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Review article

Common and distinct neural correlates of music and food-induced pleasure: A coordinate-based meta-analysis of neuroimaging studies

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ABSTRACT

Neuroimaging studies have shown that, despite the abstractness of music, it may mimic biologically rewarding stimuli (e.g., food) in its ability to engage the brain's reward circuitry. However, due to the lack of research comparing music and other types of reward, it is unclear to what extent the recruitment of reward-related structures overlaps among domains. To achieve this goal, we performed a coordinate-based meta-analysis of 38 neuroimaging studies (703 subjects) comparing the brain responses specifically to music and food-induced pleasure. Both engaged a common set of brain regions, including the ventromedial prefrontal cortex, ventral striatum, and insula. Yet, comparative analyses indicated a partial dissociation in the engagement of the reward circuitry as a function of the type of reward, as well as additional reward type-specific activations in brain regions related to perception, sensory processing, and learning. These results support the idea that hedonic reactions rely on the engagement of a common reward network, yet through specific routes of access depending on the modality and nature of the reward.

1. Introduction

Humans can feel and experience pleasure from a large variety of stimuli and activities: from primary rewards that satisfy basic biological drives, such as food, to aesthetic experiences, such as listening to music. All rewarding events and experiences, independently of their type – from primary to aesthetic – are processed by a common set of brain regions that constitute the well-known reward circuit, including the ventral tegmental area, the ventral striatum, the insula, and the ventromedial prefrontal cortex, among others (Bartra et al., 2013; Blood and Zatorre, 2001; Sescousse et al., 2013). This circuitry, through a complex interplay between dopaminergic and opioid pathways, is involved in many different aspects of reward processing: from value representation, associative learning, and incentive salience to affective processing (Bartra et al., 2013; Berridge and Kringelbach, 2008; Chase et al., 2015).

Notably, the reward circuit is highly conserved in evolution, with remarkable similarities between humans and other mammals (Haber

and Knutson, 2010; Loonen and Ivanova, 2016). Yet, the capacity to experience pleasure from aesthetic rewards, and particularly from music, is thought to be a unique human trait. Indeed, significant differences exist between music and primary rewards (e.g., food). For instance, while hedonic reactions and preference for primary tastes, such as sweetness, are mainly innate and highly preserved across species and individuals (Berridge, 2000), musical preferences are shaped by previous exposure, cognitive abilities, musical education, and cultural background; thus they are largely influenced by learning and plasticity (Gold et al., 2019a, b; Greenberg et al., 2015; Haumann et al., 2018). In this regard, recent models hold that music-induced pleasure may be driven by anticipation and prediction mechanisms, which, in turn, have been linked to predictive coding theories (Cheung et al., 2019; Gold et al., 2019b; Koelsch et al., 2019; Salimpoor et al., 2015). In line with this idea, neuroimaging studies have shown that music-induced pleasure may be mediated by the crosstalk between the ancient reward circuitry and higher-order cortical regions involved in auditory cognition and predictive coding that are phylogenetically newer and especially well

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developed in humans, such as the superior temporal gyrus and the inferior frontal gyrus (Loui et al., 2017; Martínez-Molina et al., 2016; Sachs et al., 2016; Salimpoor et al., 2013).

The engagement of both higher-order neural mechanisms and the reward system appears to be a hallmark of musical reward compared to primary and secondary rewards. However, due to the lack of comparative research comparing music and other types of rewards, it is unclear to what extent this is the case. Among all other reward types, hedonic responses to food represent an excellent control condition to assess common and distinct brain responses associated with music-induced pleasure since (i) the brain correlates of food reward have been extensively investigated in both humans and non-humans animals (particularly hedonic responses to sweetness), and (ii) food is passively delivered in real-time in human neuroimaging studies, as it is the case of music. Therefore, a direct comparison between these two reward types may help us disentangle specific- and common- brain activations during their consumption. Indeed, apart from differences in the engagement of higher-order cortical regions, differences between both may be present within the reward circuitry as well. For instance, although various parts of the striatum – the caudate, the putamen, and the nucleus accumbens – are activated by both music and food, it is not clear whether one predominates over the other as a function of the type of reward. Music reward studies have particularly emphasized the role of both the caudate and the nucleus accumbens in music-induced pleasure (Salimpoor et al., 2011), while food rewards might recruit more lateral portions of the striatum as well (Delgado, 2007). In addition, previous studies on primary and secondary rewards have shown a gradient along the posterior-anterior axis of the ventral prefrontal cortex as a function of the abstractness of the reward, with anterior parts – phylogenetically newer than posterior and medial parts – encoding more abstract representations (Klein-Flügge et al., 2013; O'Doherty et al., 2001; Rudebeck and Murray, 2014; Sescousse et al., 2013, 2010). Thus, one fundamental hypothesis is that music rewarding experiences would be represented in more anterior areas of the prefrontal cortex than food rewards.

To address these questions, we directly compared brain activations to food and music reward to identify both overlapping and specific reward-type activations by using a coordinate-based meta-analytic approach. Specifically, we conducted a meta-analysis of neuroimaging studies investigating brain responses to either music- or food-induced pleasure. In order to identify hedonic-related activations, all studies included in the meta-analysis involved either music or food “consumption” inside the scanner and reported contrasts exploring brain activations as a function of subjective reports of pleasure. By using this approach, we focus directly on hedonic or affective processes rather than perceptual or cognitive aspects of music vs. food. We first assessed the brain regions that were consistently engaged by either music or food reward, and next, we investigated common and specific reward type activations. We hypothesized that while food and music-induced pleasure would show some degree of overlapping activations within the reward network, music-induced pleasure would involve the engagement of higher-order cortical regions. We also hypothesized that differences might be present in the location and the predominance of one reward-type over the other within the reward circuitry, particularly in the ventral prefrontal cortex and the striatum (Delgado, 2007; Sescousse et al., 2010).

