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AUTONOMIC AROUSAL INDUCED BY PLEASURABLE MUSIC
CORRELATES WITH ACTIVATION OF INSULA AND ANTERIOR
CINGULATE CORTEX

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Abstract

Most people derive pleasure from listening to music, which activates limbic and paralimbic brain areas associated with processing of biologically significant rewards, such as food and sex. Music elicits various bodily responses, such as dancing, chills and autonomic nervous system (ANS) responses, such as changes in heart rate or pupil size. This study investigated how pleasurable music affects the ANS, aiming to predict brain activation based on dynamic pupil size changes during music listening. It was expected that pupil size changes would predict activation of the insula and anterior cingulate cortex (ACC), which are involved in the modulation of the ANS.

The study, conducted at the Turku PET Center, involved 36 participants who listened to self-selected pleasurable music and control auditory stimuli in two experiments. Brain activity was measured using functional magnetic resonance imaging (fMRI) during music listening in one experiment, while the other measured music induced ANS activation through pupil size changes. fMRI data were modelled with the pupil data to study the connection between the activation of the ANS and specific brain regions and with the subjective pleasure ratings to study the link between neural activity and music-induced pleasure.

The results revealed that insula and ACC activation positively correlated with ANS activity when listening to pleasurable music. Physiological arousal also predicted activation in brain regions related to auditory processing, autonomic regulation, motor control and somatosensation. Music-induced pleasure predicted activation in partly overlapping brain regions, such as the insula, ACC and orbitofrontal cortex. These findings suggest a connection between music-induced pleasure and physiological arousal mechanisms.

keywords: autonomic nervous system, anterior cingulate cortex, insula, fMRI, music, emotion

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1. Introduction

1.1 From sound to (e)motion

Music, just like other sounds, enters the ear as sound waves. This acoustic information gets transformed into neural activity in the inner ear, from where it travels to the brain. In the brain, the neural information is further processed and shaped by various neural mechanisms in areas within and outside the auditory cortex. For example, different features of music, such as pitch, melody and rhythm, get processed in separate but still overlapping networks (Zatorre et al., 2007; Koelsch, 2011). Musical information reaches brain regions in control of emotions, and triggers the sense of pleasure by activating the reward system (Koelsch, 2014). The neural activity is manifested outside of the brain, as well: music can trigger pleasurable shivers down the spine in the listener or make them cry by activating the autonomic nervous system (ANS) (Sloboda, 1991), or urge one to physically move by engaging brain areas controlling movement (Chen et al., 2008).

Human beings are universally drawn to music: it is a part of all known cultures (Mehr et al., 2019). Music induces many bodily reactions, though the responses depend on the features of the music (Gomez & Danuser, 2007). Where there's music, there's movement and dance (Mehr et al., 2019): even children as young as 5 months old move rhythmically to music (Zentner & Eerola, 2010). Even if no overt movement is occurring, activation in the motor-related areas of the brain can be detected (Zatorre et al., 2007). In addition to dancing, music can elicit other behaviors related to high arousal, like singing, shouting, or jumping (Gabrielsson & Wik, 2003). It can activate the ANS and induce subjective responses such as "chills", also known as "shivers down the spine", goosebumps, tears or lumps in the throat (de Fleurian & Pearce, 2021; Panksepp, 1995; Sloboda, 1991). Music-induced emotions reflect sensations in different parts of the body, with similar emotions raising similar bodily sensations across cultures (Putkinen et al., 2024). Listening to music has endocrinological effects as well, as it can lead to changes in cortisol, oxytocin and prolactin levels (Eerola et al., 2021; Fancourt et al., 2014; Khalifa et al., 2003).

The evolutionary role of music remains unclear. Some have even proposed that music would merely be a byproduct of other adaptations unrelated to music, something that can be pleasurable but lacks direct adaptive value (Pinker, 1997). Others have suggested that music's evolutionary function is related to promoting group cooperation and social cohesion, improving social interaction skills (Peretz & Zatorre, 2003), soothing infants (Mehr & Krasnow, 2017), controlling emotions or moods to support social functions and strengthen relationships (Juslin & Laukka, 2004; Savage et al., 2021) or signaling existing social cohesion (Mehr et al., 2021). What is common to many of these proposals is the emphasis on music's effects on the body and synchronized movement. Music allows multiple individuals to participate in social interaction through e.g. dancing, singing, or playing an instrument. Music fosters social bonding by inducing rhythmic movement, which naturally synchronizes with the music and other listeners' movement, promoting cooperation and social cohesion (Oullier et al., 2008; Toiviainen et al., 2009; Valdesolo & Desteno, 2011). For example, when dancing to music, dancers synchronize their movements to the music and other dancers, which enhances social bonding (Tarr et al., 2015).

1.2 Music and emotions

In psychology, the classification of emotions is often approached with one of two types of models: the categorical (or discrete) emotion models and the dimensional emotion models. The first define emotions as discrete categories: a classic example is the basic emotion model that includes six basic emotions: anger, disgust, fear, happiness, sadness, and surprise (Ekman, 1992; for a review of different basic emotion models, see Tracy & Randles, 2011). The dimensional emotion models, in contrast, define emotions based on where they lie on different continuous dimensions, most often valence and arousal. Valence describes whether emotion is positive or negative and arousal represents the level of activation related to the emotion, ranging from calm or relaxed to excited.

In music-related emotion research, both categorical and dimensional emotion models are often used. Where categorical emotion models have been utilized, emotion categories have usually been modified so that musically less suitable categories (e.g. disgust) have been replaced with more appropriate ones (such as tenderness). The emotion categories and their number vary considerably between studies, which makes comparing them complicated. In music studies using dimensional emotion models, valence and arousal are the most common dimensions, though they are not always able to account for the variation of music-related emotions. In general, music induces mostly positive emotions (Juslin et al., 2011; Juslin & Sloboda, 2013) while negative emotions are less common in musical experiences than in other everyday life experiences, and emotions that are typically classified as negative, such as sadness or melancholy, can be experienced as pleasant in the context of music (Eerola & Vuoskoski, 2013). To better understand the composition of music-related emotions, music-specific categorical (Zentner et al., 2008) and dimensional models have been developed: in one study, 13 separate emotion dimensions associated with music were determined, including “energizing/pump-up”, “joyful/cheerful” and “triumphant/heroic” among others (Cowen et al., 2019).

