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Feel the beat

Music exploits our brain's ability to predict and the dopamine-reward system to instill pleasure

Katrin Weigmann

Music is universally cherished across humanity. Every culture has its songs and dances, everywhere in the world people listen to music; even small children clap their hands and move to the rhythm of the beat. Music moves us in every sense of the word. We just do not know why. The musical abilities of humankind have puzzled scientists for centuries, and Charles Darwin ranked them as "one of the most mysterious with which he is endowed". Why do we make music, why do we like it, and how do we even perceive it?

> *"The musical abilities of humankind have puzzled scientists for centuries, and Charles Darwin ranked them as "one of the most mysterious with which he is endowed"."*

"Music is art in time", said Peter Vuust, a neuroscientist and music theoretician at Aarhus University in Denmark. Perceiving music has much to do with our sense of time and anticipation. Music is never perceived instantly: We need a few notes or beats before we detect a rhythm, and with the last few notes in mind, we anticipate what will happen next. Mostly, these anticipations will be met, but sometimes not. "Music plays with predictions, and this is what makes it so interesting to science", explained Vuust, because it helps to investigate the brain's predictive timing mechanisms.

"Predictive coding" is a conceptual framework of how the brain makes forecasts. It predicts incoming sensory information based on experience and context. This prediction is tightly coupled to the release of dopamine, the neurotransmitter of reward. In addition to predicting what will happen next, it is just as important to know exactly when it will happen, and an analogous system of "predictive timing" takes on this task. A school of fish or a flock of birds all turning at the same time, a dog jumping to catch a ball—predictive timing kicks in whenever animals coordinate their movements with their environment. Music makes use of both predictive coding and predictive timing. It taps into our brain's ability to sense the structure of temporal sequences and draw reward from making predictions: It may just be a means to shower ourselves in dopamine. But what exactly is it that music does to our brain? How exactly does it play with our sense of time?

Music perception is predictive timing

When we hear a rhythm, or just a series of beeps or clicks, we may or may not feel that it has a beat. Depending on the signal's regularity and structure, we can extract a meter and sense it as a three-four time or four-four time. The beat is somehow contained in the stimulus, but it may not always be obvious; beat perception is also a psychological construct.

During the past decade, a number of studies compared brain activation patterns while participants listen to a stimulus that does or does not induce beat perception. They found that beat perception activates several brain areas, including basal ganglia and parts of the secondary motor areas of the cortex [1]. "Whenever we feel the beat in a rhythm, motor areas are involved—even if we are not moving at all", explained Jessica Grahn, a cognitive neuroscientist at Western University in London, Ontario.

In addition, studies that specifically looked at interactions between brain areas found that beat perception was associated with greater connectivity between the basal ganglia, motor areas, and auditory cortex. According to Grahn, there is a physiological explanation for the engagement of the motor cortex in beat perception. "We often see motor regions involved when people are timing, not only in the context of a rhythm", she said, "This may be because the motor system operates so much in the time domain, every movement we make has to be very precisely coordinated with the timing in the outside world. The motor system is excellent for timing and therefore it is a good system to use when you are trying to perceive patterns in time".

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Sensing is predicting—the brain is constantly guessing incoming sensory information. There is increasing evidence that temporal prediction is computed in the motor system and that neuronal oscillations—synchronous electrical activity in groups of cortical neurons—play a central role in the brain's ability to make predictions. Most of all, delta (~ 1–4 Hz), theta (~ 4–8 Hz), and beta (~ 13–30 Hz) oscillations are involved. "The brain has an intrinsic dynamic. It spontaneously generates oscillations in different parts of the cortex, even when we lie quietly with our eyes closed", explained Edward Large, a neuroscientist at the University of Connecticut. But when we are listening to music, neurons in the brain adjust their oscillations to synchronize with the external stimulus. Importantly, neuronal oscillations are not just a reaction to the

Freelance Journalist, Oldenburg, Germany. E-mail: mail@k-weigmann.de
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stimulus, they are self-sustained and continue even if the external stimulus cedes. "Once they are synchronized, they can predict, because they have an intrinsic quality, a life of their own", Large said. In this sense, neuronal oscillations are basis of predictive timing in music perception.

Beat prediction

But oscillations do more than just continue a stimulus, they also interpret. "Synchronized ongoing oscillations are able to do computations and pull things out of a stimulus that are not objectively present, but implied", Large said. His research focuses on mathematical models that simulate these computations and thereby provide a rationale for a number of psychological features of beat perception.

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For example, most musical rhythms have a meter—every second, third, or fourth pulse is emphasized. This may have its roots in how our brain reacts to rhythms: According to mathematical models, a neuronal network stimulated with a regular pulse would not only entrain at the frequency of the pulse, but also at 1/2 or 1/3 the tempo, which might explain metrical accent. A study by André Mouraux and colleagues [2] showed that this is exactly what happens in the brain. They presented participants with a sequence of pulses at a rate of 2.4 Hz. Accordingly, the electroencephalographic (EEG) response of their brains showed oscillations at 2.4 Hz. But when people were asked to imagine a binary meter, like a march, an additional oscillation emerged at 1.2 Hz—half the pulse frequency. When they imagined a ternary meter, like a waltz, an additional frequency at 0.8 Hz appeared. Thus, feeling a waltz or a march emerges from the entrainment of neurons resonating to the pulse—which is probably the neuronal underpinnings of how we feel the beat.