2. Methods

2.1. Study selection for the meta-analysis

We conducted two independent searches (one for food studies, another for music studies) in PubMed to identify fMRI and Positron Emission Tomography (PET) studies exploring music and food-induced pleasure. Our search included a combination of the following: (i) the type of reward [i.e. "music"; ("food" OR "taste" OR "juice")]; (ii) reward-related terms [i.e. ("reward" OR "pleasure" OR "liking")]; and (iii)

neuroimaging terms [i.e. ("fMRI" OR "PET" OR "neuroimaging" OR "cerebral blood flow")]. The search for food reward was performed from 2012 to the present. Studies on food reward prior to 2012 were obtained from a previous meta-analysis on food reward (Sescousse et al., 2013). The searches led to 87 studies on music and 532 on food reward (Fig. 1). Articles were first selected by their title and abstract and then carefully read to make sure that they fulfilled the following selection criteria:

- (1) Whole-brain results were reported (excluding studies based on ROI analyses, without full-brain coverage, and PET studies using selective radiotracers other than H215O).
- (2) Involved healthy, drug-free adult subjects (excluding studies performed on children, teenagers, and old adults and studies with fewer than 10 subjects).
- (3) Involved the delivery, in real-time, of either food/tastes or music.
- (4) Participants reported subjective ratings of pleasure, liking, or preference.
- (5) Contrasts reported reflected hedonic processing at the time of music listening or food consumption (including contrasts such as like > dislike, positive correlations with pleasantness, correlation with individual differences in hedonic processing). Contrasts based on baseline subtraction were not included to avoid nonspecific effects.

Seventeen experiments (190 foci/330 subjects) on music rewards and twenty-one experiments (193 foci/373 subjects) on food reward (Tables 1 and 2) fulfilled our inclusion criteria. One study from the food reward meta-analysis (Green and Murphy, 2012) was split into two experiments since results were reported separately for two groups of healthy participants (diet and non-diet soda drinkers).

2.2. Meta-analysis methods

We conducted two independent coordinate-based meta-analyses, one for music experiments and one for food experiments, using anisotropic effect-size Seed-Based *d* Mapping (SDM, version 5.15, formerly "Signed Differential Mapping") meta-analysis (<http://www.sdmproject.com>). Using peak coordinates, SDM generates a voxel-level map of effect sizes by converting the reported *t* values to effect size (Hedge's *d*) and modeling an anisotropic kernel. All individual effect size maps are then combined with a random-effects model, accounting for sample size and effect size variability within and between studies. SDM *Z* maps are then recreated, dividing meta-analytic effect sizes by their standard errors across studies. Since the resulting *Z* values do not typically follow a normal distribution, SDM uses permutation statistics to estimate a null distribution. All the analyses conducted were based on 50 permutations. To test statistical significance, SDM recommends using an uncorrected $P = 0.005$ as the primary threshold, as this was found to balance sensitivity and false-positive rate optimally and be an approximate equivalent to corrected P -value = 0.05 (Radua et al., 2012). We used a more stringent threshold, $p < 0.001$ uncorrected, for the main analysis and the default threshold of $p < 0.005$ uncorrected for the exploratory analyses found in the supplementary information.

Primary analyses examined brain activity consistently engaged in either studies of music- or food-induced reward. The two resulting maps were further binarized and combined to identify "overlapping" brain regions. Next, we formally tested whole-brain differences between both reward-types by calculating the difference between both rewards in each voxel and determining its statistical significance using a randomization test as implemented in SDM.

We performed Jackknife sensitivity analyses to examine the robustness of the results and conducted Egger tests on each cluster to assess potential publication bias (Forero et al., 2019).

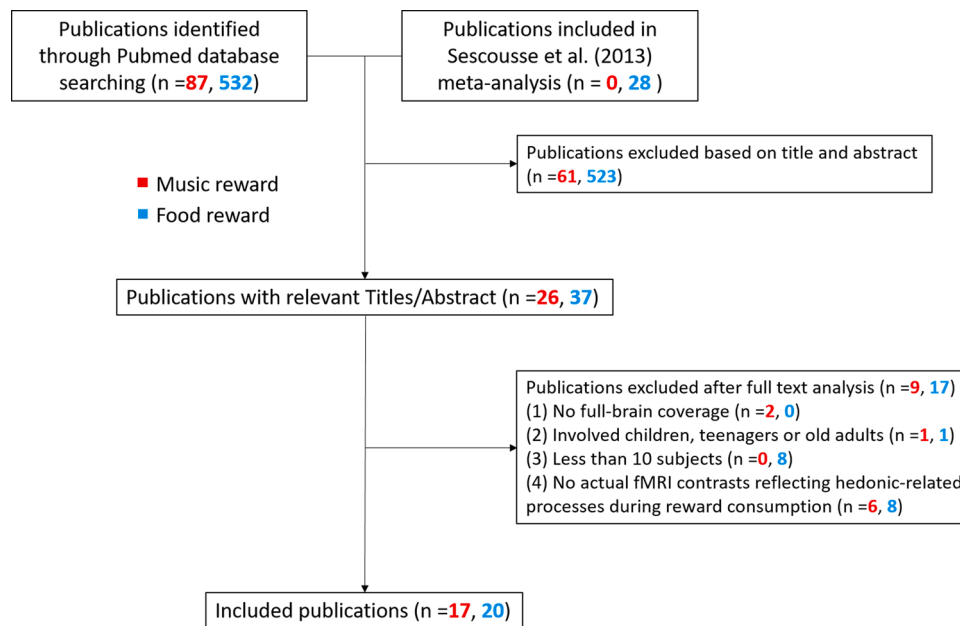


Fig. 1. Flow chart showing the study selection process for both meta-analysis.

Table 1

Music reward studies included in the meta-analysis.