Although there is variation in the propensity for musical hedonia (Martínez-Molina et al., 2016), it is generally agreed that most people find listening to music pleasant. Even though the background of strong music-related pleasure is not yet completely clear, it is thought that the pleasure stems from the emotions music evokes and the accompanying bodily responses. In line with this, music that induces strong, intense emotions seems to be related to stronger physiological arousal (Rickard, 2004) while elevated levels of arousal have been strongly linked to heightened music-induced pleasure (Salimpoor et al., 2009).

1.3 Music processing in the brain

How does the brain process the information that music provides? Just like all sounds, music consists of vibrations in air pressure. After the soundwaves have entered the ear, they travel through the auditory canal and the auditory ossicles to the cochlea, where the acoustic information turns into neural activity. From the cochlea, the neural information moves along the auditory nerve, also known as the cochlear nerve, to the brainstem. The auditory information is then projected to the auditory cortex principally via the medial geniculate body of the thalamus. The processing of auditory information begins already in the brainstem and continues in the auditory cortex. (Koelsch, 2011; Peterson et al., 2024.) For example, the primary auditory cortex, located in the superior temporal gyrus, plays a role in the fundamental processing of the auditory information, such as pitch perception (Bendor & Wang, 2005).

Music also activates the sensory-motor regions of the brain (Gordon et al., 2018) as well as the emotion- and reward-related networks (Koelsch, 2014), discussed in more detail below. The

auditory and motor systems are connected, and both are active when listening to or playing music. Motor brain regions often associated with music are the premotor cortex, supplementary motor area (SMA) and cerebellum (Chen et al., 2008; Zatorre et al., 2007). Even during passive listening, activation can be detected in some of the motor regions, such as parts of the premotor cortices and the cerebellum (Gordon et al., 2018).

Neural activity in the motor and pleasure-related areas is associated to the sensation of wanting to move to music, also known as groove. With rhythms and harmonic patterns that are of moderate complexity – not so simple that they become dull or too complex to follow - ratings of pleasure and urge to move to music are higher. With neuroimaging, activation of reward-related areas (eg. the nucleus accumbens and medial orbitofrontal cortex) and motor areas (e.g. the SMA and putamen) have been detected when listening to groovy music (Matthews et al., 2020). These findings emphasize the close connection between the motor and reward systems during music-induced pleasure and suggest that engaging the body may be one pathway through which music generates pleasure.

1.4 Music-evoked emotions in the brain

Music has the ability to evoke strong emotional responses in the listener. In the recent years, the neural correlates of music-evoked emotions have been studied in more detail to understand the relationship between everyday-emotions and emotions evoked by music. According to recent meta-analyses (Koelsch, 2014, 2020), music-induced emotions rely on a widely distributed network of regions. These include the right ventral striatum including the nucleus accumbens, dorsal striatum, insula, amygdala, mediodorsal thalamus, auditory cortex, and pre-supplementary motor area as well as the anterior cingulate cortex (ACC) and orbitofrontal cortex. Additionally, activation has been observed in the hippocampal formation.

These meta-analyses reveal common activation patterns across various emotions, but not the neural background of specific music-evoked emotions. Recent studies have approached the neural “fingerprints” of specific music-induced emotions with multivariate pattern analysis (MVPA). MVPA can reveal regularities across voxels in functional magnetic resonance imaging (fMRI) data that are specific to particular emotions, allowing for the identification of neural signatures of music-induced emotions that are undetectable with univariate analyses. A recent study by Putkinen et al. (2021) used pattern classification to identify the neural signatures of four specific music-related emotions. Discrete emotion-specific patterns were observed in the auditory and motor cortices, but no evidence of emotion-specific neural activation elsewhere was discovered. These results reinforce the link between music-related emotions and sensory-motor processes.

Music-related emotions and pleasure in particular have been proposed to rely on predictive mechanisms of the brain. Predictive processing is a general theory that suggests the brain creates predictions about sensory input and then continuously updates these predictions through perception, action and learning in order to minimize prediction error. The theory of predictive coding of music proposes that when listening to music with harmony, melody and rhythm, the brain relies on a predictive model shaped by our previous experiences to influence our perception. The brain continuously generates and updates predictions about incoming sensory information, leading to the forming of musical expectations and music-related predictive models in the brain. The brain is then able to anticipate the musical patterns, and confirmations and violations of such musical expectations lead to interactions between the auditory cortices, the motor system and limbic and reward-related brain structures, resulting in pleasure. (Vuust et al., 2022; Zatorre & Salimpoor, 2013)

As mentioned before, listening to pleasant music has been observed to activate the limbic and paralimbic regions of the brain, which have been linked with the processing of biologically significant rewards, such as food and sex. More specifically, it has been shown that the dopaminergic mesolimbic reward pathway plays a role in music-evoked pleasure. Especially brain regions such as the superficial amygdala, the nucleus accumbens (especially in association with “chills” initiated by music) and the ventral tegmental area are associated with pleasure evoked by music. (Koelsch, 2014) A PET study with D₂ receptor specific tracer [¹¹C]raclopride showed that the anticipation and experience of music-related pleasure is associated with striatal dopamine release (Salimpoor et al., 2011). Brain activation related to music-evoked pleasure has also been revealed in regions associated with autonomic arousal, such as the thalamus and ACC, and motor processes, such as the SMA (Blood & Zatorre, 2001). In a meta-analysis concerning pleasure and the reward system music, an abstract aesthetic reward, was compared to food, a primary reward. Music and food engaged similar brain networks, including the bilateral striatum and the bilateral insula, though the specific location of activation within these regions differed within the two domains. (Mas-Herrero et al., 2021.) This suggests that there is a common reward network activated by hedonic stimuli, even though the specific route of activation depends on the type of the stimulus.

