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21 In the Beginning Was the Beat: Evolutionary Origins of Musical Rhythm in Humans

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Every known culture has music with a sense of pulse, or beat, that organizes time, enlivens our bodies and can enable groups of people move in time in dance, music making, or work.[1] There can be a sheer joy in coordinated action with others, and pulse in music is one vehicle for achieving this. While the basic idea of being able to perceive and move in time with the pulse of music may seem simple, this simplicity belies a rich complexity of central interest not only to musicians, but also scientists of many stripes. The underlying neural mechanisms are fascinatingly complex, providing insights into how the brain shapes our reality and connects sensation with movement, while its evolutionary origins are matter of vigorous speculation and ongoing debate.

So, when and how did the beat begin? The universe is full of repeating patterns of light and dark, ebb and flow, swinging to and fro, and this is the milieu for all life. For organisms to be able to track *and predict*, for example the coming of day or night, has adaptive value, and synchronization with the light/dark circadian cycle is observed throughout nature. Most organisms create other rhythms of their own, of locomotion, breath, and heartbeat.

Despite the pervasiveness of oscillation and entrainment in the world, the ability to synchronize motor output to auditory input as humans do when dancing, performing, or just tapping a foot along with music turns out to be extremely rare in other animals, something Fitch has called the "paradox of rhythm."[2] There are at least two levels to this rareness: the first is basic, and often noted, that the presence of a neural link by which auditory pattern perception can influence motor pattern generation is necessary for synchronization with sound, but this link appears not to be present in most animals. It enables basic Sensory Motor Synchronization (SMS), but this does not encompass human rhythmic capacities. It is thought that in humans this auditory/motor link is bidirectional, opening rich possibilities for an internal sense of beat to affect not just how we respond to the world of rhythm, but how we actively perceive it.[3] We will call this capacity rich Beat Perception and Synchronization, or rich BPS, which we suggest is a second key development responsible for our rhythmic abilities. Highlighting the distinction between basic SMS and rich BPS is important for understanding the origins of human musical rhythm, for it emphasizes that multiple steps were likely involved. The distinction between these is not always made clear in the literature, and the majority of comparative and evolutionary accounts have focused on basic SMS, while rich BPS has not yet been demonstrated in any other animal to our knowledge.

In this chapter we will focus on a deeper origin question, asking what are the forces that shaped our ancestors to have these capacities? Frankly, It's an odd thing, to link sound and movement as we do. Adding a deep interest, remarkably, synchronized action often leads to deep feelings of bonding and oneness between individuals. Did the beat evolve because it had survival value for our distant ancestors? Is it a byproduct of our complex emotional and social brains or an invented technology for pushing our minds in pleasurable or even useful ways? We cannot know for certain. Our tangible view of the past is quite limited, with the earliest musical instruments, bone flutes, found dating from only 40,000 years ago, indicating that tonal music at least was well under

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way in our Paleolithic ancestors.[4] Nonetheless, there is a wide range of other evidence to draw from in creating theories of the origin of musical rhythm, including behavioral and neuroscientific studies of rhythm perception and production in humans, a comparative look at other animals to see what aspects of rhythmic behavior they may share with us, and why, and studies of other cultures as a way to peel back our technological and cultural developments to glimpse how music and dance may have played a role in societies of the past.

Rich Beat Perception and Synchronization: A view from cognitive neuroscience

First, what are we actually trying to explain? Here is a cognitive scientist's perspective, which may seem basic and familiar to a percussionist but with some differences in terminology and formulation. It can be boiled down to this: rhythmic patterns of sound are 'out there' in the world; the beat is entirely 'in here,' a creation of our minds. Temporal patterns of acoustic energy exist in the world. Our brains are able to find regularity and thereby form predictions about the future of these patterns, predictions that influence our perception and action. Sound patterns become rhythms *only* through an interaction with our brains: what can be predicted from a given signal is a property of the perceiver, not the signal. Just as different frequencies of light only become colors by interacting with an eye and brain—the colors we see are very different from those of a bee—so it is with rhythms: their periodicity is something we must be able to engage with. Consequently, much of our work in the cognitive science of rhythm is aimed at explaining our capacities for prediction in terms of internal mechanisms.

