Neuroecological selection for musical features through spatial reciprocity in long-term partnerships

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Abstract

Chemical sensing via olfaction constitutes a most ancient form of inter-organism communication. But acoustical signaling via tonal and rhythmic patterning is also common among higher vertebrates. Animals that live in well ventilated habitats and move in diasporic ways have further evolved more spectrally varied and discretized call structure. But unlike song in birds, researchers have struggled to locate isolated nucleii specialized for music cognition. The brain stem, midbrain, hindbrain, and forebrain, however, all largely associate with aspects of musical performance, perception, memory, and emotion. I hypothesized that spectral features of musical display evolved as honest signals of spatial cognition for precarious locomotor tasks associated with nurturing and protecting vulnerable offspring. I investigated possible connections between motor, visual, and spatial cognitive areas in relation to both signaler production and receiver processing of acoustical features of musical output. Brain component volume fractions of 42 parts from 48 primates were compiled, from a single source, and compared against a vocal complexity index (ARDI) as well as individual musical feature scores: including tone, interval, repetition, transposition rhythm, and unique syllable count. Structures for spatial and visual perception as well as motor control and emotional processing associated moderately with areas used by species who produce calls with both temporal and spectral musical features. These findings are consistent with a dual (both receiver- and signaler- side) function of musical signals. Associations with spatio-social areas (e.g. schizocortex and insula) support direct selection for a paralimbic-based neighbor orienting [PIANO] sensory modality for mapping and anticipating movement of fellow arboreal cohabitants. Associations with motor areas (e.g. LGN, mid-brain, and thalamus) support the complementary model that signaler capacities for spatio-motive emplacement [ME] are indirectly selected by conspecific receivers. This dual manifestation in low-parity species that locomote in diasporic ways through (arboreally) diffuse habitats, is compatible with musicality serving as courtship signals by long-term mates with consistent and reliable spatial capacities directly relevant to care of vulnerable (arboreal) offspring.

DOI:
First-Published: 2022/12/14
Last-Modified: 2022/12/14

Introduction

Vertebrate production of acoustic vibrations audible across great distances is realized via the passing of air over constricted nasal or throat passages (Stevens, 2000). These, often tonal, waveforms are regularly used to communicate position and emotive state to conspecifics, other niche-inhabitants, or predators. Added variation, such as in interval height, can aid in signals being heard in more occluded, arboreal environments (Morton, 1975). Other modificaitons to sound signals, such as spectral diversity in vocal units, can help to communicate a unique vocal signature of identity to conspecific receivers (Owren, Seyfarth and Cheney, 1997).

At the even more elementary, neural-cellular level, foundations for both vision (in the form of rods and cones) and hearing (in the form of c. hair cells) are known to be stable and extremely ancient (500mya) facets of vertebrate biology (Jerison, 2000). The production and perception of tone also likely pre-dates the emergence of mammals. Even some aspects of rhythm (beat entrainment) are thought to be nearly 300 million years old (Honing, 2018). And, notably, monotonic rhythm routinely appears in calls of most non-human primate species (Schruth and Jordania, 2020).

More complex, music-like patterning, approaching acoustic display, might also possibly function as a signals (Mehr *et al.*, 2020) perhaps of underlying cognition. Clustering of repeated or transposed motifs requires receivers (and learners) of such calls to possess cognition for matching of acoustic patterns (Schulz *et al.*, 2008). High-level synthesis of acoustic signals occurs in auditory cortical regions of the temporal lobe (Morley, 2012). The hippocampus, basal ganglia, and cerebellum also house circuitry utilized for fusing of sound gestures containing melodic features (Fernández, 2015). But acoustic stimulii are typically first received in the cochlea [c], and are then projected, via the spiral ganglion and c. nerve to the c. nucleus of the brain stem (Sando, 1965).

Poorly understood, still, is how these animals' brains are used to process musical features (Jacoby *et al.*, 2020). Birds, who are the most well known for song, are endowed with specialized neuclii for singing (Moore *et al.*, 2011). Primates also have proportionally large brains that correspond to long, slow (and perhaps learning conducive) life-histories (Jones, 2011). Tarisers, like birds, have exceedingly small cerebrum, and may be less dynamic in their vocal capacities than other primates (Nietsch and Niemitz, 1987). No special music or song nuclei exist in primates and their rather stereotyped calls tend not to be highly influenced by social learning (Mitani, 1988). Deducing the distributed set of brain structures consistently involved in musical calling, has therefore proven challenging.

Brain Areas

Cognitive scientists have spent decades piecing together how sounds that reach the ear trigger the cascade of mechanical, chemical, and neural events in various brain regions to produce auditory perception (Peretz and Zatorre, 2005). The production of musical sounds has a likewise complicated cascade of neural projections but in the opposite direction, from neural to mechanical. Following my predecessors, I segregated these various processes into the four principal functional domains of production, perception, memory, and emotion. Within each category, I highlight the brain regions shown to be active corresponding to these functional domains across numerous studies and sources. A key study that served as an important starting point was for musical processing of pleasurable as well as displeasing sounds (Blood and Zatorre, 2001).

Table 1. Brain areas involved in musical processing by functional domain

BRAIN	CORTEX	SYSTEM	[motor] performance	[auditory] perception	[audio] memory	[gland & inhibit] emotion
-stem			pons VPG	cochlear nuc.		
hind-			cerebellum	{olive)		cerebellum
mid-			PAG, tegmentum	colliculus		dorsal
			SN, basal ganglia	(+) thalamus		
	[sub-]		(+) striatum	corpus callosum		nucl. accumbens
	meso-		cingulate			
						hypothalamus
	paleo-	limbic				(-) amygdala
	archi-			(-) hippocampus		
fore-	periallo-	paralimbic		entorhinal (schizo) cortex		
				(+) insular cortex		
		temporal		Heshl's gyrus & medial lobe		
	neo-	parietal		sensory		
		occipital				(-) [pre] cuneus
		frontal	(+) motor, SMA	(+) orbito frontal	planum temporale	(-) prefrontal

For each brain level, cortex and system specific cortical structures involved in musical processing are specified in relation to the four functional domains of performance, perception, memory, and emotion. Colored text corresponds to a number of proposed modules as presented in this text: blue corresponds to the PIANO module components whereas brown, green, and red correspond to motive emplacement [ME] modules. Red specifically corresponds to rhythmic components. Areas prefixed with a plus (or minus) symbol correspond to positive (or negative) activation in response to consonant (or dissonant) sounding musical stimulus, according various to studies by Zatore.

Production

Music-like sounds are generated just like many other vocalized sounds, using constriction of air passages (e.g. larynx, vocal folds, syrinx) to create vibrations corresponding to different wavelengths, waveforms, and acoustic patterning. Preceding mechanical sound production are motor-neural impulses from the pons by virtue of vocal pattern generators. These projections pass through the cerebellum in the hindbrain, as well as the peri-aquiductal gray [PAG] and tegmentum in the midbrain. and thalamus (Peretz and Zatorre, 2005). Additional studies have shown varying degrees of association with subcortical nuclei of and surrounding the basal ganglia (Ackermann, Hage and Ziegler, 2014), including the substantia nigra, striatum, and meso-cortical cingulate. In the neocortex, both the frontal and sensory motor cortex have been implicated. While studies on production of specific musical features may be more elusive and inconsistent, it is clear that nearly all levels of the brain are involved in creating musical sounds.

Perception

Periodic rarefactions of air molecules reach the ear as sound patterns and are funneled towards the tympanic membrane. These patterns of air molecules induce vibrations which may reach optimal resonance with a particular bands of hair cells corresponding to particular frequencies of the initiating sounds. Frequency information is individually relayed from the cochlear spiral ganglion and is projected onto the cochlear nerve towards the cochlear nucleus of the brain-stem. From here, nerve impulses make a u-turn back up the brain-stem towards higher brain structures including the olive near the cerebellum, colliculus in the brain-stem, and the sub-cortical thalamus. At any point along the way, reflexive short-circuiting can bypass higher brain oversight by responding in a way that prioritizes survival-conducive responses to potentially dangerous stimuli.

Although both spectral and temporal features of sound are essentially (rhythmically) periodic, they are typically processed in different areas of the higher brain. The temporal lobes play a crucial part of processing spectral information. Harmonic and pitch information has been associated with processing by Heschl's gyrus in the superior part of the temporal lobe. The posterior secondary cortex has been implicated as processing pitch changes and melodic analysis. Melodic processing and recognition of contours and pitch intervals are all facilitated by both the left and right temporal lobes.

Intermediate to the lower brain relaying of auditory signals and higher brain integrative processing of harmonic, intervalic, and melodic information, the mid-brain performs a basic spatial mapping of sound sources in two dimensions. Archicortical areas such as the hippocampus and surrounding periallocortical areas of the entorhinal cortex (including the schizocortex or pre- and para- subiculum). These areas typically facilitate orientation and navigational functionality, although lower (mid-brain) areas such as the tectum and higher cortical areas such as the insula, also facilitate this process of mapping sensory input to times and places. The insula was formerly considered to be merely another part of the temporal lobe, while others consider it's extreme medial position to be essentially paralimbic. Having six cortical layers, it is considered a fifth lobe in it's own right but is deeply folded inside the lateral sulcus, underneath three other lobes including the temporal, parietal, and frontal as well as the orbital operculum. It is the least well understood of all of the other neocortical lobes but has emerged as a specialized integrator of desperate multi-modal sensory information sources into cohesive gestaltic picture of the surrounding social relevant environment in the context of proproceptive internal states.

Memory

Like the more medial paralimbic areas accessory to the hippocampus (including the schizo- and entorhinal- cortex), the insula serves as a memory hub for temporal, orientational, and navigational capacities. Unlike these lower cortical areas, the insula specializes in connecting space-time coordinates with other more socio-emotional and sensory-motor relevant information—attached, for example, to places and faces. In addition to self-monitoring physiological needs such as thirst, hunger, pain, and fatigue, the insula is responsible for governing socio-emotional capacities for compassion, empathy, and inter-personal experience. Lastly, the insula plays an important role in higher order self-awareness and risky decision making. Musical memory typically implies memory for form and structure of events along with minimal contextual, rather than the emotional, associations. But I introduce the full function of the insula and integrate with these other such areas in the next section.

