

RHYTHM IN MUSIC: WHAT IS IT? WHO HAS IT? AND WHY?

JOHN BISPHAM
*Leverhulme Centre for Evolutionary Studies/
 Centre for Music and Science,
 University of Cambridge, United Kingdom*

THIS ARTICLE EXPLORES HUMAN rhythmic abilities and behaviors within a framework of evolutionary theory highlighting the need for research in this area to be grounded upon solid psychologically valid definitions of *rhythm*. A wide-ranging cross-species comparison of rhythmic or quasi-rhythmic behaviors is presented with a view to exploring possible homologies and homoplasies to rhythm in human music. Sustained musical pulse and period correction mechanisms are put forward as human-specific and music-specific traits. Finally hypotheses as to why these abilities may have been selected for—and uniquely selected for—in the course of human evolution are explored.

Received January 31, 2006, accepted August 22, 2006

Key words: rhythm, ethology, evolution, entrainment, action, emotion

INTEREST IN THE EVOLUTION of human musical capabilities and behaviors has increased and broadened in recent years and has been the subject of numerous and wide-ranging publications (e.g., Balter, 2004; Cross & Morley, in press; Wallin, Merker, & Brown, 2000). Existing evolutionary and comparative perspectives on rhythm and pulse in music have pointed to possible homologous¹ or homoplastic²

¹Homologous traits are present in two or more species due to common descent. They may not be exactly the same but are inherited from a common ancestor.

²Homoplastic traits are similar traits that were not present in a common ancestor and hence evolved independently. However, correlations to other environmental or behavioural features can suggest parallel selection pressures that favour the evolution of any similar trait.

(sometimes termed “analogous”) behaviors in the ethological literature (Fitch, in press; McDermott & Hauser, 2005) and have attempted to account for the adaptive strength of rhythm and entrainment in the course of human evolution with reference to mother–infant interaction (Dissanayake, 2000), coalition signaling (Hagen & Bryant, 2003; Merker, 2000) and muscular bonding (McNeill, 1995). Furthermore, the principal proponents of these theories have tried to rationalize an increased evolutionary drive toward these skills in humans by linking their hypothesis to increased human infant altriciality, female exogamy, or sociality. However, none of the sources cited give clear, psychologically and behaviorally grounded, definitions of rhythm and entrainment in music and are thus restricted in terms of the precise knowledge that can be inferred from the supporting evidence. The central aim of this article is to identify, with reference to the available rhythm perception and performance literature, those features of human rhythmic behavior that are shared with other animal and human behaviors and those (if any) that are specific to—and thus key defining features of—*musical rhythm* and are hence likely to have evolved expressly for music.

Drawing upon psychological and neurophysiological literature, I have suggested (Bispham, 2003) that musical rhythmic behavior (MRB) be viewed as a constellation of concurrently operating, hierarchically organized, subskills including general timing abilities, smooth and ballistic movement (periodic and nonperiodic), the perception of pulse, a coupling of action and perception, and error correction mechanisms. Indeed, a review of current evidence appears to support the idea that all of these subskills share overlapping internal oscillatory mechanisms. As such all subskills, as well as the resulting constellation, can be viewed as being grounded in, and as having exaptively evolved from, fundamental kinesthetic abilities and modes of perceiving temporally organized events. I claim that viewing MRB in this way provides an avenue for exploring useful comparisons with other types of human and animal behavior as well as critically pointing toward putative evolutionary continuities. Furthermore, this approach mirrors influential proposals for the study of the evolution

of language (Hauser, Chomsky, & Fitch, 2002) and fits perfectly the predominant view in evolutionary theory that complex behaviors such as music evolved in a mosaic fashion, with individual components emerging or evolving independently or for independent reasons at times, and/or reforming with other components at other times. The following cross-species and intra-species comparative perspective, by focusing on individual behavioral components, is implicitly set within this constellation framework.

Periodic Production

In the introduction to *The Origins of Music* (Wallin et al., 2000), the editors state that “most animals (including humans) have the ability to move in a metric, alternating fashion” (p. 11). They contend that “what is special about humans is not their capacity to move rhythmically but their ability to entrain their movements to an external timekeeper, such as beating a drum” (p. 12). While this may well be correct it does not go far enough in distinguishing movements that are metric and alternating from those that might be considered to be “rhythmic.” Crucially, musical rhythmic production implies reference to an external timekeeper *and/or* to an internally created and volitionally controlled attentional pulse (e.g., Drake & Bertrand, 2001). As such, periodic production in nonhuman species can only be considered as being homologous (and of direct relevance) to musical behaviors if its behavioral correlates are not explicable solely in terms of biomechanical efficiencies. Nevertheless, the difficulty of delineating the mechanisms underlying periodic behaviors adds support to the case for a physiologically grounded approach to rhythmic behaviors and offers a possible avenue for comparatively exploring timing mechanisms involved in motor output and rhythmic behaviors. Changes to the human motor system, and particularly the move toward bipedalism over evolutionary time, have undoubtedly had profound impacts on rhythmic capabilities (e.g., Trevarthen, 1999). However, they are not (contra Mithen, 2005) in themselves sufficient to account for MRB in our species as they crucially do not address the fact that rhythmic behavior implies an ordering of output with reference to a sustained attentional pulse (see Bispham, 2006).

