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Rhythmic Roots: The Adaptive Functions of Vocal Isochrony and Its Role in Human Music and Language Evolution

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Abstract

Isochrony, or the regular timing of sounds, is a prominent rhythmic feature of human music and can also be found in the vocalisations of non-human animals. In the evolution of music and language, the capacity for vocal learning is hypothesised to have played a key role, with vocal learning species thought to have more advanced rhythmic capabilities. However, studies show that vocal isochrony is also present in vocal non-learners, indicating that it is perhaps a highly conserved property providing adaptive benefits across taxa. As mechanisms that are shared across multiple species are likely to have been the bedrocks of our current abilities, comparative research into vocal isochrony can give clues on how rhythms in human music and language might have evolved, even though modern speech is not typically isochronous. This review summarises possible adaptive functions of vocal isochrony by describing its presence across different species and call types found in recent

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research. Thus, it represents a narrative synthesis of the adaptive functions of vocal isochrony. Here, we highlight three major possible functions of vocal isochrony: firstly, isochrony could improve communication by enhancing signal transmission from one individual and auditory detection by others and possibly function in conveying meaning. Secondly, vocal isochrony could inform others about mate quality, indicating a role in sexual selection. Lastly, isochrony could facilitate vocal coordination between two or more individuals, as the predictability of isochrony can help individuals to adjust the timing of their vocalisations to each other more readily. These functions seem to be highly intercorrelated, which might provide clues for the evolution of human music and speech.

Keywords: vocal isochrony, rhythm, music evolution, language evolution, comparative cognition

Introduction

Music is a universal aspect of human cultures (Mehr et al., 2019). People can not only create music by singing and playing instruments, but they also entrain to it by moving along with rhythms in music. Those rhythms, defined as the temporal patterns by which sounds are spaced in time (McAuley, 2010), form the basis of music. The simplest form is isochronous rhythms (Ravignani & Madison, 2017), which are sounds produced at equal intervals, similar to a metronome or the ticking of a clock (McAuley, 2010). These are commonly found across cultures in human music (Savage et al., 2015). Although non-human animals (henceforth animals) mostly produce less complex rhythms than present in human music, it has been shown that isochrony is present in numerous natural behaviours (e.g., De Gregorio, Raimondi, et al., 2024; Norton & Scharff, 2016; Roeske et al., 2020).

Darwin already proposed in 1871 that the rhythmic abilities of humans may lie in ancient neural patterns of the brain that we share with animals, suggesting that basic rhythmic capabilities are likely shared as well (Patel, 2014). Today we may further describe these neural patterns as synchronous isochronous oscillating neurons, which are common in the brain (Buzsaki, 2006; Kanduri et al., 2015; Ukkola et al., 2009; Ukkola-Vuoti et al., 2013), making isochrony an emergent property of the nervous system (Ravignani & Madison, 2017).

Neural oscillators have previously been hypothesised to be responsible for a multitude of isochronous behaviours (Ravignani & De Reus, 2019; Ravignani & Madison, 2017), for example in the synchronised flashing of fireflies, but also in acoustic behaviours like the chorusing of crickets and frogs (Ravignani et al., 2014; Zelick & Narins, 1985). Indeed, isochrony can be found in a multitude of species, both in solo and coordinated behaviours. For example, harbour seals isochronously slap their flippers against their bodies or in water (Kocsis et al., 2024), while male palm cockatoos use sticks or seed pods to rhythmically drum on hollow tree parts (Heinsohn et al., 2017). Additionally, we can find isochrony in vocal signals, such as the song of thrush nightingales (Roeske et al., 2020) and the coordinated songs of crested gibbons (De Gregorio, Raimondi, et al., 2024) or in the temporal patterns of humpback whale vocalisations (Schneider & Mercado, 2019). Such fast endogenous rhythms in animal communication signals may be controlled by pacemakers in the central nervous system (Greenfield, 1994), which trigger a call when their excitation is at the maximum level and then return to base levels (Greenfield & Merker, 2023).

