

The Beat In Our Brains: The Neuroscience of Musical Rhythm

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In the human perception of temporality, rhythm is a concept appearing widely. Rhythm refers to periodicity, in which events repeat themselves systematically and it is seen on all scales of human observation. In astronomy, the motion of planetary bodies in space is marked by a regular transit through a repeating orbit. In physics, oscillations are found on the sub-atomic level as particles vibrate and waves of energy propagate in sinusoidal fashion. In the systems of living organisms, rhythms dictate daily cycles of wake, activity and sleep, annual cycles of breeding, migration and feeding, all of these guided by periodic changes in season as the Earth moves through its orbit. In the activity of the single human body, rhythms organize homeostasis as we breathe, as our hearts beat and as we move through our environments.

It is at this intersection of physics, biology and human behavior that rhythm achieves one of its most miraculous feats: it gives rise to music. In musicological terms, rhythm is a hierarchical organizer in time which allows a listener or performer to understand a stream of sounds as pieces of a whole, each existing on a different structural strata. Though defined in a number of different ways, rhythm specifies a basic musical pulse, or *tactus* which proceeds at a pace in Western terms referred to as *tempo* (Levitin & Tirovolas, 2009). These foundational pulses occur isochronously, or in units of fixed and equal time, and define the *meter*, which is a grouping of pulses whose periodicity, combined with differential but regular accentuation, creates a framework of expectancy to guide both musicians and listeners (Vuust, Gebauer, & Witek, 2014).

Within a piece of music's hierarchy of organization, rhythm is both expansive and reductive. From the tempo, we can zoom out to the meter, and from there to broader organizations such as phrases, refrains, movements and symphonies. We can also zoom in. Beneath the scale of tempo exist rhythmic subdivisions. In Western music, within a single tempo pulse or *beat* can exist two notes of equal duration, three, four, six, eight, sixteen or as many as are allowed by the interaction of the mechanical threshold of the instrument and the physiological capabilities of the musician's body. Further, these notes may be performed with subtle alterations in timing, intensity and duration such that different musicians reading the same piece of music may create strikingly different perceptions for the listener.

Within the span of human culture, musical rhythm manifests itself in such myriad forms that a complete categorization is impossible. The canon of Western musicology as well as the application of neuroscientific investigation to the perception and cognition of music has largely focused on the tonal concert music of pre-20th century Western Europe (Iyer, 2002). This is to the exclusion of perhaps the majority of music as it has been practiced over the geographic breadth and chronological lineage of humanity. Awareness of this academic ethnocentric myopia is of particular importance when considering rhythm, given that the music cultures of Africa, the Indian subcontinent and Latin America, as well as modern African American cultures employ musical rhythm in unique and characteristic ways (Iyer, 2002). In the study and appreciation of musical rhythm, one of the few bedrock commonalities to be found is that all musical rhythm has its origin in the human brain.

The following pages will provide a broad overview of the current neuroscientific conception of musical rhythm. A survey of brain structures and networks involved in the perception and production of rhythm will be offered along with special attention to the

phenomenon of neural entrainment. An examination of a particularly interesting recent study of neural entrainment will be offered followed by perspective on gaps in existing literature and directions for future research.

In pursuing musical rhythm within the brain, the first issue to be addressed is that of timekeeping. The human body incorporates a wide variety of mechanisms for the tracking of a range of biological and environmental periodicities, but in terms of time as it relates to musical rhythm, brief temporal intervals in the range of 200 ms to 2,000 ms are most relevant for consideration (London, 2012). Several models of neural timekeeping for this timescale exist, two of the more prominent being the interval model and the entrainment model (for a survey, see McAuley & Jones, 2003).

The interval timekeeping model comprises three components: an internal clock, a memory that stores durations marked by that clock, and a mechanism to compare durations stored in memory. The clock is started and stopped by external stimulus events, the durations are encoded and then compared against other encoded durations for the purpose of time interval judgment (Matell & Meck, 2000). Typical amongst interval models is the concept of the clock as an oscillator whose period is fixed regardless of the time stimulus being measured.

In contrast to the stop/start fixed oscillator of the interval model, entrainment models posit a continuously cycling oscillator whose period is synced or entrained to the cycle of the time stimulus being measured. Rather than an external stimulus stopping or starting the clock as in the interval model, stimulus onsets advance or delay the timing oscillator in the entrainment model. Judgments of time are accomplished by comparing stimulus onset to the momentary phase of the oscillator, as opposed to the explicit duration comparison performed by the interval

model. This allows the entrainment model to account for environmental context during timekeeping tasks (Grahn, 2012).