1.5 Music and the autonomic nervous system

The autonomic nervous system (ANS) is an important component of the peripheral nervous system, maintaining homeostasis and responding to environmental stimuli by regulating involuntary physiological processes, such as cardiovascular, respiratory and digestive functions and secretion of endocrine and exocrine glands. It is divided into three parts: the sympathetic nervous system, which triggers the “fight or flight” response by increasing heart rate, dilating pupils and inhibiting digestion during stress, and the parasympathetic nervous system, which regulates internal bodily functions such as calming the heart rate and stimulating digestion (“rest and digest” – response), and the enteric system, controlling gastrointestinal functions. The ANS integrates signals from the brain, especially regions like the hypothalamus and brainstem, with sensory feedback from the body to dynamically adjust processes like blood pressure, respiration, and thermoregulation. (Cardinali, 2018)

Listening to pleasurable music has been linked to increased activity of the sympathetic nervous system. In one study, participants listened to self-selected pleasurable music and individually selected neutral music. The participants evaluated their feeling of pleasure as they were listening to the music, and simultaneously the activation of their sympathetic nervous system was recorded as a measure of emotional arousal. The activation of the sympathetic nervous system was evaluated with measures of heart rate, respiration rate, electrodermal activity, skin temperature and blood volume pulse amplitude. A strong positive correlation between ratings of pleasure and emotional arousal was detected from the real-time reporting of subjective pleasure and the objective recording of the sympathetic nervous system activation. (Salimpoor et al., 2009.) This indicates that music-induced pleasure is closely linked with ANS activity.

People who get less pleasure from music, or people with musical anhedonia, might have reduced interaction between the auditory cortex and the mesolimbic reward system. The nucleus accumbens shows decreased activity when listening to music but not when gambling with money, which also activates the reward pathway (Martínez-Molina et al., 2016). People with this kind of specific musical anhedonia also display less music-related chills (Martínez-Molina et al., 2016; Mas-Herrero et al., 2014), meaning that people who find music less pleasant also show weaker ANS responses to music. Dopamine modulates the experience of music-induced pleasure and autonomic arousal: in a

study by Ferreri et al. (2019) it was found that dopamine precursor administered orally not only strengthened the participants' subjective abilities to experience music-induced pleasure but also increased the physiological responses. Correspondingly, when receiving dopaminergic antagonist interfering with the dopaminergic signaling, there was a reduction in both subjective pleasure and physiological arousal.

The relationship between ANS responses and brain activation is yet to be completely understood. To study this connection in more depth, brain imaging and measurement of ANS activation can be combined. For example, to investigate the activation of the ANS, changes in pupil size can be tracked, as pupillary changes reflect the activation of the sympathetic nervous system. Pupil dilation is also suggested to be strongly related to emotional arousal. (Bradley et al., 2008.) Pupil size time series can be used as a regressor in fMRI data analysis to localize regions whose activity correlate with changes in autonomic arousal. Such studies indicate that the ACC and insula are centrally involved in the autonomic regulation linked with music-induced emotions (Ferraro et al., 2022; Koelsch, 2014). However, no study to date has used this approach to examine brain basis of music-induced changes in ANS activation.

1.6 fMRI

Functional magnetic resonance imaging, or fMRI, can be used to study neural activity in different parts of the brain. It is the most commonly used method for localizing brain activity, as it allows the measurement of changes in blood flow associated with neural activity with high spatial resolution. Neural activity increases the regional blood flow and consumption of oxygen in the activated areas, leading to changes in the balance between hemoglobin's oxygenated and deoxygenated forms. Oxygenated hemoglobin is diamagnetic (i.e. less responsive to magnetic fields), whereas deoxygenated hemoglobin is paramagnetic (i.e. more responsive to magnetic fields). These changes in the oxygenation of blood and regional blood flow can be detected with fMRI. The Blood Oxygen Level Dependent (BOLD) signal can be used to measure the change in the blood oxygenation concentration. Increased blood flow increases the oxygenation of the blood and thus increases the BOLD signal. With this information, it is possible to estimate the properties of neural signals. (Logothetis & Wandell, 2004.)

1.7 Current study

In the present study, we studied how listening to pleasurable music affects the ANS. We aimed to predict brain activation with dynamic changes in pupil size during music listening, to recognize which brain regions are active in association with the autonomic responses related to music. We hypothesized that changes in pupil size predicts the activation of the insula and ACC, which are involved in the modulation of the ANS (Ferraro et al., 2022).

To study this, we used fMRI and pupil size measurement in two different settings. fMRI was utilized to map the brain regions activated during pleasurable music listening, whereas pupil size imaging was used to measure the activation of the ANS, more specifically the activation of the sympathetic nervous system. Altogether 36 participants participated in the study, half of them in both experiments. In the fMRI experiment, participants listened to self-chosen pleasurable music and random tone sequences as their brain was being imaged. Simultaneously, the participants reported their subjective feeling of pleasure and experienced music-induced chills. In the pupil size experiment, participants also listened to pleasant music of their choice and random control sounds as well as their pupil sizes were being measured. At the same time, participants evaluated

numerically how strongly both the music excerpts and the control sounds evoked feelings of joy, liking, being moved, tenderness, calming, energizing, sadness, and fear.

We modelled the fMRI data with the parametric pupil data to study the connection between the activation of the ANS and specific brain regions. As a result, activation in brain regions related to auditory processing, autonomic regulation, motor control and somatosensation was observed. The fMRI data was also modelled with the subjective pleasure ratings to study the link between neural activity and music-related pleasure. Activation was observed in several regions that have previously been linked with music-related pleasure, such as the insula, orbitofrontal cortex and ACC.