Apart from communicative behaviours, elements of isochrony can be found in heartbeats, respiration, and locomotion (Winfree, 1986), making isochronous rhythms part of the daily lives of humans and animals alike. This may in part explain why a multitude of species can discriminate between isochrony and anisochrony (i.e., the opposite of isochrony where intervals do not have the same durations). Humans can detect deviations as small as 2.5% from a perfect isochronous pulse (Friberg & Sundberg, 1995) and can also generalise to different tempos (Celma-Miralles & Toro, 2020; Van der Aa et al., 2015). In other animals, abilities to detect isochrony vary. For example, carneau pigeons are not able to discriminate between isochrony and anisochrony but do differentiate between different tempos in isochronous sequences (Hagmann & Cook, 2010). Other animals, such as harbour seals and zebra finches, can differentiate isochrony and anisochrony (Van der Aa et al., 2015; Verga et al., 2022) and rats and starlings have even been shown to generalise this differentiation to tempos they did not hear before (Celma-Miralles & Toro, 2020; Hulse et al., 1984; Mayayo & Toro, 2024). These different abilities could be explained by interspecific preferences to either use local features or the overall distribution of sounds to predict the next event (Spierings & ten Cate, 2016; ten Cate et al., 2016), as recognising isochrony may necessitate attending to the regular distribution of sounds over longer time periods.

Although isochronous rhythm perception and production seem to be widespread across taxa, much remains unknown about the role and evolution of rhythmic capabilities in vocal behaviour. Comparative research between the vocal behaviour of humans and other animal species might provide further insight into whether isochrony played a role in both the evolution of musicality – the biological and cognitive capacities that underlie the ability to perceive and produce music (Honing et al., 2015; Savage et al., 2021) – and language. As described, research has mostly focused on whether animals are capable of perceiving and producing isochronous rhythms, but little emphasis has been on the possible functions of isochrony. However, if we want to understand the role of vocal isochrony in the evolution of musicality and language, we have to know what the adaptive functions of isochrony in vocal communication are. In this review we aim to conceptually synthesize the presence and functions of isochrony across species. We searched Google Scholar for research articles (observational or playback studies) using the following search terms (vocalisations, calls, isochrony, isochronous rhythm, temporal regularity). Additionally, we took articles into account that were referred to in the articles found through these search terms. We only included studies that calculated isochrony based on the inter-onset interval, as low variance in inter-call intervals alone cannot guarantee isochrony of a sequence (see Box 1 for how isochrony is calculated in the included studies). For playback studies we only took studies into account, that used – manipulated or unaltered – naturally occurring vocalisations. The overview of included studies can be found in Table 1 (for analysis of vocalisations) and Table 2 (for playback studies).

Here we highlight and provide exemplary studies for three primary adaptive functions of isochrony, that will be described below:

1) Enhancing the transmission of signals (e.g., Hersh et al., 2024; Norton & Scharff, 2016)
2) Signalling mate quality (e.g., Demartsev et al., 2023)
3) Facilitating vocal coordination (e.g., De Gregorio et al., 2021; Ma et al., 2024)

Box 1

Calculating Isochronous Rhythms

A common method of calculating whether rhythms are isochronous is by determining rhythm ratios, based on inter-onset interval (IOI) duration (e.g., Anichini et al., 2023; Clink, 2024; De Gregorio et al., 2021; Demartsev et al., 2023):

$$r_k = \frac{i_k}{i_k + i_{k+1}}$$

where i_k is the IOI duration of the first interval, and i_{k+1} the next IOI. Say an IOI is 0.2s, and the following IOI is also 0.2s, this leads to a r_k value of 0.5, which can be categorized in the 1:1 category (isochrony).

Other methods include the calculation of a coefficient of variation (e.g., Bowling et al., 2013; De Gregorio et al., 2019), burstiness (Ravignani et al., 2019) and the generate-and-test approach (Burchardt et al., 2019; Norton & Scharff, 2016). Research only focusing on low variance in inter-call intervals cannot guarantee isochrony, as different lengths of call duration could make a sequence anisochronous. As an exception, in this review, one study was included that mentioned exceptionally low standard deviations for both the call duration and interval duration (Herzing, 2015).