Study	Modality	n	Foci	Task	Music selection	Contrast
Blood et al. (1999)	PET	10	2	Listening to 6 versions of a novel musical passage varying in degree of dissonance	Experimenter	Positive correlation with pleasantness
Blood and Zatorre (2001)	PET	10	10	Listening to music that elicits chills	Participants	Positive correlation with chill intensity
Brattico et al. (2016)	fMRI	29	21	Listening to liked and disliked musical pieces with happy and sad connotation	Participants	Like > Dislike
Caria et al. (2011)	fMRI	14	20	Listening to sad and happy music	Participants & Experimenter	Favorite > Standard (Control group)
Gold et al. (2019a)	fMRI	19	11	Decision-making task leading to consonant and dissonant musical endings	Experimenter	Consonance > Dissonance
Huang et al. (2016)	fMRI	18	26	Listening to artistic and popular music, and musical notes	Experimenter	Popular music > Notes clip Artistic music > Notes clip
Keller et al. (2013)	fMRI	21	12	Listening to both familiar and unfamiliar music, and scrambled versions	Experimenter	Negative correlation with anhedonia trait
Kim et al. (2017)	fMRI	23	7	Listening to consonant and dissonant music	Experimenter	Consonant > Dissonant
Koelsch et al. (2006)	fMRI	11	11	Listening to pleasant music and pitch-shifted versions	Experimenter	Pleasant > Unpleasant
Martínez-Molina et al. (2016)	fMRI	29	13	Listening to both pleasant and unpleasant music while reporting real-time ratings of pleasure	Participants & Experimenter	Positive correlation with pleasantness (excluding musical anhedonics)
Mas-Herrero et al. (2021)	fMRI	17	10	Listening to pleasant music while reporting real-time ratings of pleasure	Participants & Experimenter	Positive correlation with pleasantness at sham
Montag et al. (2011)	fMRI	33	6	Listening to subject-selected favorite and unlike songs	Participants	Pleasant > Unpleasant
Mueller et al. (2015)	fMRI	23	16	Listening to original (pleasant) and manipulated (unpleasant) music	Experimenter	Pleasant > Unpleasant
Pereira et al. (2011)	fMRI	14	8	Listening to a list of pop/rock music	Experimenter	Like > Dislike
Salimpoor et al. (2013)	fMRI	19	8	Listening to new released music with the possibility to buy the actual music	Experimenter	Positive correlation with the amount of money willing to pay
Trost et al. (2014)	fMRI	20	7	Listening to either consonant or dissonant piano music while performing a speeded visuo-motor detection task	Experimenter	Consonant > Dissonant
Wallmark et al. (2018)	fMRI	20	2	Listening to both familiar and unfamiliar music, either pleasant or unpleasant.	Experimenter	Like > Dislike

3. Results

We first examined brain regions that were consistently engaged when listeners reported a pleasurable experience to music. As illustrated in Fig. 2, the analysis yielded a set of brain regions including the bilateral insula (INS), the bilateral superior temporal gyrus (STG), the right inferior frontal gyrus (IFG), the bilateral ventral striatum, the anterior prefrontal cortex, and the ventromedial prefrontal cortex (vmPFC), whole-brain maps of the main results are available online on Neurovault: <https://identifiers.org/neurovault.collection:8567>.

Fig. 3 shows the main findings for the meta-analysis of neuroimaging studies investigating food-induced pleasure. The analysis revealed engagement of the bilateral insula, putamen, amygdala, ventral striatum, somatosensory cortex, posterior cingulate cortex, vmPFC, and thalamus.

Using a jackknife procedure, we found that the two activation maps (food and music) were replicated in all jackknife analyses, reflecting the consistency and robustness of our results (Figs. S1 and S2). In addition, funnel plots and Egger tests in the clusters identified showed no evidence of publication bias for either music or food studies in any clusters

Table 2
Food reward studies included in the meta-analysis.

Study	Modality	n	Foci	Task	Contrast
Berns et al. (2001)	fMRI	25	1	Passive delivery task	Preferred > Nonpreferred
Araujo et al. (2003)	fMRI	11	8	Passive delivery task	Sucrose > Tasteless drink
Felsted et al. (2010)	fMRI	40	13	Passive delivery task	Milkshake > Tasteless drink
Grabenhorst et al. (2010a)	fMRI	14	6	Passive delivery task	Positive correlation with pleasantness of milkshake flavour
Grabenhorst et al. (2010b)	fMRI	12	3	Passive delivery task	Positive correlation with pleasantness
Green and Murphy (2012)	fMRI	12	24	Passive delivery task	Sucrose > Water (soda drinkers)
Green and Murphy (2012)	fMRI	12	15	Passive delivery task	Sucrose > Water (non-soda drinkers)
Haase et al. (2009)	fMRI	18	36	Passive delivery task	Sucrose > Water
Kim et al. (2011)	fMRI	18	4	Instrumental task	Positive correlation with the value of juice
Kishi et al. (2017)	fMRI	21	6	Passive delivery task	Sweet solution > Water
McCabe and Rolls (2007)	fMRI	12	2	Passive delivery task	Positive correlation with taste pleasantness
McCabe et al. (2011)	fMRI	15	9	Passive delivery task	Chocolate > Tasteless drink
McCabe et al. (2013)	fMRI	16	12	Passive delivery task	Chocolate > Tasteless solution
Monteleone et al. (2017)	fMRI	20	13	Passive delivery task	Sucrose > Water
Murray et al. (2014)	fMRI	20	5	Passive delivery task	Chocolate > Control
			3	Passive delivery task	Milkshake > Tasteless solution
Nolan-Poupard et al. (2013)	fMRI	20	3	Passive delivery task	Positive Correlation with ad Libitum Intake
Rolls and McCabe (2007)	fMRI	16	6	Passive delivery task	Chocolate > Tasteless drink
Small et al. (2008)	fMRI	12	4	Passive delivery task	Juice > Tasteless drink
Spetter et al. (2012)	fMRI	15	3	Passive delivery task	Sweet & Savory > water
van den Bosch et al. (2014)	fMRI	34	14	Passive delivery task	Sucrose > Water
Zald et al. (1998)	PET	10	3	Passive delivery task	Chocolate > Water

identified (Figs. S4 and S5). Finally, to ensure that the effects in the music meta-analysis were not driven by those studies in which actions or decisions were made (instead of passively listening to music), we rerun our analyses excluding the 5 experiments involving real-time ratings of pleasure, decision-making, or action selection. The results remained qualitatively similar, suggesting that our main findings are not influenced by the active judgment and performance in these data sets (Figure S3)

Next, to identify those brain regions shared between both types of reward, we performed a conjunction between the two maps previously described (Fig. 4). The analysis indicated that a set of brain regions were recruited in response to either food or music reward. These regions included the bilateral ventral striatum, the bilateral insula, and the vmPFC.