Beat-based perception

It has long been known that for humans when temporal patterns have, at least loosely, certain temporal properties such has having note durations related to each other by simple ratios, or having some degree of periodicity or repetition, they can induce in us a pulse, which enables a special form of temporal perception, beat-based perception.[5] This central human mode of rhythmic engagement involves the induction, from rhythmic input, of a continuous sense of periodicity or *pulse* (termed 'beat' when reinforced by a periodic train of sonic events). A pulse can exist at multiple hierarchical levels, and all levels need not be isochronous (evenly timed), though often at least one is. The pulse tempo need not be metronomic, but can have a certain elasticity, although different levels often track each other (except, e.g., in music built incorporating multiple tempos phase slipping across each other—something that has not been much examined by science). While we can use the pulse hierarchy to organize the timing of our movements, the pulse also plays a central role in perception: one might say that the musical sense of rhythmic pulse forms a recurrent scaffold upon which time perception is organized. The timing of events is perceived relative to our internal pulse. In this way, an acoustically identical note can be perceived in very different ways: upbeat, downbeat, offbeat, afterbeat make no sense except in relation to an internal pulse through which they gain different perceptual identities and different performance realizations. Beat-relative perception also aids memory for patterns. Critically, the pulse is not slavishly determined by sound, but is something we can, to varying degrees, control: when we listen to highly syncopated rhythms, we can still 'find' and tap our toes to the pulse of the music despite the complex sequence of note durations, many not beginning 'on the beat.' Conversely, we can generate highly syncopated rhythms on an internal pulse. When the internal pulse is shared among a group of performers, they can coordinate their perception and production of rhythm. We will present below a conceptual cataloging of increasingly complex features that comprise rich BPS and distinguish it from mere SMS, keeping track of which features have and have not been demonstrated in other animals.

Basic sensory motor synchronization

Modern scientific studies of rhythm perception and production have been under way for well over a century.[6] The most basic level, and the canonical paradigm for most of our work so far is 1:1 SMS with isochronous sounds, where people move once for each sound. Most humans, even without any explicit musical training, are extremely good at this in the sense of matching the average tempo of their movement (often finger tapping) with a metronome within a few percent. Two observations point to the *existence of an internal pulse*. First, synchronization is not a reactive process, but instead a predictive and anticipatory one—synchronized movements often precede a metronome, and the movement initially synchronized to a metronome can continue when the metronome is removed.

Even simple synchronization with others has a strongly emotional and social component that develops very early. It is prosocial, meaning synchronized partners feel more positively inclined towards each other. Children are more likely to help out an adult with whom they are synchronized.[7] Basic synchronization generally develops around age four;[8] prior to that children are generally animated and moving in response to music, but not in synchrony.[9] Underscoring the importance of social interaction, if modeling an adult even two-and-a-half-year olds can synchronize.[10]

Animal evidence for basic synchronization

This basic form of 1:1 SMS has attracted the majority of attention in comparative studies and has been described in a number of animals including several species of insects and frogs who create 'synchronous choruses.'[11] These findings have inspired a number of evolutionary accounts of group synchronization because of the benefit synchronized chorusing has for increased spatial reach of calls in order to attract mates or defend territory, the so-called 'beacon effect.'[12] In contrast, non-human primates have been shown to have only limited aspects of basic synchronization. Macaques, after training, can match the tempo of auditory and visual metronomes but are unable to match the phase, always tapping after the metronome. This is in contrast to humans who can tap on or even before the metronome. This result suggests that macaques do not have the same degree of prediction, although they are able to make some predictive use of the regularity because their reaction time is shorter to regularly-timed sounds than randomly occurring ones.[13] (For comparison, budgerigars have similarly been trained with similar results.)[14] Chimpanzees can be trained to alternately tap keys on a keyboard, and their spontaneous tapping is weakly affected by a metronome, but only at tempos close to the original spontaneous tapping rate.[15] It is not yet known if they can be trained to synchronize. Comparative results have informed a number of other theories, including the vocal learning hypothesis (discussed below) as well as the "gradual audiomotor evolution hypothesis," which proposes that our primate relatives might resemble earlier stages in the gradual emergence of SMS.[16]

Tempo and subdivision

Compared to animals, humans have considerable flexibility even for basic SMS: 1) they are able to synchronize across a far wider range of tempi, from roughly 30 to 300 bpm,[17] and can predictively follow tempo changes. 2) Humans can generally change the mode of synchronization from one movement per metronome tick to subdivisions and multiples, tapping, e.g., twice per tick, or every two ticks, which we could call m:n synchronization. This is one way of establishing metrical hierarchy. Binary subdivisions and multiples are generally the easiest for non-musicians,[18] but the system can accomplish more complex divisions, meters and polyrhythms.[19] The latter implies the existence of some mechanistic distance between input and output into which pulses can be selected and manipulated, such that output need not slavishly follow the input.