Rhythm Perception

Ramus, Nespore, and Mehler (1999) showed that, like human newborns, cotton-top tamarins have the capacity to discriminate between sentences from languages

that are differentiable on the basis of their “rhythm class.”³ Hauser and McDermott (2003) draw attention to the important comparative point that “although human infants may be equipped with a capacity to discriminate languages on the basis of rhythmic cues, the presence of this ability in nonhuman primates that lack language suggests that it evolved for more general auditory purposes” (p. 667). A more recent study shows that cotton-top tamarins, like newborn babies (e.g., Ramus, 2002) and in contrast to 5-month-old infants (Nazzi, Juszyk, & Johnson, 2000), do not differentiate between languages from within rhythmic classes (Tincoff et al., 2005) supporting the idea that differentiation is based on rhythmic cues. Additionally, similar results have been found in experiments with trained rats, raising the possibility that the mechanism underlying our capacity to discriminate languages based on rhythmic cues may have evolved early within the mammalian clade (Toro, Trobalon, & Sebastián-Gallés, 2003).

While these studies are of interest to the perception of temporally structured events in humans their relevance to rhythm perception in music is limited. Most importantly the rhythmic properties of language and music, despite evidence for some overlap (e.g., Patel & Daniele, 2003), are not the same. Hauser and McDermott (2003) effectively argue for a continuum in which “music places more focus on beat and timing of particular notes and language focuses on the overall frequency contours and durations of particular phonemic clusters” (p. 667). However, they do not address the possibility that fundamental differences between rhythm in language and music exist. Distinct differences are arguably manifest in the particular nature of musical pulse where highly regular attentional pulses are sustained over time and are mutually manifest to multiple individuals. These points will be discussed in more detail below, but it is certainly the case that experiments comparing human and primate rhythmic and tempo discrimination with musical materials could provide more insight in the future.

Temporal Structuring in Communication

According to Owings and Morton’s (1998) model, animal communication occurs as a result of individuals managing and assessing signals for the purpose of regulating the behavior of others. Importantly, managers and assessors (elsewhere—e.g., Seyfarth & Cheney,

³Differentiation is based on the proportion of time occupied by vowels and appears to concur with classical taxonomies of language (e.g., Cutler, 1994).

2003—“senders” and “receivers”) need not display any awareness of their own or other’s intentionalities, but can simply be predisposed, through processes of evolution and conditioning, to behave in certain ways. In this model signals are seen to be indicative of an animal’s internal state and endow their actions with a degree of predictability through their “motivational-structural” significance (deriving from the correlations between the types of signals emitted and the motivational states of individuals). For the purposes of this discussion temporal structuring in communication is marked by aspects where the temporal structure of events acts as a communicative signal according to Owings and Morten’s model. Repeated signaling in itself is thus not considered relevant if it is explicable in terms of redundancy. Further caution is also required as what may appear to be temporal patterning may simply be the epiphenomenal outcome of conflicting signaling functions (see Owings and Morton’s, 1998, discussion of Tungara frogs, pp. 6–7).

One way in which temporal structuring is functional in animal communication is that distinctive temporal patterns can be used as a source of individuality for sounds not individually marked by the vocal tract. Screams in rhesus macaques are a well-studied example. They have clear communicative functionality and, although the nature of the scream production results in a loss of timbral individuality (Rendall, Owren, & Rodman, 1998), individuals have been shown to respond differentially depending on the identity of the caller (Ghazanfar, Flombaum, Miller, & Hauser, 2001). Other examples of temporal structuring in communication that have been viewed as relevant to human music are animal “drumming” and “song.” A range of species including palm cockatoos (Wood, 1988), woodpeckers (Dodenhoff, Stark, & Johnson, 2001), and kangaroo rats (Randall, 1997) exhibit “drumming” on hollow objects in their environments in communicative, territorial or mate attraction contexts. However, bimanual drumming in gorillas (Schaller, 1963), chimpanzees (Goodall, 1986), and bonobos (unpublished data mentioned in Fitch, in press) are putatively of even greater relevance due to phylogenetic proximity and possible homologies to human drumming in terms of the motor skills employed. Interestingly in chimpanzees, where drumming is exhibited predominantly on buttress roots by the dominant male in displays that are augmented by vocal pant-hooting, aspects of the drumming have been correlated with resting periods and future direction in group foraging, and have been shown to be both individually and culturally distinct

(Arcadi, Robert, & Boesch, 1998; Arcadi, Robert, & Mugurusi, 2004).

