Editor’s Note: While the human brain is hardwired to feel pleasure for basic survival necessities, such as eating and sex, music—although obviously pleasurable—doesn’t offer the same evolutionary advantages. So why do we respond to patterns of sounds that disappear in an instant? Why do we belt music from the top of our lungs, learn to play instruments, and empty our bank accounts to see Bruce Springsteen on Broadway? Our author offers some valuable insights.
Human beings seem to have innate musicality. That is, the capacity to understand and derive pleasure from complex musical patterns appears to be culturally universal.¹ Musicality is expressed very early in development.² In this sense, music may be compared to speech—the other cognitively interesting way that we use sound. But whereas speech is most obviously important for communicating propositions or concepts, obtaining such knowledge, this is not the primary function of music. Rather, it is music’s power to communicate emotions, moods, or affective mental states that seems beneficial to our quality of life.

Which brings us to the question that forms the title of this article: why do we love music? On its face, there is no apparent reason why a sequence or pattern of sounds that has no specific propositional meaning should elicit any kind of pleasurable response. Yet music is widely considered amongst our greatest joys.³ Where does this phenomenon come from?

There are several approaches to this question. A musicologist might have a very different answer than a social scientist. Since I’m a neuroscientist, I would like to address it from that perspective—recognizing that other perspectives may also offer valuable insights. An advantage of neuroscience is that we can relate our answer to established empirical findings and draw from two especially relevant domains: the neuroscience of auditory perception and of the reward system. To give away the punch line of my article, I believe that music derives its power from an interaction between these two systems, the first of which allows us to analyze sound patterns and make predictions about them, and the second of which evaluates the outcomes of these predictions and generates positive (or negative) emotions depending on whether the expectation was met, not met, or exceeded.

The Auditory Perception System
It’s remarkable to think that all sound—a baby crying, thunder, the strains of a waltz—is carried by nothing more than vibrations of molecules in the air. Our rich phenomenological experience of these sounds is the product of a sophisticated perceptual system that takes these vibrations and transforms them into what psychologists call internal representations (perception, thoughts, memories, emotions, etc.), which can be related to our memories of other sounds and knowledge
of the world in general. Part of the process has to do with extracting relevant acoustical features from the sounds and encoding them in the pattern of nerve firings.

This process is accomplished by operations happening in three separate brain areas: the brainstem, thalamus, and auditory cortex. A cello string when plucked, for example, will vibrate at a characteristic frequency based on the physics of its materials and its tension; if it is the first string of a conventionally tuned cello, for example, the entire length of the string would vibrate about 65 times in one second, corresponding to the musical note C. Neurons in the aforementioned nuclei and the cortex will respond in a synchronized manner with a corresponding neuronal oscillation of 65Hz, thus transforming physical energy to a pattern of neural activity representing sound frequency.

A great deal of research suggests that neurons in the auditory cortex, especially in the right cerebral hemisphere, are important for distinguishing fine gradations of frequency, creating the psychological sensation of pitch. Pitch is fundamental to most music, but it is not sufficient merely to detect that a pitch has changed; it is essential to determine the relationships between pitches within a musical system.

An introductory class in music theory would, accordingly, include a description of musical intervals, the ratio between the frequencies of two tones, which determine the patterns that form melodies (when the tones are sequential) and harmonies (when the tones are simultaneous). Importantly, intervals are defined by the relations between pitches independently of the pitch values themselves. That is, a minor third is defined (roughly) as the ratio six to five, so any frequencies in that relation will be perceived as a minor third.

This property, known as transposition, is what allows us to recognize the same song when sung in different keys (if we did not have this capacity, covers of familiar songs would not work). Several studies have indicated that the brain pathways for this kind of computation lie outside the auditory cortex proper, in regions connected to it that are also involved in other kinds of sensory transformations.
A further complication is that sounds disappear instantly from the environment—unlike, say, objects in a visual scene. Because sounds are evanescent, the brain also needs a mechanism to hold them temporarily in mind, in order to calculate pitch relationships, and other properties. (This is equally important for speech, where a sentence could not otherwise be understood since each word disappears the instant it is spoken.) This capacity depends on the faculty called working memory: roughly, the ability to retain and process information over short time periods.