Temporal-adjacent structures such as the insula and heshl's gyrus are primary cognitive regions involved in musical perception and memory (Peretz and Zatorre, 2005). Other neocortical regions, however, such as the temporal and frontal lobes, are also involved in such faculties. Dorso-lateral and inferior frontal areas were most often recruited areas for when working memory load is high. Memory becomes important not only for connecting stimulus with context, but also for higher order matching and sound stream splitting and pattern recognition. Birds and humans have converged upon abilities to perform rhythmic and perceptual grouping (ten Cate and Spierings, 2019) which underly learning and participation in complex sonic environmental contexts. In larger groups where musical displays are longer and more rhythmic, there are typically a number of contributers as opposed to small-family contexts, musical memory becomes all the more critical.

Peter Slater has described sexual selection as an open-ended process that inevitably leads to longer songs and larger song repertoires until cerebral storage space constraints are reached (Slater, 2000). In short, memory plays an important role in social signaling by vertebrates, a topic which recieves more attention below.

Emotions

Auditory stimuli are maintained in working memory in order to compare an element in a sequence to one that occurs later in time. Emotional processing of musical experience is also neurally isolable. Emotional tone, mode, and tempo are manifestations of musical emotion that correspond to particular brain areas. That is, emotional analysis of musical stimuli are mediated by a common perceptual cortical relay. Nearly the entire brain has nuclei insvolved in emotional associations with music. The the dorsal midbrain, the hindbrain cerebellum, the limbic hypothalamus and amygdala, the subcortical nucleus accumbens and ventral striatum, as well as the orbito-frontal, insular, and (pre) cuneus of the occipital lobes are all implicated in emotional processing of music. Theorietical efforts have attempted delineating the more emotionally melodic from the more lexically rhythmic (Peretz & Colthart 2003). Understandably, as we move anteriorly from the more physio-mechanical parts of the temporal lobe toward more socio-emotional parts near the frontal lobe, Broca's area, a hub for spoken language, is implicated (Brown, Martinez and Parsons, 2004).

The study of relationships between musical behavior and emotion are as old as the earliest theories on the subject. Ideas predating natural and sexual selection proposed that music was merely an advanced form of physical expression of emotion—a manifestation of “nervous excitement” (Spencer, 1875). Since the resurgence of ideas in the origins of music, many others have clamored onto this line of thought. Recent ideas on the function of music include equalization of emotional states, reinforcing of emotional coordination and promotion of conjoinment (Dissanayake, 2009), managing social uncertainty, facilitating affiliative and pro social interaction (Cross, 2011), coordinating affect for social identity, cooperation and alliance building (Bryant, 2013), increasing value through emotional contagion, social cohesion, improved well being (Snowdon, Zimmermann and Altenmüller, 2015), and thinking of it as vocal and kinesthetic communication of social emotional content (Morley, 2014), as well as stress reduction by reduction of costs of group living (Savage *et al.*, 2021).

Hormones

Less work has been done to map hormonal correlates of musicality. Many studies have looked at the relationship between testoserone and music performance in people ranging from non-musicians to elite musicians. Recently some have looked in more detail at how hormones interface with particular regions of the brain. For example, testosterone, the male sex hormone, is though to positively stimulate activity in both the amygdala and hypothalamus. Whereas oxytocin, the love hormone, is thought to stimulate activity in both the hippocampus and orbitofrontal cortex. This line of evidence has been used to support the idea of musicality as evolving as an ornament for courtship (Miani, 2015).

Spatial modules for motor control and conspecific orientation

The four functional domains can be matched to two mechanisms of evolution. The first is for performance related to motor control of the vocal apparatus. The second relates to perception, memory, and emotion (but also learning) of such acoustic output. I have recently proposed names two accompany this sender receiver pair of signaling modules: as motive emplacement and acoustic neighbor orientation.

ME This module of “motive emplacement” refers to the motor control required to realize arbitrary targets in space, but also to the motor control required to create the acoustic signals that convey such an ability. Thus motive emplacement is not only a reference to locomotor and positional targeting of substrate and dietary items, but the vocal manifestation of motor control required by small muscles to achieve such skeletal motor tasks. Furthermore, since most musical animals have eyes, and eyes have [rectus] muscles, I have proposed that the accurate function of the small muscles of the eye, hidden behind the cranial bones, are signaled by the equally small muscles of the larynx (or syrinx) for kilometers around the signaler. Thus a the skill in quickly maneuvering and focusing a highly important (yet invisible) organ for feeding, moving, and survival, is signaled by another motor controlled organ which can be much more publicly showcased, assuming the same (mid-brain, and thalamic) motor control circuitry governs both.

PIANO A second receiver side module is also proposed and is hypothesized to reside in the medial temporal lobe as both paralimbic and insular. This sub-cortical system, located surrounding and including parts of the limbic system (e.g. the hippocampal gyrus), primarily implicates the *piriform*, *parahippocampal*, and *entorhinal* cortices. These ancient structures overlap with the lowest three layers of the temporal lobe, *hippocampus*, and the olfactory structures of the *piriform*. While the *piriform cortex* is primarily concerned with sense of smell, the other two, along with the adjacent *hippocampus*, are important in facilitating spatio-temporal navigation as well as memory encoding and retrieval. Interestingly, the *schizocortex*—containing the presubiculum, parasubiculum, (involved in directing of head position and used in spatial navigation), and the enthorhinal cortex—also shares contiguity with these other spatial orientating neural areas. This proposed module also includes the aforementioned insula, an understudied fifth lobe of the neocortex. The insula is the perfect candidate for a final destination of gestaltic processing of perceptual stimulus, integrating visual, olfactory, and auditory information into a coherent whole. Importantly, I consider this final destination as being more socio-emotionally sensitive to affiliation than the lower areas (e.g. amygdala) that might short circuit into a fight-or-flight response, such as may also happen with olfactory input in the fornix or lower-frequency auditory stimulus in the cochlea. Analogous to the anterior cingulate cortex and adjacent septum, whose final stimulatory destinations tends to relate to maternal bonding and emotional, motivational, and goal directed behavior—the final reaches of the anterior insula could be similarly socio-emotionally intelligent and egalitarian.

Evolutionary Mechanisms

Human musicality and various selection models

Theories on the origins of music can be partitioned into two recently productive schools of thought. One posits it has evolved as a by-product of individualistic survival, while the other sees it as adaptive in a more pro-social capacity.

For example, music could be seen as manipulating our evolved perception for "attention worthy events" (Pinker, 1997). An example is "shrieks" and "screams" that can trigger a startle response (Bryant, 2013). We do know that dissonant sounds can easily scare us while consonant sounds have an attractive affect (Fritz *et al.*, 2009). Indeed, tonal calls tend to correspond to states of high arousal and may prescribe reorienting towards sources of sounds. Thus, the foundation of spectral differences in musical pattern creation could merely relate to manipulation of our ancestral need to navigate our sonic environment by segregating sound streams, locating sources, and categorizing them with efficiency (Bregman, 1990; Bryant, 2013).

On the opposite extreme, theories of a social bonding purpose are prevalent. Bonding ideas—ranging from those within pairs, groups, mothers and infants—abounds in the literature. One of the primary arguments supporting bonding hypotheses suggests that the repeat cost of duet-learning with a new partner or group is an honest and costly signal of partner investment that inherently discourages disillusionment (Geissmann and Orgeldinger, 2000). In all bonding theories, the ultimate objective is for the group signal to act as advertisement of the bond strength to external groups (Geissmann and Orgeldinger, 2000).

An alternative category for origins ideas rests upon the stable foundation of signaling theory. Numerous signals types are invoked under these forms of evolutionary argument. Signals can be costly or honest or both. They can be indicators of an underlying trait, possibly indicating general vigor or motor control. A new version of this form of signaling applies to signaling between groups in relation to musical display, and has been dubbed "credible signaling."

Within evolutionary ideas, there are also numerous forms of selection ranging from natural (on individuals) or selection acing on pairs or groups. Selection can also be asymmetrical, as in the case of sexual selection, with one sex [typically females] choosing the other [typically males]. Roles can also be more egalitarian, such as under mate-choice (or sexual choice). Under sexual selection, secondary (sexual) traits will tend to become exaggerated especially if there are large asymmetries in parental investment (Trivers, 1972) and males have little to offer females beyond their genes.

Evolution by (usually female) mate choice can be direct, indirect, or non-selective. Under direct selection, females choose males who can provide territory or parental care—something I have termed “nurtural security”—whereby food sources can be easily converted into offspring. Indirect selection merely has females selecting conceptions by males for purely genetic reasons. Under non-selection males will exploit biased sensitivities for copulation opportunities and songs will develop anti-habituation properties.

Bird song signaling and selection for motor control

A number of bird studies have confirmed the connection between many of the above performance features of song and some combination of earlier pairing and higher (extra-pair) copulations or fertilizations (Searcy and Yasukawa, 2019).

Partial evidence exists for non-selective, bias-exploitative, or “ornamental” signaling, driving singing in birds, which persists as a prevalent mechanism as it tends to increase copulation opportunities. On the other hand, there is stronger evidence for motor control (via indirect) signaling for "conditional" indicators of viable offspring outcomes from mating. In primates these might be motor control, for landing limbs, or for understanding parabolic trajectories for leaps.

In birds motor performance tends to reflect (indirect) genetic skill or vigor [SoV], whereas ornamental traits arise secondarily as a way to enhance this SoV (Byers 2010). Examples include repertoire size, syllable diversity, or other performance indicators: time, length, rate, amplitude (Gil and Gahr, 2002) unit repetition or trill interval consistency; often accompanied by wing, leg, or locomotor displays. Subtle differences can be useful indicators of developmental history, genetic viability, current health or condition (Byers, Hebets and Podos, 2010).

Bird song signaling and mate choice

Given that singing and musicality in birds and primates (respectively) tends to occur in monogamous species, I chose to explore various mate-choice related evolutionary mechanisms (Searcy and Yasukawa, 2019). Direct selection mechanisms for mate choice are somewhat less evidenced in birds. Examples include species recognition or decreased cost in energy or risk of choosing a mate. Direct mechanisms can also include honest handicaps (e.g. features of acoustic signals) likely mediate both conspecific recognition and mate selection. (Wilkins 2013) These direct signals translate to viable offspring via both dietary factors such as provisioning, territory defense, or other forms of care, even if the chosen partner doesn't contribute genes (Searcy and Yasukawa, 2019). Conveniently, in primates, egalitarian monogamous mating systems are common correlates of musicality (Schruth, Templeton and Holman, 2021). For mutual benefit, direct selection mechanisms should manifest via reciprocity between partners (esp. monogamous pairs) for energetic pay off in slowly reproducing species with low parity birthing. Honesty of “revealing” or costly handicap indicators is maintained by a finite cognitive storage capacity (Gil and Gahr, 2002), which can also be highly spatial in modality.

