dates back to the Greek theorists and has been debated along the whole history of music [38], the first scientific report that highlighted the affective connotation of musical modes was by Hevner (1937)[39], who asked listeners to classify musical excerpts with "sad" or "happy" adjectives. The results indicated that major mode was associated with "happy" adjectives whilst the participants selected more "sad" adjectives when the music was played in minor mode. The affective dichotomy major/happy minor/sad has been confirmed over the following decades, and other specific emotions have been studied related to this dichotomy. For example, the major mode has been associated with an experience of joy, serenity and vitality, whereas minor mode tends to be perceived as nostalgic, subdued, dark and wistful [5,6,40,41].

At its core, the valence-arousal model suggests that emotions can be described using two primary dimensions: valence and arousal. Valence refers to whether an emotion is positive (e.g., happy, content) or negative (e.g., sad, angry) [42]. Arousal, on the other hand, refers to the intensity or activation level of an emotion, ranging from low arousal (e.g., calm, relaxed) to high arousal (e.g., excited, energised) [43]. The valence-arousal model has been widely applied in music research, with studies using it to explore how different types of music affect listeners' emotional experiences [34,35,44].

Pleasure and reward

The major-minor dichotomy has been explored in various studies to understand the relationship between music, pleasure, and reward. In terms of musical pleasure, research has shown that people tend to prefer music in major mode, given the positive psychological character generally associated with it [34,45]. One influential theory is that listeners experience a sense of reward or pleasure when they are able to anticipate and predict the harmonic structure of a musical piece [46–49]. According to this theory, the major-minor dichotomy is particularly important because it creates expectations about how a piece of music will unfold. When listeners can accurately predict the next harmonic change, they experience a sense of satisfaction and pleasure. In Hunter et al. (2008)[50], for instance, participants were asked to rate musical excerpts using scales for happiness/sadness and pleasantness/unpleasantness, with the results showing that listeners found music they rated as happy also pleasant and, vice versa, sad music tended to be considered unpleasant. However, minor mode is not exclusively related to unpleasant judgments. Indeed, according to Vuoskoski and Thompson (2012)[51], two personality traits, openness to experience and empathy, are associated with liking sad music. Similarly, Bonetti & Costa (2016)[10] found that the preference for short melodies in minor mode is positively related to the level of fluid intelligence and openness to experience.

All the mentioned studies investigated Western music and Western listeners, nevertheless, other studies found some commonalities in music-induced emotions also among people of other cultures. Specifically, both Hoshino (1996)[52] and Fang et al. (2017)[53] found that excerpts in major mode induced pleasure and happiness, whereas the ones in minor mode were associated with greater tension among Japanese and Chinese people, respectively, consistently with studies on Western listeners. This evidence seems to suggest that the affective connotation of musical mode might rely on a universal dimension. However, a recent cross-cultural study conducted between Australia and Papua New Guinea, reported that major mode does not induce greater

happiness than minor in a group of people with minimal exposure to Western music [54]. This remarks that the typical major/happy minor/sad association might partly be a culturally learned association.

4.2. Association between type of stimulation and elicited behavioural and physiological responses

The reviewed studies aimed to investigate the perception of musical mode using a variety of stimuli such as chords, excerpts, musical pieces, and tone scrambles (**Table 1**). The major mode was perceived as relatively happy and bright, whereas music in minor mode tends to be perceived as dark and sad [39,55]. Isolated chords and very short melodies prove to represent sufficient stimulation to elicit these distinct affective responses [6,9,56]. Consistently, major and minor chords evoke differential responses both on a physiological and neural level regardless of whether they are presented in isolation[57], inserted in an oddball paradigm [16,32,58], or in a sequence [15]. Moreover, musical expertise is partly reflected in terms of perceptual differences of major-minor chords and its implications will be further discussed [17,31,32].

Behavioural

Regardless of stimulus duration, in studies employing pure tones, the listener's ability to discriminate between major and minor modes appears lower, resulting in a reduced perception of the characteristic major/happy and minor/sad association [2,36,59]. Most of the reviewed studies (70%) used longer-lasting stimuli, and in the bulk of them, musical excerpts and melodies were selected based on previous music research. In a few studies, the excerpts/melodies were composed for the purpose [6,21,60–62], a customised selection of real songs/excerpts [50,63–66], and partly even chosen by the participants [11]. Presumably, a longer duration increases the possible effects arising from other musical features besides mode, such as tempo, rhythm, or timbre, resulting in independent variables difficult to control for. Indeed, different durations of real-life musical stimuli may also be associated with different levels of arousal elicited by major-minor modes [35,53,55]. However, similar stimuli do not necessarily entail similar results, mainly due to the different methodological tools used to assess the elicited responses [62,67,68].

Remarkably, the sensory-perceptual discrimination between major and minor chords, as measured by the MMN paradigm, develops very early in infants [16], whereas the ability to explicitly associate emotions to the two modes emerges later, starting from 3-4 years [55], and is fully developed at the age of 8-9 years [69]. The development of this ability appears to consistently correlate with the development of fluid intelligence and cognitive maturation [10].

Autonomic

Several studies have investigated the effect of musical mode on emotional autonomic responses using physiological measures such as skin conductance level (SCL), heart rate variability (HRV), and salivary cortisol levels. Van der Zwaag et al. (2011)[35] found that musical pieces in minor mode elicited higher arousal compared to the major mode, suggesting that it is due to the higher degree of uncertainty and surprise arising from minor mode. However, the results of Kastner & Crowder (1990)[55] contradict this finding, with the major mode eliciting greater arousal. The discrepancy between these studies may be attributed to different reasons, for example, the stimuli duration and/or the age of the participants. Suda et al. (2008)[70] found that major mode music had a greater effect on reducing stress, as evidenced by a significant decrease in salivary cortisol levels compared to minor mode music and a control group without auditory stimulation. This result was supported by the activation of the dorsolateral prefrontal cortex, strongly associated with positive mood, in response to major mode music using optical topography (OT). This evidence is consistent with previous

studies which indicated that the activation of the dorsolateral prefrontal cortex is strongly associated with a positive mood [71,72].

Neural correlates

The neural correlates of musical mode have been investigated through various neuroimaging techniques, but the results have not always been consistent. For example, EEG recordings by Davidson (1988)[73] suggested that greater activity in the left frontal lobe is associated with positive emotions like happiness, while the right frontal area is related to negative emotions like sadness and fear. However, an fMRI study by Khalfa et al. (2005)[67] did not confirm this lateralization, as participants displayed stronger left activation when exposed to sad musical excerpts in minor mode and slow tempo. Specifically, the minor versus major mode contrast showed greater activity in the posterior cingulate cortex, left orbital and mid-dorsolateral prefrontal cortex, and limbic structures. These results were supported by other fMRI studies [14,74]. EEG studies have also confirmed the involvement of the medial frontal and right sensorimotor activations in musical mode processing [68].

Trochidis and Bigand (2013)[62] conducted an EEG experiment to investigate emotional responses to different musical pieces played in major, minor, and Locrian mode. Participants rated major mode pieces as happier and more serene compared to minor and Locrian modes. In EEG frontal activity, major mode was associated with increased alpha activation in the left hemisphere compared to minor and Locrian modes, which increased activation in the right hemisphere, supporting the valence lateralization model suggested by Davidson (1988)[73]. It should be noted, however, that in these studies, stimuli presented to the subjects were not specifically composed with well controlled mode for interpreting the brain responses. Thus, the presence of variable musical parameters may have caused confounding effects in the neuroimaging data, partly explaining the discordant results.

In contrast, Suzuki et al. (2008)[15] employed only major-minor chords in a positron-emission tomography (PET) study to investigate the neural correlates of major-minor modes when both are perceived as pleasurable. Results indicated that minor chords perceived as beautiful strongly activated the right striatum, associated with reward and emotion processing, while "beautiful" major chords elicited a higher activity in the left middle temporal gyrus, an area involved in cognitive processes such as orderly information and semantic memory processing [75,76].

The involvement of the motivational-reward circuit in music-induced pleasure is consistent with previous findings [45] and mainly concerns minor mode music, as reported by Green et al. (2008)[14], Pallesen et al. (2005)[57], and Pouladi et al. (2011)[74]. However, the investigation of brain responses to major and minor music yields very discordant evidence. Music in minor mode has been associated with greater brain activation than major music in both fMRI [14,77], EEG [78], and MEG-based studies [79]. On the other hand, several studies reported increased activation of major music compared with equivalent minor [44,80,81]. Interestingly, two studies using event-related fMRI, failed to find brain regions differentially activated by listening to music in major vs. minor mode, when presented as triad sequences [82], or melodic sequences [83]. Similar results were reported by Maslennikova et al. (2013)[84], showing differences in evoked EEG responses substantially based on perception of consonant and dissonant chords rather than musical mode.

Considering these divergent findings, it might be conjectured that the neural correlates of major-minor perception are a consequence of the subjective perceived emotional connotation and pleasantness rather than major and minor mode itself. This is in line with Tabei (2015)[85] who highlighted that the emotional

expression of music and emotional responses evoked in the listener are distinctly processed in the brain.

In addition to the fundamental differences between the neuroimaging methods described, the discrepancies in literature might be ascribed to the overlapping of some of the neural correlates related to happiness and sadness perceived in music [40,67,86]. Brain structures such as the amygdala, hippocampus, striatum, and regions of the reward circuit are involved in both pleasantness and unpleasantness perception in music [15,45,87]. Thus, the overlap in neural correlates between happiness and sadness in music perception can make it challenging to isolate the specific neural correlates associated with the major-minor mode dichotomy. This is because brain structures such as the amygdala, hippocampus, striatum, and regions of the reward circuit are involved in both pleasantness and unpleasantness perception in music.

For example, a study by Blood and Zatorre (2001)[45] found that listening to pleasant music activates the striatum, a brain region associated with reward and motivation, whereas listening to unpleasant music activates the amygdala, a brain region associated with negative emotions such as fear and sadness. However, these regions are also activated in response to other stimuli [88], making it difficult to determine the specific contribution of mode to these neural responses.

Therefore, while there is evidence to suggest that major and minor modes elicit different emotional responses in listeners, the specific neural correlates associated with these responses are still not fully understood and are likely to be influenced by a range of subjective and individual factors [89].