Finally, in order to identify reward type-specific activations, we performed statistical comparisons between studies (Fig. 5). The results showed that the right ventromedial striatum, the right STG, and the

anterior prefrontal cortex elicited a more reliable activation to music- than food-induced pleasure. On the contrary, the left insula, bilateral putamen, and right amygdala were more likely activated by food- than music-induced pleasure.

4. Discussion

In the current study, we performed a series of meta-analyses to examine overlapping and specific neural responses associated with music- and food-induced pleasure. This is the first attempt to explore brain regions consistently engaged in response to music-induced pleasure and investigate partial dissociations to food rewards. Previous meta-analyses on music (Koelsch, 2014) have mixed contrasts reflecting pleasantness, unpleasantness, and music-induced sadness and happiness, among others, as well as different neuroimaging modalities (PET imaging of dopamine-D2 receptor, functional connectivity, and fMRI activations). Here, we focused on hedonic-related fMRI activations to specifically identify those brain regions that are more consistently engaged when individuals experience pleasure with music and/or food. Our findings are consistent with the existence of a common reward circuit involving the ventral striatum, the insula, and the vmPFC. Yet, comparative analyses indicated a partial dissociation in the engagement of the reward circuitry as a function of the type of reward, as well as additional reward type-specific activations in brain regions related to perception, sensory processing, and learning.

4.1. The striatum

Both food and music-induced pleasure were associated with activations of the bilateral ventral striatum (VS). Although its precise functional role is still a matter of fervid debate, a wealth of fMRI studies has identified the VS in reinforcement learning, reward valuation, and incentive motivation, using either primary or secondary rewards (Bartra et al., 2013; Berridge, 2007; Chase et al., 2015; O'Doherty et al., 2004). Indeed, the VS is considered a key hub of the reward circuitry, with extensive connections to prefrontal regions and limbic structures (Haber and Knutson, 2010) and is one of the primary inputs of the mesolimbic dopaminergic neurons.

The critical role of the ventral striatum and the dopaminergic system in generating feelings of musical pleasure has been long emphasized. Previous studies have shown that (a) the degree of dopaminergic neurotransmission is related to the degree of music-induced pleasure (Salimpoor et al., 2011), (b) TMS-induced modulation of fronto-striatal circuits changes subjective feelings of pleasure bidirectionally (Mas-Herrero et al., 2018a), and (3) pharmacological dopaminergic manipulations effectively induce changes in subjective pleasure, affecting the frequency and the intensity of music-induced chills (Ferreri et al., 2019).

Interestingly, hedonic-related activations in the ventral striatum were more consistent in studies involving music. Previous meta-analyses and studies comparing brain activations to primary (e.g., food) and secondary (e.g., money) rewards have reported similar differences, with the latter showing more robust activations in the ventral striatum (Bartra et al., 2013; Sescousse et al., 2013). This effect has been attributed to the fact that monetary rewards are generally delivered in instrumental contexts in which the ventral striatum may preferentially encode reward prediction errors signals conveyed by dopaminergic neurons (Chase et al., 2015; Mas-Herrero et al., 2019; Schultz et al., 1997). In line with this idea, when food or erotic rewards are presented in an instrumental context, they tend to recruit the ventral striatum to a similar extent as monetary rewards (D'Ardenne et al., 2008; McClure et al., 2003; Sescousse et al., 2010). However, no instrumental context was present in most of the studies included in the music meta-analysis (15 out of 17). Even when studies involved action-selection, learning, and real-time pleasure ratings were excluded (n = 5), a similar pattern of activations was found in response to music-induced pleasure (see