Spatial reciprocity and mate choice in gibbons

A model example of such spatial reciprocity exists in gibbons. This socially monogamous family of primates hang precariously from branches, using just a single hand at a time, as a part of brachiating, their primary form of locomotion. Gibbons also pair up with mates for life, thus making choosing a mate especially important choice that can take many years to solidify. Similarly, since they experience concentrated weight per digit (Congdon and Ravosa, 2016) as well as acceleration during landing, such forces are further compounded when gestating or carrying infants. While there is some day to day trade off in infant carrying duties, females bear the brunt of the burden, especially in the first few months of life of the infant. Males instead may act to offset this energetic burden via defense of the vulnerable mother and infant, as well as scouting food sources and boundaries of their ever shifting home range. This reciprocity requiring exchange of spatial duties would typically include reliable motive emplacement and leap landing as well as effective memory and orientation abilities for accurately localizing their new mate and neighbors for within-tree and range spacing logistics. Long-term partnerships in complex and precarious settings require both long term memory and motor planning (and accurate execution) that can readily access corresponding higher-brain memory. Furthermore, these brain structures should be further along a given neural pathway from other more reflexive, lower-brain, fight-or-flight functionality.

Hypotheses: primate musicality via sexual choice and mate selection

I hypothesized that musicality evolved as both indirect and direct signals involved in mate selection for long-term partnerships. First, locomotion between canopy elements requires reflexive spatio-motor execution in target landing tasks given the precarious gravitational constraints of narrow inter-branch targets and precipitous above-ground distances. I predicted that conception would be biased towards conspecifics who produce consistently reappearing units in display calls, thereby indirectly selecting for genetics encoding quality motor control capacities also used in rapid grasp landing. Receivers of such signals, like the call-learners themselves, should possess perceptual cognition for accurately comparing and grouping such acoustic units. Second, longer-term pairings between inter-substrate arboreal cohabitants likely requires individuals to possess fully functioning spatial, proprioceptive, orientational, navigational, and turn-taking capacities. Given the k-selective advantages of predation-avoidance and the excessive g-forces involved in (esp. infant-laden) landing of such inter-branch locomotion—periods of weaning and learning by infants should be protracted. Thus, regardless of paternal certainty, long-term mate selection should directly entail choosiness for higher-cortical spatially-reciprocating partners capable of role switching and payoff-postponement in nurturing and protecting arboreally carried offspring (Table 2).

Table 2. Mate choice, selection, signaling, and processing associations.

selection type	signal	payoff	(long-term) benefit	processing	functionality
direct	reciprocal	energetic	♀parental care & ♂nurtural protection	perception	P.I.A.N.O.
indirect	indicator	genetic	♂motor & ♀parabolic cognition	performance	M.E. & L.L.
non-selection	ornamental	copulation	variability ↔ anti-habituation	emotional	M.E.E. & A.C.

Sexual selection can be partitioned into three sub-types corresponding to direct, indirect, (or even non-selective) payoffs to mating decisions. While indirect indicators of motive emplacement [ME] as performance signals, for example, may be more difficult to measure, they have the most theoretical support in explaining the evolution of musical calling. Direct, reciprocal signals of [mostly future] parental care are thought to be perceived by the PIANO module. Non-selective by-products of ornamental signals can also evolve via increasing chances of copulation by exploiting auditory perception centers that are biased toward emotionally sensitive response.

Music, musicality, and feature component evolution

Music is a complex whole brain phenomenon created primarily by humans. Darwin suggested it was the most mysterious of all our behaviors (Darwin, 1871). Others have suggested that, because its function has an indeterminate [adaptive] role as a whole, we should look instead for the mechanistic function of each incremental addition of individual components throughout its historical evolution (Honing *et al.*, 2015). For example tone/pitch, beat perception, and metrical rhythm likely evolved one at a time over the course of millions of years. This multi-component and pluralistic, approach naturally also lends itself to a comparative analytical methodologies while also employing an ecological perspective for selection on traits (Fitch, 2015). Elsewhere, I have developed an acoustic reappearance diversity index as such a continuous measure of musicality which can be easily used in comparative analysis across species. ARDI retains relevance to minimally capturing the complex whole of musical behavior in humans but it does little, by itself, to address multi-component aggregation of additional musical features. While I predicted that features of reappearance and diversity are the most theoretically relevant here for testing ideas in connecting musicality with ecologically relevant spatial abilities for long term partnerships, rhythm and tone may also be relevant. Thus this paper also individually investigates all six [collected] musical features as independent factors consociating with ecological and neurological aspects of musicality.

Table 3. Glossary of acronyms and terms

A.R.D.I.	acoustic reappearance diversity index {continuous index of manifest musicality measuring the average number of repeated syllable types in a call}
M.E.	motive emplacement {setting and attaining arbitrary targeted goals in space} (2021)
M.E.E.	motive emplacement and entrainment {intentionally realizing body movements with respect to socially generated acoustical cues and signals} (2022)
L.L.	leap landing: a locomotor form of motive emplacement where by leaps are landed on narrow arboreal substrate targets
A.A.H.	acoustic adaptation hypothesis {features evolved to improve propagation of acoustic signals around obstacles specific to particular habitats} (Morton 1975)
A.S.A.	auditory scene analysis {perceiver-side recovery of individual sound streams from a cacophonous mixture of multiple environmental sounds} (Bregman 1994)
A.C.	"auditory cheesecake" (Pinker 1994) or auditory chocolate, whereby biased sensitivities for environmental listening is exploited easily processed musical sounds
P.I.A.N.O.	paralimbic insular acoustic neighbor orientation {higher-cortical para-hippocampal brain areas involved in orientation and navigation tasks that facilitate spatial harmony with conspecifics and cohabitants of shared ecological niches} (2021 & 2022)
k-selection	selection in species characterized by slow (body & population) growth rates, low parity, long life spans, long weaning durations, and relatively altricial offspring
sexual selection	competition between members of the same sex (deterring rivals) in order to attract mates; can result in bizzare ornamental secondary traits (Darwin 1871)
sexual choice	more sexually symmetrical form of mate choice via indicators, in contrast to more asymmetrical sexual selection based on exaggerated or costly signals (Miller 2000)
mate choice	mate selection broadly construed around the full life-cycle: including courtship, copulation, fertilization, gestation, and parenting (Westneat & Fox 2010)
mate bonding	(possibly acoustic mode) acquaintance before cohabiting (e.g. a tree) or parenting; a part of courtship and pair formation (adapted from Savage 2020)
pair bonding	long term bonds formed by established couples typically jointly rearing offspring, post copulation; thought to co-evolve with vocal duetting (Wickler, 1980)
mate selection	process of choosing long-term mates in k-selected species (includes most of the mate choice cycle except offspring nurturing—the signal payoff)
signal selection	Includes selection for costly / honest signals (sent to all rivals, partners, enemies); but excludes utilitarian selection (e.g. fighting ability) (Zahavi & Zahavi 1997)
nurtural security	providing for offspring via both menage and range defense as well as dietary scouting or provisioning (can include infant carrying)
trophic security	evolutionary or developmental means (e.g. infant carrying) of successful deterrence or avoidance of predation within a given food web (Schruth & Jordania 2020)
spatial reciprocity	long-term mutual benefit between breeding partners or long-term neighbors where spatial-boundaries are respected in order to avoid physical collisions and falls (e.g. within tree) or resource shortages and conflicts (e.g. between trees)

Materials and Methods

I calculated brain component volume fractions on a small sample of non-human primates. Volumetric data on 42 different brain parts from 48 primate species was complied from a single source (Matano *et al.*, 1985). Part fractions were calculated by dividing the volume of each part by the overall brain volume. These were compared to a vocal complexity index and six structural acoustical features prevalent in human music and bird song. The diversity of reappearing (unique) units [ARDI] was measured as the probability of syllable reappearance—calculated as repetition plus transposition times the syllable count itself—and is used synonymously here as a measure of musicality (Schruth, Templeton and Holman, 2021). Ordinary least-squares linear regression was used to assess associations of brain volume fractions and their aggregates with both the individual musical feature scores and ARDI (Figs 1 & 3). Regressions against ARDI were also performed with and without *Tarsier spp.* (Fig 3, colored lines), as this species exhibited several signs of being an outlier, albeit an important one for inferring ancient evolution. Overlap in these datasets ranged from n=22 to n=7, variably depending on brain sub-component availability. For this reason, analysis was also performed at the general brain functional level, combining several brain components, under a weighted average, to generate composite cognition outcome variables. Functional brain regions were categorized and weighted (decreasing monotonically) according to the lists in Table 4.