2. Materials and methods

2.1 Subjects

Altogether 36 female volunteers participated in the study, 18 of which took part both in the fMRI imaging and the pupil size measurement (mean age 25.7, SD 4.) and 18 volunteers took part in the pupil size experiment only (mean age 23.3, SD 2.2, all right-handed).

The exclusion criteria included a history of neurological or psychiatric disorders, alcohol or substance abuse, current use of medication affecting the central nervous system and the standard MRI exclusion criteria. Each subject gave an informed, written consent and received compensation for their participation. The ethics board of the Hospital district of Southwest Finland had approved the protocol and the study was conducted in accordance with the Declaration of Helsinki.

2.2 Tasks

2.2.1 fMRI experiment

A 15-min fMRI experiment was conducted to map brain regions activated when listening to pleasurable music. During the experiment, the subjects listened to ten 90-sec excerpts of self-selected music and two 90-sec control stimuli in a random order. Most common music genres represented in the self-selected musical stimuli were contemporary pop, R&B and rap/hip-hop. The control stimuli were random tone sequences. Between the excerpts there was a 30-second period of silence, during which the subjects were instructed to fixate their gaze on a cross shown in the middle of the screen. During the music excerpts the subjects were instructed to rate their degree of music-evoked pleasure in real time on a scale from 1 to 10 by moving a cursor on the screen. 1 indicated no pleasure and 10 stood for “chills” evoked by the music.

2.2.2 Pupil size experiment

A pupil size experiment was carried out to measure the activation of the ANS while listening to pleasurable music. During the experiment subjects listened to 60-sec excerpts of the same self-chosen music and 45-sec control stimuli as in the fMRI experiment. In the experiment, each control stimulus was played after 2-3 music excerpts for each subject. After each music excerpt the subjects rated their experience for the following emotions on a scale from 1 to 4 (1 = very weak, 4 = very strong): joy, liking, being moved, tenderness, calming, energizing, sadness and fear.

2.3 Data acquisition

2.3.1 MRI data acquisition

The MRI data were obtained using a Phillips Ingenuity TF PET/MR 3T whole-body scanner. High-resolution (1 mm^3) structural images were acquired with a T1-weighted sequence (TR 9.8 ms, TE 4.6 ms, flip angle 7° , 250 mm FOV, 256×256 reconstruction matrix). 407 functional volumes were obtained with a T2*-weighted echo-planar imaging sequence (TR 2600 ms, TE 30 ms, 75° flipangle, 240 mm FOV, 80×80 reconstruction matrix, 62.5 kHz bandwidth, 3.0 mm slice thickness, 45 interleaved slices acquired in ascending order with no gaps).

2.3.1 Pupil data acquisition

Pupil size was recorded using EyeLink II eye-tracker (sampling rate 250 Hz, spatial accuracy better than 0.5 degrees). The recording was carried out in a dimly lit room, with participants seated, chin placed on a chin rest. A standard nine-point calibration and validation were completed in the beginning of the experiment and recalibration was carried out in the middle of the experiment. Participants were instructed to fixate their eyes on a cross shown in the middle of the screen while listening to the excerpts. Pupil size and gaze position were measured throughout the experiment. Blinks were erased from the subject-wise pupil size time series with in-house code based on PhysioData Toolbox (Kret & Sjak-Shie, 2019) and then baseline corrected (0-20 ms).

2.4. Data analysis

2.4.1 Structural and functional MRI data preprocessing

FMRIprep 1.3.0.2 (Esteban et al., 2019) was used for the preprocessing of the MRI data. The following preprocessing was performed on the anatomical T1-weighted (T1w) reference image: correction for intensity, non-uniformity, skull-stripping, brain surface reconstruction, spatial normalization to the ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009) using nonlinear registration with antsRegistration (ANTs 2.2.0) and brain tissue segmentation. On the functional data was performed the following preprocessing: co-registration to the T1w reference, slice-time correction, spatial smoothing with an 6mm Gaussian kernel, automatic removal of motion artifacts using ICA-AROMA (Pruim et al., 2015) and resampling the MNI152NL in 2009c Asym standard space.

2.4.2 Full-volume GLM data analysis

The fMRI data was analyzed with SPM12 (Wellcome Trust Center for Imaging, London, UK, <http://www.fil.ion.ucl.ac.uk/spm>). To reveal regions where the BOLD signal correlated with music-induced pleasure, a general linear model (GLM) was fitted to the data where the music sequences and control stimuli were modelled with separate boxcar regressors and dynamic pleasure ratings were included as a parametric modulator. The boxcar regressor accounted for the BOLD signal changes induced by the music and control blocks, while our primary focus was on the activity linked to the pleasure ratings. The regional effects of the pupil size were evaluated with a GLM, where the design matrix included the music and control boxcar regressor and the pupil size regressor as a parametric modulator. To control motor-related activity we added timings of the button presses as the regressor of no interest to the design matrixes, which was modelled as a stick function. Contrast images for the main effect of the pleasure ratings and the pupil size were generated for each participant and subjected to a second level analysis. Clusters surviving false discovery rate (FDR) correction ($p < 0.05$) are reported.

3. Results

3.1 Behavioral ratings

In the pupil experiment, the subjects evaluated on a scale from 1 to 4 how strongly they felt that the music excerpts and control stimuli evoked the following emotions (1 = very weak, 4 = very strong): being moved, calming, fear, energizing, joy, liking, tenderness and sadness.

In the behavioral ratings, there was a significant difference ($p < 0.01$) between the music and control ratings in each emotion except fear (**Figure 1** and **Table 1**). The difference was greatest with liking (t-value of 29.182).

