



# Social pleasures of music

Lauri Nummenmaa<sup>1,2,3,4</sup>, Vesa Putkinen<sup>1,4</sup> and Mikko Sams<sup>4,5</sup>

Humans across all societies engage in music-listening and making, which they find pleasurable, despite music having does not appear to have any obvious survival value. Here we review the recent studies on the social dimensions of music that contribute to music-induced hedonia. Meta-analysis of neuroimaging show that listening to both positively and negatively valenced music elicit largely similar activation patterns. Activation patterns found during processing of social signals and music are however remarkably similar. These similarities may reflect the inherent sociability of music, and the fact that musical pleasures are consistently associated with autobiographical events linked with musical pieces. Brain's mu-opioid receptor (OR) system governing social bonding also modulates musical pleasures, and listening to and making of music increase prosociality and OR activity. Finally, real or simulated interpersonal synchrony signals affiliation, and accordingly music-induced movements increase social closeness and pleasant feelings. We conclude that these links between music and interpersonal affiliation are an important mechanism that makes music so rewarding.

## Addresses

<sup>1</sup> Turku PET Centre, University of Turku, Finland<sup>2</sup> Department of Psychology, University of Turku, Finland<sup>3</sup> Turku University Hospital University of Turku, Finland<sup>4</sup> Department of Computer Science, Aalto University, Finland<sup>5</sup> Department of Neuroscience and Biomedical Engineering, Aalto University, FinlandCorresponding author: Nummenmaa, Lauri ([latanu@utu.fi](mailto:latanu@utu.fi))**Current Opinion in Behavioral Sciences** 2021, **39**:196–202This review comes from a themed issue on **Emotion, motivation, personality and social sciences \*positive affect\***Edited by **Gilles Pourtois, Disa Sauter, Blair Saunders** and **Henk van Steenbergen**<https://doi.org/10.1016/j.cobeha.2021.03.026>2352-1546/© 2021 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## Introduction

Human life is embedded in music. We sail through the streets with headphones on our ears, sit in the office with music blasting from the speakers, and sing, dance and party through the evenings in the midst of a

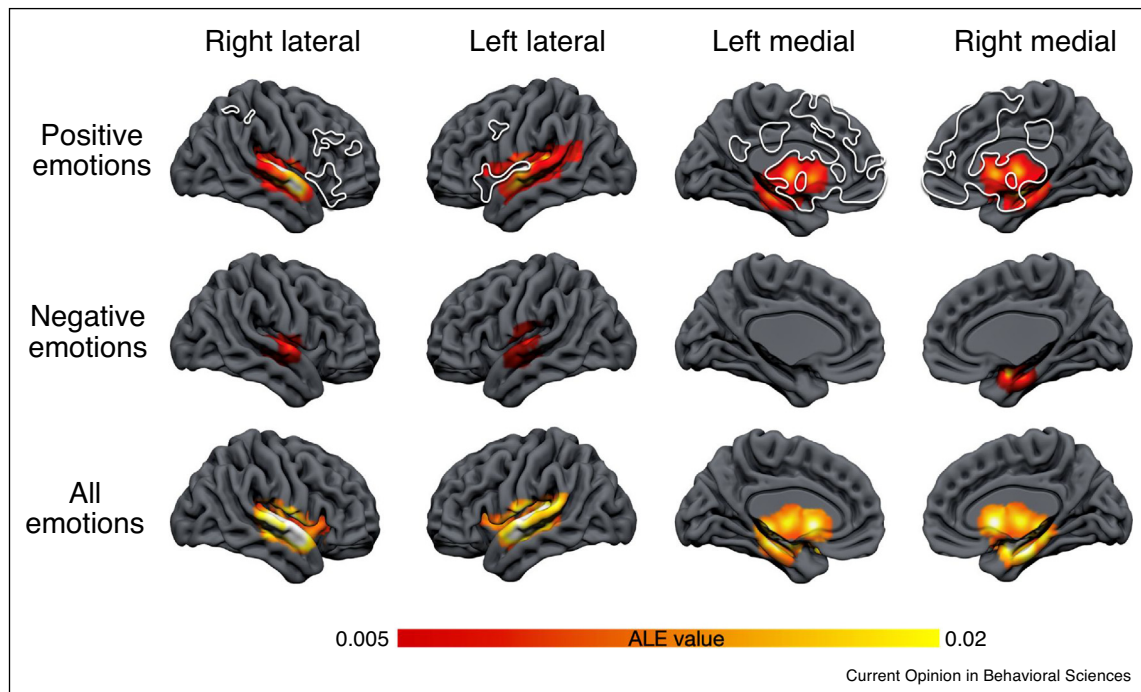
never-interrupting emotional soundtrack of our life. Emotions support survival by motivating adaptive behaviors and help maintaining physiological homeostasis [1], and positive emotions specifically promote approach motivation towards opportunities for improving survival odds, such as shelter, feeding, and increasing chances for reproduction. Music is however a curious pleasure. Emotional responses to music show many hallmarks of emotions in general including distinct subjective experience, emotional expression, action tendencies, changes in the autonomic nervous system activation [2] and distinct effects on thought and judgement [3], despite the fact that music itself serves no obvious adaptive value. Here we review recent studies on the social dimensions of music that contribute to music-induced hedonia, and discuss how sociability is an important candidate reasons for the pleasure imbued in music.