Whether or not “song”—defined as complex learned vocalization—in songbirds (Marler, 2000), cetaceans (e.g., humpback whales; Payne, 2000), and pinniped species (e.g., Sjure, Stirling, & Spencer, 2003; Van Parijs, 2003) can be considered as analogies to human song is currently under debate in the literature. McDermott and Hauser (2005) argue that human and animal song are neither homologous or homoplastic on the basis that animal song occurs only under highly restricted contexts of courtship or territorial defense; that song is functional in these contexts and never occurs for pure enjoyment or the enjoyment of others; and that in most singing species only males sing and show unique neural adaptations for song. Fitch (2006) counters this proposal, arguing that analogy is a property of mechanisms not dependent upon context or inferred adaptive function; contrasting “pure enjoyment” (a proximate causal explanation) with communicative function (an ultimate adaptive explanation) is to conflate two separate levels of biological explanation (Tinbergen, 1963); and that sex-specificity of a trait within a species need not disqualify it from analogy with a similar sex-shared trait in other species. Fitch concludes that “none of [McDermott and Hauser’s] arguments provide compelling grounds for rejecting the traditional analogy between human and animal song.” (p.184)

Although Fitch’s arguments are valid, they do not provide evidence *for* song being analogous to human song. The range of behaviors mentioned raise important and interesting issues regarding possible analogies to vocal learning, modes of perceiving temporally structured events and sequencing of complex motor actions. Nevertheless, it is doubtful if any of the above behaviors can be considered fully analogous to MRB in humans. Importantly, all of these behaviors are not only contextually distinct but also distinct in terms of the mechanisms involved. No evidence exists demonstrating that actions are guided with reference to an internally manifest pulse and as such the temporal features can be explained as resulting simply from biomechanical characteristics or from learned and stored motor output sequences. Furthermore, these behaviors display no relationship to the temporal structure of external stimuli nor coordination between the actions—overt or perceptual—of two or more individuals based on a mutually manifest and regularly structured temporal framework. In other words two features that are critical to MRB—entraining mechanisms and interpersonal interaction—appear to be absent in the examples given.

Ecological Engagement

An entraining process has been proposed as the root or facilitator of human and animal temporal perception (Jones, 1976; Jones & Boltz, 1989). According to this view, internal oscillatory mechanisms are attuned to external cues allowing us to build expectations for the timing of future events (future-directed attending) and to interact efficiently with our environment. This perspective has considerable theoretical value and its relevance to rhythm in music is well established (e.g., Large & Jones, 1999). Indeed, the likely existence of internal oscillatory mechanisms that are shared between different domains of human behavior and cognition strongly suggests that entrainment in music constitutes an evolutionary exaptation of more generally functional mechanisms for future-directed attending to temporally structured events (Bispham, 2003). Nevertheless there are crucial additional features that must be accounted for in respect of musical rhythmic behaviors. These include the creation of a mutually manifest interactive framework for communication based upon a sustained “musical” pulse, period correction mechanisms, and a coupling of action with perception. These will be discussed in the section on musical rhythmic behaviors.

Temporally Structured Duetting Interactions

In about 6% of bird species pairs combine to produce coordinated duets. In some species two birds coordinate alternating calls with such precision that it is impossible to tell that two birds are involved from the auditory signal alone (e.g., plain wren; Mann, Marshall-Ball & Slater, 2003). Duetting is most common in the tropics and is thought to relate to the fact that birds there frequently hold year-round territories and use the duets as a form of territorial advertisement (Farabaugh, 1982). This in turn is associated with birds that form long-term monogamous pair bonds. Another feature that may be associable with duetting is sexual monomorphism (similarity between the sexes). Whether or not the coordination is achieved by entrainment or, for example, synchronous commencing of fixed action patterns is not known but presents an interesting avenue for future research.

A particularly interesting case is pant hoot duets in gibbons (*Hylobates* spp.). Geissmann (2000, p. 103) explains that “Gibbons produce loud song bouts that are mostly exhibited by mated and monogamous pairs. Typically, mates combine their partly sex-specific repertoire in relatively rigid, precisely timed, and complex vocal interaction to produce well-patterned duets.”

These duets are generally thought to be involved in territorial advertisement and strengthening of pair bonds. Existing rationales for gibbon duetting include the advertising of pair strength to potential competitors, as well as the hypothesis that pair bonds involve a degree of learning and time investment and, henceforth, increase the cost of partner desertion (Geissmann & Ordeldinger, 1999). This is supported by the observation that duetting becomes increasingly well coordinated over time and by one case documenting a certain amount of adjustment in the duet structure with a partner exchange. Although as yet not understood, the mechanisms used to achieve coordination between individuals are clearly not fully analogous to MRB in humans with no evidence of a pulsed framework being employed. However, observation of the duets does suggest that, as is the case in human music, strong relationships exist between the rate of hoots, levels of kinesthetic movement and degrees of emotional excitement in both animals. As such it could be argued that the pairs are interactively affecting each other’s emotional and physiological state within a context of social bonding. This in itself marks these duets as being particularly relevant and partially analogous to MRB in humans.

Synchronous Chorusing

While impressive group coordination is displayed in, for example, schools of fish, periodically structured group synchrony of sound and/or action is rare in the animal kingdom. Documented cases include bioluminescent flashing in fireflies, claw waving in fiddler crabs, and “chorusing” in Neotropical katydid and some frog species (see Greenfield, 1994). In all cases the synchrony is based on either sight or sound, is achieved either by advanced signaling or through phase correction mechanisms, and occurs only within a narrow temporal range. The context is always that of male sexual display with synchronicity either being an indirect outcome of all participants desiring to signal first, a cooperative effort to maximize output and hence attract females to their group, or as a means of predator avoidance. Merker (2000) argues that, as periodic group synchronicity is restricted to male sexual display in the animal kingdom, it is likely to have played a similar role at some point in recent (from 6 to 7 million years ago) human evolution and supports this view with reference to female exogamy in humans and chimpanzees. However, this view does not sufficiently account for a lack of contextual, physiological, or behavioral correlations between the examples given and synchronized

behaviors in humans. In contrast to MRB in humans, correction mechanisms in the animal examples are restricted to phase correction mechanisms to individually specific quasi-eigenfrequencies with no evidence for period correction (see below for a discussion on these correction mechanisms), the temporal structure of signaling is exclusively periodic (i.e., no temporal structuring around the base periodicity), and is, in all cases, restricted to a single modality. Additionally the context of male sexual display does not correlate to the breadth of contexts in which MRB is evident in humans.