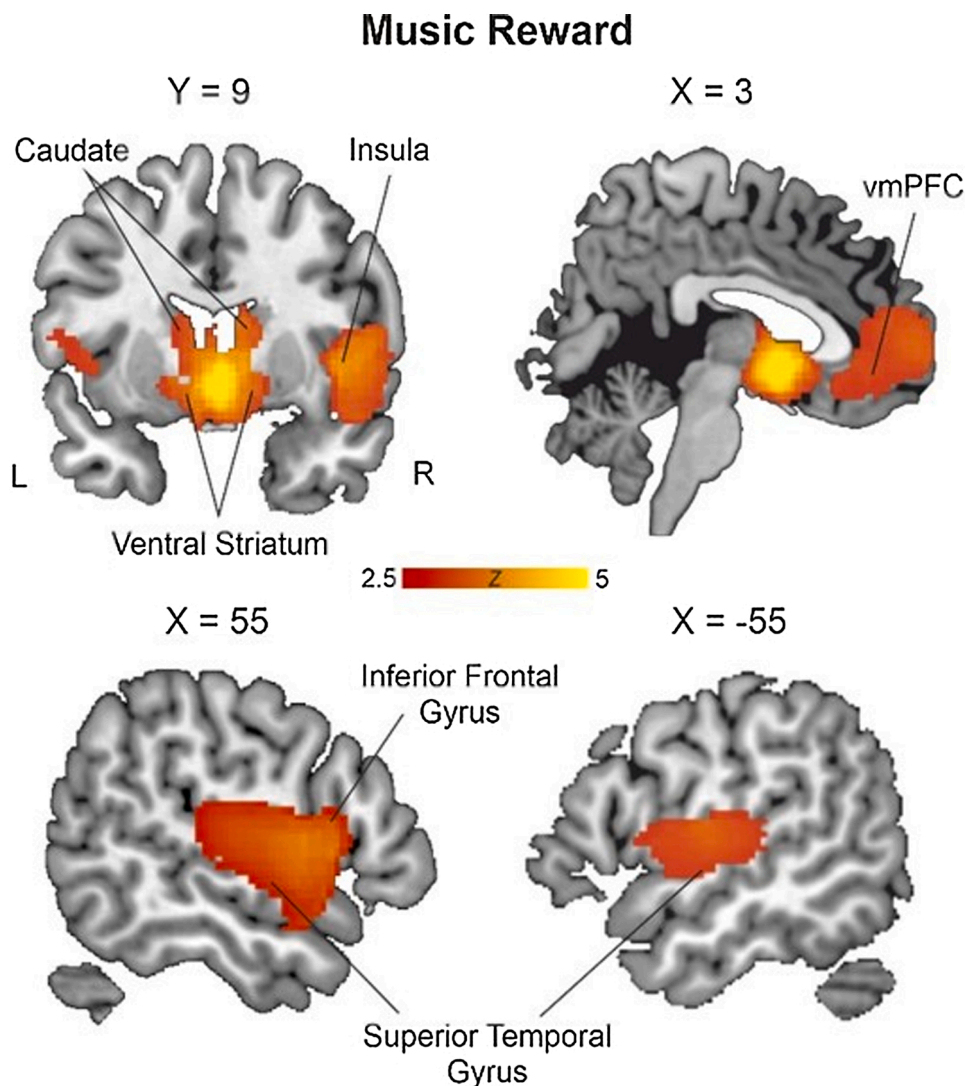


Fig. 2. Whole-brain meta-analysis of studies investigating music-induced pleasure.

Figure S3).

Thus, in the absence of any action or instrumental learning task, hedonic-related activations in the ventral striatum while passively listening to music were more consistent than in response to food reward. However, the presence of regularities in music may turn it into a learning scenario by itself, although not explicitly. Indeed, current neuro-functional models of musical pleasure suggest that the engagement of the ventral striatum, and the NAcc in particular, may be driven by music-induced expectations, particularly when those are violated (Gold et al., 2019a; Koelsch et al., 2019; Salimpoor et al., 2015; Shany et al., 2019). Notably, bodily reactions such as 'chills' which are generally associated with particularly intense and pleasurable responses to music, and have been associated with greater engagement of the NAcc (Grewe et al., 2009, 2005; Mas-Herrero et al., 2018b; Salimpoor et al., 2009), are often experienced following musical surprises (Grewe et al., 2007; Guhn et al., 2007; Harrison and Loui, 2014; Nagel et al., 2008; Panksepp, 1995; Sloboda, 1992). Finally, recent studies using an information-theoretic model of auditory expectation indicate that listeners may prefer music containing surprises, yet in a context in which those can be learned and anticipated (Cheung et al., 2019; Gold et al., 2019b). These findings resonate with learning theories that posit that the brain could intrinsically reward the information gain of balancing uncertainty and surprise (Oudeyer et al., 2016) to foster our fundamental need to generate accurate models of the world. Thus, the

information gain triggered by musical surprises and uncertainty, and our ability to successfully contextualize and resolve them, could be a potential underlying mechanism behind the rewarding properties of music and the consequent engagement of the reward circuitry in general and the VS in particular. In contrast to these aspects of music, which depend on the temporal unfolding of events over time and their anticipation, in the case of food reward, there is no temporal sequencing of events, at least not in the way the studies are conducted. A food reward is presented, but there are no cues that predict it, nor is there any surprise involved.

Furthermore, food-related studies showed more consistent activations in the bilateral putamen, which receive important projections from somatosensory regions (Sgambato-Faure et al., 2016). Interestingly, food intake activates both taste and nutrition-sensing pathways. Recent models suggest that separate striatal circuits may mediate these pathways: while ventral regions of the striatum may encode the hedonic value of food, dorso-lateral regions may convey nutritional values reflecting the energy present in aliments (de Araujo, 2016; Tellez et al., 2016). On the other hand, studies performed on non-human primates comparing food and sex-motivated behavior have shown that loss of food motivation may be driven by alterations in the lateral portions of the VS, in contrast to sexual manifestations (erection), which may be driven by the functioning of the medial regions of the VS (Sgambato-Faure et al., 2016). This dissociation within VS has been related to the