4.3. Individual factors in the perception of the major-minor dichotomy

Individual differences in major-minor discrimination

In some studies, researchers have found that there are differences in how individuals discriminate between major and minor musical stimuli. However, the effect sizes are relatively modest, meaning the differences are not very significant across individuals. Recently, Chubb et al. (2013)[2] and Dean and Chubb (2017)[59] reported that most listeners (70%) performed near chance when asked to classify rapid tone-scrambles composed of multiple copies of notes in G-major vs G-minor triads as major or minor, whereas the remaining listeners performed nearly perfectly. Interestingly, these results were replicated when the stimuli are slowed down [36].

Moreover, Adler et al. (2020)[90] demonstrated that, by employing the same stimuli, a similar bimodal distribution in 6-month-old infants. However, these latter studies have been carried out by using tone-scrambles, which are random sequences of pure tones, instead of more natural harmonic tones, typically employed in the investigation of major-minor perception. Indeed, in contrast, several studies suggest that nearly all listeners are able to sense some sort of mode-related differences when exposed to more prototypical and realistic sounds [6,9,91], including non-Western listeners [52,53], and newborn infants [16].

Effect of musical expertise on major-minor perception

As reported in **Table 2**, nearly half of the studies reviewed (n=30) investigated the effect of musical expertise on music mode perception by comparing musicians and non-musicians. Halpern et al. (2008)[92], for instance, created pairs of identical melodies except for the mode, and both musicians and non-musicians were asked to judge the melodies as major vs. minor, or happy vs. sad. The main aim of this experiment was to analyse the processing of music at the point in time of the first note that differentiated major or minor mode (critical note). The ERP showed a large N1 and P2 component in both musicians and non-musicians to the onset of

the critical note, but, interestingly, the musicians showed a late P3 (LPC) to the critical note only for minor melodies in both tasks. Non-musicians, in contrast, showed a dissociation between their behavioural and physiological responses, namely, they could easily classify the melodies as happy or sad, but they did not show any LPC response. The late P3 recorded in musicians only for minor mode stimuli is consistent with the fMRI study by Khalfa et al. (2005)[67], indicating a specific neural activity only in response to minor tunes. This tendency might be explained by the fact that minor-mode music is less common than major-mode music. Indeed, Huron (2006)[46] found that when musicians were asked to think about a random chord, 94% of them imagined a major mode chord. Hence, the major mode appears to be the most "expected" mode, and the minor mode could elicit a higher brain response as an infrequent, deviant stimulus [62,93]. Nonetheless, the modulation of musical mode perception by expertise was not systematically observed in all the studies. For instance, Pallesen and colleagues (2005)[57] did not find any consistent difference between musicians and non-musicians when they listened to major, minor, and dissonant isolated chords.

To clarify the underlying mechanisms of musical mode and their development based on musical expertise, previous studies have investigated the distinct frequency- bands connecting neuronal networks, which are involved in music processing. Lower frequency bands, such as theta and alpha, are considered to be processing "cognitive" information, whereas higher frequency bands (beta and gamma) are involved in processing more basic features [94]. Pallesen et al. (2015)[31] reported a stronger gamma-band activity in response to non-prototypical chords (i.e., dissonant and mistuned) in musicians, while beta-band activity was stronger in non-musicians listening to minor chords. Additionally, a general reduction of gamma-band activity in response to major chords was observed in both groups. This effect may reflect 'easy' processing of this mode due to its frequent occurrence in Western music. Hence, high- frequency EEG bands appear to be crucial in processing more complex musical features, and the activity may be modulated by musical expertise. This view is consistent with the findings of a recent study by Jenni and colleagues (2017)[93] who reported that minor and major compositions distinctively modulated synchronisation of neuronal activities in high-frequency ranges (beta and gamma) in frontal regions, with increased activity in response to minor compositions especially in musicians and experts. This suggests that high-frequency EEG activities also carry musical mode information in addition to highlighting the role of musical expertise in enhancing the efficient processing and sensitivity to mode. Also, the involvement of frontal regions and limbic structures in music mode processing is consistent with previous studies [14,57,67].

In terms of early musical training, previous studies suggest that minor mode chords can elicit an automatic error response in the brain (MMR) even in infants [16], whereas similar stimuli do not evoke any significant error response (MMN) in older children without musical training [17]. This inconsistency might indicate a sort of predisposition towards the major-minor neural discrimination that tends to decline during the development when musical training is absent. However, the utilisation of more complex paradigms may help to level these differences, since Tervaniemi et al. (2014)[95] found prominent MMN responses to sound changes in both musicians and non-musicians by using the melodic multi-feature paradigm. This paradigm is faster and has a higher ecological validity than previous MMN paradigms.

Finally, musical expertise does not determine only differences in terms of neural response to mode, but it also affects individual preference. In fact, well-trained musicians consider musical excerpts in minor mode as more beautiful and pleasant than non-musicians [11].

Effect of age on major-minor perception

When investigating the behavioural and neural correlates of musical mode, one of the main questions

concerns whether musical mode perception changes throughout life. Dalla Bella et al. (2001)[7] reported that 5-year-old children could discriminate between happy and sad musical excerpts, but would only describe the excerpts in terms of tempo, whereas from the ages of 6-8 they utilised both tempo and mode, like adults. Similar results were obtained when children aged 3-4 and 7-8 were asked to associate a happy or sad face to music in major and minor mode. Moreover, 7-8-year-old children responded significantly differently to popular tunes in major and minor mode, but 3-to-4-year-old children showed almost no difference [64]. Both studies suggest that the emotional response related to musical mode develops between the ages of 4 and 7.

However, the beginning of the development of the major/happy and minor/sad association around the age of 4 is not supported by all the studies reviewed here. For example, Kastner and Crowder (1990)[55] found that 3-year-old children show the ability to match schematic faces (such as sad or happy) to musical excerpts based on the musical mode. More recently, an experiment by Franco et al. (2017)[60], in which 3–to-6-year-old children were asked to match facial expressions to the music tracks heard, showed that even the youngest children were able to correctly identify the intended emotion in music, whereby the recognition of happy music appeared facilitated in the instrumental condition. To sum up, most studies reviewed suggest that the affective connotation of major and minor mode is individually developed around the age of 4 and it is entirely acquired around the age of 7-to-8.

Recently, in a cross-modal association study, Bonetti and Costa (2019)[6] found that the association between major mode and happiness, and minor mode and sadness when infants and adults were exposed to musical chords increased from 58% at the age of 4 to 61% at the age of 5, 72% at the age of 6, reaching 92% in adults. Similarly, another study found that 6-to-7-year-old children would associate happy stickers with major melodies but not sad stickers with minor melodies [69]. Both results are consistent with previous studies which indicated a “late” development of recognition of negative emotions in music, compared to positive emotions [96,97]. This might be related to cognitive and intellectual maturation, as supported by the association between fluid intelligence and the ability to associate major-minor mode to happiness/sadness [6] and preference for minor-mode music [10]. Conversely, a decline in cognitive and intellectual skills might underlie the reduced ability to recognize negative emotions in music in advancing age, whereas the recognition of happiness in music remains stable [8].

However, even adults find it difficult to identify the mode of musical excerpts in an absolute manner [98], yet there is a significant enhancement of their performance when they are explicitly instructed on the association between major-minor mode with happiness and sadness expressions [99,100]. This evidence highlights once again how mode distinction depends on both implicit and explicit learning, in addition to the individual differences in sensitivity to mode variations [2].

4.4. Clinical Observations and Implications

Clinical conditions may alter the perception of the major-minor dichotomy

Musical mode preference and perception can be significantly influenced by listener’s mood, personality profile, and psychological and/or psychiatric condition. For instance, patients with schizophrenia fail to associate minor mode music to sadness [101], as similarly seen in patients with right and left temporal resection (Khalfa et al., 2008). As regards mode preference, listeners in a sad mood do not show the typical preference for music played in major key [12]. Further, musical pieces in minor mode and slow tempo, hence with a sad connotation, tend to be more appreciated among listeners with high introversion and empathy, and low emotional stability [13,102]. In addition, high neuroticism levels are associated with stronger sad feelings in

response to music and larger use of music to regulate mood and emotions [13,103]. Considering that neuroticism predicts both depression and anxiety disorders [104], these results suggest that emotional distress might affect the preference and perception of major-minor modes.

In fact, a large body of research investigated the effect of depression on the perceived emotions in music, reporting that depression is a condition able to alter the neural responses to pleasant and favourite music [105,106]. Behavioural studies confirmed the effect of depression on emotional perception of music. Punkanen et al. (2011)[19] found that depressed patients showed higher ratings of sadness when exposed to tender music in comparison to healthy controls, with this result highlighting a bias in which positive emotions were perceived as negative. This is in line with the results reported by Gur and colleagues (1992)[107] who found that depressed patients misinterpreted neutral faces as sad and happy faces as neutral. Moreover, depressed subjects gave lower happiness ratings to happy and tender musical examples, underlying how subjects with depression slowly tend to become unresponsive to positive stimuli [108]. A possible explanation for this tendency is the "congruency bias" which determines selective attention toward negative stimuli among depressed subjects [109]. Additionally, the effect of the negative bias appears to be correlated with the level of depression, consistent with the association between severity of depression and lower ability to discriminate happy and sad expressions suggested by Surguladze et al. (2004)[110]. Also, even a few seconds of music played in minor mode elicit emotional estimate instability (expressed as high standard deviations) in patients with retarded depression [63], and more intense experience in response to sad music in depressed patients compared to the healthy population was reported by Bodner et al. (2007)[111].

Interestingly, differences in neural response to the emotional features of music occur not exclusively in major depression disorder (MDD), but also in a condition of subclinical risk of depression, which is conceptualised as an enhanced probability to develop a depressive disorder [112]. Indeed, Bonetti et al. (2017)[18] found higher mismatch negativity (MMN) amplitude to mistuned pitches within a major context compared to MMN to pitch changes in a minor context, highlighting a different responsivity to sound frequency changes among individuals with a tendency to depression. This is consistent with the results reported by Pang et al. (2014)[113] who recorded an impairment in the capacity to automatically process sad prosodies in depressed patients. Specifically, the MMN in response to sad syllables was absent, whereas the MMN to happy and angry prosodies was similar to the response in healthy participants.