## Musical pleasures in the brain

Vivid emotional terminology is used for describing music by both laypersons (e.g. 'triumphant', 'bluesy', or 'uplifting') as well as professional musicians ('maestoso', 'allegrezza', 'scatenato'). Music evokes a wide array of subjective feelings, and large-scale cross-cultural work shows that some features of emotions are described and understood in similar fashion across distant cultures [4<sup>\*</sup>,5]. But if music does not serve any immediate adaptive value, does it consistently engage the brain's emotion circuit similarly as survival-salient hedonic signals? To test this, we conducted a meta-analysis (**Supplementary Methods** and **Figure S-1** in Supplementary material) of BOLD-fMRI responses to (i) music-evoked pleasure, (ii) music-evoked displeasure and (iii) music-evoked emotions in general.<sup>6</sup> Altogether 51 studies, 1038 subjects, and 786 activation foci were included in the analysis **Table S-1** in Supplementary material). This analysis (**Figure 1**) revealed positive-emotion-related activations in bilateral temporal auditory cortical areas, ventral and dorsal striatum and amygdala, and hippocampus. Negative musical emotions elicited a similar activity pattern, with the exception of no activations in striatum and thalamus, and with auditory-cortical effects being right-lateralized. When all musical emotions were analysed together the results were similar to those for the positive emotions, with the exception of lacking thalamic cluster. This analysis yielded two important findings. First, negative and positive music-induced emotions evoke remarkably similar activations, with the exception of striatal activation. Second, the effects of

<sup>6</sup> Existing data did not pertain a finer-grained meta-analyses of for example, specific discrete emotion categories.

Figure 1



Brain regions responding consistently to music-evoked positive (a) and negative (b) emotions and to all emotions irrespective of valence (c) in activation likelihood estimation (ALE) meta-analysis. The white outline shows brain regions responding to *reward* per NeuroSynth meta-analysis ( $p < 0.01$ , retrieved June 23rd 2020).

music-induced positive emotions are distinct from those triggered by other rewards (white outline on the figure); most salient feature being the lack of pleasurable-music-induced activations in fronto-cingular and parietal areas as well as midbrain activations.

This relative unspecificity of brain basis of positive and negative emotions accords with statistical pattern recognition studies. This line of work shows that emotions evoked by non-musical stimuli [20–22] as well as spontaneously occurring emotional states during resting state [23,24] are associated with discrete neural activation patterns in the cortex and in limbic and paralimbic structures. In contrast, even in high-powered pattern recognition studies cannot decode emotions beyond the, auditory and motor cortex [25,26,27]. Studies on vocal emotional expressions yield comparable results, with above-chance level classification accuracy primarily in the auditory cortex [28–30]. This suggests that, outside the auditory cortices, musical emotional representations are less categorical in the brain than those for biologically more salient emotions. This obviously begs the question ‘why’?

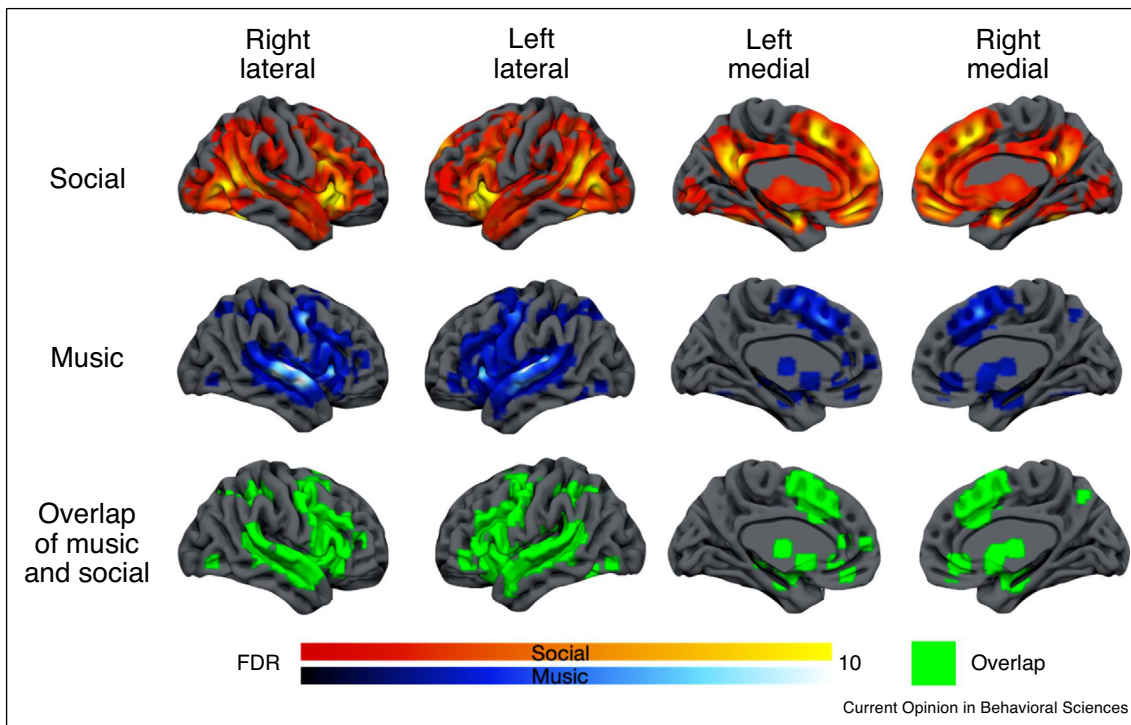
One explanation is that there is no innate coupling between specific musical exemplars and survival-salient responses, except perhaps some very low-level universals