Nonmusical Human Interaction

Musicality is part of a natural drive in human sociocultural learning which begins in infancy. (Trevarthen, 1999/2000, p. 194)

In general terms, rhythmic behaviors and abilities pervade all human social interactions; regularities combined with social knowledge provide a mutually manifest framework for interaction. Furthermore, correlations between aspects of temporal structuring in music and language (Patel & Daniele, 2003) suggest some overlap in the mechanisms employed. One way of looking at this is to postulate that interpersonal entrainment is the key rhythmic feature in human interactions. According to this view interpersonal entrainment is a multifaceted and prevalent feature of all human interactions ranging along a spectrum from (a) a loose, subconscious use of pulse as a framework for interpersonal/turn-taking interactions in, for example, mother–infant or linguistic interactions (e.g., Cutler, 1994; see Clayton, Sager, & Will, 2004) with deviations from expectancy used for affective/communicative purposes to (b) a strict adherence to pulse (groove) in group behavior and synchronicity of output where participants are aware of the pulse framework and desire to maintain a degree of temporal stability and group-coordination (e.g., music and dance). An alternative possibility is that the appearance of pulse in nonmusical interaction does not depend on entrainment mechanisms similar to those employed in music and is the result of organizing actions in relation to short-term and constantly interrupted pulses and expectancies based on temporal cues and experience. Whichever interpretation turns out to be correct, contrasting evidence that infants perceive pulse (Hannon & Johnson, 2005) and interact with reference to temporal regularities (Malloch, 1999/2000) but that children as old as four

are unable to entrain their actions to a pulsed signal (McAuley, Jones, Johnstone, & Miller, 2006) suggests that (a) precedes (b) ontogenetically (and possibly phylogenetically) and is psychologically and/or physiologically less complex. Effectively, there are features of rhythm in music that are contextually and mechanistically distinct and hence cannot be explained as having evolved with relation exclusively to nonmusical behaviors.

Musical Rhythmic Behavior

Based on the discussions leading up to this point and with reference to the available psychological and neurophysiological literature in this area I propose two interconnected features of MRB that are both human-specific and music-specific: musical pulse and period correction. As such they can be viewed as having evolved specifically for music and for reasons that are not wholly explicable through analogy to other human or animal behaviors.

Musical Pulse

Although examples of unpulsed music do exist (see Clayton, 1996) and may seem to contradict the existence of pulse being a universal feature of music, we can safely state that pulse is a highly salient feature of musical experience worldwide. Arom (1991) goes as far as to define music as “a succession of sounds capable of giving rise to a segmentation of time during which it flows in isochronous units . . . there can only be music inasmuch as it is measured and ‘danceable.’” As described above, an internally generated and/or externally guided attentional pulse is a well-modeled and widely accepted feature of temporal perception in which perceived regularities build expectations as to the timing of future events (Jones, 1976). Musical pulse, however, would appear to be distinct in that it is maintained over time and is perceived unambiguously, or at related hierarchical levels (London, 2004), by enculturated individuals (Stobart & Cross, 2000). Furthermore, the production or perception of a musical pulse involves engagement of the motor system in a particular way that enables an individual, at least potentially, to manage both fine and gross temporal control in ballistic and smooth movements (Janata & Grafton, 2003; Thaut, McIntosh, & Rice, 1997). Production and/or entrainment to a musical pulse putatively involve internal periodic oscillatory mechanisms overlapping with motor-coordination (Bispham, 2003) and provide a mechanism to affect and regulate levels of physiological arousal (Husain, Thompson, & Schellenberg, 2002).

Period Correction

Sensorimotor synchronization is of paramount importance to MRB and requires—even in cases of synchronizing with strictly periodic signals—some form of corrective mechanism without which timing errors due to internal timekeeping and motor variance (Wing & Kristofferson, 1973) would accumulate and lead to a loss of synchrony (Hary & Moore, 1985). Furthermore, musical pulse is subject to interactive involuntary fluctuations due to motor variance, features of individual style (Collier & Collier, 2002) as well as deliberate expressive and structurally motivated modulations of tempo and microtimings (e.g., Iyer, 2002; Palmer, 1997). On the basis of over a century and a quarter of timing data, as well as more recent neuroimaging studies (e.g., Stephan et al., 2002), two interacting correction mechanisms are widely accepted to be independently operational in music: phase correction and period correction (see Repp, 2005). In short, phase correction adjusts for asynchronies between the last response and stimulus events assuming an unchanged period whereas period correction modifies the next target interval on the basis of discrepancies between the timekeeper interval and the last or last few interstimulus intervals, thus altering the period of the attentional musical pulse. By enabling an interactive and sustained coupling of overt and/or covert action and perception, these two mechanisms form the basic temporal framework for real-time interpersonal musical behaviors.