Thus, emotional distress and depression may, in fact, impair the recognition and the processing of emotions conveyed by music, even in subclinical conditions. In this perspective, considering that major-minor dichotomy is one of the main determinants of emotional expression in music, its affective connotation might be further exploited to develop more effective and tailored music-based treatments.

Major-minor dichotomy as mood regulator for clinical populations

As the major-minor dichotomy in music perception has been linked to the expression of emotional valence in music, there has also been an increasing interest in the exploration of potential clinical applications of music mode as a mood-regulating tool in disorders such as depression, anxiety, insomnia, and autism, among others.

Studies have shown that listening to music can be an effective intervention for depression, potentially improving mood and reducing symptoms. For example, a randomised controlled trial conducted by Chan et al. (2011)[114] found that listening to music resulted in significant reductions in depressive symptoms among patients with major depressive disorder. Moreover, a systematic review by Maratos et al. (2008)[115] suggested

that listening to self-selected music was effective in reducing symptoms of depression and anxiety in a group of older adults. In addition to passive listening, active engagement with music in a minor key can also be a therapeutic approach for depression. For example, a study by Erkkilä et al. (2011)[116] found that improvising on a keyboard was effective in reducing symptoms of depression and anxiety among psychiatric patients.

Thus, the use of musical mode as an intervention for depression is thought to be related to the emotional and psychological responses that different modes can elicit. For example, minor keys may be particularly effective for individuals who have difficulty expressing or processing negative emotions, as they can provide a safe and non-threatening way to engage with these emotions. Indeed, minor music has been linked to a better psychological regulation and relaxation compared to major music (Wang et al., 2018)[117]. Additionally, the dichotomy may be helpful for individuals who experience symptoms such as rumination or excessive worry, as they can provide a way to shift focus away from negative thoughts and emotions [118].

Furthermore, research has shown that music may be effective in reducing arousal levels in individuals with insomnia. There are various factors that can contribute to insomnia, including stress, anxiety, and depression. One theory that explains the mechanism behind insomnia is the hyperarousal theory, which suggests that individuals with insomnia have a heightened level of arousal that prevents them from falling asleep or staying asleep. A meta-analysis of randomised controlled trials by Jespersen et al., (2022)[119] showed moderate-certainty evidence that listening to music improves sleep quality when compared to no treatment. Therefore, music in the minor mode may also be used to regulate and ameliorate the state of hyperarousal in individuals with insomnia, however, this hypothesis remains untested.

Moreover, the use of the mode dichotomy may be beneficial for children with autism spectrum disorder (ASD) who typically show altered processing of affective information within social and interpersonal domains. In fact, a study by Heaton et al., (1999)[120] showed that children with ASD and age and intelligence matched controls did not differ in their ability to ascribe affective connotations (happy/sad faces) to melodies in the major or minor mode. Therefore, the dichotomy could have potential benefits as music therapy for ASD by helping them to learn, recognize, and differentiate between different emotional states, regulate their own emotions, communicate effectively, integrate, and regulate sensory information, and develop social skills.

Overall, the major-minor dichotomy in music perception is a significant determinant of emotional expression in music and is influenced by individual factors such as mood, personality, and clinical conditions. Emotional distress and depression can impair the recognition and processing of emotions conveyed by music, including the major-minor dichotomy. However, the use of musical mode as an intervention for depression and other clinical conditions has shown promise, with minor keys being particularly effective for individuals who have difficulty expressing or processing negative emotions. Overall, further research is needed to better understand the mechanisms behind the relationship between music and emotional regulation in clinical populations. Nevertheless, the potential clinical applications of music mode highlight the importance of music in promoting emotional well-being and suggest its potential as a tool for supporting mental health.

4.5. *The Major-Minor Mode(l)*

Music has been an important part of human life for centuries, and it has been linked to emotional expression and regulation. In particular, the major-minor dichotomy has been shown to be a powerful tool in the perception and expression of emotional valence in music. This dichotomy is influenced by various individual factors, such as age, cultural background, musical expertise, mood, personality, and clinical conditions such as depression.

Based on the findings of this systematic review, we propose a comprehensive model of musical mode perception and its behavioural and physiological correlates that incorporates these factors and their interactions to better understand the complex emotional responses that major and minor musical modes elicit (**Figure 2**).

The Major-Minor Dichotomy

The major-minor dichotomy is a fundamental aspect of Western tonal music, which divides musical modes into two categories: major and minor. The major mode is often associated with positive emotions, such as happiness, excitement, and optimism, while the minor mode is associated with negative emotions, such as sadness, introspection, and longing. However, it is important to note that major and minor modes can evoke a wide range of emotions, and they are not limited to the basic affective connotations. The major-minor dichotomy is a complex and multifaceted phenomenon, and it is influenced by various individual and cultural factors.

Individual Factors

Individual factors such as age, cultural background, musical expertise, mood, personality, and clinical conditions such as depression can influence the perception of the major-minor dichotomy in music. Personality traits such as empathy and openness to experience may also affect how individuals respond to sad music in the minor mode. Cultural factors may influence the perceived emotional valence of different musical modes.

Behavioural and Physiological Correlates

Over the course of several decades, multiple neuroimaging techniques including EEG, MEG, PET, and MRI have been used in numerous studies to improve our understanding of the cognitive and neural processes involved in perceiving major and minor modes in music. Additionally, comparisons between clinical groups and healthy individuals have also played a role in refining music neuroscience models.

Clinical Implications

The major-minor dichotomy in music perception has been explored as a potential mood-regulating tool for clinical populations, including those with depression, anxiety, insomnia, and autism. Listening to music has been shown to be an effective intervention for depression, with minor keys providing a safe way to engage with negative emotions. Major-minor dichotomy can also be exploited to reduce arousal levels in individuals with insomnia and has potential as a music therapy for children with ASD in terms of emotion recognition and social skills. Further research is needed to understand the relationship between music and emotional regulation in clinical populations, but the potential applications highlight the importance of music in promoting emotional well-being.

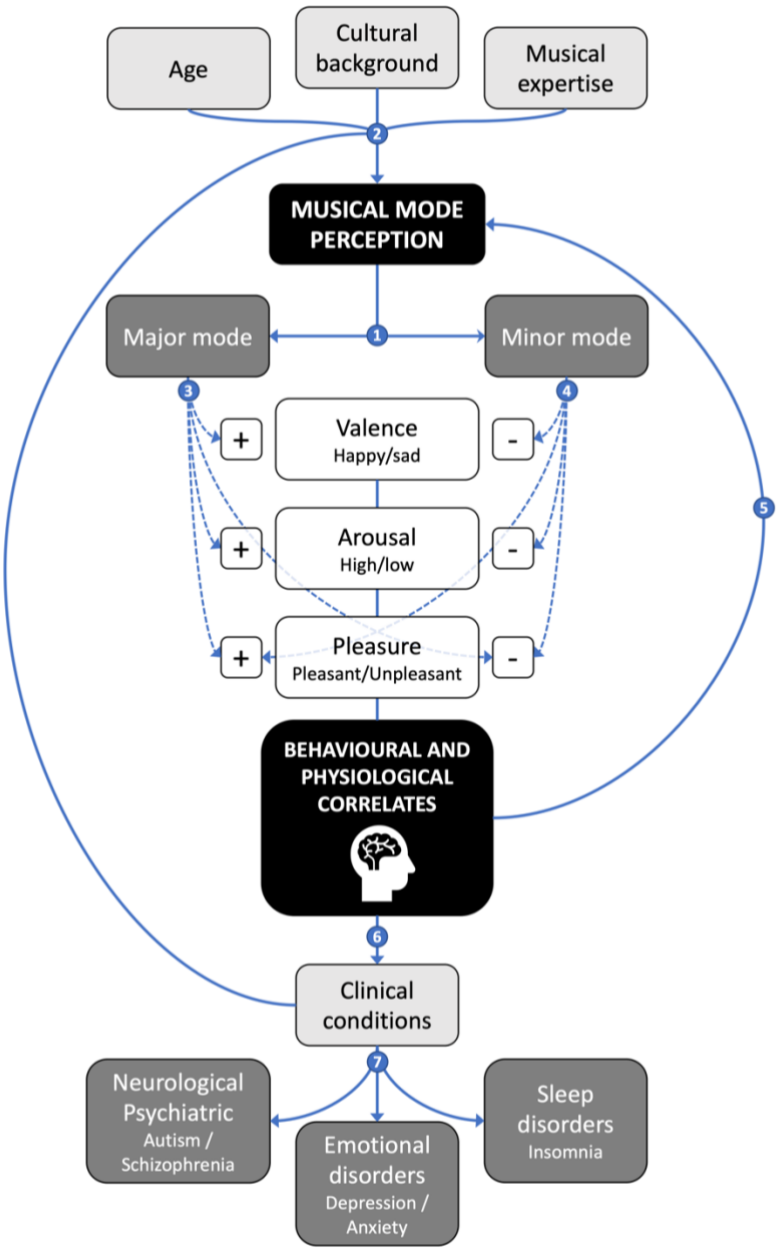

Figure 2. The *Major-Minor Mode(l)*. ① The major-minor dichotomy in music perception has been linked to the expression of emotional valence in music. ② The perception of the dichotomy may be influenced by individual factors such as age, cultural background, musical expertise, mood, personality, and/or clinical conditions such as depression. ③ The major mode has been associated to high valence and high arousal, and described as happy, uplifting, and energetic, evoking feelings of joy, excitement, and optimism. Although typically rated as pleasurable, the major mode can be unpleasant by evoking other feelings such as anger or sarcasm ④ The minor mode has been associated to low valence, low arousal, and unpleasantness, and described as nostalgic, sorrowful, and poignant, evoking feelings of sadness, introspection, and longing. However, personality traits such as openness to experience and empathy have been associated with feelings of pleasure for sad music. ⑤ Decades of behavioural and neurophysiological studies using EEG, MEG, PET, MRI, and other, have refined theories describing the processing of major and minor musical modes and their affective connotations. ⑥ Some studies have investigated the basic neurobiological mechanisms of the major-minor dichotomy and affective processing by comparing clinical populations with healthy controls, and thus further contributed to redefining music neuroscience models. ⑦ The major-minor dichotomy has potential therapeutic applications as a mood-regulating tool for individuals with depression, anxiety, insomnia, and autism, for example. It may be effective for individuals with anxiety and depression who have difficulty expressing or processing negative emotions, it may reduce arousal levels in individuals with insomnia, and it may have potential benefits for individuals with autism spectrum disorder by helping them to recognize and differentiate between emotional states, regulate their emotions, and develop social skills. Figure created with Microsoft® PowerPoint version 16.71.