The entrainment model has several strengths including its compatibility with dynamic attending theory (DAT; Jones, 2008). DAT suggests that attention capture is driven by rhythmic oscillation and the salience of meter relates to the strength of attention to individual rhythmic events (Vuust et al., 2014). DAT and the entrainment model deal with entrainment, or internal synchronization to external events, on the conceptual level. However, recent neuroscientific findings indicate that populations of neurons synchronize their firing to periodic external events (Will & Berg, 2007) and this lends biophysical support to the entrainment model.

Regarding the anatomical substrate of the brain's rhythmic clock and perception of rhythm more broadly, there exists some ambiguity. Whereas perception of tonal information such as pitch is well established as occupying a tonotopically organized region of the primary auditory cortex and whereas phenomena such as harmonic interval, melody and contour are localized within the superior temporal gyrus and planum polare (Koelsch & Siebel, 2005; Levitin & Tirovolas, 2009), localization of timing, rhythm perception and production is less clear (Thaut et al., 2009). In a 2015 meta-analysis of neuroimaging studies on musical processing, Janata found that, other than regions TE1 and TE3 of the auditory cortex, which are activated by all dimensions of music, no other temporal lobe foci were activated by rhythm. Instead, processing of rhythm was found in regions associated with motor control. Double-dissociation evidence from neuropsychological studies strongly suggest that pitch and rhythm are processed through separate pathways (Levitin & Tirovolas, 2009).

Cortical and sub-cortical structures related to movement have been identified as active during the processing of rhythm, in particular the cerebellum, basal ganglia, the supplementary

motor area (SMA) and premotor cortex (PMC; Zatorre, Chen, & Penhune, 2007). The basal ganglia is commonly associated with motor control and action selection while the cerebellum is conceived as maintaining coordination and error-correction during movement. Acting as intermediaries between these structures, the PMC and SMA have roles in planning and execution of motor action (Grahn, 2012).

In the understanding of differentiated roles for brain structures involved in timing and movement, a distinction is drawn between systems operating on sub-second timescales and those operating on longer timescales. At timescales longer than 1 second, the basal ganglia and possibly the SMA are at work, whereas in the millisecond range, cerebellar functions are active (Zatorre et al., 2007). This distinction is suggestive of an automatic process in the cerebellum for very fast action and a more cognitively controlled process in the basal ganglia for movement occurring over longer timescales. However, Grahn (2012) finds this distinction to be too simplistic given that, despite an intuitive sense that longer actions require more conscious control, sub-second actions can require significant conscious control and longer actions can be learned and subsequently automatic.

Beyond the perception and production of timing, the cerebellum, basal ganglia, PMC and SMA have a role in motor learning and motor sequencing. The basal ganglia, in conjunction with the frontal cortex, has been implicated in the learning of movement sequences, while the cerebellum is considered important for integrating learned sequences into unified actions (Thaut et al., 2009). Further, the pre-SMA and SMA are implicated in the process of *chunking*, wherein complex motor sequences are divided into simpler action components for the purpose of organizing those complex behaviors (Zatorre et al., 2007).

Of particular interest, given the relationship between motor activity, music perception and learning, as well as the emerging concept that rhythm perception depends on interaction between motor and auditory systems (Zatorre et al., 2007), is the mirror neuron system. First observed in single cell recordings of pre-motor cortices of macaque monkeys, and now observed in humans, the term ‘mirror neuron system’ describes sensorimotor neurons that discharge when an individual performs an action or observes another being performing the same action (Rizzolatti & Craighero, 2004). A number of studies have sought to investigate the role of mirror neuron activity in the auditory domain and findings have shown activity in motor regions of the brain such as the PMC, SMA and cerebellum when individuals observe musical performance (Meister et al., 2004) and when they listen to music (Baumann et al., 2007; Chen, Penhune, & Zatorre, 2008). Evidence suggests the linkage between auditory and motor systems in the human brain is mediated by the PMC with subdivisions thereof conducting both basic functions (the ventral PMC conducts direct sound-movement mappings) and those of a higher-order (selection of movements based on sensory cues performed by the dorsal PMC; Chen, Penhune & Zatorre, 2008). In my personal experience as a drummer who works in live/electronic settings where a drum machine is present, I have always maintained that when an audience watches a human hit a drum, their reaction is stronger than if they simply hear the sound emanate from a box, even if the sonic qualities of the sound are identical.