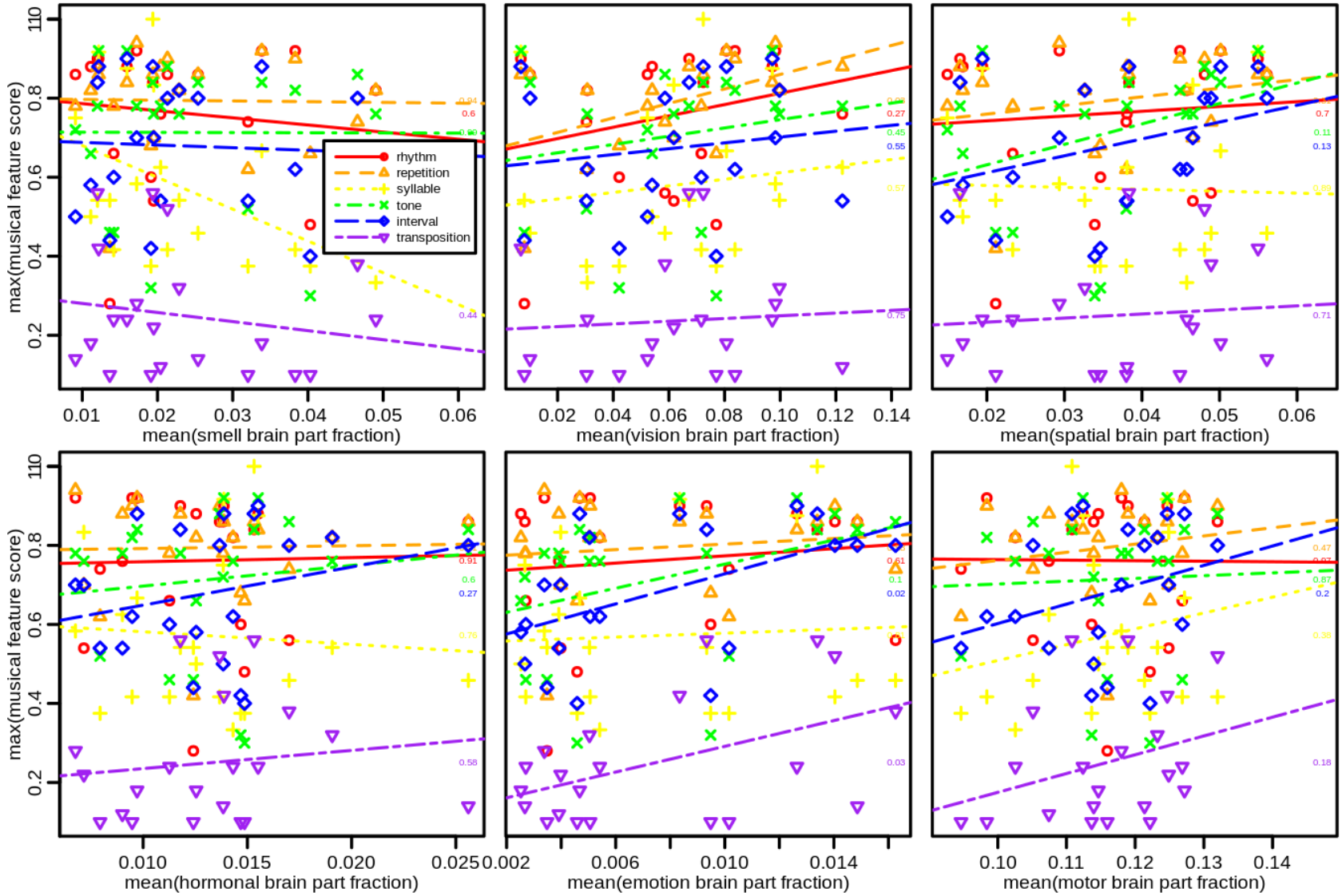
Table 4. Functional brain areas and their underlying components

smell	bulbus olfactorius, lobus piriformis, bulbus olfactorius accessorius, nucleus olfactorii lateralis
vision	area striata, visual cortex, tractus opticus, corpus geniculatum laterale, nucl_amygd_basal_IMC, vestibularis medialis
spatial	hippocampus, schizocortex, septalis triangularis, nucl_amygd_basal_IMC, subcommissurale
motor	mesencephalon, thalamus, basal ganglia ,cerebellum, nucl_amygd_basal_IMC
emotion	amygdala, pineale, septum, habenularis medialis, complexus cortico basolateralis
hormonal	hypothalamus, pineale, septum, meninges hypophysis nerves

Results

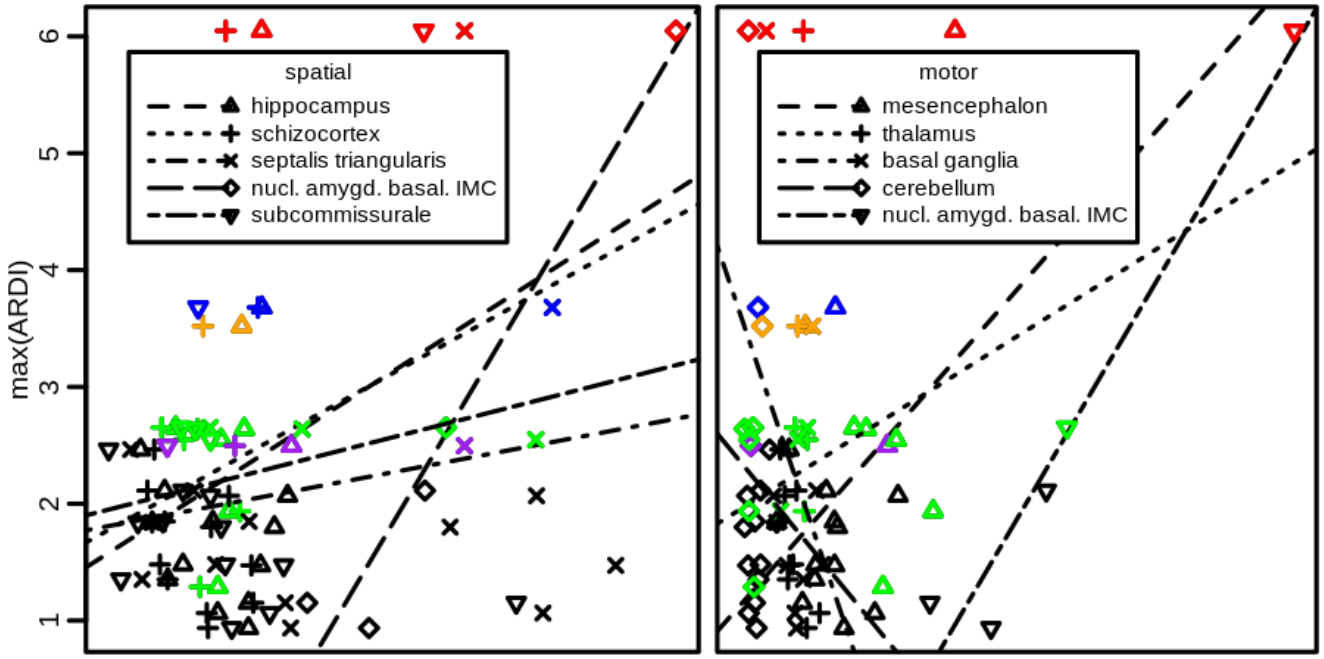
There were negative associations of vocal complexity with brain components associated with olfaction—including the *bulb*, *accessorius*, and *piriform*—and was strongest between *piriform* and *syllable* ($p<0.05$). Inversely, there were uniformly positive associations of all musical features with brain components associated with vision (Fig 1)—including *tractus opticus*, *striata*, and *corpus geniculatum laterale* [LGN]—and was strongest between ARDI and the LGN ($p<0.01$). Additionally applying ARDI to brain volumes unveils an association with the visual cortex ($p<0.1$), but only weakly confirms positive associations (Figs 1 & 2b) with areas related to spatial capacities (*hippocampus*, $p=0.3$; *schizocortex,* $p=0.4$). When spatial areas were aggregated, their correlation with ARDI was moderate. ($p=0.2$) and consistently positive across all five sub components (Fig 2a). Tone and interval had particularly strong associations with the weighted mean of spatial areas ($p\sim0.1$). Subcortical areas involved with motor control were more mixed in comparison with ARDI (Figs 2b & 3) with syllable transposition, and interval showing the highest correlations ($p\sim0.2$). Basal ganglia (including just *striatum* and *subthalamus*) was surprisingly negatively associated with ARDI whereas *thalamus* and *mesencephalon* (midbrain) were positive ($p=0.1$). If tarsiers are removed from these regressions, the trends are reversed into positive associations. While hormonal areas only showed weak correlations (with interval, $p\sim0.3$) emotional areas had strong positive correlations both interval ($p\sim0.02$) and transposition ($p\sim0.03$) but only a moderate association with ARDI. Other lower brain areas that showed strong associations with areas including motor control (*nucleus basalis*, $p<0.3$ and *vistibularis*, $p<0.4$) as well as those involved in motivation (*habenularis* $p=0.01$), sleep/wake (*pineale* $p<0.001$), and arousal (*cortico-basolateralis* $p=0.2$)--although these were primarily driven by *Tarsier spp*.

Figure 1. Weighted mean brain function versus max musical feature scores for six brain functions.



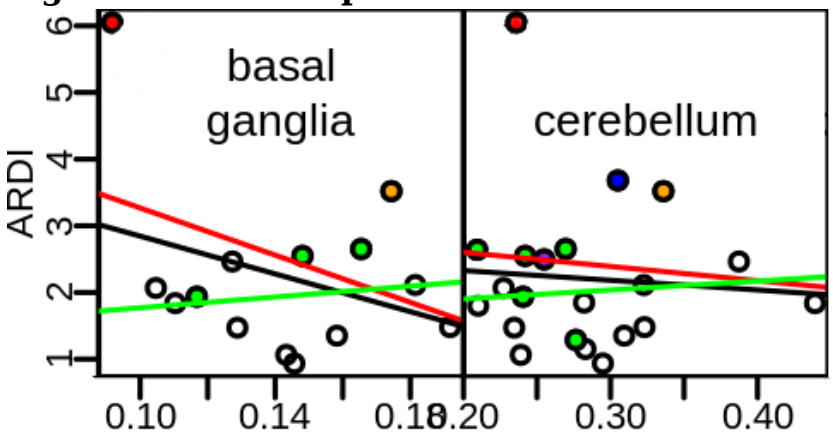
Using the functional brain area definitions (Table 4) monotonically decreasing weighted means of these fractions were compared with the maximum musical feature scores for each species. *Syllable count* was rescaled to 0 to 1 to facilitate comparison with the other features. Linear regression fit lines were plotted across each of the six feature score datasets.

Figure 2. Spatial and motor brain regions associated with ARDI



Unaggregated volumetric fractions (per non-neocortical whole brain volumes) from individual brain components (x-axis) plotted against ARDI scores. Linear regression trend lines are individually plotted for each sub-component of motor and spatial areas. With the exception of the basal ganglia and cerebellum, all spatial and motor associations are positive.

Figure 3. Detailed plots of two contraindicative spatial brain regions.



The *Tarsier* outlier drives the negative association of basal ganglia and cerebellum volumetric fractions with ARDI. But *H. lar,* the only gibbon, has high values for both both volumetric fractions and ARDI, indicating motor planning could be higher in larger (e.g. anthropoid) primates than in (e.g. tarsiers). Colored points represent “musical” primates: green=titi, tamarin, and marmoset monkeys, purple=galagos, blue=indri, orange=gibbon, red=tarsier.

Discussion

A striking, yet unsurprising, primary finding of this work are that primates have diminished neurological capabilities for smell which appears to have been supplanted by spectrally complex vocal communication. This behavioral overhaul, implies possible co-opting of visual areas for “seeing” acoustic gestures, a possible prioritization of spatial-navigational structures (over faculties associated with smell), as well as possible use of vocal signals as indicators for motor control. More tenuously implicated parts correspond to emotive states of motivation, wakefulness, and fear—perhaps regulated in response to and signaled by vocal complexity. Such compensation for arboreally diluted olfactory signaling and inter-substrate leaping, could be related to such ancient factors as target landing, predation avoidance, or some combination thereof, especially in callers.