Complex temporal patterns, hierarchy

A second type of elaboration concerns the complexity of input and output patterns that can be represented and produced. Synchronizing with complex multi-part music is an example of the former, while playing a complex drum pattern to a click track is an example of the latter. Of course, complex sounds can also lead to complex movements, and this is indeed the most common configuration. Key, however, is the existence of an internal pulse to tie it together. Basic auditory perception processes such as grouping of sounds, separation of different sources, and measuring event rate appear widespread in animals and are present in human newborns,[20] so this is not itself a necessary feature of SMS, but rather an enricher of it by providing a wider variety of sound representations with which to synchronize.[21] A fully hierarchical, metrical, system of beats may further require brain regions that in humans are essential to language, which have been hypothesized to more generally implement nested hierarchies of action,[22] as well as require associated development of motor system complexity.[23] In animals, synchronization with actual music, with its multiple temporal scales, has been demonstrated to date in only cockatoos,[24] parrots,[25] and California sea lions,[26] with only cockatoos so far displaying hierarchical movement patterns—moving different parts of the body (head, trunk, feet) in sync with different metrical levels, as in human dance.[27]

Active perception

A third elaboration, which we believe to be critical for the fuller set of behaviors associated with rich BPS is for the motor pulse to influence auditory perception, even in the absence of movement. In support of this blurring of the distinction between hearing and moving, it has frequently been observed that during the perception of strongly pulse-inducing rhythms, motor planning regions are activated even in absence of movement,[28] suggesting they may play a role in generating an internal pulse. By studying multiple metrical interpretations of a single ambiguous rhythm, we have demonstrated that the pulse can influence auditory responses.[29] We have proposed the Action Simulation for Auditory Prediction (ASAP) hypothesis to formalize the idea that the motor system plays a causal role in perception through reciprocal transformations of auditory and motor pulses via the parietal cortex, and that one explanation for human abilities is the presence of robust bidirectional connections in this network.[30] The active influence of pulse on auditory perception has not been demonstrated in any other animals to date though it has only been tested in a few species.[31]

Human expertise and training

Though all of the foregoing mechanisms exist in humans they may have varying levels of efficacy in different individuals and be dependent on implicit experience or training to be fully functional. For example, while synchronization with a metronome, simple subdivisions, or simple, strongly metrical patterns, is easy for most non-musicians, for many, synchronization with more highly syncopated patterns is more challenging.[32] Similarly, more complex m:n polyrhythmic synchronization ratios generally have to be learned. Active perception, by which our internal pulse shapes how we hear rhythm is often challenged when we hear unfamiliar music from a different culture; only through experience can we begin to understand an intended pulse structures.[33] Many first time salsa or West African dancers are acutely aware of this, and face the need to learn, usually through the body, how to hear the pulse of these rhythms. Musicianship demonstrates the human ability to build, maintain, and assert an internal sense of pulse even based on audiovisual input streams with complex, shifting temporal relationships to a central but not directly expressed or reinforced pulse.

There are other levels of elaboration that we will not deal with in this short treatment, including the involvement of short- and long-term memory, the potential for complex syntactic structures of nested rhythmic patterns within patterns, and the connection of these more mechanistic aspects of rhythm perception and production with goals, motivations, and emotions. Notably, these higher levels are what strike us as most musical, and it is these that are often accounted for most directly in evolutionary accounts of the origin of human musical rhythm.

Accounts of the origin of beat perception and synchronization

The first question is if musical behaviors evolved at all. Have we evolved to be rhythmic because of some fitness or survival benefit conferred to our distant ancestors that enabled those with the rhythmic skills outlined above to better survive to pass on their genes to the next generation? Alternatively, if rhythm is thought to confer no survival value, it cannot have been shaped by natural selection. In this case, is BPS merely a byproduct of other adaptations which we have learned to use for musical purposes?

Non-adaptation views

Most famous of the non-adaptation views is Pinker's[34] argument that music is 'auditory cheesecake' in the sense that it was invented in order to stimulate existing auditory sensitivities (to vocal emotion, language, auditory scene analysis, etc.) in much the same way cheesecake was invented to titillate our (presumably evolved) desires for foods high in fats and sugars. In his view, music is a mere 'pleasure technology' with no biological utility, a statement that proved surprisingly offensive to many, perhaps because it appeared to trivialize one of humanities dearest attributes. Pinker was criticized for a view too rooted in our modern, Western relationship to music where listening to recorded music predominates: indeed superficially, being deprived of one’s iTunes, Spotify, or music videos should have no effect on an individual’s survival. This claim is debatable, given pervasive uses of music for motivation and emotional regulation, which surely impact our well-being and worldly and reproductive success. Music as pleasure technology seems even less tenable in a world prior to on-demand recorded music, or in other cultures in which music and dance performance still play a more central and participatory role in daily life.