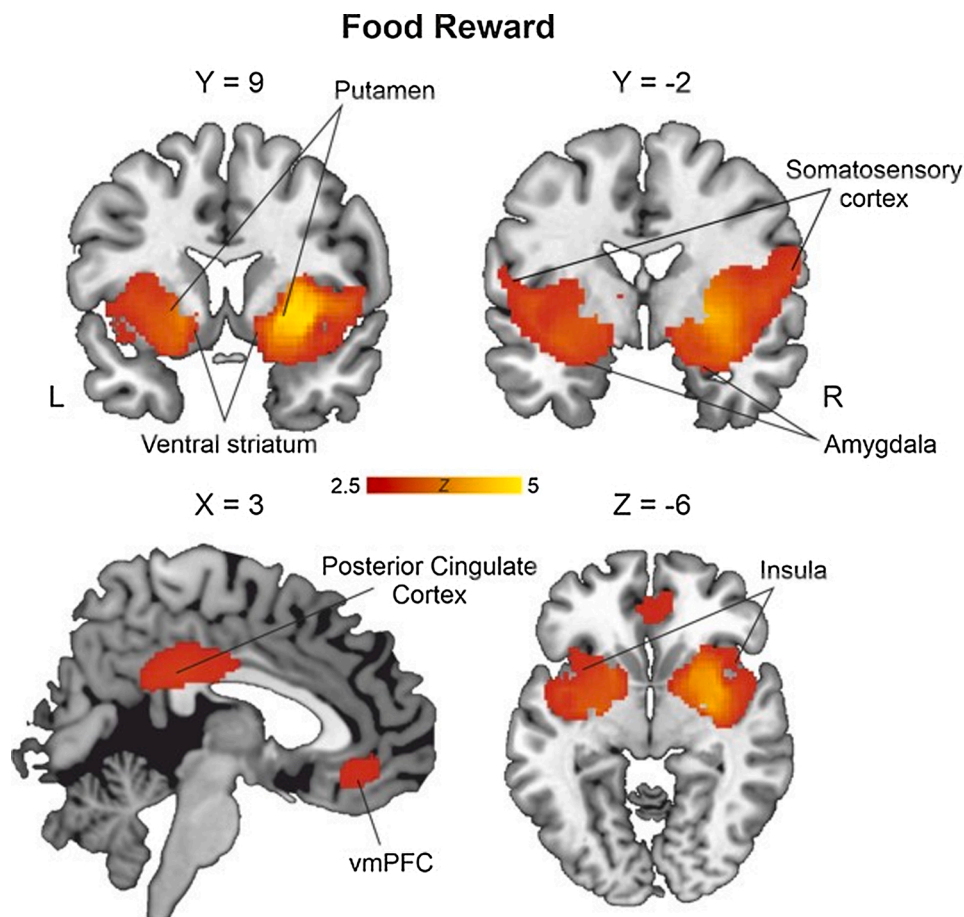


Fig. 3. Whole-brain meta-analysis of studies investigating food-induced pleasure.

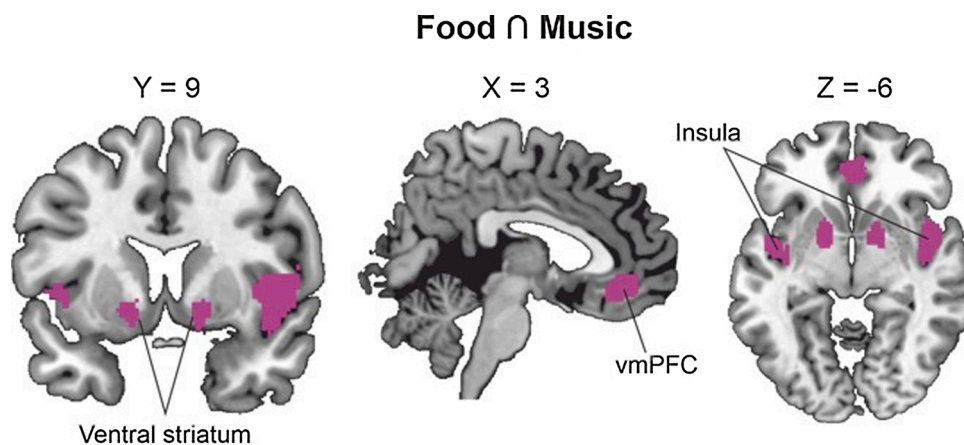


Fig. 4. Overlap between both food- and music-induced pleasures.

existence of separate fronto-striatal circuits associated with different reward-types. The mediolateral striatal dissociation between music and food reward found in our meta-analysis further supports the presence of distinct pathways associated with different rewards and the relevance of specific-reward type circuits in motivated behaviors.

4.2. Auditory cortical regions

The greater engagement of brain structures particularly involved in auditory cognition and predictive coding while listening to pleasant music, such as the right STG and the right IFG, further reinforces the idea

that learning is crucial for the experience of musical pleasure. The right STG has been consistently implicated in various processes relevant for music perception, including pitch representation (Coffey et al., 2016; Johnsrude et al., 2000), tonal pattern processing (Foster and Zatorre, 2010a; Patterson et al., 2002), tonal working memory (Albouy et al., 2019), tonal learning (Herholz et al., 2016), and musical imagery (Herholz et al., 2012). Recent findings indicate that this right hemisphere specialization in music may arise from differential sensitivity to acoustical cues between the left and the right auditory cortices, with specific sensitivity to spectral information in the right hemisphere and greater sensitivity to temporal information in the left (Albouy et al.,