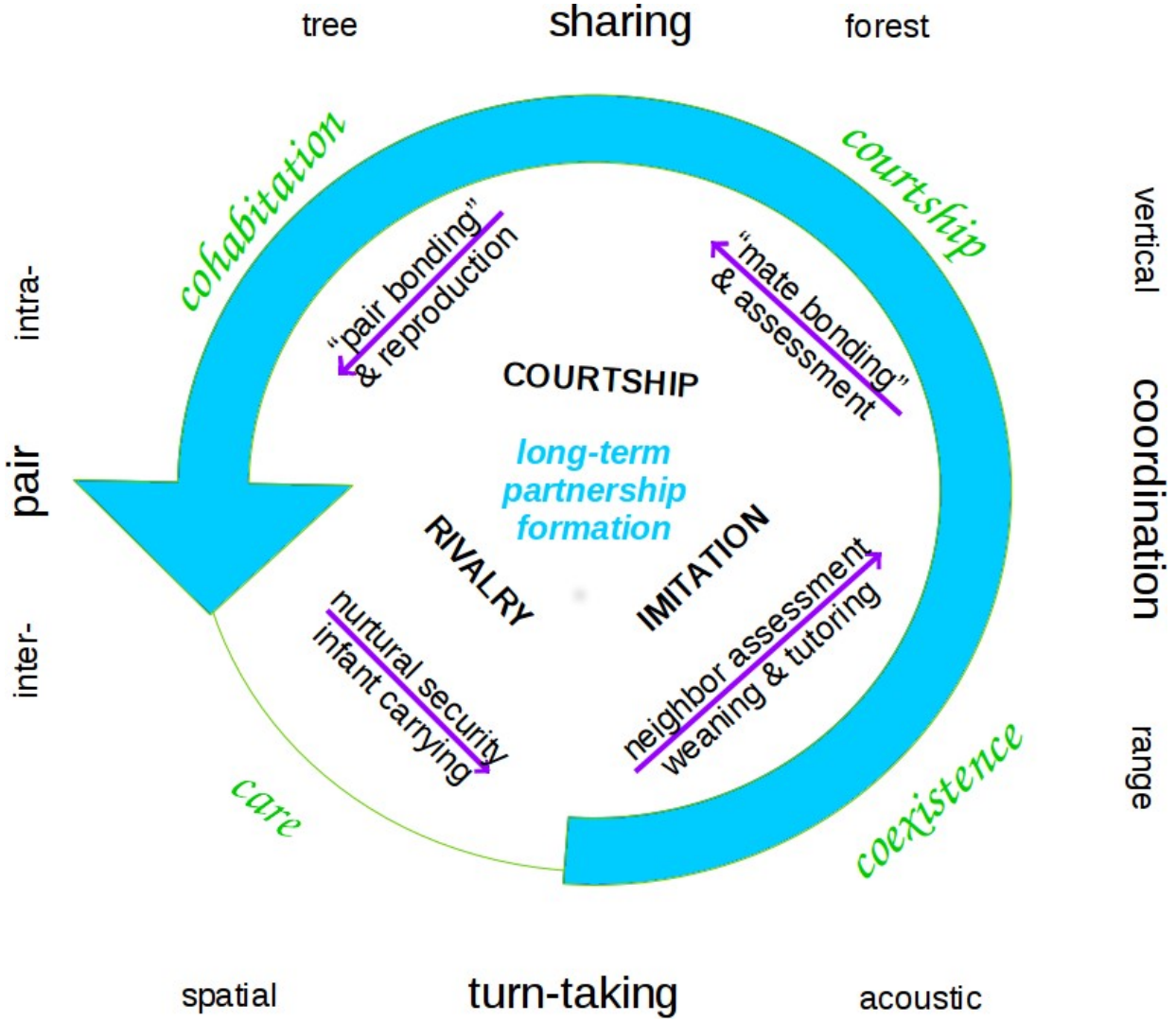
More socially, the findings presented here suggest that higher-cortical paralimbic and medial temporal areas, ranging from the schizocortex to the insula, utilize spatial and temporal information to link musical stimulii to form longer-term memories for harmonious cohabitation, here of trees and forests. These motor control and spatial orientation ideas are integrated under a full-cognitive-stack concept with a discussion on the basal-ganglia’s role in motor planning in larger primates, including apes. A chronology of the accrual of individual features underlying musical behavior is explored with special attention to the development of longer rhythmic and song-like musical production. Lastly, the adaptive significance of musicality in [terrestrial] humans is explored with respect to sub-features that are likely in decline (e.g. spectral) versus those that might be under positive selection (e.g. temporal) as well as those that are being maintained (e.g. syllable).

Indicators of motor control. The clearest motor-control areas associated with ARDI are the *mesencephalon* (midbrain) and, to a lesser extent, the thalamus (upper *diencephalon*). The midbrain relays sensory-motor signals to the cerebral cortex while the *thalamus* relays movement and motor planning as well as sensory (e.g. vision and hearing) information. It is possible that this increased importance of precise (post-cranial) motor control (e.g. of wrists) co-evolved with expansion of distinctly elaborate acoustic display. Stronger support for (cranial area) motor control is evidenced by greater vocal complexity association with lower-brain areas of *nucleus basalis* and *vestibularis medialis*. The former is known to release the motor-neuron activator acetylcholine, whereas the later is involved in fine control over head, neck, and eye movements. This evidence supports a hand-eye coordination and locomotor signaling origin for ancient primate musicality. The preceding motor-control evidence argument for such a musicality-origins module is nicely complimented by the highly corroborative associations with spontaneous visual-spatial circuitry running conterminously with the diencephalon (e.g. LGN).

Spatio-social mechanisms across the mate-choice life cycle

Charles Darwin envisioned the evolution of music as a sexually selected trait strongly embedded in the social context of “imitation, courtship, and rivalry” (Darwin, 1871). Since then others have proposed pair bonding, group selection, territoriality, and range defense as mechanisms driving the evolution of musicality in myriad species. Here I attempt to bring all of these social mechanisms into a single coherent picture organized around the mate-choice life cycle including courtship, copulation, fertilization, parenting, and weaning—from ME to PIANO.

Figure 5. Mate selection, arboreal cohabitation, care, and range spacing.



Numerous proposed mechanisms of musical evolution, including Darwin's original socio-emotional contexts, can be organized into a behavioral-ecological mate-choice life-cycle under the four phases of *courtship*, *cohabitation*, *care*, and *coexistence*. While *care* (including 'nurtural security' and infant carrying) is excluded from partner formation, it arguably constitutes the end goal of such long-term mutual pairings. The cycle repeats when weaning infants begin learning and imitating the musicality of parents and are overheard by potential mates in neighboring ranges.

Courtship: remote mate assessment and bond formation

Darwin originally viewed courtship between the sexes to be the original function of the music-like calling in our lineage. Like myself, he preferred to focus on the social dynamics of gibbons as a model organism, from which to rest his ideas on human socially-monogamous courtship.

As we have seen from our results correlating intervalic vocalizations in primates with hormonal and motor control areas of the brain (e.g. mid-brain and thalamus), it's reasonable to speculate that such call features have replaced scent as the primary way in which breeding pairs discover interest in one another. Naturally, this motor control element of adjacency to highly intervalic calls (Fig. 5), like those of gibbons and tarsiers, reflect fine motor control of the small muscles. As stated in the ME hypothesis above, these vocal motor control signals could indicate functioning muscular control for inter-orbital visual resolution of relatively narrow substrate targets, including branches and tree trunks, for more acrobatic landings. Because both lemurs and gibbons perform daring inter-arboreal airborne feats—where gravity demands split-second visual resolution and skeletal execution of limb landing—effective motor-control signaling via lower brain areas, could be a primary function of highly intervalic song.

As discussed in the introductory material on musical production and perception above, indicators of [ME] areas possibly reside in the same general sensory-motor control centers where humans experience pleasurable involuntarily chills, namely just inside the back of neck. These proposed areas possibly include the mid-brain (e.g. PAG, tegmentum, optic tectum, and colliculus) as well as the thalamus.

Socio-ecologically, this mechanism of selecting a sexual partner for their genetically encoded motor-control reflexes, could theoretically, and likely does, happen well before such individuals even come into close contact. Singing (ones own) and listening to others' song components, could preemptively facilitate a coordination of the timing logistics of sharing acoustic space, remotely, before even sharing a tree or having an up-close encounter. Even frequency based aspects of joint calling could be determined before ever duetting together.

Ultimately, like any k-selected species, however, longer term signals of future commitment and care are required to transpire between mates as well as the short term motor signaling. K-selected species, those with few offspring, invest more in each than r-selected species. Thus potential mates must factor infant-care and tree-cohabitation considerations, in order to perform precarious joint-arboreal locomotion. Therefore, both ME and PIANO related signaling factor into such a long-term selection processes.

Coordination: locomotor logistics of copulation and bonded cohabitation

While short-term copulations are likely fundamentally rooted in transferring genetic material, even such short encounters require intra-arboreal coordination. Even if parenting and monogamy may not necessarily require constantly sharing or even sleeping in the same tree, copulation by arboreal primates certainly does. While signaling ME to potential genetic mates is important, signaling of PIANO capabilities should be as well. Thus, both working out kinks of one-armed mating [ME] as well as tree cohabitation [PIANO] are arguably both critical social aspects of making any type of pairing happen. However, while the N in PIANO currently stands for ‘neighbor’, it could just as easily stand for ‘newlywed’ for the primary focus in this manuscript is on such long-term pairs that spend much greater time together in select trees, executing coordinated locomotion, than with any other individuals.

PIANO is also fundamentally an orientational and navigational module that helps couples quickly identify and relocate to one another upon regular daily periods of separation and reunion. Therefore, it ultimately constitutes a form of contact calling ideas on the origins of musicality. However, PIANO is specifically proposed to enable rapid identification of specific spectral features of long-term partners. These features are most directly tied to emotional centers and may even have been co-opted from maternal-infant locational signaling which was only later co-opted to long-term mates (Miani, 2015).