Table 1

Overview of Included Studies Investigating the Presence of Isochrony in Naturally Occurring Vocalisations

Species category	**Species**	**Vocal learner**	**Call type**	**Call function**	**Isochrony**	**Reference**
Primates	*Homo sapiens*	1	Speech		X	Bowling et al. (2013)
Passerine	*Cracticus nigrogularis*	1	Song	Territorial/mate attraction[1]	I	Xing et al. (2022)
	Taeniopygia guttata	1	Song	Territorial/mate attraction	I	Norton & Scharff (2016)
	Luscinia luscinia *Taeniopygia guttata*	1	Song	Territorial/mate attraction	I	Roeske et al. (2020)
Pinnipeds	*Arctocephalus pusillus pusillus*	1	Barks (adult females)	Threat	I	Osiecka et al. (2024)
			Barks (pups)		V	
	Arctocephalus pusillus pusillus	1	Mother attraction calls	Mother-pup recognition	X	Osiecka et al. (2022)
			Pup attraction calls		X	
	Phoca vitulina	1	Mother attraction calls	Mother-pup recognition	X	Anichini et al. (2023)
	Phoca vitulina	1	Mother attraction calls	Mother-pup recognition	X	Ravignani et al. (2019)
Cetaceans	*Stenella frontalis*	1	Synchronized squawks	Interspecific aggression	I	Herzing (2015)
	Megaptera novaeangliae	2	Whale song	Mate attraction[2]	V	Schneider & Mercado (2019)
Bats	*Saccopteryx bilineata*	2	Echolocation calls	Navigation/locating prey	I	Burchardt et al. (2019)
			Male song	Territorial/mate attraction	I	
			Pup isolation calls	Solicit maternal care	I	

Species category	Species	Vocal learner	Call type	Call function	Isochrony	Reference
Primates	*Hylobates lar*	3	Solo	Courtship	I	Raimondi et al. (2023)
			Duet	Territorial/bond strength	I	
	Indri indri	3	Duet/chorus	Territorial/bond strength	I	De Gregorio et al. (2019)
			Duet/chorus	Territorial/bond strength	I	De Gregorio et al. (2021)
			Duet/chorus	Territorial/bond strength	I	De Gregorio, Maiolini, et al. (2024)
			Honks	Terrestrial predator	I	
			Alarm roars	Aerial predator	X	
			Song roars	Attention gathering before singing	X	
	Nomascus gabriellae	3	Duet/chorus	Territorial/bond strength	I	De Gregorio, Raimondi, et al. (2024)
	Nomascus leucogenys					
	Nomascus siki					
	Nomascus concolor	3	Duet/chorus	Territorial/bond strength	I	Ma et al. (2024)
	Nomascus hainanus					
	Nomascus nasutus					
	Pongo pygmaeus	3	Flanged male long calls	Territorial/mate attraction[3]	I	Lameira et al. (2024)
Fish	*Halobactrachus didactylus*	-	Boatwhistle	Mate attraction	V	Vieira et al. (2021)
	Sciaena umbra	-	R-calls	Signalling reproductive state	I	Picciulin et al. (2024)
Hyraxes	*Procavia capensis*	-	Male song	Mate attraction	I	Demartsev et al. (2023)

[1] Collins (2004); [2] Herman (2017); [3] Setia & van Schaik (2007).

Note. The numbers indicate the order of vocal learning this species belongs to (1 = highest order, 2 = middle order, 3 = lowest order, - = vocal non-learner or unknown; Arriaga & Jarvis, 2013; Janik & Knörnschild, 2021). The isochrony column indicates whether isochrony was found in the call type (I = isochrony, V = variable, X = absent).

Table 2

Overview of Included Playback Studies Using Sequences of Isochronous (and Anisochronous) Conspecific Vocalisations

Species category	**Species**	**Vocal learner**	**Call type**	**Call function**	**Result**	**Reference**
Passerine	*Grallina cyanoleuca*	1	Duet	Territorial	Birds responded more to isochronous duets than to irregular duets	Ręk & Magrath (2023)
Pinnipeds	*Phoca vitulina*	1	Mother attraction calls	Mother-pup recognition	Pups look more often when isochronous playbacks are presented compared to random	Verga et al. (2022)
Rodents	*Mus musculus*	3	Courtship song	Mate attraction	Females approached regular sequences more than irregular sequences; no preference for perfectly isochronous over regular playbacks	Perrodin et al. (2023)
Gruiformes	*Crex crex*	-	Loud calls	Indicate aggressiveness	Males learned new association and started employing it in their own calling behaviour	Ręk (2013)

Note. The numbers indicate the order of vocal learning this species belongs to (1 = highest order, 2 = middle order, 3 = lowest order, - = vocal non-learner or unknown; Arriaga & Jarvis, 2013; Janik & Knörnschild, 2021).