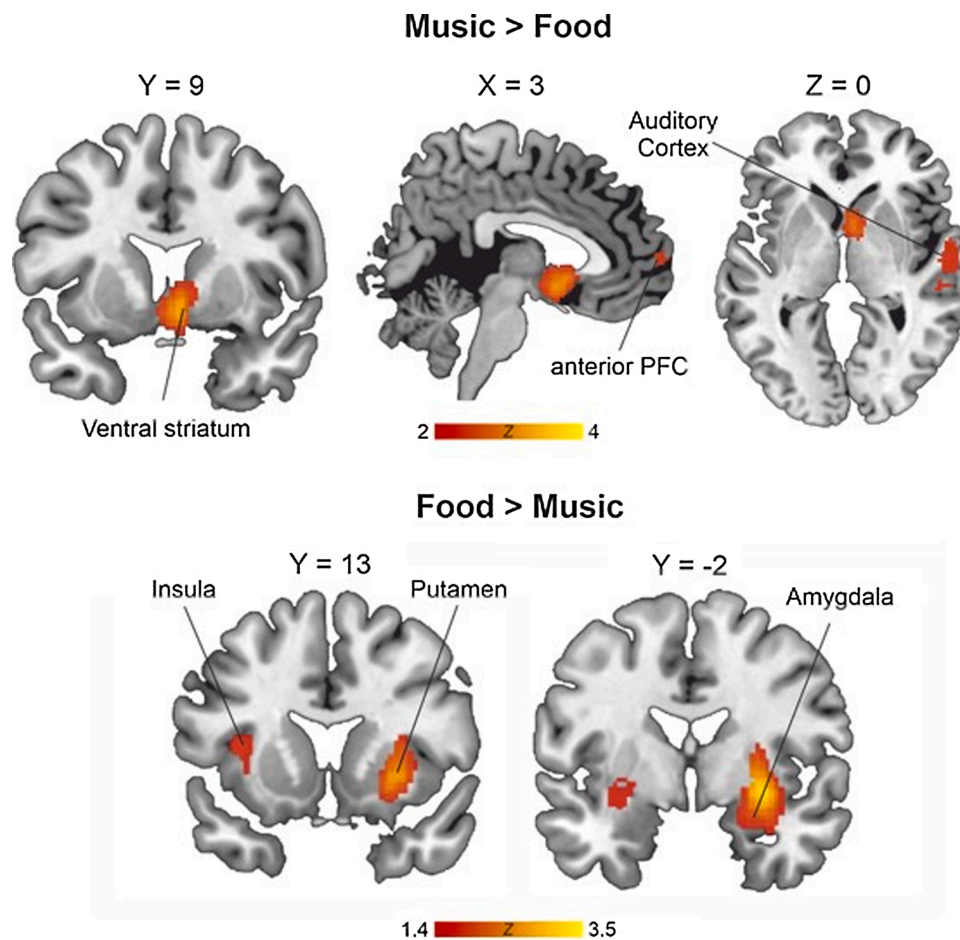


Fig. 5. Brain regions more reliably activated by one reward compared to the other.

2020). Notably, our meta-analysis also indicates the engagement of the right IFG while listening to pleasant music, which goes in line with the right-hemispheric dominance in music processing. Previous fMRI and MEG studies have implicated the right IFG in musical structure processing – responding to musically unexpected events (Koelsch et al., 2005; Tillmann et al., 2006, 2003)–, and tonal working memory –while retaining, manipulating, and retrieving tonal information (Albouy et al., 2018, 2017; Foster and Zatorre, 2010b). Consistent with the importance of these structures for music processing, individuals suffering from amusia (a deficit in music perception and production abilities, particularly in pitch processing) present morphological brain anomalies both in white and grey matter concentrations in the right IFG (Albouy et al., 2013) and the connectivity between the STG and the IFG (Loui et al., 2009). It is important to note that the engagement of both the right STG and IFG in the current meta-analysis does not merely reflect perceptual or cognitive aspects related to general music processing (independently of its pleasantness) since all the contrasts included in the meta-analysis focus directly on hedonic or affective processes.

Previous fMRI studies have already shown that these high-order cortical regions involved in auditory cognition and predictive coding show enhanced coupling with reward-related structures, such as the NAcc, while listening to pleasant music (Salimpoor et al., 2013), coinciding with music-induced surprises (Shany et al., 2019). Besides, individual differences in music reward sensitivity are accompanied by similar differences in functional and structural connectivity between the right STG and reward- and emotion-related structures such as the vmPFC, the ventral striatum, and the insula (Loui et al., 2017; Martínez-Molina et al., 2019, 2016; Sachs et al., 2016). In particular, specific musical anhedonics – individuals who do not derive pleasure from music

but show intact music perceptual abilities as well as intact affective reactions to other reward types (Mas-Herrero et al., 2018b, 2014) – showed disrupted auditory-striatal coupling while listening to music. Conversely, individuals with high sensitivity to music presented the reverse pattern, with greater functional connectivity between auditory cortices and reward centers (Martínez-Molina et al., 2019, 2016).

Altogether, these findings fit well with the idea that the exchange of information between high-order cortical regions involved in auditory perception and cognition, on the one hand, and reward systems, on the other hand, plays a crucial role in musical pleasure.

4.3. The ventromedial prefrontal cortex

In a similar fashion as the ventral striatum, the vmPFC also responded to both food and music-induced pleasure. The ventral prefrontal cortex is a multisensory hub that receives inputs from sensory modalities such as taste, olfaction, audition, vision, and somatic sensation and projects primarily to the ventral striatum (Haber and Knutson, 2010). Early fMRI studies have shown that vmPFC activations consistently correlates with subjective reports of pleasure in response to various types of rewards – including primary, secondary, and abstract (Blood and Zatorre, 2001; Elliott et al., 2003; Knutson et al., 2001; O'Doherty et al., 2001; Rolls, 2000). The vmPFC is thought to integrate signals from different sensory modalities and represent them on a common scale, reflecting the attractiveness or value of rewards for the purpose of comparison and evaluation (Kringelbach, 2005). Following this view, both food and music-induced pleasure were associated with activations in the vmPFC (Fig. 4). The cluster identified nicely overlaps with previous meta-analyses on subjective value comparing primary and

monetary rewards, which agrees with its role in representing reward value independently of the reward's nature (Bartra et al., 2013; Sescousse et al., 2013).

Besides, our results show that music recruits anterior portions of the prefrontal cortex more reliably than food rewards (Fig. 5). The cluster identified falls within the ventral portions of Brodmann area 10. Previous studies have implicated this region in coordinating information processing in tasks involving multiple cognitive operations (Ramnani and Owen, 2004). Indeed, music requires the coordination and integration of several cognitive operations involving temporal expectations, predictions, working memory, and learning across multiple hierarchical timescales. Notably, this area has multiple connections with the superior temporal gyrus (Petrides and Pandya, 2007; Saleem et al., 2008). Evidence in favor of the role of frontotemporal connections in music-induced pleasure comes from patients with frontotemporal lobe dementia (FTLD). Previous studies have shown that patients with FTLD may develop musicophilia, a specific craving for music (Fletcher et al., 2015, 2013). This particular phenotype has been associated with grey matter volume changes in a distributed network, including the right temporal cortex and the anterior prefrontal cortex, among others (Fletcher et al., 2015, 2013). Overall, together with our results, these findings suggest a key role of frontotemporal pathways in musical pleasure.