4.6. Limitations and future directions

Published studies exploring the perception of major-minor dichotomy are several and difficult to synthesise due to differences in methodologies, stimuli, and population. This probably underlies the discrepancies in the pattern of results among the papers we reviewed, especially concerning neuroimaging studies. From this work, we offer some recommendations for future directions that empirical research on major and minor modes could pursue, and we discuss the potential implications.

Primarily, we highlighted how intrapersonal factors may substantially contribute to the recognition and emotional connotation attributed to major and minor modes. Therefore, we suggest that future studies aiming at exploring the neural and physiological response to music mode should always consider the subjective psychological perception of pleasantness and listener's level of musical expertise, since these factors may significantly affect brain activation and perceived emotions in response to stimuli differing in mode. The combination of subjective questionnaires and physiological measures would provide reliable information about the effective consonance between physiological state and perceived emotion.

On this note, we also suggest that future studies in musical mode and music in general, should include more information about the participants. We found that very few of the included studies reported years of education, year of musical training, onset of musical training, and current music practice time. Furthermore, we found, through the quality assessment, that items related to subject characterization and confounding effects got lower scores. Including such variables in scientific studies of human behaviour and music neuroscience allows researchers to control for individual differences, measure expertise, investigate developmental effects, and understand plasticity in response to musical training [121].

A further crucial question in musical mode investigation concerns the type of stimulation to employ. For instance, some studies here reviewed used musical chords as stimuli, namely single sounds, whereas other studies, to achieve a higher ecological validity, exposed participants to longer musical excerpts or even whole songs in major or minor keys. In the latter case, it appears quite complicated to identify the specific role of musical mode in determining the emotional response, since other variables such as tempo and lyrics do affect the perceived emotions in music [5,40]. Also, during the exposure to longer musical stimuli, motivation and attention are more likely to influence the subjective responses. Accordingly, papers employing chords or short excerpts showed higher consistency of results than those eliciting responses with longer or less natural harmonic sounds. However, longer real-life musical stimuli seem to be more appropriate than shorter sounds when the investigation is focused on the experienced mood [34], or on the association with personality traits [13,122]. In fact, longer sounds are necessary to induce and maintain an emotional response in the listener [89], as well as to allow for an evaluation of elicited responses overtime during the exposure. It might be proposed that, since longer stimuli result in a higher involvement of cognitive processes, the emotional responses produced should be evaluated not only in terms of happiness/sadness dichotomy, as mainly done in existing musical mode studies, but considering a wider range of emotions, more refined and complex. On the contrary, in addition to help reducing the effect of other musical features, shorter stimuli are more suitable when the investigation is aimed at evaluating basic emotions, since as reported by Peretz et al. (2001)[123] a very short duration of music (250 ms) is enough to differentiate sadness from happiness. However, to identify the effect of major-minor dichotomy in a context of either longer or shorter stimuli, it is suggested to minimise the variations of other musical features during the exposure, limiting the changes solely to musical mode.

Lastly, the findings of this study have several implications for future research on musical mode perception also in a clinical perspective. For instance, this systematic review reveals that the preference towards music in minor mode is often aimed at regulating mood and providing emotional benefits, but it might also underlie a condition of emotional distress which, in turn can lead to pathological conditions [12,13,124]. Consistently, prior evidence indicated that depression may affect the emotional evaluation of musical stimuli by eliciting lower responsivity to positive stimuli as well as eliciting a stronger response to negative stimuli [19,111].

From this perspective, the subjective differences in the affective evaluation of musical mode might represent a promising tool for an early behavioural evaluation of depression. Similar results might also be obtained associating the performance of emotional recognition of musical mode with the listeners' level of anxiety, since previous studies suggested that also patients with anxiety show a negative bias in emotion recognition tasks [125]. Given the above, the affective evaluation of musical mode fragments might help to identify emotional disorders, with the advantages of (1) not involving complex cognitive mediation, since it implies a rapid evaluation of short sounds, (2) bypassing the verbal barriers in assessment and (3), exploiting the generally positive attitude towards exposure to music. Moreover, if on one side there is evidence of large and systematic effect of individual differences in major-minor distinction, which might make it difficult to use judgments of mode to identify emotional disorders, on the other, studies employing shorter and unambiguous stimuli, such as diatonic scales [126] or triad chords [9,127] seem to limit this tendency. In this perspective, the use of musical mode as a clinical stimulation paradigm is worth further investigation. Furthermore, neuroimaging evidence of the effect of depression level in the automatic discrimination of major-minor stimuli, as indexed by the auditory component of mismatch negativity (MMN) [18] suggests that the preference for sad music among depressed subjects could have a basis or, at least, a neural correlate in the sensory processes on the auditory cortex level.

5. Conclusions

The major-minor dichotomy has long been of interest in music research studies. Although extensive literature exists exploring this fundamental musical feature, this is the first attempt to comprehensively and systematically review and synthesise research specifically investigating physiological and behavioural correlates of major and minor modes, as well as summarise how this dichotomy has been investigated in empirical research. The papers were analysed in qualitative terms, instead of a quantitative meta-analysis, mainly due to the great variability of methods and approaches in literature.

The typical affective connotation attributed to the major-minor dichotomy, hence major-happy and minor-sad association, has been substantially confirmed in the examined literature, including cross-cultural studies which hence suggest a universal component of this affective categorization [52,53,128] . In other words, the emotional dimension associated with major and minor modes might primarily arise from their different psychoacoustic features, such as harmonicity, spectral entropy, and roughness, rather than from cultural factors. In line with this view, some authors speculated that minor mode music chords share similar harmonic relationships to sad speech prosody. Nonetheless, empirical research aimed at establishing the universality of major/minor affective dimension is increasingly hindered by the difficulty in finding population groups totally unfamiliar with Western culture and music [1]. In the latter case, the typical affective perception of major and minor appears significantly reduced [52,53]. A comprehensive view might be that psychoacoustics characteristics predispose to the development of the conventional affective association of major with happiness, and minor with sadness, leading to established cultural-based emotional connotations. In this sense, levels, and types of exposure to Western-like music might contribute to these associations by modulating familiarity and the ensuing ability to discriminate between the two modes.

The centrality of the perceived affective connotation in major-minor processing is confirmed by neuroimaging studies which, moreover, point out a crucial point: neural and physiological activity appears to be more associated with basic emotional responses and evaluation of pleasantness rather than musical mode itself [15,82]. This may partly underlie the discordant results that arose in studies investigating the neural correlates of mode perception, in addition to the differences of methods and stimuli.

In this perspective, any study exploring the realm of major-minor dichotomy cannot disregard the investigation of the intra-personal factors contributing to its perception and processing, as pointed out in our proposed model. For instance, in this review we reported several studies suggesting that individual difference in processing of major-minor mode partly arises from musical expertise, since musicians show more neural activity and appreciation for minor-mode music than non-musicians [11,67,92] as well as a greater ability to discriminate between the two modes [52,92,99]. Therefore, studies reviewed agree in considering musical expertise a determinant of the major-minor representation and its affective processing as well as a factor which significantly speeds up the musical mode categorization process in children [17]. The fact that major-minor perception is mostly related to its affective connotation might also explain why its explicit perception and affective recognition (mainly regarding minor/sad association) are established only after the age of 3-4, concomitantly with cognitive and intellectual maturation, such as fluid intelligence [6,7,55]. Accordingly, ageing leads to a reduced ability to perceive the emotional connotation of musical mode, especially concerning negative emotions conveyed by minor mode excerpts [7]. In other words, the ability to explicitly perceive (and supposedly discriminate) major and minor modes is strongly related to the ability of recognizing their emotional connotation, supporting the conjecture that the ensuing behavioural and physiological responses are not related to the musical mode *per se*.

To sum up, musical mode has been a central topic in musical studies since Greek theorists, including Gregorian, Renaissance-polyphony and tonal- harmonic studies [129]. The phenomenon that mainly captured the attention of theorists and musicians was how the structure of musical scales related to their specific emotional expression, a phenomenon that was largely demonstrated in controlled studies, as reported in this systematic review. Although the literature on musical mode has reached a voluminous corpus that we have summarised in this review, we still miss a comprehensive explanation of the reasons why different modes are associated with different emotional expressions in music. The study of musical mode, in this perspective, could be central for gaining significant insights into the central theme of emotional valence perception and processing in affect theory.

Declaration of conflicting interests

The authors declare no conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors. The Center for Music in the Brain is funded by the Danish National Research Foundation (project number 117). LB is supported by Carlsberg Foundation (CF20-0239), Lundbeck Foundation (Talent Prize 2022), Center for Music in the Brain, Linacre College of the University of Oxford (Lucy Halsall fund), and Nordic Mensa Fund.