A related view is Patel's[35] suggestion that while music is non adaptive, it is biological useful in the life of an individual. Music is not a mere pleasure technology, but a 'transformative technology of the mind' that has impacts on more general cognitive functions like attention and language, and provokes emotions by exploiting existing reward mechanisms, such as the reward for correct temporal predictions. Its universality is explained by analogy to another human technology, the control of fire. With regard to rhythm, Patel's "Vocal Learning Hypothesis" accounts for the emergence of BPS as a byproduct of adaptations for vocal learning, which is assumed to require strong connections between auditory and motor systems to enable the tuning of motor acts to match the acoustics of sounds to be imitated.[36] If such circuitry extended to the whole body, not just vocal musculature, Patel suggested it could be a foundation for BPS. The hypothesis predicts that only vocal-learning species, among them parrots and dolphins, should be capable of BPS. This excludes other primates who are not vocal learners. The hypothesis was initially confirmed by the discovery of the first non-human animal that could synchronize with a musical beat, a sulfur-crested cockatoo named Snowball, that was able to intermittently synchronize head-bobs to music of different tempos, demonstrating the ability to abstract a pulse from music and couple it to movement.[37] Subsequent support came from a survey of public videos that showed the only animals that quantitatively synchronized with music were cockatoos, parrots, and an elephant, all vocal learners.[38] The relative inability of non-human primates to synchronize is likewise consistent with the hypothesis. Similar abilities were demonstrated in a California sea lion, not a known vocal learner,[39] possibly contradicting the vocal learning hypothesis, although there remains some controversy on this point given their close relation to walruses and harbor seals, which are known vocal learners.[40]

Non-adaptation views, perhaps surprisingly, are in the minority. For one thing, they do not accord particularly well with the use of music in small-scale cultures, where ritual aspects predominate, and if music was invented for its cognitive benefits, it seems a rather roundabout way of transforming the mind. Beyond this, other thinkers, for better or worse, seem unable to resist the sense that music must be an adaptation, with distinct survival or reproductive advantages, given the universality of music in human culture, and the fact that music is, at least in some sense, unique to humans, that aspects of it appear innate and are deeply linked to emotion and groups. We will turn to these accounts next.

A brief introduction to evolution

Natural selection was defined by Darwin as the principle "by which each slight variation, if useful, is preserved."[41] “Useful” in this case means a variation in a trait that enhances an individual's chance of surviving long enough to create progeny. This concept was proposed in the context that there is naturally occurring variation between individuals, and there is considerable struggle for existence—because of geometric increases in population, many individuals will not survive. Over time, traits consistent with survival in the current environment will become enriched in the population. (The use of 'natural' was chosen in contrast to artificial selection by man, as in selective breeding.) Traits compatible with survival are often called *adaptations*, and discussed as being *selected* by the environment, though both these terms are arguably too active to describe the phenomenon, and should be understood without their usual sense of agency and goal direction. The beauty of this simple principle is it that it can amplify traits at any level (so long as they can be inherited).

Darwin next defined *sexual selection* as a “less rigorous” form of selection not in terms of life or death, but an individual's chance of securing mates, which then impacts their ability to create offspring. Sexually selected traits tend to differ in males and females, and include those involved in direct competition within a sex (such as the size of a stag's horns) and those involved in attracting the opposite sex, the canonical example of which is a peacock's plumage. Two additional forms of selection are often discussed but are more controversial: *kin selection* as a way of explaining traits that give benefit to ones relatives, though at the expense of oneself; and *group selection* as a way to explain traits that benefit the larger group, even though they may not directly benefit the individual. Group selection is controversial as it implies that groups are the units of selection, mutation, and reproduction (i.e. groups generate new groups). We'll sidestep this interesting argument. I think the most helpful view is that traits can have effects at multiple scales: to recognize that humans are inexorably bound up in groups, and thus may have some traits that enhance their ability to be in a group; and that if these traits have overall positive impacts on their individual fitness, then this is all that matters in the end as humans are individuals that reproduce and mutate. Indeed Darwin noted in the context of natural selection that, "In social animals [natural selection] will adapt the structure of each individual for the benefit of the community; if each in consequence profits by the selected change."[42] That will do just fine for our purposes in understanding social aspects of rhythm.

Adaptational theories focused on the individual

Sexual selection

Darwin predates Pinker's skepticism: "As neither the enjoyment nor the capacity of producing musical notes are faculties of the least direct use to man in reference to his ordinary habits of life, they must be ranked amongst the most mysterious with which he is endowed."[43] He solved the mystery by suggesting, by analogy with bird song, that music must have played a role in our ancestors' courtship, but colorfully suggests that cultural developments have eliminated any original sexual dimorphism in the trait.