Phase correction mechanisms can be supposed to be operational in all activities involving future-directed attending where expectations are constantly updated based upon asynchronies between attentional pulses and stimulus events. In contrast period correction is almost by definition functional specifically within the framework of a sustained musical pulse. As Repp (2004) states, “It is likely that period correction is a specifically human ability [and] is a manifestation of the more general human ability to set the tempo of a rhythmic activity at will.” Importantly, and in contrast to phase correction, which seems to represent independent processes of largely automatic action control, period correction is facilitated by or incurs conscious awareness of the tempo change and can thus be interpreted as a representation of intentional cognitive control (Repp, 2001). This is supported by a recent study into the effects of intention, attention and awareness, on adaptation to tempo changes in sensorimotor synchronization (Repp & Keller, 2004), which shows that period correction is strongly dependent on all three variables whereas phase correction depended only on intention.

The concluding sections discuss hypotheses concerning the possible functionality of MRB in human evolution. While largely conjectural they are intended to exploit the strength of an evolutionary perspective in highlighting gaps in our understanding and in guiding us toward productive areas for future research.

Why?

A wealth of persuasive arguments for music being an adaptive trait (Huron, 2001), strong evidence against a sexual selection hypothesis (Brown, 2004), the fact that musical pulse and period correction cannot be accounted for by theories relating to mother–infant interactions (e.g., Dissanayake, 2000), the inherently interactive and social nature of period correction as well as the social contextualization (Gregory, 1997) and social embeddedness (Tolbert, 2001) of music strongly suggest that music (and subsequently MRB) is (or was) functional at the group level and in group ceremony. A hypothesis of this nature with regard to music generally was proposed by Roederer (1984), who states that “the role of music in superstitious or sexual rites, religion, ideological proselytism and military arousal clearly demonstrates the value of music as a means of establishing behavioral coherency in masses of people.” Cross (2001) builds on this by arguing that music’s ubiquity and efficacy in encounters with the numinous are best accounted for by reference to proto-music’s “floating intentionality”⁴ (see Cross, 2005). With reference to Sperber’s (1996) notion of relevant mysteries,⁵ Cross explains that music, like religious ideas, is distinguished from everyday beliefs by its paradoxicality and relevance, by its broad applicability and ambiguity. He concludes that “by virtue of these attributes music may thus be particularly appropriate as a means of amplifying, exemplifying or reinforcing in the course of ongoing experience just these attributes of belief that are interpretable as religious; music’s indeterminacy may suit it for use as a means of pursuing and perhaps even parsing the numinous” (p. 37). Crucially the creation of collective alternate realities or beliefs is prospectively

⁴The key point that Cross is making by ascribing transposable intentionality to music is that meaning in music is both culturally constructed and individually flexible (depending on, for example, experience, social status or mood). In other words, it retains a high level of ambiguity and can mean different things to different people while remaining collectively meaningful.

⁵Defined as situations where beliefs or mental representations arise which are contradictory but are each separately related to (and hence relevant in respect of) other mental representations and beliefs.

functional at the group level by endowing the actions of others with a degree of predictability (Shennan, 2002).

A challenge for future research will be modeling the distinct functionality of rhythm in these contexts. Arguably the most likely hypothesis is that MRB is primarily rooted in providing a temporal framework, collective emotionality, a feeling of shared experience, and cohesiveness to group activities and ritualistic ceremonies. Effects of tempo on arousal levels (Husain et al., 2002), the consistent use of music in altering states (Thayer, Newman, & McLain, 1994), and the clear relationship between rhythmic behaviors and physical action (Janata & Grafton, 2003) suggest that musical pulse is functional in regulating emotions and motivational states by means of affecting states of action-readiness (Frijda, 1986; Frijda & Zeelenberg, 2001). A crucial point to make at this stage is that, contrary to the focus of research undertaken in the area of music and emotion (e.g., Juslin & Sloboda, 2001), music can be viewed as being functional in regulating emotions and as communicating strategies for the regulation of emotion rather than as raw emotional expression per se (Joel Swaine, personal communication). In this framework period correction mechanisms could provide the means for expanding a strategy for self-regulation to one that functions in co-regulating and achieving a convergence of emotional and motivational state with regularities providing joint focus, redundancy, and attentive efficiency as well as a feeling of shared experience. These features may in turn generate nonconflicting modes of appraisal and interpretation of ritualistic and symbolic acts and representations in ceremonial activities and enable or support the creation of joint belief systems. Supporting this hypothesis will require working within a framework that allows us to conceptually relate issues of music, rhythm, emotional self and co-regulation, action, attention, and functionality at the individual and/or group level.

An equally pertinent and potentially informative question is, why us? When such simple acts as marching together in time have been hypothesized to create feelings of group bondedness, solidarity, and cohesion (McNeill, 1995), why is that other social animals (in par-

ticular primate species) appear to be not able or motivated to employ musical pulse or period correction mechanisms? One possibility is that the adaptive strength or functioning of MRB is dependent on other species-specific characteristics. These may include the ability to sustain attention to events—active or imaginary—and volitionally control actions (Norman & Shallice, 1980) the ability to rehearse events in working memory (Baddeley, 1997); joint intentionality and the ability and/or motivation to manage the cognitive environment of others in communication (Sperber & Wilson, 1986; Tomasello, Carpenter, Call, Behne, & Moll, 2005); and complex emotions. Alternatively, increased infant altriciality, expanding group size, and increased sociality in the hominine lineage (Dunbar, 1996; Joffe, 1997) may have uniquely provided selection pressures toward the use of affective and contingent modes of communication, providing a necessary stepping-stone to MRBs.