Care: direct signals to mates realized as parental investment

While every phase of the mate-choice life-cycle leading up to this point has been related to building bonds, the ultimate point of all bonding is arguably to then invest such coordinative efficiency into rearing offspring. That is, in order to turn the caloric payoffs of scouting, nurturing, and even provisioning, into manifest offspring, pairs must put those signaled promises into parental action. Stated using a more classical formulation, there exists adaptive challenges in the logistics of not only mate *selection* but also in mate *cooperation* in order to successfully bring forth offspring (Zahavi and Zahavi, 1999). This form stands in marked contrast to more recent forms of [credible] signal, such as from a parents who reliably indicate infant offspring attention (Mehr and Krasnow, 2017).

Researchers have long investigated different variations on a theme of parental investment related to music evolution. Ellen Dissanayake has hypothesized that parental care had direct fitness benefits for improving the survival of offspring due to [musically] improved parent offspring communication. Under more recent views, introduced above, costly forms of parental attention [PA] constituting honest attention can signal PA *to* infants and are indicative of devout infant care and manifested as infant-directed song (Mehr *et al.*, 2018). This thesis has recently been incorporated into the “credible signaling” framework where parental attention is signaled to helpless infants via simple lullabies between parents and infants (Mehr *et al.*, 2020) and where crying (distress, separation, isolation calls) carries information about the timing of investment. While these ideas sound similar to PIANO, my proposal constitutes a signal of promises of future parental investment to potential mates, usually between a male partner to a long-term female partner with whom he has yet to pair. In contrast to conflicting interests between human mothers and infants—a model that fails to recognize the similarly high degree of [arboreal] helplessness of primate infants—the form of PI signal I explore is between potential mates.

The PI I explore here exposes a different conflict—that *between* sexes—in the form of a possibly collaborative division of labor. Where more ‘gravid’ (or ‘gravis’) infant carrying (predominantly by the female) is juxtaposed by the future nurtural roles assumed by the (presumably more nimble) male, including of food-scouting and range-defense. Although this form of specialization need not necessarily be so sexually asymmetrical, as many male gibbons and callitrichids will carry infants as well as females. But specialization does tend toward such a manifestation—as infants may become predisposed to a higher degree of attachment to their mothers, especially in clades with proximity to potentially prolonged nursing associated with ventral carrying. As primates breastfeed for years in some apes, for example, this specialization tends to manifest as this female carrying and feeding while the male scouting duties and defense of the range his mate and infant occupy.

The signaled promise between pairs is that of PI for nurtural security for the offspring where both help to convert the calories afforded to them by their home range into successful growth of their offspring. Nurtural security gets at the heart of evolution because it focuses on turning genes and food into embodied offspring. Because dietary factors affecting mate choice are highly confounded with many other measures (e.g. size, health), it is often instead assessed analytically via more direct measures of home range and care.

In other musically singing animals like birds, gametes (here, eggs) are larger in the female and she is therefore undually burdened by extra weight for flying, and therefore that much more vulnerable to predators. It remains unclear how this logic might effects larger cetaceans, except perhaps in that they may also face a similar form of obstetrical dilemma when carrying fetuses that could interfere with efficient swimming.

Coexistence: inter-pair re-orientive spacing upon pair relocation

Coming full circle back to offspring weaning and independent feeding, we note that pairs likely also begin to explore their own range and the boundaries with others. The calls offspring began to assimilate by virtue of physical attachment to their mother may begin to manifest as their own ranging calls. These short (not necessarily repeated), melodic, and initially just intra-group-directed may function in a spatial orientating [PIANO] capacity.

With locomotor independence, comes visual-motor competence in resolving branch shapes for themselves. Thus, even though their calls serve in a largely PIANO sense of orientating towards their own, they also may also begin to experiment with longer more repetitive calls signaling mid-brain and thalamic binocular vision and branch-shapes limb-landing capabilities.

But as a k-selected long-term family unit, these sub-adults may still be dependent upon their parents for physical protection and seasonal foraging. In visually (arboreally) occluded habitats where not only spectral precision but spatial orientation is required. The archicortical/limbic hippocampus as well as allocortical/paralimbic entorhinal areas are both involved in processing the full range of auditory stimulus, any initial attempts at auditory grouping, and potentially also spectral binding of acoustic elements. Researchers have demonstrated negative associations between dissonance and hippocampal regions, which could possibly be interpreted to undermine any affiliative consequences implicit to PIANO. Noisy, dissonant, short staccato are the key parameters that characterize alarm calls (Snowdon 2001), where as affiliative contact calls tend to be more harmonic (Fischer 2000)

But it’s possible that these more dissonant alarm calls could have been counter-intuitively co-opted to stimulate range-spacing and reproductive *suppression* in neighbors that have been perceived by the callers as encroaching upon their range. Use of harsher and more dissonant alarm and aggression calls may stimulate (such neighbors’) nervous-systems at the (sub-)thalamic level (Blood and Zatorre, 2001) and possibly into reflexive (ME) response for fight or flight reaction. The data presented here further support highly intervalic calls replacing smell as the primary means of stimulating sub-cortical brain areas involved in fear (e.g. amygdala) and thereby also possibly suppressing reproduction and facilitating inter-range buffering. That is, dissonant or piercingly intervalic calls could directly impart to neighbors signals to relocate or otherwise suppress reproductive impacts on overlapping habitat. While highly intervalic calls are not dissonant in human music, in other animals, they may be considered as both dissonant and cooperatively affiliative, in this proposed form of range-spacing coexistence.

In contrast to the harsh crescendoing frequency sweeps of territorial gibbon great calls, adult quaver phrases of this ape family are considerably more assuasive. These quaver phrases may be understood as more affiliative, and may signal a more acquiescent adult (PIANO-esque) signal—something along the lines of when and where to relocate or cross-gaps in the canopy. This shift from slightly lower-brain hippocampus (and amygdala) level processing (e.g. stimulus binding) of harsher territorial signals to those that are higher up and further away from the medial temporal lobe. The insula, forms a more gestalticly coherent environmental scene for planning more elaborate, unusual, and risky locomotor maneuvers. Also, while still medial, the insula is lateral of much of the limbic and paralimbic areas involved in more simplistic processing of stimulus. The insula is responsible for more socially informed emotional processing like compassion, empathy, and interpersonal self-awareness. This functionality corroborates the typically affiliative nature of most music-like calls and higher brain appreciation and awareness of others, as well as possible suppression of lower-brain reproductive urges.

A final piece of the coexistence theme is that of imitation, or mimicry, of the calls of neighbors. In birds, songs tend to function as signals (or “threats”) of readiness or willingness to defend their territory. Mimicry of a neighbors’ songs addresses the threats of that neighbor in particular. It also gives them a chance to show off their age, experience, learning, and memory (in a very directed fashion) in their reply to a specific neighbor.

Charles Darwin thought of music as the supreme mystery of the science of man and the most mysterious trait with which we are endowed (Darwin, 1871). He also thought of music as the best example of mate choice playing a role in a human behavioral trait (Darwin, 1871). Geoffrey Miller has been Darwin’s most vociferous supporter (on this topic) in the last hundred years (Miller, 2000). He champion’s Darwin’s view on sexual selection “through” mate choice for “brains as indicators” as a way to preempt natural selection. He viewed sexual courtship as the principal biological function of music dividing mate choice for either indicators or aesthetic display. Here have I have proposed a third way, via PIANO’s spatial reciprocity in long term parental investment through care as nurtural security or infant carrying or both.

Paralimbic / Insular Acoustic Neighbor Orientation versus ASA

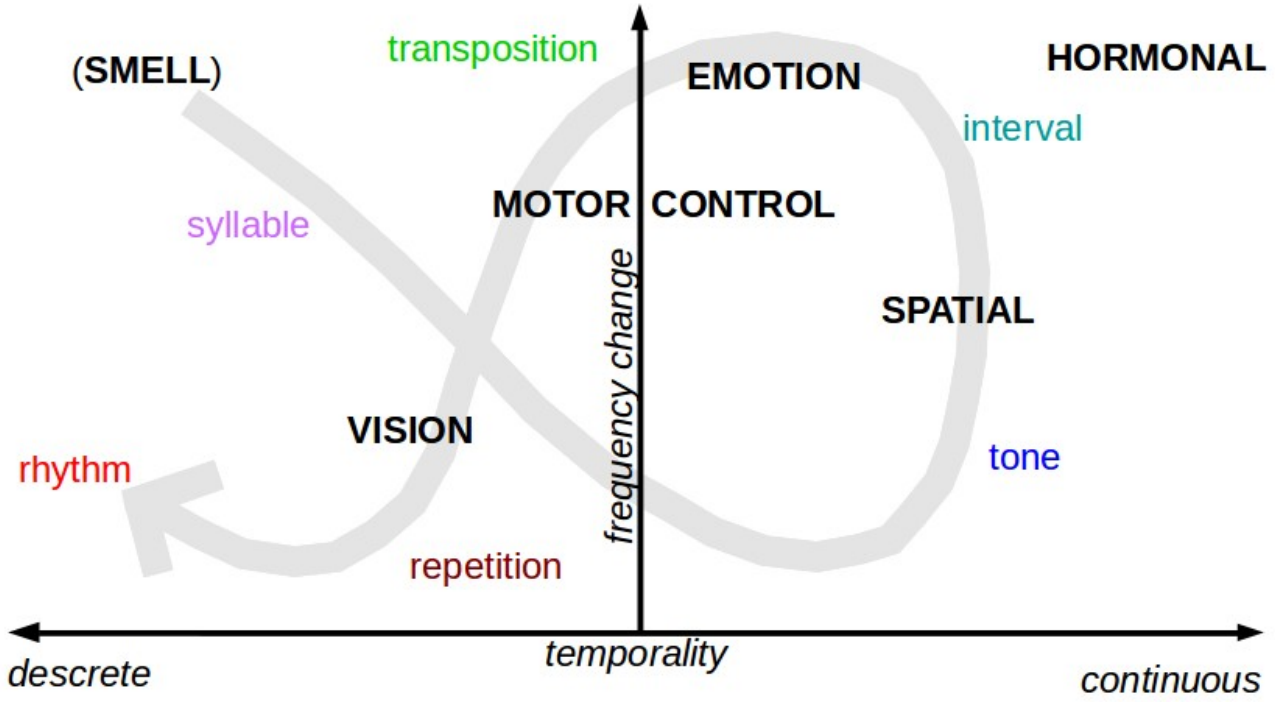
There has been a respectable research effort levied against the theoretical framework of *auditory scene analysis* [ASA] (Bregman, 1990; Trainor, 2015). But very little of this work specifically addresses spatial aptitude aspects of cognition (in the signal sender) and instead focuses on distillation of contiguous shapes across topographically equivalent representations of cognition (in the signal receiver). I suggest a refocusing towards neural representations (of *both* the signaler and receiver), specifically those interconnected to the (para)limbic regions of the brain.