Isochrony Enhances Signal Transmission

One adaptive function of isochrony might be the enhancement of signals to make transmission more effective. The predictability provided by isochrony could reduce the attentional energy to rhythmic properties in receivers, which in turn could lead to benefits such as better auditory detection in noisy environments (Norton & Scharff, 2016) or an increased ability to focus on other properties of the call (Hersh et al., 2024). Indeed, humans perform better in detecting target noise bursts in a noisy environment when they are presented in a temporally predictable way (Lawrance et al., 2014). Furthermore, in humans the pitch of regularly timed tones is guessed more accurately than with irregularly timed tones (Jones et al., 2002). To date there is no study directly supporting this hypothesis in other animals. However, studies suggest that isochronous rhythms may support vocal learning (Bruno, 2017; Ravignani, 2021; Roeske et al., 2020). In addition, a study on greater sac-winged bats, who exhibit three different isochronous calls, shows that these calls are coupled to the rhythm of the wingbeat. This coupling might make them easier for listeners to detect, as bats might be neurally attuned to wingbeat rhythms (Burchardt et al., 2019).

Isochrony could also expand the options for information transmission. As an animal´s vocal repertoire is limited compared to humans (Hammerschmidt & Fischer, 2008), other strategies could be used, such as combining calls, varying the acoustic structure (Coye et al., 2018) or using different rhythms such as isochrony as additional components to expand the communicative possibilities. A playback study on corncrake males has shown that they can expand their repertoire by learning to associate specific artificial rhythms to new contexts and using those rhythms themselves in a way not previously present in their behaviour (Ręk, 2013). Orangutans' isochronous long calls have been found to contain different levels of faster isochronous tempos occurring within the overarching slower isochronous tempo of the sequence, which could serve a similar function as recursion in human language, where a language element placed inside another language element can add meaning to a sentence (Lameira et al., 2024).

Additionally, isochrony could be used to add individual ‘signatures’ to acoustic signals. Chimpanzee drumming is thought to encode individual identity with chimps using individual rhythms, including isochrony, during travels (Eleuteri et al., 2022). Northern elephant seals’ male barks contain individual specific regular rhythms and remain stable over time. Individuals retreat from unaltered playbacks as well as calls altered within the individual’s natural range, while manipulated calls outside the intra-individual range are ignored (Mathevon et al., 2017). However, while the barks of both female adult and pup cape fur seals are isochronous (Osiecka et al., 2024), there is no isochrony in mother- or pup attraction calls (Osiecka et al., 2022). Taking these results together, it is therefore still not fully clear whether and how isochrony functions as an indicator for identity in vocalisations.

Isochrony Signals Mate Quality

Vocal behaviour as a whole has often been hypothesised to have evolved in the context of sexual selection. Different vocalisation properties have been linked to indicators of mate quality, such as food availability (Berg et al., 2005), body size (Kagawa & Soma, 2013), lung capacity (Fitch & Hauser, 2003), nesting success (Hoi-Leitner et al., 1995) and immune function (Puts et al., 2016). Additionally, it has been shown that in some bird species more elaborate singing and higher singing rates are preferred by females (e.g., pied flycatcher, Alatalo et al., 1990; song sparrow, Nowicki et al., 2002b; white-throated sparrow, Wasserman & Cigliano, 1991).

Bird song, as one of the most elaborate vocal behaviours, is energetically costly to produce (Berg et al., 2005) and depends on brain structures that cannot withstand poor nutrition or developmental stress (Nowicki et al., 2002a), thus possibly serving as a handicap (Zahavi, 1975). This may specifically affect rhythmic behaviours, since repetition over time has been shown to indicate developmental stability and the amount of neural noise (Van den Broek & Todd, 2009). Deviations from isochronic rhythms could heighten the salience of neural noise, making it easier for females to detect (Van den Broek & Todd, 2003). Interestingly, a study on zebra finches showed that males downregulate the levels of neuronal noise when singing in the presence of a female compared to undirected singing (Hessler & Doupe, 1999). Although there is little direct evidence for this relationship, isochrony can be found in the courtship songs of zebra finches and thrush nightingales (Norton & Scharff, 2016; Roeske et al., 2020), and in the inter-phrase interval of Australian pied butcherbirds (Xing et al., 2022), but also brown meagres (e.g., Picciulin et al., 2024). Being able to maintain a regular rhythm might indicate higher energy reserves and better respiratory capabilities (Van den Broek & Todd, 2009). Lusitanian toadfish switch between a harder to maintain isochronous and an anisochronous calling rate (Vieira et al., 2021), possibly signalling their body condition through the relative proportion of isochronic calling (Amorim et al., 2010; Vieira et al., 2021). Furthermore, the offspring of rock hyrax males with more isochronous precision have a higher chance of surviving to be at least 1 year old (Demartsev et al., 2023). Moreover, if isochrony is an indicator of mate quality, we would expect potential mates to prefer regularity over irregularity. Indeed, mice have been shown to approach temporally regular courtship songs more often than irregular ones (Perrodin et al., 2023). When tested with perfectly isochronous songs, the mice, however, showed no preference compared to naturally regular songs, indicating a ceiling effect (Perrodin et al., 2023). The fact that zebra finch males do not adjust the isochrony of their song to the presence of a female (Norton & Scharff, 2016) further suggests that isochrony could be an inflexible property of vocalisations that may serve as an honest signal of mate quality.