Of further interest in the pursuit of musical rhythm as it manifests in neural activity is the concept of neural entrainment. While the idea of entrainment is used in a variety of contexts within the study of music perception, often in a conceptual or phenomenological way to suggest that a listener has cognitively or experientially joined the pulse of the music, there is a neurophysiological application to the term in which the meaning is significantly more literal. A

long observed phenomenon in electrophysiology is that when a regularly repeating stimulus is presented to a subject, a similarly repeating change in neural voltage amplitude is measured by EEG. This response is, in the correct conditions, stable in phase and amplitude over time and is thus referred to as a steady state evoked potential or ‘SS-EP’ (Nozaradan, 2014).

An SS-EP is a periodic response and is thus observed to occur as narrow-band peaks at frequencies related to the stimulus. In this usage, ‘frequency’ refers not to pitch, though the human perception of tonal pitch is indeed related to oscillatory frequency, but rather to the periodic pace at which a rhythmic stimulus is presented or an SS-EP occurs. Thus, an isochronous pulse at 120 beats per minute can be said to exist at a frequency of 2 Hz. In this case, a subject presented with such a stimulus and examined with EEG would show SS-EP spectra occurring at a periodicity of 2 Hz and/or harmonics thereof (Large & Snyder, 2009).

Phase-locked bursting of neuronal firing is considered to be a means by which different populations of neurons communicate or coordinate (Large & Snyder, 2009). Beta band oscillations (12.5 – 30 Hz) are observed in sensory and motor cortices as well as the cerebellum and basal ganglia and are associated with motor activity (Grahn, 2012). Given research showing that beta oscillations are modulated by the rate of rhythmic auditory stimuli (Fujioka, Trainor, Large, & Ross, 2012) there is evidence to suggest that auditory-motor coupling is achieved through an entrainment process not unlike that of musical rhythm perception.

Using a paradigm referred to as ‘frequency tagging’, Nozaradan and colleagues (Nozaradan, 2014) use EEG and stimuli of varying number and periodicities to isolate SS-EPs and identify relationships between stimuli and their resulting oscillatory spectra. Fascinatingly, this approach has been applied to sensory modalities other than audition such that higher-order visual phenomena such as figure-ground separation and face perception have been addressed in

the context of neural oscillation (Appelbaum, Wade, Pettet, Vildavski, & Norcia, 2008; Rossion, 2014).

In the same way that the brain infers information about spatial relationships between figure and background from a visual image which may not code that specific information, the brain infers the periodic percepts of musical beat and meter from auditory stimuli, whether or not that stimulus is perfectly periodic. Thus, the perception of rhythm is not a property of the stimulus, though it is induced by the stimulus. Rather, it is a cognitive construct of a perceptual process. In this way, and given the multiple period and phase combinations possible from a particular musical stimulus, listeners may extract many different beats from the music they hear, though culture strongly guides this extraction (Nozaradan, 2014).

A recent noteworthy study on neural entrainment to rhythmic structure was carried out by Tierney and Krauss at Northwestern University in Chicago (Tierney & Kraus, 2014). Existing literature on neural entrainment via auditory/musical perception has employed stimuli of a very simple nature. Using simple sound stimuli has the advantage of allowing researchers to control for a wide variety of variables in order to more clearly isolate entrainment phenomena. However, the trade-off in a carefully controlled laboratory setting is the sacrificing of ecological validity. It is fairly uncommon for people in their daily lives to attend to a long series of isochronous clicks.

The intent of Tierney and Krauss' effort was to evaluate neural entrainment in a more musically natural setting. To this end, the researchers replaced the isolated and simplified sonic stimuli typically used in such studies with a popular American rhythm & blues song from the late 1950's, "Pills" by Bo Diddley. Further widening the generalizability of the study is the fact that the researchers sought their 98 subjects from Chicago high schools, as opposed to the

demographically narrower population of college undergraduates typically sourced for such research.