References

1. Virtala, P. & Tervaniemi, M. Neurocognition of Major-Minor and Consonance-Dissonance. *Music Percept.* **34**, 387–404 (2017).
2. Chubb, C. *et al.* Bimodal distribution of performance in discriminating major/minor modes. *J. Acoust. Soc. Am.* **134**, 3067–3078 (2013).
3. Casas-Mas, A., Pozo, J. I. & Scheuer, N. Musical Learning and Teaching Conceptions as Sociocultural Productions in Classical, Flamenco, and Jazz Cultures. *J. Cross-Cult. Psychol.* **46**, 1191–1225 (2015).
4. Koelsch, S. Neural substrates of processing syntax and semantics in music. in *Music that Works: Contributions of Biology, Neurophysiology, Psychology, Sociology, Medicine and Musicology* 143–153 (2009). doi:10.1007/978-3-211-75121-3_9.
5. Peretz, I., Gagnon, L. & Bouchard, B. Music and emotion: perceptual determinants, immediacy, and isolation after brain damage. *Cognition* **68**, 111–141 (1998).
6. Bonetti, L. & Costa, M. Musical mode and visual-spatial cross-modal associations in infants and adults. *Music. Sci.* **23**, 50–68 (2019).
7. Dalla Bella, S., Peretz, I., Rousseau, L. & Gosselin, N. A developmental study of the affective value of tempo and mode in music. *Cognition* **80**, B1-10 (2001).
8. Castro, S. L. & Lima, C. F. Age and Musical Expertise Influence Emotion Recognition in Music. *Music Percept.* **32**, 125–142 (2014).
9. Pallesen, K., Brattico, E. & Carlson, S. Emotional connotations of major and minor musical chords in musically untrained listeners. *Brain Cogn.* **51**, 188–190 (2003).
10. Bonetti, L. & Costa, M. Intelligence and Musical Mode Preference. *Empir. Stud. Arts* **34**, 160–176 (2016).
11. Brattico, E. *et al.* It's sad but I like it: The neural dissociation between musical emotions and liking in experts and laypersons. *Front. Hum. Neurosci.* **9**, 21 (2016).
12. Hunter, P., Schellenberg, E. & Griffith, A. Misery Loves Company: Mood-Congruent Emotional Responding to Music. *Emot. Wash. DC* **11**, 1068–72 (2011).
13. Ladinig, O. & Schellenberg, E. Liking Unfamiliar Music: Effects of Felt Emotion and Individual Differences. *Psychol. Aesthet. Creat. Arts* **6**, 146–154 (2012).
14. Green, A. C. *et al.* Music in minor activates limbic structures: A relationship with dissonance? *NeuroReport* **19**, 711–715 (2008).
15. Suzuki, M. *et al.* Discrete cortical regions associated with the musical beauty of major and minor chords. *Cogn. Affect. Behav. Neurosci.* **8**, 126–131 (2008).
16. Virtala, P., Huotilainen, M., Partanen, E., Fellman, V. & Tervaniemi, M. Newborn infants' auditory system is sensitive to Western music chord categories. *Front. Psychol.* **4**, (2013).
17. Virtala, P., Huotilainen, M., Putkinen, V., Makkonen, T. & Tervaniemi, M. Musical training facilitates the neural discrimination of major versus minor chords in 13-year-old children. *Psychophysiology* **49**, 1125–1132 (2012).
18. Bonetti, L., Haumann, N. T., Vuust, P., Kliuchko, M. & Brattico, E. Risk of depression enhances auditory Pitch discrimination in the brain as indexed by the mismatch negativity. *Clin. Neurophysiol.* **128**, 1923–1936 (2017).
19. Punkanen, M., Eerola, T. & Erkkilä, J. Biased emotional preferences in depression: Decreased liking of angry and energetic music by depressed patients. *Music Med.* **3**, 114–120 (2011).
20. Zhao, H., Jiang, J., Zhou, L. & Jiang, C. Role of the human mirror system in automatic processing of musical emotion: Evidence from EEG. *Acta Psychol. Sin.* (2019).
21. Gosselin, N. Impaired recognition of scary music following unilateral temporal lobe excision. *Brain* **128**, 628–640 (2005).
22. Koelsch, S. Toward a neural basis of music perception - a review and updated model. *Front. Psychol.* **2**, (2011).
23. Peretz, I. & Zatorre, R. J. BRAIN ORGANIZATION FOR MUSIC PROCESSING. *Annu Rev Psychol* **56**, 89–114 (2005).
24. Cook, N. D., Fujisawa, T. X. & Takami, K. Evaluation of the affective valence of speech using pitch substructure. *IEEE Trans. Audio Speech Lang. Process.* **14**, 142–151 (2006).

25. Asano, R., Lo, V. & Brown, S. The Neural Basis of Tonal Processing in Music: An ALE Meta-Analysis. *Music Sci.* **5**, 20592043221109960 (2022).
26. Higgins, J. P. & Green, S. Cochrane Handbook for Systematic Reviews of Interventions. (2011).
27. Culyer, A. J. *Centre for Reviews and Dissemination*. *The Dictionary of Health Economics, Third Edition* (Edward Elgar Publishing Limited, 2014).
28. Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & PRISMA Group. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Med.* **6**, e1000097 (2009).
29. Covidence systematic review software, Veritas Health Innovation, Melbourne, Australia. Available at www.covidence.org. https://support.covidence.org/help/how-can-i-cite-covidence.
30. Kmet, L. M., Cook, L. S. & Lee, R. C. Standard Quality Assessment Criteria for Evaluating Primary Research Papers from a Variety of Fields. *ERA* https://era.library.ualberta.ca/items/48b9b989-c221-4df6-9e35-af782082280e (2004) doi:10.7939/R37M04F16.
31. Pallesen, K. J. *et al.* Experience drives synchronization: The phase and amplitude dynamics of neural oscillations to musical chords are differentially modulated by musical expertise. *PLoS ONE* **10**, (2015).
32. Putkinen, V., Tervaniemi, M., Saarikivi, K., Ojala, P. & Huotilainen, M. Enhanced development of auditory change detection in musically trained school-aged children: a longitudinal event-related potential study. *Dev. Sci.* **17**, 282–297 (2014).
33. Steinbeis, N. & Koelsch, S. Affective priming effects of musical sounds on the processing of word meaning. *J. Cogn. Neurosci.* **23**, 604–621 (2011).
34. McConnell, M. M. & Shore, D. I. Upbeat and happy: Arousal as an important factor in studying attention. *Cogn. Emot.* **25**, 1184–1195 (2011).
35. van der Zwaag, M. D., Westerink, J. H. D. M. & van den Broek, E. L. Emotional and psychophysiological responses to tempo, mode, and percussiveness. *Music. Sci.* **15**, 250–269 (2011).
36. Mednicoff, S., Mejia, S., Rashid, J. A. & Chubb, C. Many listeners cannot discriminate major vs minor tone-scrambles regardless of presentation rate. *J. Acoust. Soc. Am.* **144**, 2242–2255 (2018).
37. Pilcher, N., Cortazzi, M. & Jin, L. Da capo: A musical technique to evoke narrative recall. *Psychol. Music* **42**, 483–502 (2014).
38. Wiering, F. *Tonal Structures in Early Music*. (Routledge, 1998).
39. Hevner, K. The Affective Value of Pitch and Tempo in Music. *Am. J. Psychol.* **49**, 621–630 (1937).
40. Brattico, E. *et al.* A functional MRI study of happy and sad emotions in music with and without lyrics. (2011) doi:10.3389/fpsyg.2011.00308.
41. Crowder, R. G. Perception of the major/minor distinction: II. Experimental investigations. *Psychomusicology Music Mind Brain* **5**, 3–24 (1985).
42. Koelsch, S., Fritz, T., Yves Cramon, D., Mü ller, K. & Friederici, A. D. Investigating Emotion With Music: An fMRI Study. *Hum Brain Mapp* **27**, 239–250 (2006).
43. Reisenzein, R. Pleasure-Arousal Theory and the Intensity of Emotions. *J. Pers. Soc. Psychol.* **67**, 525–39 (1994).
44. Chang, Y.-H. *et al.* Experiencing affective music in eyes-closed and eyes-open states: An electroencephalography study. *Front. Psychol.* **6**, (2015).
45. Blood, A. J. & Zatorre, R. J. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci.* **98**, 11818–11823 (2001).
46. Huron, D. *Sweet Anticipation: Music and the Psychology of Expectation*. *MIT Press* (2006). doi:10.1525/mp.2007.24.5.511.
47. Koelsch, S. Brain correlates of music-evoked emotions. *Nat. Rev. Neurosci.* **15**, 170–180 (2014).
48. Pearce, M. T. The construction and evaluation of statistical models of melodic structure in music perception and composition. (City University London, 2005).
49. Pando-Naude, V., Patyczek, A., Bonetti, L. & Vuust, P. An ALE meta-analytic review of top-down and bottom-up processing of music in the brain. *Sci. Rep.* **11**, 20813 (2021).
50. Hunter, P. G., Schellenberg, E. G. & Schimmack, U. Mixed affective responses to music with conflicting cues. *Cogn. Emot.* **22**, 327–352 (2008).
51. Vuoskoski, J. K. & Eerola, T. Can sad music really make you sad? Indirect measures of affective states induced by music and autobiographical memories. *Psychol. Aesthet. Creat. Arts* **6**, 204–213 (2012).
52. Hoshino, E. The Feeling of Musical Mode and its Emotional Character in a Melody. *Psychol. Music* **24**,