Several brain circuits emanating from the auditory cortex, mainly the dorsolateral frontal cortex and posterior areas in the parietal lobe, are important for this ability, and hence indispensable for musical perception.⁷,⁸ People with congenital amusia (sometimes called tone-deafness)—the inability to comprehend musical relationships and hence to perceive melodies or other musical structures—have been found to have reduced connections between auditory areas and frontal regions, and therefore struggle to figure out the relationships between sounds.⁸

**The Prediction System**

The foregoing description gives a brief and highly simplified glimpse of some of the machinery that allows us to perceive tones and determine relationships between them. But, of course, that barely scratches the surface of what’s involved in responding to musical sounds. One of the most important aspects of perception, and one that is critical for music, is the ability to anticipate future events based on past experience.⁹

This is an essential ability for survival, because an organism can more effectively prepare an appropriate response to an event if that event can be predicted. In the case of music—and, it is thought, of language—there is a rich statistical relationship between patterns of sounds. Every musical system, like every language, has a syntax, that is, a set of rules concerning which sounds follow other sounds. The auditory brain is exquisitely sensitive to such regularities and can learn statistical relationships quickly and efficiently, even early in life, via exposure to exemplars of the system in question (melodies, rhythms, words, and sentences). This is how babies learn about sound patterns in their environments.¹⁰
To test the neural substrates of this ability, researchers have devised procedures presenting a set of sounds that follows standard, expected rules (e.g., a sequence of chords), and then introducing a new item that either should or should not follow, based on the context (e.g., an out-of-key chord). In this situation, violations of expectancy yield a characteristic brain response that originates in auditory areas and frontal regions.\textsuperscript{11}

Such results reveal that when we listen to music we not only encode sound properties and their relationships, but also make predictions about what’s coming up (otherwise we would not find the out of key chord jarring). Such predictions are based not only on what has just been experienced in the moment, but also on a knowledge of sound patterns in general drawn from our entire listening history. If one lacks sufficient exposure to the rule system of a different culture, appropriate predictions are often difficult, and that culture’s music may be hard to understand. The same principle would apply to another culture’s language.

**What about Pleasure?**

The brain mechanisms sketched very roughly above provide the substrates for a number of perceptual and cognitive skills without which, I argue, music would not be possible. If we could not extract pitch information, or hold it in memory, or understand pitch relationships, or make predictions, we could not have what we call music. But none of this explains why we like music so much. For insights into that question, we need to consider a totally different set of brain structures: the reward system.

Scientists have accumulated a great deal of evidence, from both animal models and human studies, to identify the system that signals the presence of a stimulus that has value for the organism. An obvious example would be a hungry rat that is trained to press a lever in response to a cue (such as a light coming on) to receive food. Early studies showed that in this situation certain neurons situated deep in the subcortex, in a structure called the striatum, responded with bursts of dopamine release when the food was delivered.\textsuperscript{12}

But it soon became apparent that these responses were doing much more than merely signaling the presence of food, because after a time, these neurons stopped responding if the amount of food
was constant. That is, when the food was expected the neural responses decreased; but if the amount suddenly became larger, a vigorous dopamine response would return; and if less or no food was delivered, the response would actually be inhibited below baseline level. Thus, this reward system was encoding the difference between what was expected and what was actually obtained, a concept that became known as reward prediction error (where positive reward prediction error corresponds to a better outcome than was anticipated).

The reward system has been shown to be responsive to a wide range of complex stimuli in both humans and animals. Human neuroimaging studies consistently show activity in the striatum and other components of the reward system when people are shown images of food, or allowed to win money in gambling, or by playing video games, or are shown erotic stimuli. Thus, the reward system is thought to underlie the response to many different kinds of inputs that are, globally speaking, beneficial to the organism’s survival or well-being. Food and sex are, of course, biologically necessary for survival (of the individual and the species, respectively); and money may be thought of as having value based on the fact that one may exchange it for other desired items. Imaging studies have also shown reward-system activity for various drugs, including cocaine and amphetamines.

Music and the Reward System
So what does music have to do with rats pressing levers or people taking drugs? When our group first started to research music-induced pleasure, we did not know whether the same reward system that reacts to biologically relevant stimuli would also be engaged by an entirely abstract stimulus such as music. After all, music is not necessary for survival, nor is it a medium of exchange like money, nor a chemical substance like a drug that can trigger direct neuronal responses.

Our team set out to explore this question using brain imaging techniques that would allow us to measure activity in the striatum during the experience of high pleasure from music. But we immediately ran into a methodological problem: how to measure a subjective response, such as pleasure, in a rigorous, objective, scientifically viable manner? The study of something as complex and potentially uncontrolled as musical emotion represented a particular hurdle. In our first
approach to this question, we came up with the idea of studying “chills,” the pleasurable physical response that many people experience while listening to certain musical passages.

The advantage of this approach was that chills are accompanied by physiological changes (increased heart rate, respiration, skin conductance, and so forth), from which we could derive an objective index of the timing and intensity of maximal pleasure. To implement this idea, we asked each participating individual to select their own favorite music, guaranteed to elicit maximal pleasure. Thus armed, we were able to demonstrate in a series of studies that both dorsal and ventral striatum does indeed respond to moments of peak pleasure induced by music and, using a neurochemically specific radioligand (a radioactive biochemical substance that binds to a relevant molecule), that dopamine release occurred in the striatum during these moments.