The researchers created two conditions of the same musical stimulus in order to investigate neural entrainment using EEG. In an ‘on the beat’ condition, the Bo Diddley song was presented with a synthesized bassoon superimposed onto the music such that its onsets coincided with the stimulus song’s onsets. In the ‘off the beat’ condition, the superimposed bassoon part was shifted off the song’s beat by 25% of the average interbeat interval, such that it occurred at the same tempo as the stimulus song but in a different phase, resulting in a stimulus whose rhythmic coherence was reduced. The added bassoon part was controlled for amplitude by a hard limiter, as was the stimulus song, to prevent variations in acoustic energy from confounding the results. The authors make no explanation of why they chose a bassoon, nor any mention of how weird Bo Diddley must sound accompanied by that instrument.

Results of the study showed clear differences in neural oscillation spectra between the two conditions. In both the on-beat condition and the off-beat, narrow-band peaks were observed at 2.4 Hz, which was the basic beat frequency. However, the on-beat condition showed a narrow-band peak at 4.8 Hz, or twice the basic beat frequency, whereas the off-the-beat stimulus did not. Additionally, the off-the-beat condition showed weaker response to the basic beat frequency.

These results are interesting for a variety of implications. First, given that the off-the-beat condition tracked the beat frequency (2.4 Hz) but not its higher harmonic (4.8 Hz) suggests that tracking of the beat and its metrical subdivisions may be an independent and separable process. In the case of the present study, it would seem that subjects in the off-the-beat condition were tracking the beat, but not its metrical subdivisions. Tierney and Krauss support this idea

with references to neuropsychological literature describing similar phenomena. This finding is an interesting contribution to the concept that human perception of rhythm is a hierarchical process in terms of cognition, but also in the neurophysiology that underlies that cognition.

However, subjects in this study watched a (silent, subtitled) movie as they listened to the audio stimuli and data were collected. The authors state that this was in order to maintain attention during data collection and subjects were told they didn't need to concentrate on the auditory stimulus. This is a weak point in the methodology. Possibly, the authors believed that non-attending subjects would provide data isolating perceptual processes, but given that the construct being sought involves cognition, the experimental paradigm should create circumstances which maximize subjects' attention to the musical stimulus.

Additionally, the use of Bo Diddley as the source for musical stimuli is excellent for ecological validity (as well as the enjoyment, or even sanity, of subjects and experimenters). However, this style of rhythm & blues, and particularly Bo Diddley's band, feature subtle tempo variations across a song that could reduce entrainment. Despite mostly holding to a fixed pattern, the song features full-stops for dramatic effect at points, and there is a certain amount of timing variation which results from the physiology of the human performers. Also, the musical contribution of Bo Diddley's famous maraca player, Jerome Green, adds a blurring quality to the rhythmic content, which is pleasant for listening but possibly impactful on the data of neural entrainment. Future research could employ music produced electronically, and thus of digitally perfect timing reliability and sonic isolation.

Of course, the above concerns are characteristic of the trade-off between control and real-world validity. The work by Tierney and Krauss (2014) represents a move toward greater ecological validity in the study of the neuroscience of musical perception and cognition. This

study had a large number of subjects from outside the university system and stimuli that were of the type encountered by music listeners every day. That the study showed evidence of neural entrainment in this setting is a good step forward, as is its evidence for a hierarchy of rhythmic perception, which is subject to the coherence of the music stimuli.

As research continues on neural entrainment and its relationship with rhythm perception, there are a number of interesting paths it should follow. Just as ecological validity is important to ensure that laboratory investigations are indeed measuring a phenomenon as it exists in the outside world, it is imperative that researchers explore rhythm in the brain as it manifests in cultures outside Western contexts (Nozaradan, 2014; Iyer, 2002). Latin, African and African-American cultures in particular are fascinatingly nuanced and subtly different in the way they manifest musical rhythm and the neural underpinnings of these expressions should be investigated.

Pertaining to the mechanics of neural entrainment, one of the matters to be explored is whether the observed enhancement of SS-EPs at beat-related frequencies is the result of the physiological response of the neuron to the auditory stimulus itself, or whether what we observe is the neural signature of a cognitive process. This challenge lies at the heart of much neuroscience as we seek to understand the way physiological processes support and somehow constitute the activity of higher thought. The study of rhythm is an excellent vehicle for the elucidating the human brain's means of processing external stimuli, creating a schema in which to understand that stimuli, and then manipulating those schemas to serve interaction with the stimuli. Knowing more deeply the human capacity for and love of rhythm will bring light to many shadows in our understanding of how the brain tracks time, how the movement of our

bodies is intertwined with our processing of sound and how oscillations of brain activity reflect both our external environment and our internal processes.

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