More recently, Miller[44] renewed the argument stating, "Music is what happens when a smart, group-living, anthropoid ape stumbles into the evolutionary wonderland of runaway sexual selection for complex acoustic displays." Music is thus like Darwin's famous example of selection, the peacock tail. Miller amusingly applies a common trope that rock and rollers have lots of sex, but don't always live so long (so, music may actually be maladaptive for survival). Extrapolating to a time prior to birth control, he suggests this would have been a powerful means of enhancing reproductive success. Musical performance is an indicator of mate quality (though working through "pre-existing perceptual and cognitive preferences" shaped by evolution). Musical expertise and prowess advertise stamina, physical coordination, and creative ability (a serious concern in novelty-craving species).

Others have rejected sexual selection accounts, perhaps too strictly, based on the fact that both sexes are musical (while most sexually selected traits are seen only in one sex). As we saw above, this is not a serious problem, as the differences could have been erased historically, or mate selection could be in both directions. Sexual selection may appear at odds with the group role of music in many small-scale societies, so sexual selection proponents tend to hark back to a time when music was more of a solo activity, which seems to be their major flaw. However, this seems not a critical objection, as who can doubt the ability of music and dance to introduce us to an individual intimately, whether they are alone or in a group, and play a role in attraction? For a social animal, part of attractiveness could well be the ability to stand out in a group while simultaneously displaying ones ability to cooperate with others in a group. Group music making could have developed as a more efficient way of finding mates in larger groups, compared to one-on-one interactions.

Natural Selection: adaptation for survival

One of the first of the recent writers to speculate on the survival value of music, Roederer[45] identified music as a kind of acoustical-emotional pattern perception training tool that would enable the mother/child dyad to tune up the infant's brain for both the complex auditory pattern perception needed for speech perception as well as in emotional relationships. Infants and mothers deficient in necessary skills would be at a disadvantage in the social world. This view does not deal with rhythm or synchronization explicitly, but as emotionally laden elements of music, accounts for a suggested role in maintaining group cohesion by establishing ways to equalize or synchronize emotions. This view bears a striking similarity to Patel's transformative technology of the mind.

Theories rooted in bipedalism

A number of accounts have identified the special development of bipedalism as a reason for the emergence of rhythmic synchronization. Bipedalism had numerous survival advantages, including freeing up the hands and arms for tasks other than supporting the body. Unlike quadrupedal locomotion, the energetically most efficient gaits for bipeds are all isochronous, with strict left/right alternation.[46] Thus all humans would have endless experience with producing and hearing isochronous rhythms, as well as have the ability to smoothly modulate tempo. This could explain the motoric substrates for synchronization, as well as explain the human preference for walking-tempo isochrony,[47] but it does not immediately explain synchronization of movement to sound.

One suggestion, by Riggle,[48] explains the emergence of synchronization as a byproduct of a system that rewards periodic vestibular and auditory inputs, a system that is proposed to motivate infants to begin walking and reward their production of steady gaits. Larsson[49] identifies bipedal locomotion as providing an opportunity for groups to match their walking and running gaits to reduce the continuous auditory masking that unsynchronized footfalls would create. By evolving the ability to synchronize gait, windows of quiet would be available to detect other important sounds of predators and prey. This could enable groups to move around more stealthily by obscuring the size of a group and confer a survival advantage.

Theories rooted in caregiving

Bipedalism brought with it disadvantages, including the need for a smaller birth canal due to constraints on pelvic shape, which in turn necessitated giving birth to helpless infants born at an early stage of development. Dissanyake[50] proposes that a motivational system had to evolve to ensure that bipedal mothers would become committed to the extended caregiving required by their immature infants, and that this selective pressure led to a structured form of rhythmic emotional bonding that depended on abilities to predict the timing of others actions, and to feel bonded because of it. This initial foundation supports the continuous use of musical interactions throughout life, and exemplifies the grander sweep of more holistic origin hypotheses—embedded in a supramodal framework of ritual and imitation, rhythmic synchrony becomes just one piece in the whole that combines emotion, sociality and rhythm.

Adaptational theories focused on groups

Rhythm as facilitator or marker of social groups

Music making is often done in groups. Brown[51] has argued core features of music, including a temporal structure that readily encourages group synchronization, are optimal for making this so. The communal participatory use of music in small-scale cultures reinforces this notion of music's central use. Not surprisingly then, many evolutionary accounts of music emphasize its ability to create cohesive groups, some going so far as to state that the capacity to synchronize is the critical developmental milestone that enabled the growth of human culture by enabling earlier humans to form larger groups, using the power of joint synchronization to ease the inevitable social tensions that forced earlier groups to fracture.[52] Many others have pointed out that music can serve as a sort of social glue and medium for group emotional regulation and communication, that builds group identity.[53]