Isochrony Facilitates Vocal Coordination

Isochrony may also play an important role in vocal coordination (Ma et al., 2024) by enabling listeners to predict the start of the next call and allowing senders to adjust their call timing to either synchronise or alternate with one or more individuals (Ravignani & Madison, 2017; Roeske et al., 2020). In synchronising – where individuals time their vocalisations to onset at the same time (Greenfield & Merker, 2023) – isochrony seems to have three different functions: firstly, synchrony is thought to help attract mates to an area by intensifying the signal or indicating high habitat resource availability (Greenfield & Merker, 2023; Ravignani et al., 2014). Japanese treefrog females, for example, are more likely to approach playbacks of a synchronised chorus than an asynchronous one (Legett et al., 2021). Secondly, synchrony might lower the individual predation risk, by making it more difficult for eavesdropping predators to localise single individuals (Greenfield & Merker, 2023). For example, bats that predate on pug-nosed treefrogs are less likely to respond to synchronous choruses than asynchronous choruses (Tuttle & Ryan, 1982). Thirdly, vocal synchrony could play a role in group cohesion and social bonding (Launay et al., 2016). This has been shown in multiple studies investigating the effect of synchronous singing on humans (Kreutz, 2014; Pearce et al., 2015, 2017). Moreover, Atlantic spotted dolphin males synchronise their squawks, a call type produced during intra- and interspecific aggression, possibly to display the strength of their alliance (Herzing, 2015). Additionally, although isochrony is usually absent in modern human speech, human speech rhythms can move towards isochrony to facilitate vocal synchronisation in artificial tasks (Bowling et al., 2013; Filippi et al., 2019).

In contrast, one of the main adaptive functions of alternation – where individuals signal out of phase – may lie in avoiding overlaps masking advertisement signals, preventing potential mates from perceiving the signal (Greenfield & Merker, 2023). Indeed, túngara frog females prefer non-overlapping calls (Legett et al., 2019). Furthermore, isochrony enables turn-taking, which can foster (perceived) group cohesion and territorial defence. Playing back regular conspecifics' duets triggered stronger territorial responses than irregular duets in Australian magpie-larks (Ręk & Magrath, 2023), suggesting that coordinated duets are stronger territorial signals. Alternation might have led to turn-taking like we find in human speech today, as it helps speakers to avoid overlapping each other, while still continuing the conversation with relatively little silence between two speakers (Ravignani & Madison, 2017).

In duetting and coordinated songs, synchronisation and alternation are often combined. Evidence that isochrony indeed facilitates vocal coordination comes from recent research in gibbons and indris, which found isochrony in songs that play a role in territorial defence and signalling social bond strength (De Gregorio et al., 2019, 2021, 2022; Gregorio, Maiolini, et al 2024; Gregorio, Raimondi, et al. 2024; Ma et al., 2022, 2024; Raimondi et al., 2023; Torti et al., 2013). In crested gibbons, more isochronous male singing leads to a higher proportion of females successfully completing a great call (Ma et al., 2024). Most studies point to the predictability of isochrony facilitating vocal coordination in duetting and chorusing species, however, in Lusitanian toadfish for example, alternation occurs with isochronous rhythms, while synchrony is more common with irregular rhythms, showing it might be species-specific whether isochrony leads to improved synchrony or alternation (Vieira et al., 2021). In lar gibbons, isochrony does not necessarily lead to more synchronous songs and vice versa, as females start singing less isochronous with an increase in synchronisation, suggesting that the calls not only indicate mate status but also potentially serve as signals to female competitors and higher quality males (Raimondi et al., 2023). Additionally, work investigating whether harbour seal pups might call isochronously to be able to alternate, and thereby avoid overlap of their mother attraction calls, found no evidence for isochrony (Anichini et al., 2023; Ravignani et al., 2019). Thus, although isochrony might facilitate vocal coordination, its functions seem to be multifold.