in harmony, rhythm and acoustics [31]. Thus music-evoked emotions have a significant learning-based component. This leads to more idiosyncratic emotional responses in the brain, and due inconsistent brain responses across individuals their classification is impossible at group level. Another possible explanation is the ubiquitous pleasantness of music: even though music can be described in a wide variety of positive (e.g. tender, romantic, joyful) and negative (sad, fearful, suspenseful, creepy) terms, all these categories typically receive high ‘liking’ ratings [27], thus the intrinsic coupling between music and pleasure makes the music-evoked emotions categorically diffuse. We next explore the possibility that this ubiquitous pleasantness of music stems from role in social bonding.

### Social pleasures of music

Music listening has been fundamentally social until fairly recently when storing acoustic information became possible. First mechanical musical instruments were developed around as late as 1000AD, music boxes become available around late 1700, and analogue recording and playback of voice was invented by Thomas Edison in 1877. Social and music processing engage remarkably overlapping areas in the human brain, as evidenced in the meta-analytic maps derived from NeuroSynth database [32] shown in (Figure 2). Overlap is observed not just

Figure 2



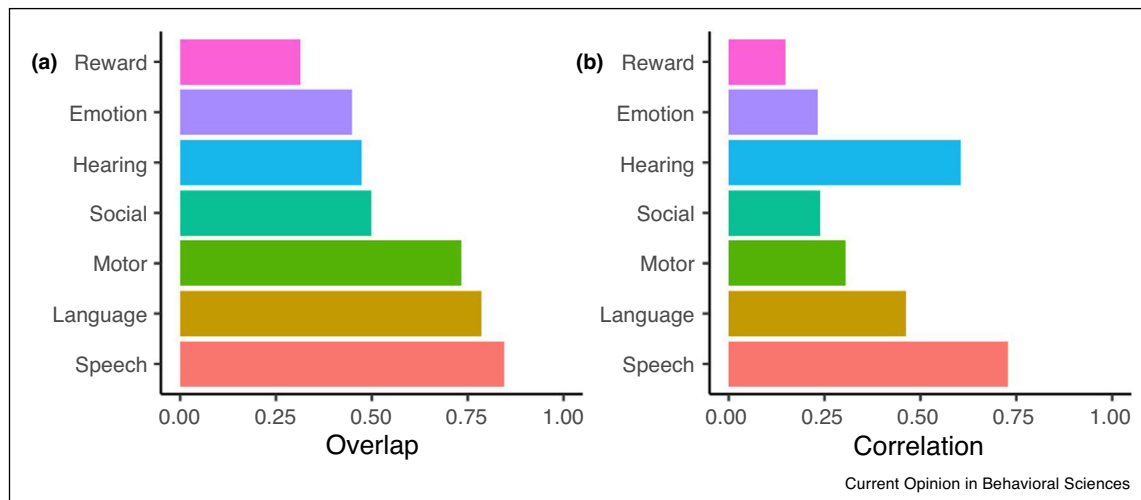
Meta-analytic maps for brain regions involved in social processing (hot colours), music perception (cool colours) and their overlap (green). The data show uniformity test maps thresholded at  $p < 0.05$  retrieved from NeuroSynth on May 8th 2020.

in the auditory cortices, but also in posterior temporal polysensory areas, motor cortex, thalamus, amygdala, midcingulate cortex, anterior insula and ventral striatum. Music and social processing thus recruit partially similar neural subsystems, which however go significantly beyond sensory and associative cortices (Figure 3): When music-evoked activations are compared with meta-analytic activation maps for language, socioemotional and motor functions, clearest overlap is obviously found for motor and language functions; however overlap with the regions involved in social processes is also substantial and also larger than with, for example, emotions or reward. Such parallels in the brain can be accounted by multiple factors, and similarity of activations across tasks does not obviously mean that the tasks would recruit similar neural mechanisms. First, music might bolster interpersonal bonds, as music preferences serve as cues for similar values [33,34]. Experiments using artificial ‘music markets’ have indeed found that peer preferences shape musical tastes strongly – when people know their peers’ music preferences (such as playlists), they have a tendency to follow them somewhat independently of their own tastes or the population-level appeal of the songs [35]. Yet, musical emotions are present in the absence of face-to-face social contact, and pleasant emotions evoked by music are not necessarily amplified in groups [36].