Related to the idea that music serves to build groups is the parallel that music serves to advertise the quality of a group. Merker,[54] explains the emergence of isochronous group synchronization as a modification of a behavior like the chimpanzee "carnival display," a riotous group movement and noisemaking session in response to finding a fruit tree. He supposes that if a common ancestor of chimpanzees and humans was able to develop means of synchronizing such vocalizations as a group, the summed super-voice could advertise food abundance more broadly to migrating females and draw them in. This 'beacon effect' was previously used to explain group chorusing in other synchronously chorusing species. He further hypothesizes that, because of the linkage of breathing, vocalization and locomotion, such displays might be at around the walking pace, the rate that modern humans prefer to synchronize. In contrast to Fitch,[55] Merker dismisses primate 'drumming' displays as merely individual noisemaking often presented at biophysically-limited maximum rates (one might think of a captive animal rattling a cage door), and thus not a promising foundation for synchronization.

Hagen and Bryant[56] suggest music is at the heart of an even higher level of human social organization: the existence of intergroup relationships in the absence of any kinship ties. They propose that music and dance enabled this more complex social organization by acting as both a group identifier, as well as a credible indicator of group quality for the purpose of forming mutually beneficial alliances with other groups. Music and dance performances take much longer to prepare than to perform, and thus a short performance can instantly communicate a large degree of credible information about group stability and ability to act in a coordinated way. Only established groups with adequate time and traditions could prepare impressive displays. This account is proposed to explain why humans with greater musicality both in production as well as discrimination of quality would be better adapted to signal group quality. This argument is quite similar to a sexual selection hypothesis, only operating at the levels of groups. While compelling ethnographic evidence for the model of using music and dance to court other groups for alliances is presented, this account seems to fit equally well with a non-adaptational account such as TTM in which cultural innovation built on a pre-existing abilities replaces biological adaptation.

Future Directions

We have tried to lay out the wide spectrum of accounts for the origin of human beat-based rhythm. It is a fascinating, though admittedly incomplete, set of views. Each one seems to have made one or more leaps, and most focus intently on only part of the evidence available. As unsatisfying a conclusion as it might be, it seems likely that all of the foregoing accounts have some aspects that are correct: music and rich BPS are complexes of many individual components, and most accounts so far have simplified this. Every account, even non-adaptation accounts, presumes that functional aspects evolved, but disagree on what selective pressure led to this. On top of these adaptations we have apparently invented vast and varied traditional repertoires of music and dance for a range of purposes. It remains to sharpen the conceptual account of the components of human rich BPS and to find neural mechanisms accounting for these different components. The input of percussionists would be most welcome here. Ultimately, we need an account for the evolution of each aspect of rich BPS, and determine if they are separable, evolved for specific reasons, or are best considered as a whole. There are of course many other questions left unanswered: If the benefits of group music making are so powerful, why have they not evolved more often? Is it that the neural change needed to link auditory and motor systems is difficult to evolve, or is it that other species lacked the social milieu and essential prerequisites for the addition of this link to be of any value? We hope the reader is sufficiently stimulated to read further, and join the debate.

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NOTES

[1] B. Nettl, "An Ethnomusicologist Contemplates Universals in Musical Sound and Musical Culture," in N. L. Wallin and B. H. Merker (eds.), *Origins of Music* (MIT Press, 2000)

[2] W. T. Fitch, "The Biology and Evolution of Rhythm: Unraveling a Paradox," in P. Rebuschat, M. Rohrmeier, J. A. Hawkins, and I. Cross (eds.), *Language and Music as Cognitive Systems* (Oxford University Press, 2012)

[3] A. D. Patel and J. R. Iversen, "The Evolutionary Neuroscience of Musical Beat Perception: the Action Simulation for Auditory Prediction (ASAP) Hypothesis," *Frontiers in Systems Neuroscience,* 8 (2014) 57

[4] N. J. Conard, M. Malina, and S. C. Münzel, "New Flutes Document the Earliest Musical Tradition in Southwestern Germany," *Nature,* 460 (2009), 737–40

[5] D-J Povel and P. J. Essens,"Perception of Temporal Patterns," *Music Perception,* 2 (1985) 411–40

[6] For example, T. L. Bolton, "Rhythm," *The American Journal of Psychology*, 6 (2), (1894), 145-238. For comprehensive reviews, see: B. H. Repp, "Sensorimotor Synchronization: A Review of the Tapping Literature, *Psychonomic Bulletin and Review,* 12 (2005), 969–92; B. H. Repp and Y-H Su, "Sensorimotor Synchronization: A Review of Recent Research (2006–2012)," *Psychonomic Bulletin and Review,* 20 (2013), 403–53.

[7] For a recent review, see L. J. Trainor and L. Cirelli, "Rhythm and Interpersonal Synchrony in Early Social Development, *Annals of the New York Academy of Science,* 1337 (2015) 45–52.