29–46 (1996).
53. Fang, L., Shang, J. & Chen, N. Perception of Western Musical Modes: A Chinese Study. *Front. Psychol.* **8**, (2017).
54. Smit, E. A., Milne, A. J., Sarvasy, H. S. & Dean, R. T. Emotional responses in Papua New Guinea show negligible evidence for a universal effect of major versus minor music. *PLOS ONE* **17**, e0269597 (2022).
55. Kastner, M. P. & Crowder, R. G. Perception of the Major/Minor Distinction: IV. Emotional Connotations in Young Children. *Music Percept. Interdiscip. J.* **8**, 189–201 (1990).
56. Ellison, D., Moisseinen, N., Fachner, J. & Brattico, E. Affective versus cognitive responses to musical chords: An ERP and behavioral study. *Psychomusicology Music Mind Brain* **25**, 423–434 (2015).
57. Pallesen, K. J. *et al.* Emotion processing of major, minor, and dissonant chords: a functional magnetic resonance imaging study. *Ann. N. Y. Acad. Sci.* **1060**, 450–453 (2005).
58. Virtala, P. *et al.* The preattentive processing of major vs. minor chords in the human brain: An event-related potential study. *Neurosci. Lett.* **487**, 406–410 (2011).
59. Dean, T. & Chubb, C. Scale-sensitivity: A cognitive resource basic to music perception. *J. Acoust. Soc. Am.* **142**, 1432–1440 (2017).
60. Franco, F., Chew, M. & Swaine, J. S. Preschoolers' attribution of affect to music: A comparison between vocal and instrumental performance. *Psychol. Music* **45**, 131–149 (2017).
61. Halpern, A. R. Perception of structure in novel music. *Mem. Cognit.* **12**, 163–170 (1984).
62. Trochidis, K. & Bigand, E. Investigation of the Effect of Mode and Tempo on Emotional Responses to Music Using EEG Power Asymmetry. *J. Psychophysiol.* **27**, 142–148 (2013).
63. Al'tman, Ya. A., Alyanchikova, Yu. O., Guzikov, B. M. & Zakharova, L. E. Estimation of short musical fragments in normal subjects and patients with chronic depression. *Hum. Physiol.* **26**, 553–557 (2000).
64. Gregory, A. H., Worrall, L. & Sarge, A. The development of emotional responses to music in young children. *Motiv. Emot.* **20**, 341–348 (1996).
65. Schellenberg, E. G., Peretz, I. & Vieillard, S. Liking for happy- and sad-sounding music: Effects of exposure. *Cogn. Emot.* **22**, 218–237 (2008).
66. Tai, S.-K. & Kuo, Y.-J. Alterations in brainwaves caused by different Music Genres. in *2019 IEEE 10th International Conference on Awareness Science and Technology (iCAST)* 1–4 (2019). doi:10.1109/ICAwST.2019.8923257.
67. Khalfa, S., Schon, D., Anton, J.-L. & Liégeois-Chauvel, C. Brain regions involved in the recognition of happiness and sadness in music. *NeuroReport Rapid Commun. Neurosci. Res.* **16**, 1981–1984 (2005).
68. Lin, Y.-P., Duann, J.-R., Feng, W., Chen, J.-H. & Jung, T.-P. Revealing spatio-spectral electroencephalographic dynamics of musical mode and tempo perception by independent component analysis. *J. NeuroEngineering Rehabil.* **11**, (2014).
69. Nieminen, S., Istók, E., Brattico, E. & Tervaniemi, M. The development of the aesthetic experience of music: Preference, emotions, and beauty. *Music. Sci.* **16**, 372–391 (2012).
70. Suda, M., Morimoto, K., Obata, A., Koizumi, H. & Maki, A. Emotional responses to music: towards scientific perspectives on music therapy. *NeuroReport* **19**, 75 (2008).
71. Habel, U., Klein, M., Kellermann, T., Shah, N. J. & Schneider, F. Same or different? Neural correlates of happy and sad mood in healthy males. *NeuroImage* **26**, 206–214 (2005).
72. Markowitsch, H. J., Vandekerckhove, M. M. P., Lanfermann, H. & Russ, M. O. Engagement of Lateral and Medial Prefrontal Areas in the Ecphory of Sad and Happy Autobiographical Memories. *Cortex* **39**, 643–665 (2003).
73. Davidson, R. J. EEG Measures of Cerebral Asymmetry: Conceptual and Methodological Issues. *Int. J. Neurosci.* **39**, 71–89 (1988).
74. Pouladi, F., Ganjgahi, H., Zadehmohammadi, A. & Oghabian, M. A. Homayoun as a Persian music scale on non-musician's brain: An fMRI study. *Basic Clin. Neurosci.* **3**, 22–29 (2011).
75. Gernsbacher, M. A. & Kaschak, M. P. Neuroimaging Studies of Language Production and Comprehension. *Annu. Rev. Psychol.* **54**, 91–114 (2003).
76. Onitsuka, T. *et al.* Middle and Inferior Temporal Gyrus Gray Matter Volume Abnormalities in Chronic Schizophrenia: An MRI Study. *Am. J. Psychiatry* **161**, 1603–1611 (2004).
77. Nemoto, I., Fujimaki, T. & Wang, L. fMRI Measurement of Brain Activities to Major and Minor Chords

and Cadence Sequences. *Conf. Proc. Annu. Int. Conf. IEEE Eng. Med. Biol. Soc. IEEE Eng. Med. Biol. Soc. Conf.* **2010**, 5640–3 (2010).
78. Proverbio, A. M. & Russo, F. Multimodal recognition of emotions in music and language. *Psychol. Music* **50**, 54–68 (2022).
79. Jomori, I. *et al.* Effects of emotional music on visual processes in inferior temporal area. *Cogn. Neurosci.* **4**, 21–30 (2013).
80. Jeong, J.-W. *et al.* Congruence of happy and sad emotion in music and faces modifies cortical audiovisual activation. *NeuroImage* **54**, 2973–2982 (2011).
81. Tsang, C., Trainor, L., Santesso, D., Tasker, S. & Schmidt, L. Frontal EEG Responses as a Function of Affective Musical Features. *Ann. N. Y. Acad. Sci.* **930**, 439–42 (2001).
82. Mizuno, T. & Sugishita, M. Neural correlates underlying perception of tonality-related emotional contents. *NeuroReport* **18**, 1651–1655 (2007).
83. Lee, Y.-S., Janata, P., Frost, C., Hanke, M. & Granger, R. Investigation of melodic contour processing in the brain using multivariate pattern-based fMRI. *NeuroImage* **57**, 293–300 (2011).
84. Maslennikova, A. V., Varlamov, A. A. & Strelets, V. B. Evoked changes in EEG band power on perception of consonant and dissonant chords. *Neurosci. Behav. Physiol.* **43**, 670–673 (2013).
85. Tabei, K.-I. Inferior Frontal Gyrus Activation Underlies the Perception of Emotions, while Precuneus Activation Underlies the Feeling of Emotions during Music Listening. *Behav. Neurol.* **2015**, (2015).
86. Mitterschiffthaler, M. T., Fu, C. H. Y., Dalton, J. A., Andrew, C. M. & Williams, S. C. R. A functional MRI study of happy and sad affective states induced by classical music. *Hum. Brain Mapp.* **28**, 1150–1162 (2007).
87. Blood, A. J., Zatorre, R. J., Bermudez, P. & Evans, A. C. Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nat. Neurosci.* **2**, 382–387 (1999).
88. Kim, S. H. & Hamann, S. Neural Correlates of Positive and Negative Emotion Regulation. *J. Cogn. Neurosci.* **19**, 776–798 (2007).
89. Eerola, T. & Vuoskoski, J. K. A review of music and emotion studies: Approaches, emotion models, and stimuli. *Music Percept.* **30**, 307–340 (2013).
90. Adler, S. A., Comishen, K. J., Wong-Kee-You, A. M. B. & Chubb, C. Sensitivity to major versus minor musical modes is bimodally distributed in young infants. *J. Acoust. Soc. Am.* **147**, 3758 (2020).
91. Temperley, D. & Tan, D. Emotional Connotations of Diatonic Modes. *Music Percept.* **30**, 237–257 (2013).
92. Halpern, A. R., Martin, J. S. & Reed, T. D. An ERP Study of Major-Minor Classification in Melodies. *Music Percept.* **25**, 181–191 (2008).
93. Jenni, R., Oechslin, M. S. & James, C. E. Impact of major and minor mode on EEG frequency range activities of music processing as a function of expertise. *Neurosci. Lett.* **647**, 159–164 (2017).
94. von Stein, A., Chiang, C. & König, P. Top-down processing mediated by interareal synchronization. *Proc. Natl. Acad. Sci.* **97**, 14748–14753 (2000).
95. Tervaniemi, M., Huotilainen, M. & Brattico, E. Melodic multi-feature paradigm reveals auditory profiles in music-sound encoding. *Front. Hum. Neurosci.* **8**, (2014).
96. Cunningham, J. G. & Sterling, R. S. Developmental change in the understanding of affective meaning in music. *Motiv. Emot.* **12**, 399–413 (1988).
97. Dolgin, K. G. & Adelson, E. H. Age Changes in the Ability to Interpret Affect in Sung and Instrumentally-Presented Melodies. *Psychol. Music* **18**, 87–98 (1990).
98. Halpern, A. R., Bartlett, J. C. & Dowling, W. J. Perception of Mode, Rhythm, and Contour in Unfamiliar Melodies: Effects of Age and Experience. *Music Percept.* **15**, 335–355 (1998).
99. Leaver, A. M. & Halpern, A. R. Effects of Training and Melodic Features on Mode Perception. *Music Percept.* **22**, 117–143 (2004).
100. Thompson, C. A. & Opfer, J. E. Affective constraints on acquisition of musical concepts: Children's and adults' development of the major–minor distinction. *Psychol. Music* **42**, 3–28 (2014).
101. Abe, D., Arai, M. & Itokawa, M. Music-evoked emotions in schizophrenia. *Schizophr. Res.* **185**, 144–147 (2017).
102. Taruffi, L., Pehrs, C., Skouras, S. & Koelsch, S. Effects of Sad and Happy Music on Mind-Wandering and the Default Mode Network. *Sci. Rep.* **7**, (2017).