Conclusion

A comparative perspective on musical rhythmic behaviors suggests that musical pulse and period correction are unique to humans and to the context of music and can thus be supposed to have evolved specifically for music. Additionally this article demonstrates the value of a clear model of rhythm in music as a constellation of partially shared and partially specific abilities as well as the need for the study of rhythm to be positioned within a wider framework of human cognition and behavior.

Author Note

I would like to thank Ian Cross and Joel Swaine, who kindly discussed contents of the article with me and offered many invaluable and insightful comments and suggestions.

Address correspondence to: John Bispham, Leverhulme Centre for Evolutionary Studies, University of Cambridge, Fitzwilliam Street, Cambridge CB2 1QH, UK. E-MAIL jcb59@cam.ac.uk

References

- ARCADI, C., ROBERT, D., & BOESCH, C. (1998). Buttress drumming by wild chimpanzees: Temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. *Primates*, 39, 505–518.
- ARCADI, C., ROBERT, D., & MUGURUSI, F. (2004). A comparison of buttress drumming by wild chimpanzees from two populations. *Primates*, 45, 135–139.
- AROM, S. (1991). *African polyphony and polyrhythm: Musical structure and methodology*. Cambridge: Cambridge University Press.

- BADDELEY, A. (1997). *Human memory: Theory and practice (revised edition)*. Howe: Psychology Press.
- BALTER, M. (2004). Seeking the key to music. *Science*, 306, 1120–1122.
- BISPHAM, J. (2003). *An evolutionary perspective on the human skill of interpersonal musical entrainment*. Unpublished MPhil dissertation, University of Cambridge.
- BISPHAM, J. (2006). “Music” means nothing if we don’t know what it means. Lead review of *The singing Neanderthals: The evolution of music, language, mind and body* by S. Mithen. *Journal of Human Evolution*, 50, 587–593.
- BROWN, S. (2004). Evolutionary models of music: From sexual selection to group selection. In F. Tonneau & N. S. Thompson (Eds.), *Perspectives in ethology 13: Behavior, evolution and culture* (pp. 231–281). New York: Plenum Publishers.
- CLAYTON, M. (1996). Free music: Ethnomusicology and the study of music without metre. *Bulletin of the School of Oriental and African Studies*, 59, 323–332.
- CLAYTON, M., SAGER, R., & WILL, U. (2004). In time with the music: The concept of entrainment and its significance for ethnomusicology. *ESEM Counterpoint*, 1, 1–45.
- COLLIER, G., & COLLIER, J. (2002). A study of timing in two Louis Armstrong solos. *Music Perception*, 19(3), 463–483.
- CROSS, I. (2001). Music, cognition, culture and evolution. *Annals of the New York Academy of Sciences*, 930, 28–42.
- CROSS, I. (2005). Music and meaning, ambiguity and evolution. In D. Miell, R. MacDonald, & D. Hargreaves (Eds.), *Musical communication* (pp. 27–43). Oxford: Oxford University Press.
- CROSS, I., & MORLEY, I. (in press). Music in evolution and evolutionary theory: The nature of the evidence. In S. Malloch & C. Trevarthen (Eds.), *Communicative musicality: Narratives of expressive gesture and being human*. Oxford: Oxford University Press.
- CUTLER, A. (1994). The perception of rhythm in language. *Cognition*, 50, 79–81.
- DISSANAYAKE, E. (2000). Antecedents of the temporal arts in early mother-infant interaction. In N. Wallin, B. Merker, & S. Brown (Eds.), *The origins of music* (pp. 389–410). Cambridge, MA: MIT Press.
- DODENHOFF, D., STARK, R., & JOHNSON, E. (2001). Do woodpecker drums encode information for species recognition? *Condor*, 103, 143–150.
- DRAKE, C., & BERTRAND, D. (2001). The quest for universals in temporal processing in music. *Annals of the New York Academy of Science*, 930, 17–27.
- DUNBAR, R. (1996). *Grooming, gossip and the evolution of language*. Cambridge, MA: Harvard University Press.
- FARABAUGH, S. (1982). The ecological and social significance of duetting. In D. E. Kroodsma, E. H. Miller, & H. Ouellet (Eds.), *Acoustic communication in birds* (pp. 85–124). New York: Academic Press.
- FITCH, T. (2006). The biology and evolution of music: A comparative perspective. *Cognition*, 100(1), 173–215.
- FRIJDA, N. (1986). *The emotions: Studies in emotion and social interaction*. New York: Cambridge University Press.
- FRIJDA, N., & ZEELLENBERG, M. (2001). Appraisal: What is the dependent? In R. J. Davidson, P. Ekman, & K. R. Scherer (Eds.), *Appraisal processes in emotion* (pp. 141–155). Oxford: Oxford University Press.
- GEISSMANN, T. (2000). Duet songs of the siamang, *Hylobates syndactylus*: I. Structure and organisation. *Primate Report*, 56, 103–123.
- GEISSMANN, T., & ORDELDINGER, M. (2000). The relationship between duet songs and pair bonds in siamangs *Hylobates syndactylus*. *Animal Behaviour*, 60, 805–809.
- HAZANFAR, A., FLOMBAUM, J., MILLER, C., & HAUSER, M. (2001). The units of perception in the antiphonal calling behavior of cotton-top tamarins (*Saguinus oedipus*): Playback experiments with long calls. *Journal of Comparative Physiology, A*, 187, 27–35.
- GOODALL, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
- GREENFIELD, M. (1994). Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecological Systems*, 25, 97–126.
- GREGORY, A. (1997). The roles of music in society: The ethnomusicological perspective. In D. Hargreaves & A. North (Eds.), *The social psychology of music* (pp. 123–140). Oxford: Oxford University Press.
- HAGEN, E., & BRYANT, G. (2003). Music and dance as a coalition signaling system. *Human Nature*, 14(1), 21–51.
- HANNON, E., & JOHNSON, S. (2005). Infants use meter to categorize rhythms and melodies: Implications for musical structure learning. *Cognitive Psychology*, 50, 354–377.
- HARY, D., & MOORE, G. (1985). Temporal tracking and synchronisation strategies. *Human Neurobiology*, 4, 73–77.
- HAUSER, M., CHOMSKY, N., & FITCH, T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, 298, 1569–1577.
- HAUSER, M., & McDERMOTT, J. (2003). The evolution of the music faculty: A comparative perspective. *Nature Neuroscience*, 6, 663–668.
- HURON, D. (2001). Is music an evolutionary adaptation? *Annals of the New York Academy of Science*, 930, 43–61.
- HUSAIN, G., THOMPSON, W., & SCHELLENBERG, E. (2002). Effects of musical tempo and mode on arousal, mood, and spatial abilities. *Music Perception*, 20, 151–171.
- IYER, V. (2002). Embodied mind, situated cognition, and expressive microtiming in African-American music. *Music Perception*, 19(3), 387–414.
- JANATA, P., & GRAFTON, S. (2003). Swinging in the brain: Shared neural substrates for behaviours related to sequencing and music. *Nature Neuroscience*, 6, 682–687.