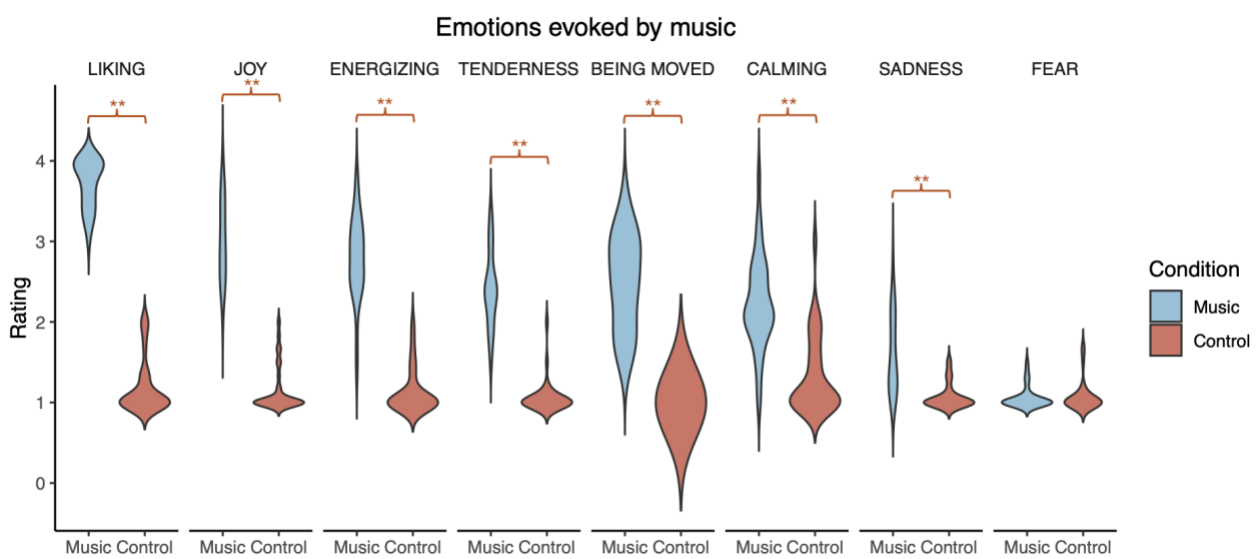


Figure 1. Graphical representation of how the subjects evaluated the strength of the emotions evoked by the music and control stimuli. ** = $p < 0.01$

Emotion	t-value	p-value
Liking	29.182	< 0.01
Joy	16.584	< 0.01
Energizing	16.066	< 0.01
Tenderness	14.354	< 0.01
Being moved	14.348	< 0.01
Calming	6.2104	< 0.01
Sadness	6.0039	< 0.01
Fear	-0.36066	0.7207

Table 1. T- and p-values of the measured ratings of the strength of different emotions for the self-chosen music excerpts vs control stimuli.

3.2 Pupil size during music listening

In the pupil experiment, the pupil sizes of the subjects were tracked when the subject was listening to pleasurable music and neutral control stimuli. Average pupil size between 1-6 sec was computed, and during that time period the average pupil size was significantly greater ($p < 0.05$) when listening to self-selected, pleasurable music, in comparison to control stimuli (**Figure 2**).

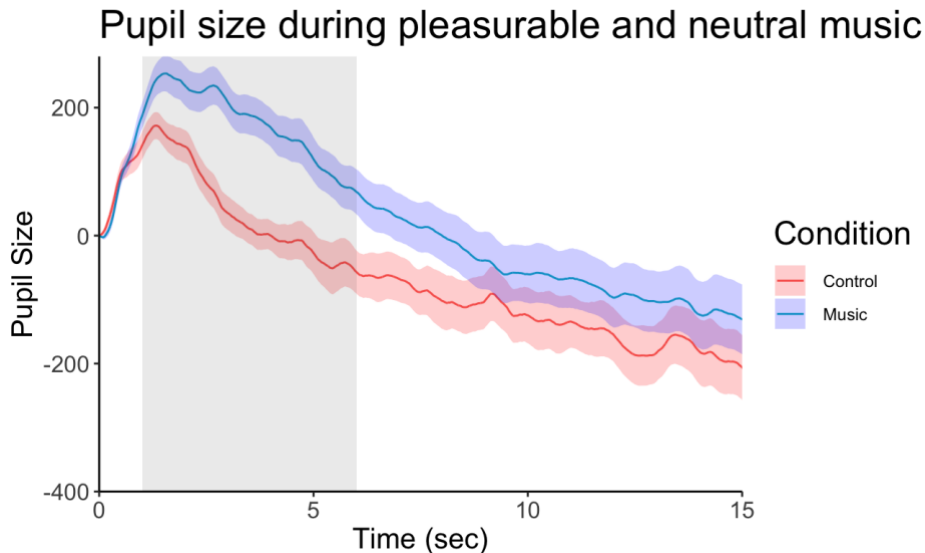


Figure 2. Mean size of the pupil during both the music excerpts and the control stimuli. During the highlighted period, the average pupil size was significantly greater ($p < 0.05$) when listening to music in comparison to the control stimuli.

3.3 Pupil diameter-dependent BOLD responses

Modelling the BOLD data with the parametric pupil size when listening to pleasurable music revealed activation in the SMA extending to the ACC, as well as activation of the insula and superior temporal gyrus. Activation was also observed in the supramarginal gyrus, extending to the pre- and postcentral gyri (**Figure 3**).

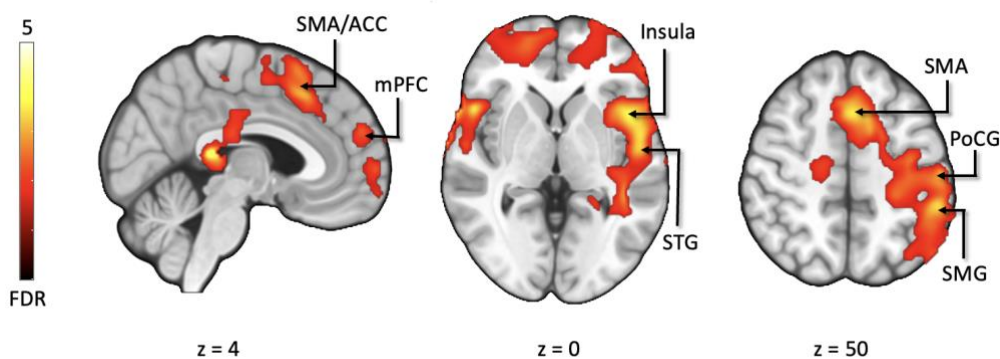


Figure 3. Pupil diameter-dependent BOLD-responses (thresholded at $p < 0.05$, FDR corrected at cluster level). SMA = Supplementary motor area, ACC = Anterior cingulate cortex, mPFC = Medial prefrontal cortex, STG = Superior temporal gyrus, PoCG = Postcentral gyrus, SMG = Supramarginal gyrus. The colourbar indicates the t statistic range.