Second, humans spontaneously attribute mental states to others and even to inanimate objects [37], and social interaction might be the default mode via which humans communicate with their environment [38,39]. Music provides powerful ways of such social communication, and social features also influence music preferences. Vocal music is more popular than instrumental music, as clearly evidenced by Spotify playlists (e.g. <https://spotifycharts.com/regional>). This preference may stem from the capability of vocals for communicating emotional states effectively, but also from inherent craving for ‘social stimulation’ even in the form of song texts [40]. In line with this, sex and romantic relationships have remained the most common lyrical content of popular music throughout the past 50 years [41]. These and other semantic features of song lyrics are associated with the pleasantness of the mood evoked by the music [42]. Large-scale analysis also suggests a close link between harmony and lyrics, that is, presence of major/minor chords and concurrent emotional semantics of the lyrics [43], suggesting that musical and semantic features both contribute to the mood of a musical piece.

Third, the lyrical content of the songs also contributes to their emotional quality via the autobiographical memories they activate. One study found that on average a 30% of

Figure 3



Overlap (A; proportion of joint voxels) and spatial correlation (Pearson) between music-related activation and related socioemotional and sensorimotor processes. The results are based on uniformity test maps thresholded at  $p < 0.05$  retrieved from NeuroSynth on March 10th 2020.

tested songs from a large corpus of popular music pieces evoked vivid autobiographical memories and often also concomitant strong, primarily positive emotions [44,45]. In a subsequent fMRI study, it was found that the saliency of these autobiographical memories was predictive of activity in the medial prefrontal cortex [46] — a brain region that is consistently associated with social cognition [47]. Because mPFC also responded to faster frequency of the musical stimulus features, it was proposed that mPFC would associate music with emotionally salient episodic memories. Functional theories of autobiographical memory postulate that this memory system is centrally involved in social bonding via retrieving and sharing personal memories [48,49], thus these data suggest that music and its lyrics might support social attachment functions via the emotional and autobiographical memories it evokes. Finally, due to the centrality of music in the social life, musical anhedonia (the inability to enjoy music) can be experienced as socially debilitating [50]. In line with this, anatomical studies have found that both lower enjoyment of music as well as musical anhedonia is associated with lowered connectivity between the auditory cortex and regions involved in socioemotional processing [50,51], further supporting the link between sociability and musical pleasures.

### Musical social bodies

Our social bodies are embedded in music and we often have an irresistible urge to move with the beat of the music. Such rhythmic movements are evident already in young children [52] and also in some non-human primates [53••]. These movements are specific with respect to the emotions induced by the music [54], and meta-analysis point towards consistent activation of the motor system

during passive music listening [55]. These embodied somatomotor responses to music might be a key pathway for eliciting the musical emotions, as it has been well established that different emotional states are associated with distinct ‘bodily fingerprints’ [56••,57]. Indeed, studies have shown that spontaneous dance movements during music listening enhance the subjective experience of pleasantness [58] and in line with this, music-induced emotional states can be reliably decoded from the activity of the motor cortex [27].

Humans automatically mimic each others’ expressions and postures, and such synchrony is routinely interpreted as a signal of affiliation [59,60]. Music-induced movements and pleasures facilitate social bonding, as rhythmic movements during dancing and singing help individuals to synchronize their actions. Studies in nonhuman primates suggest a causal role of endogenous opioid receptor (OR) system in modulating social bonding [61,62]. Human experiments have found that both synchronous movements during dancing [63•,64] as well as joint music making heighten social closeness and increase pain threshold — a proxy of central opioid release [65,66], and experimental work shows that singing together significantly facilitates social bonding when compared to other social activities [67]. Making music together promotes spontaneous cooperation already in four-year old children, suggesting that this mechanism could be intrinsic or at least functional at very early age [68].

Specific midbrain dopamine neurons respond more strongly to unpredicted versus predicted rewards [69]. It has been proposed that such ‘positive prediction error’ responses to musical events contributes to music-induced



pleasure via concomitant striatal dopamine release [70]. Yet, familiar and thus fully predictive music can retain its hedonic impact, and humans can easily listen their favorite songs for thousands of times and still enjoy them. Thus, positive prediction error processing cannot fully account for music-induced pleasure. Indeed, predictability (e.g. a steady beat) is crucial music's ability to induce social entrainment between listeners, and it is possible that this predictability-driven social entrainment is a central source of musical enjoyment [71].