A renewed and expanded reconsideration of ASA, in both how and why the auditory scene is connected to specific cognitive systems, is contended. I propose that an ecologically relevant capacity for orientation within an organism's acoustic neighborhood—one comprised of uniquely (and perhaps musically) identifiable auditory stimulii—could plausibly run conterminously with the paralimbic system. It's further possible that these ancient, formerly *olfactory*, cortical structures were re-purposed to encode pertinent *acoustic* landmarks for orientation (e.g. conspecifics). This is in spite of the fact that the evidence presented here, for any such putative exaptation of olfaction adjacent regions towards acoustic processing, is still quite limited.

Ancient primate homology and the multifactorial evolution of music

Recent studies of the brain provide evidence—in the form of circadian activity period, respiration, and even brain waves—that rhythmicity is ancient in animals. Others have further suggested that processing of rhythm has deeply ancient underpinnings (Honing, 2019). Buy while my own investigations into individual musical features confirms monotonic rhythm is pervasive in primates (Schruth, 2022), higher order rhythmic complexity has only increased very recently in larger more terrestrial forms. In other works, I have demonstrated how a minimalistic definition of human musicality (e.g. as ARDI) is all-inclusively derivable across all human cultures. This (rhythm and tone agnostic) definition also applies across deep-clades to the origins of the primate order itself with spectral complexity (e.g. melody) as the default state for primates. Presumably, spectral features replaced chemical signaling in crucial social communications such as those for mating. Using the neural correlations underlying Figure 1, I outline a rough chronology within the organizing context of both temporality and spectral dynamics (Fig. 5) in the sub-sections in remainder of the discussion.

Figure 5. Musical features and brain areas mapped along axes of temporality and frequency dynamics.



Musical feature score categories of tone, interval, syllable, repetition, transposition, and rhythm (colored font) and general brain functions (bold all-caps) are mapped in relation to each other and along two types of temporal (reddish) and spectral (bluish) delineations. Temporality (x-axis) distinguishes highly discrete features, like rhythm and syllable, from continuous ones, like tone. Frequency change (y-axis) distinguishes highly intervalic features, including transposition and interval (top), from features that do not modulate in frequency, like repetition (bottom). The evolution of musical signals from the earliest primates to modern humans likely took a path (gray arrow) from reduced smell to a more visually occluded spatial- and tonal- signaling, to intervallic motor signaling, and then ornamental visual-motor control signaling manifested as repetition and rhythm. Parentheses (around ‘SMELL’) indicates a negative correlation.

From olfactory signals to discretized acoustic referents

The observed trade off between sense of smell—diminished olfactory and piriform areas—with other areas observed here (Fig 1) is unsurprising. Because complex auditory and visual processing primarily localize to the temporal and occipital regions of the cerebral cortex, the conversely decreased correspondence in brain parts for reduced olfaction was expected. Arguably, the more intriguing observation, however, is that primates may have adjusted allocation for parts of their lower cortical areas, originally evolved in ancient piscine ancestors hundreds of millions of years ago, for more auditory based spatial orientating. As mentioned above, ancient cortical areas for smell seem to have been efficiently reduced and out-competed for adjacent space. Also plausible is the idea of overlapping functionality, or shared contiguity, with regions of both higher cortical areas involved in processing of auditory input (and temporal events) as well as lower cortical areas involved in spatial processing, perhaps also by recruiting hippocampal regions. These two sensory system reside on opposite extremes of the well inter-connected hippocampal gyrus—with the (lower) limbic areas primarily processing chemical stimulus and the higher temporal regions primarily processing acoustic gestures.

Emotional cries, wails, and moans: weaning, attention, and predation.

The results of the regression of brain volume fractions upon complex calling most strongly implicates diencephalic-contiguous areas including the midbrain and forebrain. Due to the disproportionately extreme values for *Tarsier spp.*, these parts—including the *pineale* (sleep/wake), *amygdala* (arousal/fear), and *hebernularis* (motivation/addiction)—exhibited strong associations with musical calling. The strong associations of the pineal gland and habernularis with musical complexity suggests PIANO could benefit from expanded consideration to lower brain areas involved in wakefulness and arousal. But strong associations of vocal complexity with wakefulness are not surprising considering the reduced remote-sensing of conspecific emotive-states among arboreally dispersal and constant repositioning of possibly nocturnal and leaping ancestral primates. Each of these could factor into an broader model including both sensory trade-offs and predation avoidance strategies (Schruth and Jordania, 2020; Schruth, 2021).

As a final consideration about inter-arboreal pressures and predation avoidance driving arboreality and eventually music like calling, I also address the puzzle of culogos. Culogos are tropical arboreal inter-tree gliders who, along with tree-shrews, are close contenders for being the most closely related taxon the primate order. It is natural to suspect, given the logic of both ME and PIANO outlined above, that culogos should likewise have developed musical calling, given their inevitable separation. However, I would argue that several key differences have stifled such development towards musicality in their lineage related to claws instead of nails, infant carrying, gliding anatomy, and the infrequency of inter-tree leaps. Primates have nails which presumably make infant carrying more comfortable. Cologos, by contrast, have slightly higher parity as afforded by leaving their infants in nests instead of carrying them. Furthermore, cologos only glide less than one percent of their locomotor bouts, in comparison to more than half for leaping by lemurs. Lastly, gliding has major (natural selection alleviating) advantages over primate limb-landing. Cologos’ targets (tree trunk) are broader and forces may be more gentle for (their parachute-style) landing than in wing-less primates.

Trade-off for sense of vision.

A similar co-opting of visual cortical areas by cognitive processing of music-like gestures, are arguably evidenced here. It is possible that nocturnal and leaping near stem-primates re-purposed the *striata* (Fig 2), a cortical area normally used for processing optical inputs, for visualizing auditory input instead. Something analogous is known to occur with elite, but visually blind, musicians (e.g. piano players)—who recruit the occipital lobe in facilitating musical performance (Ross, Olson and Gore, 2003). The similar phenomena of mental representation of exogenous spectral contiguities to internal spatial cortical maps has been covered in *auditory scene analysis* [ASA]. However, much of ASA is typically concerned with tracking of continuous streams of auditory sensory input rather than matching of discrete acoustic gestures for limb landing (e.g. ME) or mapping of these gestures into ecologically relevant spatial coordinates (e.g. PIANO), as I have proposed here.

Visual-spatial signals.

The strongest evidence of a correlation between any of these vocal complexity scores and visual brain structures (Fig 2) lies, interestingly, in the LGN. The LGN obtains information directly from retinal ganglion cells. It also has strong feedback connections with the visual striata. Thus a large LGN indicates exceptional prioritization of visual input and a need for instantaneous spatio-temporal calculations perhaps for rapid motor reflexes. Further, the LGN also plays an important role in integration of directives for visual attention with other sensory input, such as sound cues. Output signals from the LGN determine the spatial dimensions of the raw visual inputs from anatomically corresponding points along both retina. This information is used as feedback for visual focus on objects of interest in the external environment. Thus, the LGN could serve in locating conspecifics who might be separated in arboreal, visually occluded, environs where transposition-rich musical calls would propagate most efficiently.

Terrestrial Ecology

Spectral attributes of acoustic output seem to decline for most terrestrial species. But syllables may be maintained via neutral or balancing selection. In humans, who have noses that rise meters above the (relatively odoriferous) earth, such selection may have even been positive. But other spectral qualities are likely undergoing decline like they have in other terrestrial primates and birds. A few exceptional possibilities for spatio-motor emplacement [ME] persisting to manifest include throwing as part of ballistic hunting in humans. Features of PIANO could have also applied to more nomadic hunter-gatherers or pastoralists who still needed to orient to repositioning of nearby tribes—ever shifting acoustic landmarks on the nomadic ancestral plain. A more postural application of ME could be hammering for stone tool making. Even more intricate tool making, such as those that don't fossilize or last millions of years, could also have comprised the underlying trait bolstering such being signaling via musicality. These other less ballistic forms may have entailed more complex motor plans with numerous lengthy steps and could have corresponded to longer more hierarchically elaborate songs. This scenario thereby possibly Implicates a final missing piece in a full stack of vertically connected brain components—including cerebellum and basal ganglia—which lie intermediate to areas involved in ME (below) and PIANO (above).

Yet evidence suggests that only temporal qualities should increase, and then for max not mean levels of patterning. Thus even such temporal acoustic signals in humans may have been more ornamental for sexual signals rather than for more routine egalitarian ones. If larger visual areas are primarily associated with repetition, for example, and my proposal concerning inter-orbital pattern matching (as part of ME) is correct—occasional rapid climbing could have been the primary target of signal selection. This scenario is coherent if early homo only used trees for sleeping and protection during the night. Even later members of genus homo would likely still climb trees to gather fruit or honey. This preservation of repetitive acoustics as a sexually selected ornament in males would be compatible with provisioning behavior by males during high calorie demands of gestation and lactation. Furthermore, assuming a more gibbon- or bonobo- like, free and egalitarian mating system, this increasing sexual dimorphism could explain the carryover into our modest imbalance of singer sex-ratios in popular music today.

Sexual selection and temporal display

There is an undeniable strangeness about the popularity and fervor us (western civilization) humans have for our music, particularly because our practice is so commonly decoupled from any obvious survival value, Even the astonishing genius of Charles Darwin struggled with the problem of music in humans and accordingly allocated additional decades of labor to tackle such curious emotional traits, inventing a new form of (sexual) selection, en route. That its ultimate function is so mystifying is a major clue that he may have been on the right track by looking at the difference in mating goals of sexual dimorphic species. I have argued above that musicality evolved in more committed partnerships: in k-selected species, for the mutualistic goals of rearing offspring in arboreally precarious habitats. But I have also shared evidence that terrrestriality tends to diminish the very spectral qualities that are signaled by an increasingly irrelevant form of locomotion. Thus, while musicality may have initially evolved via sexual choice or mate selection for monogamous arborealists, terrestrial descendant appears to have only atrophied manifestations. I have proposed that musicality in formerly arboreal and now terrestrial species, like ours, are experiencing a split between vestigial spectral qualities to their musicality.