- JOFFE, T. (1997). Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution*, 32, 593–605.
- JONES, M. (1976). Time, our lost dimension: Toward a new theory of perception, attention, and memory. *Psychological Review*, 83, 325–335.
- JONES, M., & BOLTZ, M. (1989). Dynamic attending and responses to time. *Psychological Review*, 96, 459–491.
- JUSLIN, P., & SLOBODA, J. (2001). *Music and emotion: Theory and research in affective science*. Oxford: Oxford University Press.
- LARGE, E., & JONES, M. (1999). The dynamics of attending: How people track time-varying events. *Psychological Review*, 106, 121–156.
- LONDON, J. (2004). *Hearing in time: Psychological aspects of musical meter*. Oxford: Oxford University Press.
- MALLOCH, S. (1999/2000). Mothers and infants and communicative musicality. *Musicae Scientiae, Special Issue: Rhythm, Musical Narrative, and the Origins of Human Communication*, 29–58.
- MANN, N., MARSHALL-BALL, L., & SLATER, P. (2003). The complex song duet of the plain wren. *Condor*, 105, 672–682.
- MARLER, P. (2000). Origins of music and speech: Insights from animals. In N. Wallin, B. Merker, & S. Brown (Eds.), *The origins of music* (pp. 31–48). Cambridge, MA: MIT Press.
- MCAULEY, J., JONES, M., JOHNSTONE, H., & MILLER, N. (2006). The time of our lives: Life span development of timing and event tracking. *Journal of Experimental Psychological Genetics*, 135, 348–367.
- MCDERMOTT, J., & HAUSER, M. (2005). The origins of music: Innateness, uniqueness and evolution. *Music Perception*, 23(1), 29–60.
- MCNEILL, W. (1995). *Keeping together in time: Dance and drill in human history*. Cambridge, MA: Harvard University Press.
- MERKER, B. (2000). Synchronous chorusing and human origins. In N. Wallin, B. Merker, & S. Brown (Eds.), *The origins of music* (pp. 315–327). Cambridge, MA: MIT Press.
- MITHEN, S. (2005). *The singing Neanderthals: The origins of music, language, mind and body*. London: Weidenfeld and Nicolson.
- NAZZI, T., JUSCZYK, P., & JOHNSON, E. (2000). Language discrimination by English-learning 5-month-olds: Effects of rhythm and familiarity. *Journal of Memory and Language*, 43, 1–19.
- NORMAN, D., & SHALLICE, T. (1980). *Attention to action: Willed and automatic control of behavior*. CHIP 99, University of California, San Diego.
- OWINGS, D., & MORTEN, E. (1998). *Animal vocal communication: A new approach*. Cambridge: Cambridge University Press.
- PALMER, C. (1997). Music performance. *Annual Review of Psychology*, 48, 115–138.
- PATEL, A., & DANIELE, J. (2003). An empirical comparison of rhythm in language and music. *Cognition*, 87, 35–45.
- PAYNE, K. (2000). The progressively changing songs of humpback whales: A window on the creative process in a wild animal. In N. Wallin, B. Merker, & S. Brown (Eds.), *The origins of music* (pp. 135–150). Cambridge, MA: MIT Press.
- RAMUS, F., NESPOR, M., & MEHLER, J. (1999). Correlates of linguistic rhythm in the speech signal. *Cognition*, 73, 265–292.
- RAMUS, F. (2002). Language discrimination by newborns: Teasing apart phonotactic, rhythmic, and intonational cues. *Annual Review of Language Acquisition*, 2, 85–115.
- RANDALL, J. (1997). Species-specific footdrumming in kangaroo rats: *Dipodomys ingens*, *D. deserti*, *D. spectabilis*. *Animal Behaviour*, 54, 1167–1175.
- RENDALL, D., OWREN, M., & RODMAN, P. (1998). The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *Journal of the Acoustical Society of America*, 103, 602–614.
- REPP, B. (2001). Phase correction, phase resetting, and phase shifts after subliminal timing perturbations in sensorimotor synchronization. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 600–621.
- REPP, B. (2004). Comments on “Rapid motor adaptations to subliminal frequency shifts during syncopated rhythmic sensorimotor synchronization” by M. Thaut & G. Kenyon. *Human Movement Science*, 21, 61–78.
- REPP, B. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin & Review*, 12, 969–992.
- REPP, B., & KELLER, P. (2004). Adaptation to tempo changes in sensorimotor synchronization: Effects of intention, attention, and awareness. *Quarterly Journal of Experimental Psychology*, 57, 499–521.
- ROEDERER, J. (1984). The search for a survival value of music. *Music Perception*, 1, 350–356.
- SCHALLER, G. (1963). *The mountain gorilla*. Chicago: University of Chicago Press.
- SEYFARTH, R., & CHENEY, D. (2003). Signalers and receivers in animal communication. *Annual Review of Psychology*, 54, 145–173.
- SHENNAN, S. (2002). *Genes, memes and human history*. London: Thames and Hudson.
- SJARE, B., STIRLING, I., & SPENCER, C. (2003). Structural variation in the songs of Atlantic walrus breeding in the Canadian High Arctic. *Aquatic Mammals*, 29, 297–318.
- SPERBER, D. (1996). *Explaining culture*. Oxford: Blackwell.
- SPERBER, D., & WILSON, D. (1986). *Relevance: Communication and cognition*. Oxford: Blackwell.
- STEPHAN, K., THAUT, M., WUNDERLICH, G., SCHICKS, W., TIAN, B., TELLMANN, L., SCHMITZ, T., HERZOG, H., MCINTOSH, G., SEITZ, R., & HOMBERG, V. (2002).