It is possible music may tickle our social brains by providing a means for a feeling of 'simulated synchrony' with others – the pulsating beat of a song may trick our brains into thinking that we are actually synchronizing with another person, and this behavioural synchronization and concomitant opioid release could promote feelings of social contact [72]. Human positron emission tomography (PET) studies have indeed shown that OR activity during affiliative behaviors, such as touching or laughing, is an important molecular mechanism supporting social bonding in humans [73<sup>\*\*</sup>,74], and the relaxing pleasurable sensations evoked by endogenous opioid peptides could act as a safety signal promoting establishment of social bonds. Opioidergic neurotransmission contributes to pleasures ranging from social laughter and physical exercise [73<sup>\*\*</sup>,75], yet there exists no direct *in vivo* imaging data demonstrating OR involvement in musical hedonia. However, pharmacological studies indicate that blocking  $\mu$ -opioid receptors dampens musical hedonia [76].

## Conclusions

We conclude that the musical pleasures stem at least partially from the role of music in human sociability. Although on surface level music seems to serve no obvious survival function to make it pleasurable, we argue that the link between music, interpersonal synchrony and affiliation is an important factor that makes music so rewarding. Musical autobiographical memories and social and emotional lyrics in music further provide means for rehearsing and maintaining various social scripts. Because of their episodic nature, music-evoked autobiographical memories are oftentimes imbued with feeling of nostalgia [45,77]. Because such memories are activated automatically during low retrieval demands and as one key function of nostalgic feelings is counteracting loneliness [78], it is possible that music can even serve as an artificial social companion during moments of social isolation and distress. For these reasons, music is a fascinating tool and target for emotion researcher, as music allows bringing, real, naturalistic pleasures to the laboratory.

## Conflict of interest statement

Nothing declared.

## Acknowledgements

This study was supported by the Academy of Finland (grants #294897 and #332225 to LN) and Sigrid Juselius foundation.

## Uncited references

[6–19,79<sup>\*\*</sup>].

## 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.cobeha.2021.03.026>.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
  - of outstanding interest
1. Ekman P: **An argument for basic emotions.** *Cogn Emot* 1992, **6**:169-200.
  2. Juslin PN, Västfjäll D: **Emotional responses to music: the need to consider underlying mechanisms.** *Behav Brain Sci* 2008, **31**:559-575.
  3. Vuoskoski JK, Eerola T: **Can sad music really make you sad? Indirect measures of affective states induced by music and autobiographical memories.** *Psychol Aesthet Creat Arts* 2012, **6**:204-213.
  4. Cowen AS, Fang X, Sauter D, Keltner D: **What music makes us feel: at least 13 dimensions organize subjective experiences associated with music across different cultures.** *Proc Natl Acad Sci U S A* 2020, **117**:1924.
  - Shows that music evokes a broad set of culturally universal discrete emotions with fuzzy boundaries between categories.
  5. Fritz T, Jentschke S, Gosselin N, Sammler D, Peretz I, Turner R, Friederici AD, Koelsch S: **Universal recognition of three basic emotions in music.** *Curr Biol* 2009, **19**:573-576.
  6. Bencherif B, Fuchs PN, Sheth R, Dannals RF, Campbell JN, Frost JJ: **Pain activation of human supraspinal opioid pathways as demonstrated by C-11-carfentanil and positron emission tomography (PET).** *Pain* 2002, **99**:589-598.
  7. Boecker H, Sprenger T, Spilker ME, Henriksen G, Koppenhoefer M, Wagner KJ, Valet M, Berthele A, Tolle TR: **The runner's high: opioidergic mechanisms in the human brain.** *Cereb Cortex* 2008, **18**:2523-2531.
  8. Burghardt PR, Rothberg AE, Dykhuis KE, Burant CF, Zubieta JK: **Endogenous opioid mechanisms are implicated in obesity and weight loss in humans.** *J Clin Endocrinol Metab* 2015, **100**:3193-3201.
  9. Hsu DT, Sanford BJ, Meyers KK, Love TM, Hazlett KE, Wang H, Ni L, Walker SJ, Mickey BJ, Korycinski ST *et al.*: **Response of the mu-opioid system to social rejection and acceptance.** *Mol Psychiatry* 2013, **18**:1211-1217.
  10. Koeppe MJ, Hammers A, Lawrence AD, Asselin MC, Grasby PM, Bench CJ: **Evidence for endogenous opioid release in the amygdala during positive emotion.** *NeuroImage* 2009, **44**:252-256.
  11. Prossin AR, Koch AE, Campbell PL, Barichello T, Zalzman SS, Zubieta JK: **Acute experimental changes in mood state regulate immune function in relation to central opioid neurotransmission: a model of human CNS-peripheral inflammatory interaction.** *Mol Psychiatry* 2016, **21**:243-251.
  12. Scott DJ, Stohler CS, Egnatuk CM, Wang H, Koeppe RA, Zubieta JK: **Placebo and nocebo effects are defined by opposite opioid and dopaminergic responses.** *Arch Gen Psychiatry* 2008, **65**:220-231.