103. Chamorro-Premuzic, T., Fagan, P. & Furnham, A. Personality and uses of music as predictors of preferences for music consensually classified as happy, sad, complex, and social. *Psychol. Aesthet. Creat. Arts* **4**, 205–213 (2010).
104. Zinbarg, R. E. *et al.* Testing a Hierarchical Model of Neuroticism and Its Cognitive Facets: Latent Structure and Prospective Prediction of First Onsets of Anxiety and Unipolar Mood Disorders During 3 Years in Late Adolescence. *Clin. Psychol. Sci.* **4**, 805–824 (2016).
105. Keller, J. *et al.* Trait anhedonia is associated with reduced reactivity and connectivity of mesolimbic and paralimbic reward pathways. *J. Psychiatr. Res.* **47**, 1319–1328 (2013).
106. Osuch, E. A. *et al.* Brain activation to favorite music in healthy controls and depressed patients. *NeuroReport* **20**, 1204–1208 (2009).
107. Gur, R. C. *et al.* Facial emotion discrimination: II. Behavioral findings in depression. *Psychiatry Res.* **42**, 241–251 (1992).
108. J. Tomarkenand, A. & Keener, A. D. Frontal Brain Asymmetry and Depression: A Self-regulatory Perspective. *Cogn. Emot.* **12**, 387–420 (1998).
109. Gollan, J. K., Pane, H. T., McCloskey, M. S. & Coccaro, E. F. Identifying differences in biased affective information processing in major depression. *Psychiatry Res.* **159**, 18–24 (2008).
110. Surguladze, S. A. *et al.* Recognition Accuracy and Response Bias to Happy and Sad Facial Expressions in Patients With Major Depression. *Neuropsychology* **18**, 212–218 (2004).
111. Bodner, E. *et al.* Finding words for emotions: The reactions of patients with major depressive disorder towards various musical excerpts. *Arts Psychother.* **34**, 142–150 (2007).
112. Carlson, E. *et al.* Maladaptive and adaptive emotion regulation through music: a behavioral and neuroimaging study of males and females. *Front. Hum. Neurosci.* **9**, 466 (2015).
113. Pang, X. *et al.* Mismatch Negativity of Sad Syllables Is Absent in Patients with Major Depressive Disorder. *PLOS ONE* **9**, e91995 (2014).
114. Chan, M. F., Wong, Z. Y., Onishi, H. & Thayala, N. V. Effects of music on depression in older people: a randomised controlled trial. *J. Clin. Nurs.* **21**, 776–783 (2012).
115. Maratos, A., Gold, C., Wang, X. & Crawford, M. Music therapy for depression. *Cochrane Database Syst. Rev.* (2008) doi:10.1002/14651858.CD004517.pub2.
116. Erkkilä, J. *et al.* Individual music therapy for depression: randomised controlled trial. *Br. J. Psychiatry* **199**, 132–139 (2011).
117. Wang, D., Liu, S. & Wang, X. Study on the Impact of Different Music Education on Emotional Regulation of Adolescents Based on EEG Signals. *Educ. Sci. Theory Pract.* **18**, (2018).
118. Garrido, S., Eerola, T. & McFerran, K. Group Rumination: Social Interactions Around Music in People with Depression. *Front. Psychol.* **8**, 490 (2017).
119. Jespersen, K. V., Pando-Naude, V., Koenig, J., Jennum, P. & Vuust, P. Listening to music for insomnia in adults. *Cochrane Database Syst. Rev.* (2022) doi:10.1002/14651858.CD010459.pub3.
120. Heaton, P., Hermelin, B. & Pring, L. Can children with autistic spectrum disorders perceive affect in music? An experimental investigation. *Psychol. Med.* **29**, 1405–1410 (1999).
121. Criscuolo, A., Pando-Naude, V., Bonetti, L., Vuust, P. & Brattico, E. An ALE meta-analytic review of musical expertise. *Sci. Rep.* **12**, 11726 (2022).
122. Dobrota, S. & Reić Ercegovac, I. The relationship between music preferences of different mode and tempo and personality traits – implications for music pedagogy. *Music Educ. Res.* **17**, 234–247 (2015).
123. Peretz, I. Listen to the brain: A biological perspective on musical emotions. in *Music and emotion: Theory and research* 105–134 (Oxford University Press, 2001).
124. Taruffi, L. & Koelsch, S. The Paradox of Music-Evoked Sadness: An Online Survey. *PLOS ONE* **9**, e110490 (2014).
125. Quadflieg, S., Wendt, B., Mohr, A., Miltner, W. H. R. & Straube, T. Recognition and evaluation of emotional prosody in individuals with generalized social phobia: A pilot study. *Behav. Res. Ther.* **45**, 3096–3103 (2007).
126. Tan, D. & Temperley, D. Perception and Familiarity of Diatonic Modes. *Music Percept.* **34**, 352–365 (2017).
127. Bakker, D. R. & Martin, F. H. Musical chords and emotion: major and minor triads are processed for emotion. *Cogn. Affect. Behav. Neurosci.* **15**, 15–31 (2015).

128. Mao, M. & Rau, P.-L. P. EEG-Based Measurement of Emotion Induced by Mode, Rhythm, and MV of Chinese Pop Music. in *Cross-Cultural Design* (ed. Rau, P. L. P.) 89–100 (Springer International Publishing, 2014). doi:10.1007/978-3-319-07308-8_9.
129. Powers, H. *et al.* Mode. *Oxf. Grove Music* (2001).

Figure captions.

Figure 1. The major and minor modes in Western tonal music. The difference between major and minor modes is rooted in the interval between the tonic note and the third degree of the scale. Major keys are generally considered to sound bright, happy, and uplifting, while minor keys are associated with sombre, melancholy, or dramatic emotion. The natural minor scale has no alterations to any of the scale degrees, while the melodic minor scale raises the sixth and seventh scale degrees when ascending but reverts to the natural minor scale when descending. The harmonic minor scale raises the seventh scale degree by a semitone, and the Dorian mode is a minor mode based on the second degree of the major scale. These scales have different unique characteristics and are often used in different contexts in Western music.

Figure 2. The Major-Minor Mode(l). ① The major-minor dichotomy in music perception has been linked to the expression of emotional valence in music. ② The perception of the dichotomy may be influenced by individual factors such as age, cultural background, musical expertise, mood, personality, and/or clinical conditions such as depression. ③ The major mode has been associated to high valence and high arousal, and described as happy, uplifting, and energetic, evoking feelings of joy, excitement, and optimism. Although typically rated as pleasurable, the major mode can be unpleasant by evoking other feelings such as anger or sarcasm ④ The minor mode has been associated to low valence, low arousal, and unpleasantness, and described as nostalgic, sorrowful, and poignant, evoking feelings of sadness, introspection, and longing. However, personality traits such as openness to experience and empathy have been associated with feelings of pleasure for sad music. ⑤ Decades of behavioural and neurophysiological studies using EEG, MEG, PET, MRI, and other, have refined theories describing the processing of major and minor musical modes and their affective connotations. ⑥ Some studies have investigated the basic neurobiological mechanisms of the major-minor dichotomy and affective processing by comparing clinical populations with healthy controls, and thus further contributed to redefining music neuroscience models. ⑦ The major-minor dichotomy has potential therapeutic applications as a mood-regulating tool for individuals with depression, anxiety, insomnia, and autism, for example. It may be effective for individuals with anxiety and depression who have difficulty expressing or processing negative emotions, it may reduce arousal levels in individuals with insomnia, and it may have potential benefits for individuals with autism spectrum disorder by helping them to recognize and differentiate between emotional states, regulate their emotions, and develop social skills. Figure created with Microsoft® PowerPoint version 16.71.

Table 1. Characteristics of included studies.

	Author (year)	Country	*N*	Age	Age group	Males	Females	Years of education	Musical expertise	Years of musical training	Onset of musical training	Training time (hr/wk)	Method	Modality	Stimuli	MODE-Centred	Familiarity	Feature/Paradigm	Clinical
1	*Abe et al. (2017)*	Japan	*58*	42	Adult	20	38	>9	U	-	-	-	Beh	-	Musical chords	Yes	-	Happy/Sad	Yes
2	*Al'tmann et al. (2000)*	Russia	*18*	31.5	Adult	13	5	-	U	-	-	-	Beh	-	Musical excerpts	No	-	Aversion/Delight	Yes
3	*Bakker & Martin (2015)*	Australia	*30*	20	Adult	15	15	-	NM	-	-	-	Phys/Beh	EEG	Musical chords	Yes	-	ERP	No
4	*Bonetti & Costa (2016)*	Italy	*80*	21.4	Adult	20	60	-	M/NM	8.57	-	-	Beh	-	Musical excerpts	Yes	-	Preference	No
5	*Bonetti & Costa (2019)*	Italy	*219*	20.8	B	121	98	-	M/NM	6.95	-	-	Beh	-	Musical chords	Yes	-	Happy/Sad, Pleasant/Unpleasant	No
6	*Bonetti et al. (2017)*	Denmark	*88*	28.4	Adult	40	48	-	M/NM	21	-	-	Phys	MEG/EEG	Musical excerpts	No	Yes	Passive listening	Yes
7	*Brattico et al. (2009)*	Finland	*20*	26.4	Adult	6	14	-	M/NM	18.2	-	14	Phys/Beh	MEG	Musical chords	No	-	Happy/Sad, Pleasant/Unpleasant	No
8	*Brattico et al. (2011)*	Finland	*15*	23.9	Adult	9	6	-	M/NM	14	-	-	Phys/Beh	fMRI	Musical excerpts	No	Yes	Happy/Sad, Pleasant/Unpleasant, Like/Dislike, Beauty/Ugly	No
9	*Brattico et al. (2016)*	Denmark	*29*	23.9	Adult	14	15	-	M/NM	16.2	9.1	18.6	Phys/Beh	fMRI	Musical excerpts	No	Yes	Happy/Sad, Pleasant/Unpleasant, Like/Dislike, Beauty/Ugly	No
10	*Castro & Lima (2014)*	Portugal	*80*	23	Adult	40	40	-	M/NM	≥ 9	-	-	Beh	-	Musical excerpts	No	-	Happy/Sad, Scary/Peaceful	No
11	*Chang et al. (2015)*	Taiwan	*30*	21.6	Adult	20	10	-	U	-	-	-	Phys/Beh	EEG	Musical excerpts	No	-	Positive/Negative valence	No
12	*Chubb et al. (2013)*	USA	*184*	-	Adult	-	-	-	M/NM	-	-	-	Beh	-	Tone scrambles	Yes	-	Happy/Sad	No
13	*Costa (2013)*	Italy	*152*	23.6	Adult	19	133	-	NM	-	-	-	Beh	-	Musical chords	Yes	-	Happy/Sad	No
14	*Costa et al. (2004)*	Italy	*29*	22.1	Adult	12	17	-	NM	-	-	-	Beh	-	Musical pieces	No	-	Valence, Aesthetic judgement	No
15	*Dalla Bella et al. (2001)*	Canada	*91*	23	B	42	49	-	NM	-	-	-	Beh	-	Musical excerpts	Yes	-	Happy/Sad	No
16	*Dobrota & Ervegovac (2015)*	Croatia	*323*	21.7	Adult	89	234	-	U	-	-	-	Beh	-	Musical pieces	Yes	-	Preference	No
17	*Eerola et al. (2013)*	Finland	*46*	30.2	Adult	25	20	-	M/NM	-	-	-	Beh	-	Musical excerpts	No	-	Tender/Peaceful, Happy/Sad, Angry/Scary	No
18	*Ellison et al. (2015)*	Finland	*24*	24.6	Adult	9	15	-	NM	-	-	-	Phys/Beh	EEG	Musical chords	No	-	Happiy/Sad	No