3.4 Pleasure dependent BOLD responses

We modelled the BOLD responses with the subjective pleasure ratings during music listening. This analysis revealed activity in the insula, orbitofrontal cortex and ACC as well as in the middle frontal gyrus and frontal pole. Subcortically, activation was observed particularly in the right caudate and bilateral putamen. There was also activation in sensorimotor regions in the pre- and postcentral gyri, SMA, and supramarginal gyrus as well as in the visual cortex (**Figure 4**).

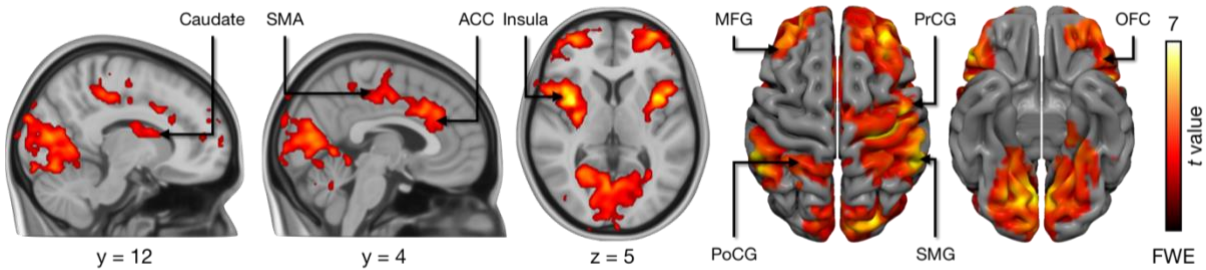


Figure 4. Pleasure-dependent BOLD responses (thresholded at $p < 0.05$, FWE corrected at cluster level). SMA = Supplementary motor area, ACC = Anterior cingulate cortex, MFG = Middle frontal gyrus, PoCG = Postcentral gyrus, PrCG = Precentral gyrus, SMG = Supramarginal gyrus, OFC = Orbitofrontal cortex. The colourbar indicates the t statistic range.

4. Discussion

4.1 Summary of main findings

We investigated the neural correlates of the sympathetic nervous system activation during music listening with fMRI. To achieve this, we used pupil size as a physiological marker of sympathetic activity and employed it to predict BOLD responses during listening to pleasurable music and neutral control stimuli.

Our main finding was that the activation of the insula and the anterior cingulate cortex (ACC) were positively associated with sympathetic nervous system activity when listening to pleasurable music. This result confirmed our hypothesis stemming from prior findings that pleasurable music activates the sympathetic nervous system (Salimpoor et al., 2009), and the ACC and insula are centrally involved in the modulation of ANS activity (Beissner et al., 2013; Ferraro et al., 2022).

Physiological arousal also predicted activation in the superior temporal gyrus, where the auditory cortex is located, as well as activation in the sensory-motor areas, such as the supplementary motor area (SMA), pre- and postcentral gyri and supramarginal gyrus. These results indicate that sympathetic nervous system activity induced by pleasurable music relies on brain circuits associated with interoceptive awareness, viscerosensory processing, and action preparation.

We also modelled the BOLD responses with the ratings of subjective pleasure. This analysis revealed activity in the insula, ACC, orbitofrontal cortex, middle frontal gyrus and frontal pole. Subcortically, activation was observed particularly in the right caudate and bilateral putamen. There was also activation in the sensorimotor regions in the pre- and postcentral gyri, SMA, supramarginal gyrus and visual cortex. Majority of these regions have been associated with music-related pleasure (Blood & Zatorre, 2001; Mas-Herrero et al., 2021). The pupil size-dependent and the pleasure-related BOLD responses partly overlap, suggesting that certain connections within the neural circuits associated with pleasure are specifically linked to arousal, while others are connected to distinct elements of the pleasure experience.

4.2 Pleasurable music increases sympathetic activity

In previous music-related studies, activation of the ANS has been measured using various physiological indicators, including changes in skin conductance responses, heart rate, respiration rate, blood volume pulse, body or skin temperature, and salivary cortisol levels (Khalfa et al., 2002; Rickard, 2004; Salimpoor et al., 2009). However, even though pupil size is a valid tool for measuring ANS activation (Bradley et al., 2008) and has been utilized in fMRI studies regarding ANS activation before (Ferraro et al., 2022), it has rarely been employed to study music-induced changes in sympathetic nervous system activity. We used pupil size changes as a marker of the sympathetic nervous system activation and found that the average pupil size was significantly greater when listening to pleasurable music than the control stimuli. These findings highlight the utility of pupil size as a marker for capturing sympathetic nervous system activation during music listening and indicate that the sympathetic nervous system was more active when listening to pleasurable music than the control stimuli.

When modelling the BOLD data with the pupil size as the regressor, activation was revealed in the ACC and insula, as predicted. Insula and ACC are centrally involved in the modulation of the ANS (Beissner et al., 2013; Ferraro et al., 2022). Insula is linked to interoceptive processing and has been associated with subjective feelings, attentional processes, music and time perception as well as

awareness of movement and sensation ((Bud) Craig & D, 2009; Ferraro et al., 2022; Koelsch, 2014). ACC is involved in action preparation and regulation of the ANS, especially sympathetic responses (Beissner et al., 2013; Ferraro et al., 2022). The connection between ACC and insular cortex and ANS activation has been studied in different settings and with different mental processes, such as cognitive tasks or with stimuli inducing nausea or pain (Ferraro et al., 2022). In some of these studies, pupil size changes have been used as a measurement of ANS activation (Breedon et al., 2017; Causse et al., 2022; Critchley et al., 2005; Harrison et al., 2009).