13. Scott DJ, Stohler CS, Koeppe RA, Zubieta JK: **Time-course of change in C-11 carfentanil and C-11 raclopride binding potential after a nonpharmacological challenge.** *Synapse* 2007, **61**:707-714.
14. Smith YR, Stohler CS, Nichols TE, Bueller JA, Koeppe RA, Zubieta JK: **Pronociceptive and antinociceptive effects of estradiol through endogenous opioid neurotransmission in women.** *J Neurosci* 2006, **26**:5777-5785.
15. Wager TD, Scott DJ, Zubieta JK: **Placebo effects on human mu-opioid activity during pain.** *Proc Natl Acad Sci U S A* 2007, **104**:11056-11061.
16. Zubieta JK, Smith YR, Bueller JA, Xu YJ, Kilbourn MR, Jewett DM, Meyer CR, Koeppe RA, Stohler CS: **Regional mu opioid receptor regulation of sensory and affective dimensions of pain.** *Science* 2001, **293**:311-315.
17. Liberzon I, Zubieta JK, Fig LM, Phan KL, Koeppe RA, Taylor SF: **Mu-opioid receptors and limbic responses to aversive emotional stimuli.** *Proc Natl Acad Sci U S A* 2002, **99**:7084-7089.
18. Zubieta JK, Ketter TA, Bueller JA, Xu YJ, Kilbourn MR, Young EA, Koeppe RA: **Regulation of human affective responses by anterior cingulate and limbic mu-opioid neurotransmission.** *Arch Gen Psychiatry* 2003, **60**:1145-1153.
19. Zubieta JK, Heitzeg MM, Smith YR, Bueller JA, Xu K, Xu YJ, Koeppe RA, Stohler CS, Goldman D: **COMT val(158)met genotype affects mu-opioid neurotransmitter responses to a pain stressor.** *Science* 2003, **299**:1240-1243.
20. Kassam KS, Markey AR, Cherkassky VL, Loewenstein G, Just MA: **Identifying emotions on the basis of neural activation.** *PLoS One* 2013, **8**:e66032.
21. Saarimäki H, Gotsopoulos A, Jääskeläinen IP, Lampinen J, Vuilleumier P, Hari R, Sams M, Nummenmaa L: **Discrete neural signatures of basic emotions.** *Cereb Cortex* 2016, **6**:2563-2573.
22. Kragel PA, Labar KS: **Multivariate neural biomarkers of emotional states are categorically distinct.** *Soc Cogn Affect Neurosci* 2015, **10**:1437-1448.
23. Kragel PA, Knodt AR, Hariri AR, LaBar KS: **Decoding spontaneous emotional states in the human brain.** *PLoS Biol* 2016, **14**:e2000106.
24. Tusche A, Smallwood J, Bernhardt BC, Singer T: **Classifying the wandering mind: revealing the affective content of thoughts during task-free rest periods.** *Neuroimage* 2014, **97**:107-116.
25. Paquette S, Takerkart S, Saget S, Peretz I, Belin P: **Cross-classification of musical and vocal emotions in the auditory cortex.** *Ann N Y Acad Sci* 2018, **1423**:329-337.
- Multivariate pattern recognition study showing that musical and vocal emotions elicit similar neural activation patterns in auditory cortex, yet no emotion-specific patterns could be established elsewhere in the brain.
26. Sachs ME, Habibi A, Damasio A, Kaplan JT: **Decoding the neural signatures of emotions expressed through sound.** *Neuroimage* 2018, **174**:1-10.
27. Putkinen V, Nazari-Farsani S, Seppälä K, Karjalainen T, Sun L, Karlsson HK, Hudson M, Heikkilä TT, Hirvonen J, Nummenmaa L: **Decoding music-evoked emotions in the auditory and motor cortex.** *Cereb Cortex* 2021. 2020.2005.2024.101667.
28. Kotz SA, Kalberlah C, Bahlmann J, Friederici AD, Haynes J-D: **Predicting vocal emotion expressions from the human brain.** *Hum Brain Mapp* 2013, **34**:1971-1981.
29. Ethofer T, Van De Ville D, Scherer K, Vuilleumier P: **Decoding of emotional information in voice-sensitive cortices.** *Curr Biol* 2009, **19**:1028-1033.
30. Peelen MV, Atkinson AP, Vuilleumier P: **Supramodal representations of perceived emotions in the human brain.** *J Neurosci* 2010, **30**:10127.
31. Patel AD: *Music, Language and the Brain.* Oxford: Oxford University Press; 2010.
32. Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, Wager TD: **NeuroSynth: a new platform for large-scale automated synthesis of human functional neuroimaging data.** *Front Neuroinf* 2011.
33. Boer D, Fischer R, Strack M, Bond MH, Lo E, Lam J: **How shared preferences in music create bonds between people: values as the missing link.** *Pers Soc Psychol Bull* 2011, **37**:1159-1171.
34. Savage PE, Loui P, Tarr B, Schachner A, Glowacki L, Mithen S, Fitch WT: **Music as a coevolved system for social bonding.** *Behav Brain Sci* 2020:1-36.
35. Salganik MJ, Dodds PS, Watts DJ: **Experimental study of inequality and unpredictability in an artificial cultural market.** *Science* 2006, **311**:854.
36. Egermann H, Sutherland ME, Grewe O, Nagel F, Kopiez R, Altenmüller E: **Does music listening in a social context alter experience? A physiological and psychological perspective on emotion.** *Musicae Scientiae* 2011, **15**:307-323.
37. Heider F, Simmel M: **An experimental study of apparent behavior.** *Am J Psychol* 1944, **57**:243-259.
38. Hari R, Sams M, Nummenmaa L: **Attending to and neglecting people: bridging neuroscience, psychology and sociology.** *Philos Trans R Soc B Biol Sci* 2016, **371**:1-9.
39. Hari R, Henriksson L, Malinen S, Parkkonen L: **Centrality of social interaction in human brain function.** *Neuron* 2015, **88**:181-193.
40. Zunshine L: *Why We Read Fiction: Theory of Mind and the Novel.* Columbus: Ohio State University Press; 2006.
41. Christenson PG, de Haan-Rietdijk S, Roberts DF, ter Bogt TFM: **What has America been singing about? Trends in themes in the U.S. top-40 songs: 1960-2010.** *Psychol Music* 2019, **47**:194-212.
42. Laurier C, Grivolla J, Herrera P: **Multimodal music mood classification using audio and lyrics.** *2008 Seventh International Conference on Machine Learning and Applications; 11-13 December 2008: 2008:688-693.*
43. Kolchinsky A, Dhande N, Park K, Ahn Y-Y: **The minor fall, the major lift: inferring emotional valence of musical chords through lyrics.** *R Soc Open Sci* 2017, **4**:170952.
44. Janata P, Tomic ST, Rakowski SK: **Characterisation of music-evoked autobiographical memories.** *Memory* 2007, **15**:845-860.
45. Barrett FS, Grimm KJ, Robins RW, Wildschut T, Sedikides C, Janata P: **Music-evoked nostalgia: affect, memory, and personality.** *Emotion* 2010, **10**:390-403.
46. Janata P: **The neural architecture of music-evoked autobiographical memories.** *Cereb Cortex* 2009, **19**:2579-2594.
47. Amodio DM, Frith CD: **Meeting of minds: the medial frontal cortex and social cognition.** *Nat Rev Neurosci* 2006, **7**:268-277.
48. Pillemer DB: **Remembering personal circumstances: a functional analysis.** *Affect and Accuracy in Recall: Studies of "flashbulb" Memories.* Cambridge University Press; 1992:236-264. Edited by Emory symposia in cognition, 4.
49. Nelson K: **THE psychological and social origins of autobiographical memory.** *Psychol Sci* 1993, **4**:7-13.
50. Loui P, Patterson S, Sachs ME, Leung Y, Zeng T, Przyssinda E: **White matter correlates of musical anhedonia: implications for evolution of Music.** *Front Psychol* 2017, **8**.
51. Sachs ME, Ellis RJ, Schlaug G, Loui P: **Brain connectivity reflects human aesthetic responses to music.** *Soc Cogn Affect Neurosci* 2016, **11**:884-891.
52. Zentner M, Eerola T: **Rhythmic engagement with music in infancy.** *Proc Natl Acad Sci U S A* 2010, **107**:5768.
53. Hattori Y, Tomonaga M: **Rhythmic swaying induced by sound in chimpanzees (Pan troglodytes).** *Proc Natl Acad Sci U S A* 2020, **117**:936.
- Demonstrates that auditory beat induces rhythmic swaying in chimpanzees, supporting the evolutionary origins of musicality.
54. Burger B, Saarikallio S, Luck G, Thompson MR, Toiviainen P: **Relationships between perceived emotions in music and**