[8] J. D. McAuley, M. R. Jones, S. Holub, H. M. Johnston, and N. S. Miller, "The Time of our Lives: Life Span Development of Timing and Event Tracking," *Journal of Experimental Psychology*: *General*, 135 (2006) 348–67

[9] T. Eerola, G. Luck, and P. Toiviainen, "An Investigation of Pre-schoolers' Corporeal Synchronization with Music," *Proceedings of the 9th International Conference on Music Perception and Cognition*, (2006)

[10] S. Kirschner and M. Tomasell, "Joint Drumming: Social Context Facilitates Synchronization in Preschool Children," *Journal of Experimental Child Psychology*, 102 (2009), 299–314

[11] A. Ravignani, D. L. Bowling, and W. T. Fitch, "Chorusing, Synchrony, and the Evolutionary Functions of Rhythm," *Frontiers in Psychology*, 5 (2014), 1118

[12] B. H. Merker, "Synchronous Chorusing and Human Origins," in Wallin, et al., *The Origins of Music*, pp. 315–27

[13] H. Merchant and H. Honing, "Are Non-human Primates Capable of Rhythmic Entrainment? Evidence for the Gradual Audiomotor Evolution Hypothesis," *Frontiers in Neuroscience*, 7 (2014), 274

[14] A. Hasegawa, K. Okanoya, and T. Hasegawa, "Rhythmic Synchronization Tapping to an Audio-visual Metronome in Budgerigars," *Science Report*, 1 (2011), 120

[15] Y. Hattori, M. Tomonaga, and T. Matsuzawa, "Distractor Effect of Auditory Rhythms on Self-paced Tapping in Chimpanzees and Humans," *PLOS ONE* (*Public Library of Science*) (2015), in press

[16] Merchant and Honing, "Non-human Primates," 274

[17] J. London, *Hearing in Time* (Oxford University Press, 2004)

[18] E. E. Hannon and S. E. Trehub, "Metrical Categories in Infancy and Adulthood," *Psychological Science*, 16 (2005), 48–55

[19] P. Vuust, M. Wallentin, K. Mouridsen, L. Ostergaard, and A. Roepstorff, "Tapping Polyrhythms in Music Activates Language Areas," *Neuroscience Letters*, 494 (2011), 211–6

[20] C. E. Hagmann and R. G. Cook, "Testing Meter, Rhythm, and Tempo Discriminations in Pigeons, *Behavioral Processes*, 85 (2010), 99–110; L. J. Trainor and L. Cirelli, "Rhythm and Interpersonal Synchrony in Early Social Development," *Annals of the New York Academy of Science*, 1337 (2015), 45–52

[21] W. T. Fitch, "Rhythmic Cognition in Humans and Animals: Distinguishing Meter and Pulse Perception," *Frontiers in Systems Neuroscience*, 7 (2013), 68

[22] L. Fadiga, L. Craighero, and A. D'Ausilio, "Broca's Area in Language, Action, and Music," *Annals of the New York Academy of Science*, 1169 (2009), 448–58

[23] G. Mendoza and H. Merchant, "Motor System Evolution and the Emergence of High Cognitive Functions," *Progress in Neurobiology*, 122 (2014), 73–93

[24] A. D. Patel, J. R. Iversen, M. R. Bregman, and I. Schulz, "Experimental Evidence for Synchronization to a Musical Beat in a Non-human Animal," *Current Biology*, 19 (2009), 827–30

[25] A. Schachner, T. F. Brady, I. M. Pepperberg, and M. D. Hauser, "Spontaneous Motor Entrainment to Music in Multiple Vocal Mimicking Species," *Current Biology*, 19 (2009), 831–6

[26] P. Cook, A. Rouse, M. Wilson, and C. Reichmuth, "A California Sea Lion (Zalophus californianus) can Keep the Beat: Motor Entrainment to Rhythmic Auditory Stimuli in a Non-vocal Mimic," *Journal of Comparative Psychology*, 127 (2013), 412–27

[27] P. Toiviainen, G. Luck, and M. R. Thompson, "Embodied Meter: Hierarchical Eigenmodes in Music-Induced Movement," *Music Perception*, 28 (2010), 59–70

[28] For example, J. A. Grahn and J. B. Rowe, "Feeling the Beat: Premotor and Striatal Interactions in Musicians and Non-musicians During Beat Perception, *Journal of Neuroscience*, 29 (2009), 7540–8

[29] J. R. Iversen, B. H. Repp, and A. D. Patel, "Top-down Control of Rhythm Perception Modulates Early Auditory Responses," *Annals of the New York Academy of Science,* 1169 (2009), 58–73