These studies transformed our understanding of the neurobiology of musical pleasure but left unanswered precisely how or why the reward system is thus engaged. A clue to this question was our observation that there were two phases to the dopamine response: an anticipatory phase, occurring a few seconds prior to peak pleasure in one sub-portion of the striatum, and a second response in a different sub-region at the actual point of pleasure. This finding indicates that expectations are as important a source of pleasure as resolutions. Interestingly, music theorists have posited something similar for many years: that emotional arousal and pleasure in music arise from creating tension and then leading the listener to expect its resolution, which resolution is sometimes delayed or manipulated to increase the expectation even further.

Using the chills response proved very useful; but one could ask whether the engagement of the reward system is limited to this experience; since not everyone gets chills, and since music can be very pleasurable even without any chills, it seemed important to test musical pleasure without any chills being involved. To do so we used a paradigm adapted from neuroeconomics, in which people listen to music excerpts and decide how much money they would be willing to spend to buy a recording of it. The monetary amount is then a proxy for value, and indirectly, for pleasure. With this approach we also found that the ventral striatum showed increased activity as value increased.
But a second clue emerged from this study because we also found that as value increased, and the response in the striatum increased, the higher was its coupling (measured in terms of correlated brain activity) to the auditory cortex and its associated network: the more listeners liked a given musical piece (indexed by their willingness to spend more money), the greater the cross-talk between striatum and auditory system. This finding is important because it links the activity of the perceptual system, as reviewed above, with that of the reward system. Thus, we propose that the two systems have different functions: the perceptual mechanism computes the relationships between sounds and generates expectancies based on those patterns (“I just heard this sound, followed by that sound, therefore the next one should be X”); the outcome of the prediction (sound X compared to the actual sound perceived) is then evaluated by the reward system (“X is not as good as I expected, therefore it is not pleasurable, or X is surprising and better than expected therefore it is highly pleasurable”).

And just as one might expect from our reward prediction model, the reward response is greatest neither when the outcome is exactly as expected (which is boring), nor when the outcome is completely unpredictable (confusing), but when it hits the “sweet spot” of being somehow better than expected. This concept, though still lacking full definition, is one that musicians find intuitive: the best music, typically, neither formulaically follows conventions nor is too complex to follow, but has the virtue of moderation in its ability to surprise the listener with novelty within a predictable framework.

If the account of musical pleasure presented in the preceding paragraphs is roughly correct, it leads to some testable predictions. First, we reasoned that if musical pleasure arises from interactions between auditory networks and the reward system, then such interactions should be disrupted in persons who are unable to experience musical pleasure. To assess this idea, we sought out such individuals, and discovered that three to four percent of the general population exhibits what we labelled “specific musical anhedonia.” These people have reasonably intact overall hedonic capacity (they enjoy food, sex, social activities, money, even visual art), nor do they have a perceptual disorder such as amusia (tone deafness); they just don’t enjoy or appreciate music, as shown by their lack of physiological responses to it.
When we scanned their brains, we discovered that their reward system responded normally to a gambling game, but not to music; and the coupling between auditory and reward systems was essentially absent during music listening. Thus, as predicted by our model, musical anhedonia emerges in the absence of the typical interaction between the two systems.

One might say that musical anhedonia represents a chicken and egg problem: perhaps it is the lack of musical pleasure that leads to decreased connectivity between auditory and reward systems, and not vice versa. To exclude such a possibility, it is critical to test a second prediction arising from our model: if activity in the reward system really underpins musical pleasure, then we should be able to modulate that pleasure by manipulating activity within that system in the normal brain.

Previous work had shown it possible to excite or inhibit the reward system, by changing dopamine activity in the striatum with a noninvasive brain stimulation technique known as transcranial magnetic stimulation. We recently implemented this technique while people listened to music (their own favorites and some choses by us) and found that, just as we predicted, listeners reported more pleasure and showed greater physiological responses (skin conductance) to music in the context of excitatory stimulation, and reported less pleasure, even to their own selected music, and showed diminished physiological responses during the inhibitory stimulation. This finding provides causal evidence that musical pleasure is directly linked to reward system activity.

I am very pleased to see that music neuroscience has shifted over the past decades from a fringe area to a solid research domain, with labs in many countries making important contributions and substantial progress reported in respected journals. What not long ago seemed like an intractable problem—how music can result in strong affective and pleasurable responses—is now a topic that we understand well enough to have significant insights into and testable hypotheses about. It is an exciting time to be working in this domain; we look forward to future developments which, based on the science discussed in this piece, we hope will include applications to clinical, educational, and even artistic domains.
Bio

Robert Zatorre, Ph.D., is a cognitive neuroscientist at the Montreal Neurological Institute of McGill University. His laboratory studies the neural substrate for auditory cognition, with special emphasis on two characteristically human abilities: speech and music. He and his collaborators have published about 300 scientific papers on topics including pitch perception, auditory imagery, brain plasticity, and musical pleasure. In 2006 he became the founding co-director of the international laboratory for Brain, Music, and Sound research (BRAMS), a unique multi-university consortium dedicated to the cognitive neuroscience of music. He tries to keep up his baroque repertoire on the organ whenever he gets a chance.