- music-induced movement.** *Music Percept Interdiscip J* 2013, **30**:517-533.
55. Gordon CL, Cobb PR, Balasubramaniam R: **Recruitment of the motor system during music listening: an ALE meta-analysis of fMRI data.** *PLoS One* 2018, **13**:e0207213.
56. Nummenmaa L, Hari R, Hietanen JK, Glerean E: **Maps of subjective feelings.** *Proc Natl Acad Sci U S A* 2018, **115**:9198-9203.  
Reveals high-resolution maps of emotions and other feelings in the body, suggesting bodily basis of emotional feelings.
57. Nummenmaa L, Glerean E, Hari R, Hietanen JK: **Bodily maps of emotions.** *Proc Natl Acad Sci U S A* 2014, **111**:646-651.
58. Bernardi NF, Bellemare-Pepin A, Peretz I: **Enhancement of pleasure during spontaneous dance.** *Front Hum Neurosci* 2017, **11**:572.
59. Lakin JL, Jefferis VE, Cheng CM, Chartrand TL: **The chameleon effect as social glue: evidence for the evolutionary significance of nonconscious mimicry.** *J Nonverbal Behav* 2003, **27**:145-162.
60. Nummenmaa L, Lahnakoski JM, Glerean E: **Sharing the social world via intersubject neural synchronisation.** *Curr Opin Psychol* 2018, **24**:7-14.
61. Keverne EB, Martensz ND, Tuite B: **Beta-endorphin concentrations in cerebrospinal-fluid of monkeys are influenced by grooming relationships.** *Psychoneuroendocrinology* 1989, **14**:155-161.
62. Fabre-Nys C, Meller RE, Keverne EB: **Opiate antagonists stimulate affiliative behaviour in monkeys.** *Pharmacol Biochem Behav* 1982, **16**:653-659.
63. Tarr B, Launay J, Dunbar RIM: **Silent disco: dancing in synchrony leads to elevated pain thresholds and social closeness.** *Evol Hum Behav* 2016, **37**:343-349.  
Using pain threshold as a proxy for exogenous opioid release, the authors shows that synchronized dancing leads to endogenous opioid peptide release, possibly promoting social boundedness.
64. Tarr B, Launay J, Cohen E, Dunbar R: **Synchrony and exertion during dance independently raise pain threshold and encourage social bonding.** *Biol Lett* 2015, **11**.
65. Dunbar RIM, Kaskatis K, MacDonald I, Barra V: **Performance of music elevates pain threshold and positive affect: implications for the evolutionary function of music.** *Evol Psychol* 2012, **10** 147470491201000403.
66. Weinstein D, Launay J, Pearce E, Dunbar RIM, Stewart L: **Singing and social bonding: changes in connectivity and pain threshold as a function of group size.** *Evol Hum Behav* 2016, **37**:152-158.
67. Pearce E, Launay J, Dunbar RIM: **The ice-breaker effect: singing mediates fast social bonding.** *R Soc Open Sci* 2015, **2**:150221.
68. Kirschner S, Tomasello M: **Joint music making promotes prosocial behavior in 4-year-old children.** *Evol Hum Behav* 2010, **31**:354-364.
69. Schultz W: **Updating dopamine reward signals.** *Curr Opin Neurobiol* 2013, **23**:229-238.
70. Salimpoor VN, Zald DH, Zatorre RJ, Dagher A, McIntosh AR: **Predictions and the brain: how musical sounds become rewarding.** *Trends Cogn Sci* 2015, **19**:86-91.
71. Trost WJ, Labbé C, Grandjean D: **Rhythmic entrainment as a musical affect induction mechanism.** *Neuropsychologia* 2017, **96**:96-110.
72. Cohen EEA, Ejsmond-Frey R, Knight N, Dunbar RIM: **Rowers' high: behavioural synchrony is correlated with elevated pain thresholds.** *Biol Lett* 2009.
73. Manninen S, Tuominen L, Dunbar RIM, Karjalainen T, Hirvonen J, Arponen E, Jääskeläinen IP, Hari R, Sams M, Nummenmaa L: **Social laughter triggers endogenous opioid release in humans.** *J Neurosci* 2017, **37**:6125-6131.  
Using positron emission tomography, this study shows that social bonding signals such as laughter engage the brain's opioid receptor system.
74. Nummenmaa L, Tuominen L, Dunbar R, Hirvonen J, Manninen S, Arponen E, Machin A, Hari R, Jääskeläinen IP, Sams M: **Social touch modulates endogenous  $\mu$ -opioid system activity in humans.** *NeuroImage* 2016, **138**:242-247.
75. Saanijoki T, Tuominen L, Tuulari JJ, Nummenmaa L, Arponen E, Kalliokoski K, Hirvonen J: **Opioid release after high-intensity interval training in healthy human subjects.** *Neuropsychopharmacology* 2017.
76. Mallik A, Chanda ML, Levitin DJ: **Anhedonia to music and mu-opioids: evidence from the administration of naltrexone.** *Sci Rep* 2017, **7**:41952.
77. Zentner M, Grandjean D, Scherer KR: **Emotions evoked by the sound of music: characterization, classification, and measurement.** *Emotion* 2008, **8**:494-521.
78. Wildschut T, Sedikides C, Arndt J, Routledge C: **Nostalgia: content, triggers, functions.** *J Pers Soc Psychol* 2006, **91**:975-993.
79. Ferreri L, Mas-Herrero E, Zatorre RJ, Ripollés P, Gomez-Andres A, Alicart H, Olivé G, Marco-Pallarés J, Antonjoan RM, Valle M *et al.*: **Dopamine modulates the reward experiences elicited by music.** *Proc Natl Acad Sci U S A* 2019, **116**:3793.  
Using pharmacological manipulations, this study shows that dopaminergic system has a key role in mediating musical pleasures.