- Conscious and subconscious sensorimotor synchronization—prefrontal cortex and the influence of awareness. *NeuroImage*, 15, 345–352.
- STOBART, H., & CROSS, I. (2000). The Andean anacrusis? Rhythmic structure and perception in Easter songs of Northern Potosí, Bolivia. *British Journal of Ethnomusicology*, 9(2), 63–94.
- THAUT, M., MCINTOSH, G., & RICE, R. (1997). Rhythmic facilitation of gait training in hemiparetic stroke rehabilitation. *Journal of Neurological Sciences*, 151, 207–212.
- THAYER, R., NEWMAN, J., & MCLAIN, T. (1994). The self-regulation of mood: Strategies for changing a bad mood, raising energy, and reducing tension. *Journal of Personality and Social Psychology*, 67, 910–925.
- TINBERGEN, N. (1963). On aims and methods of ethology. *Zeitschrift fuer Tierpsychologie*, 20, 410–433.
- TINCOFF, R., HAUSER, M., TSAO, F., SPAEPEN, G., RAMUS, F., & MEHLER, J. (2005). The role of speech rhythm in language discrimination: Further tests with a non-human primate. *Developmental Science*, 8(1), 26–35.
- TOLBERT, E. (2001). Music and meaning: An evolutionary story. *Psychology of Music*, 29, 89–94.
- TOMASELLO, M., CARPENTER, M., CALL, J., BEHNE, T., & MOLL, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioural and Brain Sciences*, 28, 675–691.
- TORO, J., TROBALON, J., & SEBASTIÁN-GALLÉS, N. (2003). The use of prosodic cues in language discrimination tasks by rats. *Animal Cognition*, 6(2), 131–136.
- TREVARTHEN, C. (1999/2000). Musicality and the intrinsic motive pulse: Evidence from human psychobiology and infant communication. *Musicae Scientiae, Special Issue: Rhythm, Musical Narrative, and the Origins of Human Communication*, 155–215.
- VAN PARIJS, S. (2003). Aquatic mating in pinnipeds: A review. *Aquatic Mammals*, 29, 214–226.
- WALLIN, N., MERKER, B., & BROWN, S. (Eds.). (2000). *The origins of music*. Cambridge, MA: MIT Press.
- WING, A., & KRISTOFFERSON, A. (1973). The timing of interresponse intervals. *Perception & Psychophysics*, 13, 455–460.
- WOOD, G. (1988). Further field observations of the palm cockatoo *Probosciger aterrimus* in the Cape York Peninsula, Queensland. *Corella*, 12, 48–55.