References

1. Savage, P. E., Brown, S., Sakai, E., & Currie, T. E. (2015). Statistical universals reveal the structures and functions of human music. Proceedings of the National Academy of Sciences, 112(29), 8987-8992.
2. Honing, H. (2018) The origins of musicality. MIT Press
3. Brattico, E., & Jacobsen, T. (2009). Subjective Appraisal of Music. Annals of the New York Academy of Sciences, 1169(1), 308–317.
4. Kraus, N., Anderson, S., White-Schwoch, T., Fay, R.R., and Popper, R.N. (2017) The Frequency-Following Response. Springer Handbook of Auditory Research.
5. Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: music and speech. Trends in cognitive sciences, 6(1), 37-46.
6. Klein, M. E., & Zatorre, R. J. (2014). Representations of invariant musical categories are decodable by pattern analysis of locally distributed BOLD responses in superior temporal and intraparietal sulci. Cerebral Cortex, 25(7), 1947-1957.
7. Kumar, S., Joseph, S., Gander, P. E., Barascud, N., Halpern, A. R., & Griffiths, T. D. (2016). A brain system for auditory working memory. Journal of Neuroscience, 36(16), 4492-4505.
8. Albouy, P., Mattout, J., Bouet, R., Maby, E., Sanchez, G., Aguera, P. E., ... & Tillmann, B. (2013). Impaired pitch perception and memory in congenital amusia: the deficit starts in the auditory cortex. Brain, 136(5), 1639-1661.
9. Huron, D. B. (2006). Sweet anticipation: Music and the psychology of expectation. MIT press.
10. Saffran, J. R., Johnson, E. K., Aslin, R. N., & Newport, E. L. (1999). Statistical learning of tone sequences by human infants and adults. *Cognition, 70*(1), 27-52.

11. Maess, B., Koelsch, S., Gunter, T. C., & Friederici, A. D. (2001). Musical syntax is processed in Broca’s area: an MEG study. *Nature neuroscience, 4*(5), 540.

12. Schultz, W. (2002). Getting formal with dopamine and reward. *Neuron, 36*(2), 241-263.

13. Sescousse, G., Caldú, X., Segura, B., & Dreher, J. C. (2013). Processing of primary and secondary rewards: a quantitative meta-analysis and review of human functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews, 37*(4), 681-696.

14. Drevets, W. C., Gautier, C., Price, J. C., Kupfer, D. J., Kinahan, P. E., Grace, A. A., ... & Mathis, C. A. (2001). Amphetamine-induced dopamine release in human ventral striatum correlates with euphoria. *Biological psychiatry, 49*(2), 81-96.

15. Blood, A. J., & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences, 98*(20), 11818-11823.

16. Salimpoor, V. N., Benovoy, M., Larcher, K., Dagher, A., & Zatorre, R. J. (2011). Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nature neuroscience, 14*(2), 257.

17. Salimpoor, V. N., van den Bosch, I., Kovacevic, N., McIntosh, A. R., Dagher, A., & Zatorre, R. J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science, 340*(6129), 216-219.

18. Chmiel, A., & Schubert, E. (2017). Back to the inverted-U for music preference: A review of the literature. *Psychology of Music, 45*(6), 886–909.

19. Mas-Herrero, E., Zatorre, R. J., Rodríguez-Fornells, A., & Marco-Pallarés, J. (2014). Dissociation between musical and monetary reward responses in specific musical anhedonia. *Current Biology, 24*(6), 699-704.

20. Martínez-Molina, N., Mas-Herrero, E., Rodríguez-Fornells, A., Zatorre, R. J., & Marco-Pallarés, J. (2016). Neural correlates of specific musical anhedonia. *Proceedings of the National Academy of Sciences, 113*(46) E7337-E7345.

21. Strafella, A. P., Paus, T., Barrett, J., & Dagher, A. (2001). Repetitive transcranial magnetic stimulation of the human prefrontal cortex induces dopamine release in the caudate nucleus. *Journal of Neuroscience, 21*(15), RC157-RC157.
22. Mas-Herrero, E., Dagher, A., & Zatorre, R. J. (2018). Modulating musical reward sensitivity up and down with transcranial magnetic stimulation. *Nature Human Behaviour, 2*(1), 27.