[30] A. D. Patel and J. R. Iversen, "The Evolutionary Neuroscience of Musical Beat Perception: the Action Simulation for Auditory Prediction (ASAP) Hypothesis," *Frontiers in Systems Neuroscience*, 8 (2014), 57

[31] C. E. Hagmann and R. G. Cook, "Testing Meter, Rhythm, and Tempo Discriminations in Pigeons," *Behavioral Processes*, 85 (2010), 99–110; H. Honing, H. Merchant, G. P. Háden, L. Prado, and R. Bartolo, "Rhesus Monkeys (Macaca mulatta) detect Rhythmic Groups in Music, but not the Beat," *PLOS ONE*, 7 (2012), e51369

[32] A. D. Patel, J. R. Iversen, Y. Chen, and B. H. Repp, "The Influence of Metricality and Modality on Synchronization with a Beat," *Experimental Brain Research*, 163 (2005), 226–38

[33] P. Toiviainen and T. Eerola, "Where Is the Beat?: Comparison of Finnish and South-African Listeners.," *Proceedings of the 5th Triennial ESCOM Conference*, (2003), 501–4

[34] S. Pinker, *How the Mind Works* (New York: Norton, 1997)

[35] A. D. Patel, "Music, Biological Evolution, and the Brain," in M. Bailar (ed.), *Emerging Disciplines* (Rice University Press, 2010), pp 91–144

[36] A. D. Patel, "Musical Rhythm, Linguistic Rhythm, and Human Evolution," *Music Perception,* 24 (2006), 99–104

[37] Patel, et al., "Experimental Evidence," 827-30

[38] A. Schachner, "Auditory-motor Entrainment in Vocal Mimicking Species: Additional Ontogenetic and Phylogenetic Factors," *Communicative and Integrative Biology*, 3 (2010), 290–3

[39] Cook, et al., "A California Sea Lion," 412-27

[40] A. D. Patel, "The Evolutionary Biology of Musical Rhythm: Was Darwin Wrong?" *PLOS Biology*, 12 (2014), e1001821

[41] C. Darwin, *On the Origin of Species by Means of Natural Selection*, 1st ed., (London: John Murray, 1859)

[42] *Ibid.*

[43] C. Darwin, *The Descent of Man and Selection in Relation to Sex*, 1st ed., vol. 2 (London: John Murray, 1871), p. 333

[44] G. Miller, "Evolution of Human Music through Sexual Selection," in Wallin, et al., *The Origins of Music*, pp 329–60

[45] J. G. Roederer, "The Search for a Survival Value of Music," *Music Perception*, 1 (1984), 350–6

[46] T. A. McMahon, *Muscles, Reflexes, and Locomotion* (Princeton University Press, 1984)

[47] M. F. McKinney and D. Moelants, "Ambiguity in Tempo Perception: What Draws Listeners to Different Metrical Levels?" *Music Perception*, 24 (2006), 155–66

[48] M. Riggle, "A Simpler Explanation for Vestibular Influence on Beat Perception: No Specialized Unit Needed," *Empirical Musicology Review,* 4 (2009), 19–22

[49] M. Larsson, "Self-generated Sounds of Locomotion and Ventilation and the Evolution of Human Rhythmic Abilities," *Animal Cognition*, 17 (2013), 1–14

[50] E. Dissanayake, "Ritual and Ritualization: Musical Means of Conveying and Shaping Emotion in Humans and other Animals, in S. Brown and U. Voglsten (eds.), *Music and Manipulation: on the Social Uses and Social Control of Music* (Oxford: Berghahn Books, 2006), pp 31–56

[51] S. Brown, "Evolutionary Models of Music: From Sexual Selection to Group Selection," *Perspectives in Ethology*, 13 (2000), 234–84

[52] W. H. McNeill, *Keeping Together in Time: Dance and Drill in Human History* (Harvard University Press, 1997)

[53] Brown, "Evolutionary Models," 234-84; S. Mithin, *The Singing Neanderthals: The Origins of Music, Language, Mind and Body* (Harvard University Press, 2006)

[54] B. H. Merker, G. S. Madison, and P. Eckerdal, "On the Role and Origin of Isochrony in Human Rhythmic Entrainment," *Cortex*, 45 (2009), 4–17

[55] W. T. Fitch, "The Biology and Evolution of Rhythm: Unraveling a Paradox," in P. Rebuschat, M. Rohrmeier, J. A. Hawkins, and I. Cross (eds.), *Language and Music as Cognitive Systems* (Oxford University Press, 2012)

[56] E. H. Hagen and G. A. Bryant, (2003) "Music and Dance as a Coalition Signaling System," *Human Nature*, 14 (2003), 21–51