In addition, the brain can infer a regular pulse from a more complex rhythm. For example, we can easily tap at the quarter notes of a four-four time, even if the rhythm we hear has syncopations or pulses between the counts. A recent study by Large and his colleagues suggests that this ability is also generated by neuronal oscillations [3]. They played rhythms to people asking them to tap at a regular count and compared people's behavior to predictions from a mathematical model that simulates oscillatory circuits of the brain. "We designed rhythms that had no energy at the frequency people are most likely to tap to", said Large. In other words, no two clicks would ever be one count apart—but nonetheless people would tap on the count. Likewise, the mathematical model predicted that the brain—or, more precisely, the motor regions—would entrain at the frequency of the count in response to the stimulus. Again, this suggests that neuronal oscillations explain how beat perception arises in our brains.

The main rhythmic pulse of music may vary, but it is usually at a frequency between 0.5 and 5 Hz. Neural oscillations that entrain to the pulse will be in the delta (~ 1–4 Hz) or theta (~ 4–8 Hz) range, and they work together with faster oscillations in the beta range (~ 13–30 Hz) in predictive timing. "The motor system seems to do its computations in the beta range", commented Large, "our hypothesis is that delta oscillations are controlling the amplitude of the beta oscillations, and that this is really how auditory and motor cortices are communicating".

Indeed, it has recently been shown that, when participants listen to a regular rhythm, activity in the beta-band drops after each beat, and recovers just before the next. Importantly, the beta rebound reaches its maximum just prior to the next beat, no matter the tempo of the rhythm. Thus, beta rebound comes at the tempo of the beat, but it leads the way and predicts the next event. Moreover, beta oscillations not only predict the next note, but also the meter. The drop in amplitude is larger when the next pulse is an upbeat [4]. This is compelling evidence for a central role of beta oscillations in predictive timing.

Music rewards the brain

Listening to music is a joyous experience, because music exploits the brain's competence for predictive coding, according to Vuust. "It is not completely clear how, but dopamine is in some way related to prediction", he said. Current theories of reward-processing postulate that the dopamine response reflects the prediction error—dopamine neurons respond when the reward is higher than predicted. This may explain why we appreciate music that is slightly more complex: It is less predictable and thus generates more prediction errors, as Vuust explained. According to a study from his research group, a simple rhythm that was too predictable did not appeal to people; but adding a few aberrations to the regular beat improved its popularity. "The more prediction error, the more we want to move and the more we feel pleasure", Vuust commented. But this only applies as long as the rhythm is still simple enough to make predictions. "When the rhythm gets too complex, we lose the model. Even though there is a lot of irregularity, we don't have a prediction to hold it up against", Vuust explained [5].

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Taken together, we perceive the beat and we enjoy music because our brain uses oscillations to predict timing and because we draw reward from these predictions. But these features have a much broader function. For one, neural oscillations are a general principle of predictive timing, not just for regular, reoccurring stimuli. "Any given stimulus can turn on a number of different oscillators at different frequencies. In effect, you could predict any kind of temporal pattern, especially given the ability to learn", said Large, "but the more regular ones are probably easier". Music, of course, is regular and therefore has a pronounced effect on oscillations. "Music just happens to stimulate the system in a way in which all these oscillations line up", Large explained. Our brain is prone to keep time in music, to predict the next note and to extract meter from a rhythm. In addition, we enjoy music because it plays with predictions. "The dopamine system rewards us for learning to make correct predictions, and music makes use of the brain's predictive abilities and of the brain's dopamine system", Vuust added.

Most animals do not dance

As natural it is to for us to pick up a beat, this ability is rare in the animal kingdom. Dogs do not waggle their tail to a beat and cats do not tap their paws, even though these animals have lived with humans for centuries. If musicality builds on oscillations and the dopamine system, if it taps into the timing of the motor system, why can't animals dance? "Maybe they are better than we know", suggested Large, "the research with animals is ongoing and in the past 10 years, a number of animals have been discovered that can move to the beat".

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One of the first indications that humans are not the only species capable of beat perception came from a sulfur-crested cockatoo named Snowball in 2008. A bird rescue center in Indiana had posted videos on YouTube showing Snowball bobbing his head and lifting his feet to the rhythm of pop songs. Aniruddh Patel, a neuroscientist, then at the Neurosciences Institute in San Diego, took a closer look and found that Snowball was, indeed, synchronizing his movement to the beat; he was capable of entraining to slower or faster rhythms. Inspired by these observations, Adena Schachner, then at Harvard University, conducted a systematic YouTube search for dancing animals. After carefully excluding all possible fakes, she found 14 more parrot species and, surprisingly, an Asian elephant capable of entraining to the beat [6].