4.4. The insula

The third brain region consistently engaged across both music and food rewards is the posterior insula bilaterally. The insular cortex also represents an integration hub and is at the crossroad of several circuits involved in sensory, cognitive, motivational, and emotional functions (Benarroch, 2019; Gogolla, 2017; Uddin et al., 2017). Studies conducted in humans and non-human primates have identified a posterior-to-anterior connectivity gradient, with the anterior parts mostly connected to the frontal cortex and limbic regions, and the posterior portions heavily connected with sensorimotor, visual, and auditory cortices (Benarroch, 2019; Gogolla, 2017; Uddin et al., 2017). These differences in connectivity pattern have been associated with different functionality: while anterior regions have been related to introspective awareness of emotion and bodily states (Critchley, 2004; Paulus and Stein, 2006), posterior sections have been involved in somatosensory processing and integration (Rodgers et al., 2008; Stephani et al., 2011). In particular, previous studies have shown the pINS is activated by sounds (reflecting auditory responses that resemble those described in the auditory cortex, Blenkmann et al., 2019) and mouth movements (Woolnough et al., 2019). Thus, given the role of the pINS in somatosensory function, the recruitment of the pINS by both food- and music-induced pleasure in our data may reflect greater auditory and sensorimotor processing to pleasant music and food, respectively.

On the other hand, our results indicate that food rewards robustly and specifically activated the anterior insula (aINS). The aINS also includes the primary taste cortex, which receives multiple sensory inputs of gustatory cues, such as smell, taste, and texture, among others (de Araujo and Simon, 2009). This finding is consistent with the activations found in the somatosensory cortex in the meta-analysis of neuroimaging studies investigating food-induced pleasure (Fig. 3). Similar to models of music, food-induced reward may rely on the interaction between brain regions involved in food perceptual processing and the common reward circuitry. Altogether, the results highlight the existence of specific routes of access into the reward circuitry depending on the modality and nature of the stimulus, which may provide a plausible mechanism explaining the existence of specific anhedonias (and hyperhedonias) in response to a particular type of reward.

4.5. The amygdala

Our meta-analysis also revealed food-specific activations in the

amygdala. The amygdala is especially well-known to mediate emotional processing, particularly aversive emotional reactions such as fear (LeDoux, 2000). Yet, accumulating evidence indicates that the amygdala is equally sensitive to rewarding stimuli (Bermudez and Schultz, 2010; Janak and Tye, 2015; Sugase-Miyamoto and Richmond, 2005). Besides, the engagement of the amygdala seems to scale with the emotional intensity and salience of the stimuli, regardless of their valence (Bonnet et al., 2015; Lang and Bradley, 2013). These findings have led to the idea that the amygdala's predominant role may be the detection of motivationally salient information, rather than a specific role in valence processing as it was initially thought. Particularly, the amygdala may be involved in assigning an emotional tag to salient stimuli to guide decision-making (Gottfried et al., 2003) and acquire and retain lasting memories involving emotional experiences (Inman et al., 2018). Notably, we did not find amygdala activation associated with music-induced pleasure. This finding may be considered surprising given the rich emotional content of music. One potential explanation is that this lack of effect may be driven by differences in the fMRI contrasts generally used in music studies compared to those employed in food-reward studies. While most of the food studies included in our meta-analysis compared brain activations between pleasant (sugar, chocolate, juice, etc.) and neutral food (tasteless solutions, water, etc.), most of the fMRI studies in music-induced pleasure compared pleasant to unpleasant music (particularly dissonant music). In this regard, dissonant and unpleasant music has been shown to activate paralimbic structures, including the amygdala and the parahippocampal gyrus (Blood et al., 1999; Gosselin et al., 2007; Koelsch et al., 2006). Therefore, the dissociation found in the amygdala between food- and music-induced pleasures may reflect an imbalance in emotional salience between pleasant and neutral food and an equivalent emotional intensity between pleasant and unpleasant music. Besides, in most food studies, individuals were tested after a short period of fasting, which likely contributed to experiencing the actual food more emotionally arousing. Therefore, the amygdala activations that we found in response to food-induced pleasure are more likely to reflect discrepancies in the emotional impact between target and baseline conditions in food- than music-reward studies, rather than a specific role in the hedonic evaluation of primary rewards.

5. Limitations

One main limitation of coordinate-based meta-analyses is their susceptibility to "threshold bias" since only the coordinates that reached a particular statistical significance are included, leaving out potentially relevant brain regions. Besides, fMRI data are susceptible to signal dropout in certain brain regions, while coordinate-based meta-analysis cannot adjust for these signal loss. This is important since brain regions that are particularly susceptible to suffer from signal dropouts, such as the vmPFC or temporal cortices, can show false negatives. However, our meta-analysis shows consistent activation in those brain regions in response to either music or food reward. Nevertheless, future studies may take advantage of image-based meta-analysis approaches to solve these problems as they are less prone to the threshold bias, and signal dropout adjustments can be applied (Cutler et al., 2018).

6. Conclusions

The current meta-analysis is the first to systematically compare the neuroanatomical substrates of both a primary reward (food) and an abstract aesthetic reward (music). Our results indicate the existence of a set of brain regions that are consistently engaged while either listening to pleasant music or savoring palatable food. These brain regions constitute a common reward circuitry and include the bilateral striatum, the ventromedial prefrontal cortex, and the bilateral insula. However, comparative analyses indicated that the location of the activity within these regions varied somewhat across both rewards and the presence of

reward type-specific activations. Overall, the current results support the idea that hedonic reactions rely on the engagement of a common reward network, yet through specific routes of access depending on the modality and nature of the input. In addition, the current findings support the interpretation that music-induced pleasure relies on the engagement of both higher-order cortical regions involved in auditory cognition and predictive coding and reward-related structures.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neubiorev.2020.12.008>.

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