The relationship between ANS activation and music remains understudied. Some studies regarding music-related arousal have been conducted: subjective ratings of music-related pleasure have been found to positively correlate with the activation of the sympathetic nervous system and increased arousal (Salimpoor et al., 2009), though it remains unclear, whether increased arousal would also be associated with music that is especially calming but nevertheless pleasant to the listener.

To our knowledge, the current study is the first to examine the neural correlates of dynamic changes in physiological arousal using fMRI. An early study with 10 musically trained participants used PET to measure cerebral blood flow and found that ACC activation as well as activation of ventral striatum, insula, thalamus, orbitofrontal cortex, amygdala, ventral medial prefrontal cortex, SMA and cerebellum are linked with heightened physiological responses when listening to pleasurable music (Blood & Zatorre, 2001). Our findings support the positive association between increased sympathetic activity and activation of ACC and insula. Additionally, we observed activation in SMA and medial prefrontal cortex, in line with the results of Blood and Zatorre (2001). Activation of medial prefrontal cortex here may be related to the emotions evoked by the music, as it has been priorly associated with emotions in non-musical context (Saarimäki et al., 2016).

As mentioned before, our results revealed activity in the SMA and precentral gyrus, where the primary motor cortex is located. These regions support the control of voluntary movement. SMA has been associated with timing, planning and preparation of movement (Grèzes & Decety, 2002; Picard & Strick, 1996; Rao et al., 1997). Previously, neural activity induced by musical stimuli has been found in the brain regions that are in charge of motor control, even if overt movement is absent. It has been speculated that music activates predictive processes and starts preparing the brain for action in case the activation of the motor system would be relevant. (Chen et al., 2008; Gordon et al., 2018.) It seems evident that the processing of perceived music engages areas usually considered substantial for only action-related information. In our study, increased BOLD-signal was also observed in the postcentral and supramarginal gyri, which partially answer for the somatosensory functions of the brain. Our results confirm the previous findings of heightened motor cortical activity during music listening and show that elevated autonomic activation due to pleasurable music is related to increased activity in the motor and somatosensory areas of the brain.

Pupil size was also found to predict activation in the superior temporal gyrus, where the auditory cortex is situated. Auditory cortex has been observed to show strong activation in context of music-related emotions (Putkinen et al., 2021), and happy and sad music activate the auditory cortex stronger than neutral music (Mitterschiffthaler et al., 2007). Auditory cortex activity has also been proven to be more enhanced when listening to pleasant music, as opposed to unpleasant sounds (Mueller et al., 2015). This phenomenon might be associated to an increase in the current state of sensory focus due to a pleasant stimulus. Pleasant stimuli tend to draw attention to themselves, and an elevated level of attention strengthens the activation of the sensory regions of the brain. For example, when attention is focused on an auditory stimulus, elevated activity of the auditory cortex can be detected. (Petkov et al., 2004.)

4.3 Music, emotion and pleasure

In the pupil experiment, the participants rated how strongly they felt specific, discrete emotions during the self-chosen musical excerpts and the control stimuli. The music excerpts evoked all the emotions (being moved, calming, energizing, joy, liking, tenderness and sadness) aside from fear significantly stronger than the control stimuli. Greatest difference between the music excerpts and control stimuli was for liking, which is most likely due to the fact that the participants were free to choose music that they found pleasurable. These results notably point out that even when pleasurable music is self-selected, it may still evoke emotions classically thought of as negative, such as sadness. Listening to sad music has been associated with regulating negative moods or negative emotions, seeking consolidation, retrieving memories of past live events, or evoking other emotions with at least partly positive undertones, such as nostalgia or tenderness (Taruffi & Koelsch, 2014). These kind of observations are common with music-induced emotions (Eerola & Vuoskoski, 2013), and are indicative of the complex nature of music-induced emotions and highlight their distinctiveness from emotions triggered by “real-life“ events.

We also modelled fMRI data with ratings of subjective pleasure. Activity was revealed in the insula, orbitofrontal cortex and ACC as well as in the sensory-motor regions including the pre- and postcentral gyri, SMA and supramarginal gyrus. Additionally, the right caudate, bilateral putamen and visual cortex showed activity. The activation of many of these regions has previously been linked with music-related pleasure, especially the insula, orbitofrontal cortex, ACC, SMA and right caudate (Blood & Zatorre, 2001; Mas-Herrero et al., 2021). In previous studies using fMRI to investigate brain responses to pleasurable music, activation of the insula, Rolandic operculum and ventral striatum have been detected, as well as activation of the caudate nucleus (Koelsch et al., 2006; Montag et al., 2011).

Music-related pleasure, its anticipation and music-related chills, which are strongly associated with physiological arousal, have been linked with activation of the striatal dopaminergic system, including the nucleus accumbens (Koelsch, 2014; Salimpoor et al., 2011). Activation of the nucleus accumbens predicts music-related pleasure, correlates with the reward value of music (e.g.; willingness to pay; Salimpoor et al., 2013), is reduced in musical anhedonia (Martínez-Molina et al., 2016), and peaks at the onset of pleasurable stimuli before declining over time (Mueller et al., 2015). When listening to music with high reward value, increased functional connectivity between nucleus accumbens and the auditory cortices has been revealed (Salimpoor et al., 2013; Zatorre & Salimpoor, 2013), highlighting the role of interaction between sensory and reward circuits in music-induced pleasure. Despite its roles in pleasure and music-induced emotion, no activation of the nucleus accumbens was revealed in this study. However, in this study the BOLD data was not specifically modelled in relation to the experienced chills. Nucleus accumbens activation could be more readily observed during music-induced chills, which represent peak levels of music-induced physiological arousal, as opposed to the wider range of music-induced arousal examined in the current study.