A link to vocal learning

Parrots, humans, and elephants share, aside from their ability to "dance", another commonality: They are vocal learners; they can imitate sounds. According to Patel's "vocal learning hypothesis", this may be a prerequisite for beat perception, since both abilities require a close coupling between auditory and motoric brain regions. The vocal learning hypothesis in its very strict sense is debatable. There are animals—or at least one animal—that is not a vocal learner and can nonetheless entrain to the beat: a sea lion named Ronan, who has been trained to nod her head to the beat. But then, sea lions are in the same family as walruses and phocids or "true seals", who are vocal learners. Taken together, there seems to be some connection between vocal learning and beat perception.

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Non-human primates, our closest relatives, are no vocal learners and show only moderate rhythmic abilities. According to the "gradual audiomotor evolution hypothesis", formulated by Hugo Merchant and Henkjan Honing, beat-based timing evolved gradually in the primate lineage, and peaked in humans [7]. Macaque monkeys can tap to a metronome, but it takes them more than a year of training. Moreover, they seem to use a slightly different strategy; their movements lag about 250 ms behind the beat. This does not mean that they only react to each single pulse: If they would do so, their lag time would be much longer. They do have some predictive abilities, just not as pronounced as humans. Monkeys seem more sensitive to visuomotor than to audiomotor integration.

Again, our superior rhythmic abilities mirror the stronger coupling between the auditory and motor system. "Non-human primates have very good auditory and motoric systems, but the underlying representational system that allows the exchange between the two is not well developed", explained David Poeppel, a neuroscientist at New York University and the Max Planck Institute for Empirical Esthetics in Frankfurt, Germany. This coupling supports both language and music abilities. "The 'dorsal stream' of sound processing that connects the auditory and motor cortex is important in speech learning. It maps an incoming auditory signal onto articulatory motor representations, so that we can repeat a word that we have just heard", Poeppel explained.

Music and language: similar and different

Language and rhythm perception are not only built on the same anatomy, they also use the same oscillatory mechanism of predictive timing. "The physical signal of language has a very specific quasi-rhythm of volume change between 4 and 5 Hz", Poeppel said. It is the same for all languages and, according to Poeppel, it correlates with the length of a syllable and reflects the average rate at which we open and close our mouth. "Language moves forwards in time units of about 200 ms and neural entrainment in the theta range allows us to track this rhythm", he added. In a recent study, Poeppel and his colleagues showed that this entrainment is required to actually understand what is being said: When they filtered out the theta-information from a speech signal, it became incomprehensible. However, when a theta-rhythm was reintroduced in the form of simple click-sounds, which was not adding any language information, intelligibility came back [8]. "The brain needs this rhythm to align to the acoustic stimulus. It uses oscillations to segment the incoming signal, creating chunks that can then be decoded", Poeppel explained. The rhythm of music may vary somewhat more—there are slower pieces and faster pieces. But in principle, both language and music perception are based on oscillations that are used to analyze the physical sound signal. "Resolving the temporal granularity is very similar in music and language", Poeppel said.

"Music has this enormous ability to harmonize us as a group emotionally at an abstract level."

There is, of course, more to language and music than merely decoding an acoustic signal. "Music works on many different time scales and there are probably different mechanisms involved at different time scales", Vuust said—and this applies to language as well: Both have complex hierarchies. We know when to expect a verb in a sentence, or when to expect a specific chord in music. We learn the structure of language as well as we learn music, the types of harmonies and rhythms we grew up with. "We are not nearly as good at processing music that has different structures from another culture", Grahn said. "I think this is because predictions are not going to be accurate any more. And this extends beyond rhythm, to pitch structures and harmonic progressions". But how we memorize music is quite a mystery. “We memorize whole melodies. This is quite different from how we store language. We don’t store whole conversations; we store words in a content-addressable memory”, Poeppel said. “The kinds of mental objects used for calculating predictions are quite dissimilar, and that makes a huge difference”.

Music as an instrument for social cohesion

The cognitive scientist Steven Pinker once called music “auditory cheesecake”—a mere by-product of language evolution. But there are good reasons to believe that music does confer some selective advantage. It could have played a role for sexual selection and mate seeking, or in promoting group cohesion and social bonding. Vuust argues for the latter. “The use of music in rituals is probably as old as humans themselves”, he said. “Music has this enormous ability to harmonize us as a group emotionally at an abstract level”.

The origin of musicality will probably remain in the mists of time, as there are no fossil records to trace the evolution of cognitive abilities. How did humans develop an increased connectivity between the auditory cortex and premotor areas? Was the evolutionary selection on language, on musicality, or on both or on something else? But whatever its evolutionary origin—music builds on some very fundamental faculties of the brain, the use of oscillations for temporal predictions. “Music has a very special structure and this makes it so interesting to neuroscience. It allows us to stimulate the brain in a particular way that makes it reveal its secrets”, Large said.

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