However, I have also reported an increase in temporal patterning that has increased. For example, the average of the most rhythmic calls in terrestrial species is more rhythmic than the average of the most rhythmic calls in arboreal species. Thus, it appears that temporal features of terrestrial primates is becoming more ornamental and perhaps therefore also dimorphic and truly sexually selected. A display that comes to mind, to solidify this point, is that of a chest beating gorilla who may spend most of his life on the ground, but may only very occasionally need to use pattern matching (for ME) to rapidly climb a tree, perhaps, in rare circumstances, when not the largest animal around. This form of terrestrial signal, where upper and lower body motor functions are decoupled, could be the norm for signaling full functionality in such semi-vestigial limbs. Similar dimorphism appears to have manifested in more rhythmic displays of humans (e.g. dancing) around the globe as well.

A higher degree of rhythmic patterning of vocalizations have been shown to result in greater reproductive success in birds. Longer more rhythmically precise singing may signal status in being unperturbed by predators in spite of giving away location. Uniformity of trilling, to use another related example, may likewise signal confidence as only those individuals who can afford to concentrate full attention on the calling are able to make the pattern so reliably (Zahavi and Zahavi, 1999). Thus rhythm, like melodic matching, can have a similar signaling mechanism, here illustrated via more costly than indicative for branch landing.

Group factors on motive emplacement and entrainment

This paper began by forwarding the weak assertion that motive emplacement was the neuro-modular substrate acted upon by indirect selection for genes by the opposite sex. And while much of the rest of the paper argues for higher brain processing of these signals in a way that facilitates higher order social functioning (e.g. child-rearing and spacing), here I return, full circle, to motive emplacement, but now in a larger group context. The primary way in which entrainment becomes important is for rhythmic group performances. But instead of placing limbs on branches, we now grasp each other. Dancing has essentially become a (loco)motor-visual display using semi-vestigial limbs accompanying temporally dominating musical-auditory signals. These signals possibly evolved to demonstrate that such limbs still can, in-fact, function, for other occasional secondary uses.

Despite the recent finding that rhythmicity tends to decrease as group sizes grow larger across primate species (Schruth, 2022), there is something unmistakably inviting about a (visible) instrumental rhythmic performance. Other researchers have noted that metrical rhythm easy for an outsider to join (Savage *et al.*, 2021). I have recently noted that there even appears to be more room for additional performers beyond the typical small-family spectral-performance of gibbons, to something more on the order of six individuals. There is an undeniable relationship between terrestriaity and group size, and in order for our progenitors to survive terrestrially for long, they needed to learn how to work together in larger groups: for example to team up on more ferocious terrestrial carnivores, for scavenging or hunting or both.

Thus musicality seems to run the full gamut of associations from those involving infant care, to mate bonding, to intra- and inter- group signaling. I therefore concur with efforts to develop a broad and inclusive theory where signaling and bonding theories can coexist under one framework (Savage *et al.*, 2021). Others have argued that this spectrum is actually U-shaped from mother infant to pair to group (Lehmann, Welker and Schiefenhövel, 2009), more akin to what I have attempted to do above from a mostly signaling perspective. And yet, with the curious case of human music, this paper has come (chronologically) full circle back to the (short term) sexually selective signaling for copulation opportunities presented by the visio-motor flavor of ME modules I have presented here. Rhythmic patterning has turned out to be not only the most ancient (monotonic), but paradoxically also the most modern (complex). And while there were not strong correlations for monotonic rhythm, others have noted an important role of the cerebellum and embodied motor areas.

Motor planning, basal ganglia, and the full cognitive stack of music

Above I have made the case that MEE may have been important for movement in precarious proximity (e.g. acrobatic tree sharing by gibbons or other aerial primates). But its not entirely clear why MEE might be important in humans except for the occasional intense bout of hand to hand fighting. The answer could come in the form of complex motor planning and execution. While vocal production learning is largely absent in primates (Janik and Slater, 1997; Fitch, 2015) sequencing of song elements (Petkov and Wilson, 2012) may show some signs of manifesting in certain species. Primates are notorious for being unable to use their lips and tongues in a way that even comes close to what humans can do for language. But with gesture, apes are extremely proficient at communicating. This has led some researches to even go as far as defining musicality around the ideas—as "deliberately controlled and metrically organized gesture" (Morley, 2014). There is an undeniable sequencing overlap of music with language (Merker, Morley and Zuidema, 2015) with corresponding requisite motor sequencing (Brown, Martinez and Parsons, 2004) and the maintaining selection on syllables diversity could translate into the lexical processing areas surrounding the temporal lobe (e.g. Broca's & Heschl's areas). This line of thinking requires a bit of punctuated leap in abilities from the motor-planning of limbs (in apes) to that of the vocal apparatus (in humans). While some plasticity demonstrated in primate calls, in marmosets and spectral features of tamarins (Weiss, Hotchkin and Parks, 2014) and loudness and duration in macaques (Bryant, 2013). Gibbons have high degree of heritability of a fixed syntax to their calls (Geissmann, 2000; Fitch, 2015), although the spacing, timing, amplitude and spectral qualities are obviously improved upon between infancy and adulthood.

The basal ganglia [BG], an area thought to be central for complex motor planing, was negatively correlated with the ARDI musicality measure. A reconsideration, however, is possible if we are willing to assuming tarsiers represent an exceptional outlier. If the BG is involved in higher order musicality to signal higher order locomotor planning—for example convoluted terminal branch landing in gibbons or complex multi-person (e.g. swing) dancing in humans—it may represent a recent addition to a complete (and possibly integrated) stack of motor control underlying musical signaling. Thus human music may represent a full cognitive stack of motor control through many levels, cortices, and systems.

Adaptive significance to modern societies and civilizations

Music has been described as a non-selected by-product of biased predispositions for other evolved capacities. Steven Pinker famously called music "Auditory cheesecake." Music may merely be a culturally created yet highly evocative system of sounds designed to exploit unconscious and biologically evolved perceptual response biases to distinguish the affiliative from the threatening (Bryant, 2013). Just because certain display traits may originated via non-selective mating preference, however, doesn't mean they have to remain non-selective (Searcy, 1992). Recently there has been a call to move beyond the idea of by-products as final evolutionary dead ends, towards thinking about exaptation instead (Savage *et al.*, 2021). Rather than thinking of music exploiting auditory scene analysis modules, we can invoke culture as salvaging this perceptual apparatus as exaptation (Trainor, 2015, p. 2). In fact, the entire history of musical feature accrual could be re-construed in this way. Music is composed of components that correspond to different adaptive pressures over evolutionary time (Honing *et al.*, 2015; Trainor, 2015).

On the opposite extreme, some have claimed that human music is entirely unique. Despite claims that animal musicality and singing has no homology or analogy with human forms (Hauser and McDermott, 2003; Savage *et al.*, 2021), the data suggests otherwise. I have shown elsewhere (Schruth, 2020) that musicality (as measured via ARDI) has a strong evolutionary signal (lambda=.8) evidencing a deep homology in primates. Further, while singing is likely not homologous with birds, and constitutes a more rare form in primates, humans do share substantial homology with gibbons. Gibbons do have the lowest average of the family's species' most rhythmic calls, among apes (Schruth, 2022). But unlike increasingly vestigial melody, terrestriality seems to have increased selection for ornamental rhythm in humans. This combined with complex motor planning required for dancing and language leaves vocal rhythmic display as tirelessly engaging topic of study.

Conclusion

In conclusion, music-like signaling appears to have evolved with fundamental visual, motor, emotive, and spatial-orientating structures of the mid-brain, allo-archi- and paralimbic cortical areas. Associations of temporally aesthetic features with visual-spatial areas confirm auditory grouping predictions of both PIANO and ME. These further indicate possible ornamental selection for vision related function associated with ME in terrestrial primates who practice only semi-vestigial use of fore-limbs. Spectral feature associations with spatial areas, notably, may be more relevant in visually occluded environments. Further, these acoustic features have strong phylogenetic signal and their cognitive associations coincide in deep-clade primate lineages such as tarsiers.

The paralimbic and archicortical areas, in particular, seem well situated between the most ancient sense (of smell) and more recently evolved senses (e.g. of hearing)—both highly integral in localization of the moving landmarks of conspecifics and predators alike. Intervalic associations with motor areas, on the other hand, suggest musical frequency changes in calls could serve as indirect signals for fine muscle control in (also formerly) arboreally acrobatic species. It is possible that cognition for in-motion binocular visual resolution of branch-shapes required to accurately land high-speed locomotor bouts—may have also occasionally been co-opted for auditory signal assessment when stationary. The comparative processing of auditory-spectral gestures was likely not only used for identification and localization, but could have supplementally been recruited for assessment of display quality. Such a receiver-side function of display quality assessment, rather than a strictly orientational capacity, is evidenced by the higher correlation of musical calling with orbital-motor (LGN) over paralimbic regions, though both associate positively.

Strong emotional associations with intervalic spectral features suggest musical calls may have early maternal-infant locational roots. But these signals may have been co-opted by adults to signal reliable motor control capacities to long term mates. The model presented here further suggests that (arboreal) signal receivers use spectral qualities of possibly direct signals of nurtural security to assess quality of long-term mates. It is also possible that a harmonious inter-family coexistence driven by range spacing is enforced via hormonal-reproductive suppression via these very same highly intervalic calls. Rhythmic complexity has independently evolved in several disparate terrestrial primates, but in humans this has coincided with exceptionally longer songs and linguistic sequences. Thus while rhythmic aspects may currently persist in humans as indirect opportunistic indicators of occasional motor-control capacities, more fully featured musical complexity appears to have evolved in longer-term arboreal mate-choice consistency contexts. Only through a life-time and life-history holistic perspective, considering the complete mate-choice cycle, can we understand both the indirect and direct selection effects driving musical courtship signaling, for both genetics and nurture of viable offspring.

Acknowledgements

I thank Rob, Aditya, Sarah, and Jeannie, and Tiffany for scoring spectrograms. I also thank my former collaborators Chris Templeton, Darryl Holman, and Eric Smith for their ongoing contributions to related projects. I also thank Eliot Brenowitz and Joseph Sisneiros for granting me permission to audit their neuroetholgy course.

Statement of Ethics

No live animals were used in the compilation of our data.

Conflict of Interest Statement

The authors declare no obvious conflicts of interest.

Funding Sources

The author declares no funding sources.

Data Availability Statement

The data is available on-line at http://osf.io/bvsfz

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