In summary, our results indicate that activity in some of these regions correlate with subjective pleasure as well as objective arousal, that is elevated sympathetic nervous system activity. Such regions include the insula, ACC, SMA, supramarginal gyrus and pre- and post-central gyri. However, some regions only show enhanced activity with relation to only subjective pleasure, such as the orbitofrontal cortex, bilateral putamen or the right caudate. Our results suggest that certain connections within the neural networks associated with pleasure are specifically linked to arousal, while others could be related to other components of pleasure such as attentional engagement and reward valuation.

4.4 Music, pleasure and the body

A key finding in this study was that the sympathetic nervous system activates when listening to pleasurable music when compared to neutral auditory stimulus. Activation of the sympathetic nervous system involuntarily triggers several physiological responses related to the “fight or flight”-response, such as increased heart rate in order to pump more oxygenated blood to muscles and vital organs, dilated pupils to enhance vision, elevated blood pressure due to the constriction of blood vessels and redirection of blood flow to enhance physical performance. Lungs dilate to enhance oxygen flow, and sweating may occur to cool the body down. Even though the autonomic responses to music can be subtle and the background of such connection is not yet established, pleasurable music clearly increases the state of arousal.

Pleasure and physiological arousal seem to intertwine. Most people gain pleasure from listening to music, and the motivations for listening to music are typically connected to the emotional responses or processes related to it (Juslin & Laukka, 2004). In a study by Salimpoor (2009), a strong dynamic relationship between increased music-related pleasure and arousal was recorded. These findings demonstrate a dissociation between the physiological responses of individuals who find a particular piece of music pleasurable and those who do not, as no significant changes in physiological arousal were measured from participants who did not experience the music pleasant. The results reinforce the expected link between emotional arousal and pleasure, suggesting that physiological response is strongly influenced by the listener’s subjective preference. However, as musical preferences are very subjective, it is hard to conduct studies that can reliably examine this phenomenon. Subjective feelings are hard to measure, and it is also important to consider that other emotional states besides pleasure activate the sympathetic nervous system, such as anxiety or fear. It has also been studied that certain features of music (e.g. familiarity, tempo or modes) as well as traits of the listeners (e.g. personality) contribute to the enjoyment of the music and the emotions it evokes (Hevner, 1935, 1937; Montag et al., 2011; Pereira et al., 2011; Peretz et al., 1998). Additionally, as stated before, music classified as “sad” can still be perceived as pleasant (Eerola & Vuoskoski, 2013), highlighting that music can be categorized according to its musical features (e.g. minor key or slow tempo), but the emotions evoked by it do not always correlate with such categorization.

In this study, pleasurable music activated sensory-motor brain regions, such as the SMA, more than the control stimuli. This suggests that the experience of music-induced pleasure is not supported solely by brain regions governing emotional or auditory processing but also involves motor regions, potentially reflecting an embodied response to music. The underlying mechanisms of this connection, however, remain to be explored in greater detail. One possible explanation is that pleasurable music might trigger involuntary motor responses, such as tapping or moving to the rhythm, which could enhance the overall pleasurable experience. Additionally, music’s ability to activate the sympathetic nervous system could be contributing to increased arousal or physical engagement, making the experience more rewarding. Music may also be perceived as pleasant because it engages the motor regions and activates the sympathetic nervous system.

Bodily responses related to music can also be studied from another point of view. In a study by Putkinen et al. (2024), bodily sensations related to emotions induced by music were mapped, visually illustrating where specific music-related emotions are felt in the body. Notably, the study highlighted that music does generate strong subjective bodily sensations that correlate with the emotions it evokes across the participants. The origin of these sensations likely ties to the activation of the motor system and ANS. Body mapping emphasizes the role of music-induced emotions in shaping bodily sensations. For example, music related to emotions such as happiness and

danceability were linked to the activation of the limbs in participants from both Western and Chinese cultures. Our fMRI results showing that motor areas as well as areas related to sympathetic responses are active when listening to pleasurable music suggest that the activation of these regions could be central in the formation of these emotion-specific bodily sensations.

Further study of the interactions between the sensory, motor, and autonomic systems could provide deeper insights into why music is experienced as pleasurable and why brain regions typically linked to biologically significant rewards or motor processes activate when listening to music.

4.5 Limitations

A larger sample size would improve the reliability of defining the relationship between autonomic responses and brain activation, allowing for the detection of weaker effects. Nonetheless, this study successfully identified activation in the regions that were anticipated to be active. Additionally, all the participants in this study were female to maximize statistical power, as the spatial distribution of specific opioid receptors regulating reward and mood varies between the sexes (Kantonen et al., 2020). Also, a sample group consisting of females only can be expected to maximize the effects of the study, as women tend to report stronger emotional responses (Lench et al., 2011). This leaves open whether our results generalize to men. However, no major differences between the sexes in relation to themes concerning the topic has come up in literature.

4.6 Conclusion

In the present study we investigated how listening to pleasurable music affects the ANS. We proposed that changes in pupil size predict the activation of the insula and ACC, brain regions associated with ANS modulation. Our hypothesis was confirmed, and our results suggest that listening to pleasurable music is associated with the activation of the ANS, specifically the sympathetic branch. This activation is linked to increased activity in brain regions such as the insula and ACC. These findings suggest a direct connection between emotional experiences evoked by music and physiological arousal mechanisms.

Additionally, activation was observed in the brain regions responsible for auditory processing, autonomic regulation, motor control and somatosensation. These results shed light on the connection between music and bodily reactions beyond those governed by the ANS. The connection between music-induced pleasure was also examined with fMRI, pointing out that the brain areas activated during peak sympathetic nervous system activity and when music is perceived as most pleasant partially overlap but are not identical. This distinction indicates that music-related pleasure and arousal are aspects of the same phenomenon but involve distinct neural networks.

Here, we have provided insights into the relationship between physiological and emotional responses to pleasurable music. With further research, the multidimensional aspects of music-induced pleasure – encompassing ANS activation, motor processes and emotional responses – can be better understood.

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