19	*Fang et al. (2017)*	China	*70*	21.4	Adult	25	45	14.7	NM	-	-	-	Beh	-	Musical excerpts	Yes	Yes	Pleasure, Arousal, Emotional tension, Liking	No
20	*Franco et al. (2017)*	UK	*112*	22.2	B	44	68	-	NM	-	-	-	Beh	-	Musical pieces	No	-	Happy/Sad	No
21	*Gosselin et al. (2005)*	Canada	*32*	39.8	Adult	14	18	13	NM	-	-	-	Beh	-	Muiscal excerpts	No	-	Happiness/Sadness, Threat, Peacefulness	Yes
22	*Green et al. (2008)*	Denmark	*21*	27.3	Adult	-	-	-	NM	-	-	-	Phys/Beh	fMRI	Musical excerpts	Yes	-	Happy/Sad, Like/Dislike	No
23	*Gregory et al. (1996)*	UK	*96*	-/3-8	B	-	-	-	U	-	-	-	Beh	-	Musical pieces	No	-	Happy/Sad	No
24	*Halpern (1984)*	USA	*45*	-	Adult	-	-	-	M/NM	≥ 5	-	-	Beh	-	Musical excerpts	Yes	-	Mode discrimination	No
25	*Halpern et al. (1998)*	USA	*103*	18.8	Adult	-	-	-	M/NM	11.7/11.2	-	-	Beh	-	Musical excerpts	Yes	Yes	Mode discrimination	No
26	*Halpern et al. (2008)*	USA	*36*	19-34	Adult	12	24	15.9	M/NM	11.3	-	-	Phys/Beh	EEG	Musical excerpts	Yes	Yes	Happy/Sad, Mode discrimination	No
27	*Heaton et al. (1999)*	UK	*42*	10	Child	NA	NA	NA	U	NA	NA	NA	Beh		Musical excerpts	Yes	No	Happy/Sad	Yes
28	*Hevner (1935)*	USA	*205*	-	Adult	-	-	-	M/NM	-	-	-	Beh	-	Musical excerpts	Yes	Yes	Affective evaluation	No
29	*Hoshino (1996)*	Japan	*66*	20.1	Adult	0	66	-	M/NM	14	-	-	Beh	-	Musical excerpts	Yes	-	Affective evaluation	No
30	*Hunter et al. (2008)*	Canada	*80*	-	Adult	28	52	-	M/NM	4.6	-	-	Beh	-	Musical pieces	No	-	Happy/Sad, Pleasant/Unpleasant	No
31	*Hunter et al. (2011)*	Canada	*102*	-	Adult	-	-	-	U	-	-	-	Beh	-	Musical pieces	No	Yes	Happy/Sad, Pleasant/Unpleasant	No
32	*Jenni et al. (2017)*	Switzerland	*59*	23.5	Adult	-	-	-	M/NM	16.2	6.5	-	Phys	EEG	Musical excerpts	Yes	-	Passive listening	No
33	*Jeong et al. (2011)*	USA	*15*	22.8	Adult	5	10	-	NM	-	-	-	Phys/Beh	fMRI	Musical excerpts	No	Yes	Happy/Sad	No
34	*Jomori et al. (2013)*	Japan	*14*	26.5	Adult	5	9	-	NM				Phys/Beh	MEG	Musical excerpts	No		Bright/Dark, Fearful	-
35	*Kastner & Crowder (1990)*	USA	*38*	3-12	Child	-	-	-	U	-	-	-	Beh	-	Musical excerpts	Yes	-	Happy/Sad, Contented/Angry	No
36	*Khalfa et al. (2005)*	France	*13*	28	Adult	8	5	-	U	-	-	-	Phys/Beh	fMRI	Musical excerpts	No	-	Happy/Sad	No
37	*Khalfa et al. (2008)*	France	*86*	31.5	Adult	40	46	12.5	M/NM	-	-	-	Beh	-	Musical excerpts	No	-	Happy, Sad	Yes
38	*Ladinig & Schellenberg (2012)*	Ca-da	*61*	18.3	Adult	8	53	-	M/NM	1.8	-	-	Beh	-	Musical pieces	No	Yes	Happy/Sad, Like/Dislike	No
39	*Leaver & Halpern (2004)*	USA	*165*	18.7	Adult	94	71	-	M/NM	9.8	-	-	Beh	-	Musical excerpts	Yes	-	Happy/Sad, Mode discrimination	No

40	*Lee et al. (2011)*	USA	*12*	20.4	Adult	7	5	-	M/NM	5.7	-	-	Phys/Beh	fMRI	Musical excerpts	No	-	Happy, Sad	No
41	*Lin et al. (2014)*	USA	*24*	24.6	Adult	14	10	-	NM	-	-	-	Phys	EEG	Musical pieces	Yes	-	Passive listening	No
42	*Mao & Rau (2014)*	UK	*12*	23.1	Adult	7	5	-	U	-	-	-	Phys/Beh	EEG	Musical pieces	Yes	-	Sublimity, Vitality, Unease	No
43	*Maslennikova et al. (2013)*	Russia	*15*	24.5	Adult	1	14	-	NM	-	-	-	Phys/Beh	EEG	Musical chords	No	-	Pleasant, Unpleasant	No
44	*McConnel & Shore (2011)*	Canada	*90*	19.5	Adult	24	66	-	U	-	-	-	Beh	-	Musical pieces	No	-	Mood evaluation	No
45	*Mednicoff et al. (2018)*	USA	*73*	-	Adult	-	-	-	M/NM	3.1	-	-	Beh	-	Tone scrambles	Yes	-	Mode discrimination	No
46	*Mizuno & Sugishita (2007)*	Japan	*18*	23.1	Adult	10	8	-	M	12.4	-	-	Phys	fMRI	Musical chords	No	-	Cheerful, Sad, Neutral (Affective evaluation)	No
47	*Nemoto et al. (2010)*	Japan	*17*	21	Adult	17	0	-	U	-	-	-	Phys	fMRI	Musical chords	Yes	-	-	No
48	*Nieminen et al. (2012)*	Finland	*78*	7.4	Child	38	40	-	M/NM	-	-	-	Beh	-	Musical excerpts	No	-	Like/Dislike, Beautiful/Ugly, Happy/Sad	No
49	*Pallesen et al. (2003)*	Denmark	*12*	25	Adult	5	7	-	NM	-	-	-	Phys/Beh	fMRI	Musical chords	Yes	-	Happy/Sad	No
50	*Pallesen et al. (2005)*	Denmark	*21*	26	Adult	12	14	-	M/NM	-	-	-	Phys/Beh	fMRI	Musical chords	Yes	-	Happy/Sad, Pleasant/Unpleasant	No
51	*Pallesen et al. (2015)*	Denmark	*22*	26.8	Adult	6	16	-	M/NM	18.2	-	14	Phys	MEG	Musical chords	Yes	-	Passive listening	No
52	*Pilcher et al. (2014)*	UK	*15*	20s	Adult	5	10	-	NM	-	-	-	Beh	-	Musical pieces	No	-	Subjective descriptions	No
53	*Proverbio et al. (2020)*	Italy	*16*	22.3	Adult	8	8	-	U	-	-	-	Phys/Beh	EEG	Musical excerpts	No	-	-	No
54	*Putkinen et al. (2014)*	Finland	*133*	7-13	Child	-	-	-	M/NM	-	-	-	Phys	EEG	Musical chords	No	-	Passive listening	No
55	*Schellenberg et al. (2008)*	Canada	*108*	-	Adult	-	-	-	M/NM	1.9	-	-	Beh	-	Musical excerpts	No	Yes	Like/Dislike	No
56	*Smit et al. (2022)*	Australia	*249*	27.4	Adult	103	146	-	M/NM/U	<5	-	-	Beh	-	Musical chords/Musical excerpts	Yes	Yes	Happy/Sad	No
57	*Steinbeis & Koelsch (2011)*	Germany	*40*	22.7	Adult	20	20		M/NM	12.32			Phys/Beh	EEG	Musical chords	Yes	-	ERP	No
58	*Suda et al. (2008)*	Japan	*10*	25-35	Adult	5	5	-	U	-	-	-	Phys/Beh	OT	Musical pieces	No	-	Happy/Sad	No
59	*Suzuki et al. (2008)*	Japan	*13*	20-26	Adult	13	0	-	M/NM	3.3	-	-	Phys/Beh	PET	Musical chords	Yes	-	Beauty	No
60	*Tabei (2015)*	Japan	*17*	21	Adult	7	10	-	M	-	-	-	Phys/Beh	fMRI	Musical excerpts	No	-	Happy/sad	No
61	*Tai & Kuo (2019)*	China	*8*	20-25	Adult	-	-	-	U	-	-	-	Phys/Beh	EEG	Musical pieces	No	-	Valence/Arousal	No

62	*Thompson & Opfer (2014)*	USA	*240*	19.7/7.9	B	131	109	-	U	-	-	-	Beh	-	Musical excerpts	Yes	-	Affective valence, Mode discrimination	No
63	*Trochidis & Bigand (2013)*	Canada	*16*	16	Adult	8	8	-	NM	-	-	-	Phys/Beh	EEG	Musical pieces	Yes	No	Happy/sad/anger/serenity	No
64	*Tsang et al., (2001)*	Canada	*55*	-	Adult	-	-	-	U	-	-	-	Phys/Beh	EEG	Musical excerpts	Yes	-	Happy/sad	No
65	*van der Zwaag et al. (2011)*	Netherlands	*20*	22	Adult	5	15	-	NM	-	-	-	Phys/Beh	ECG and respiration	Musical pieces	Yes	-	Pleasure	No
66	*Virtala et al. (2011)*	Finland	*16*	28	Adult	6	10	-	NM	-	-	-	Phys	EEG	Musical chords	Yes	-	MMN	No
67	*Virtala et al. (2012)*	Finland	*24*	13	Child	11	13	7	M/NM	-	-	-	Phys	EEG	Musical chords	Yes	No	Musical training	No
68	*Virtala et al. (2013)*	Finland	*19*	<1	Child	-	-	-	NM	-	-	-	Phys	EEG	Musical chords	Yes	-	-	No
69	*Wang et al. (2018)*	China	*47*	51	Adult	23	24	-	U	-	-	-	Phys/Beh	EEG	Musical pieces	Yes	No	Emotion regulation	Yes
70	*Zhou et al. (2019)*	UK	*32*	24	Adult	10	22	17	NM	-	-	-	Phys/Beh	EEG	Musical chords	Yes	No	Happy/Sad	Yes

Note. Age group: B = Adults and Children; Musical expertise: U = Undefined, M = Musicians, NM = Non-musicians; Method: Beh = Behavioral, Phys = Physiological.

Table 2. Cross-tabulation of the studies as a function of method, expertise, and sample.

	Physiological	**Behavioural**	**Physiological & Behavioural**
Children	3	3	0
Adults	7	25	27
Children & Adults	0	5	0
Musicians	1	0	1
Non-musicians	3	7	10
Musicians & Non- musicians	5	17	8
Undefined expertise	1	9	8