In humans, rhythmic synchrony is thought to have evolved in our ancestors as a means to attract migrating females (Merker et al., 2009; Ravignani & Madison, 2017). Combining vocal efforts to maximise the amplitude of their calls, using isochrony as predictable time points, could help in outcompeting other groups (Merker et al., 2009). This rhythmic vocal synchrony could then have further evolved as a coalition signal in humans drumming with their limbs, leading to what we now know as music (Hagen & Bryant, 2003; Merker et al., 2009). These isochronous vocal and non-vocal behaviours together with additional adaptations such as vocal learning and entrainment might have been one of the building blocks to the complex patterns we find in music and speech today.

Vocal Learning and Entrainment as Preadaptations for Musicality and Language

Similar brain areas activate when processing speech and music (Levitin & Menon, 2003; Ma et al., 2019; Peretz et al., 2015), suggesting that musicality and language may share the same evolutionary precursors. However, this topic is still widely debated. Other authors argue that although speech and music share overlapping brain areas, distinct areas can be found that are only activated in one or the other tasks, which is further supported by studies on patients with brain damages or developmental disorders affecting specific areas (see Leongómez et al., 2021 for a review and discussion). Darwin (1871) proposed that musicality and language may be based on the ability to imitate and modify sounds in nature, or sounds produced by con- or heterospecifics. This reinforces the role of vocal learning in human music and language evolution and has since been reframed as the musical protolanguage hypothesis (Fitch, 2013). How isochrony production and perception played a role here is not yet clear. Temporal rhythmic aspects of speech are, for example, provided by the duration of speech units and the pauses between them, or by the alternation of stressed and unstressed syllables (Filippi et al., 2019). Still, humans consistently rate song as more regular than speech (Yu et al., 2023). Different languages exhibit isochrony at different levels (Grabe & Low, 2002; Ravignani & Madison, 2017), but it has also been suggested that isochrony might only be a perceived trait of speech and not actually be present in speech (Jadoul et al., 2016; Lehiste, 1977). Regardless, isochrony may have been the dominant temporal structure in early human speech and thus may have provided anchoring points for speech elements to grab onto (De Gregorio, Maiolini, et al., 2024; Hersh et al., 2024; Jadoul et al., 2016; Patel, 2006; Ravignani et al., 2019). Consequently, isochrony may have been a building block of the more elaborate rhythms we find in speech today.

Additionally, vocal and rhythmic flexibility may be preadaptations for more complex traits like musicality and language, such as suggested by the vocal learning rhythmic synchronisation hypothesis (Patel, 2006, 2014, 2021). Vocal learning is a crucial mechanism for the evolution of human speech, enabling the production of a large repertoire of sounds and words (Lattenkamp & Vernes, 2018). In recent years, however, vocal learning has been proposed to exist on a continuum (Ten Cate et al., 2016), with humans, pinnipeds and songbirds in the highest order (Arriaga & Jarvis, 2013; Janik & Knörnschild, 2021). Non-human primates are considered lower order vocal learners (Janik & Knörnschild, 2021), but coordinated songs of indris and crested gibbons show both synchrony and alternation, and duet contributions can start and stop flexibly (De Reus et al., 2021; Gamba et al., 2016; Terleph et al., 2018). The presence of isochrony in some but not other call types in different species (De Gregorio, Maiolini, et al., 2024; Osiecka et al., 2022, 2024) further shows a flexible inclusion of it in call repertoires across multiple orders of vocal learners with varying degrees of vocal flexibility. Vocal learning capabilities have also been hypothesized to be the precursors for advanced rhythmic capabilities (Patel, 2021), such as beat-based timing and entrainment – the synchrony of behaviour with external rhythms (Merker et al., 2009) – which are theorised to be especially prominent in higher order vocal learners (Arriaga & Jarvis, 2013; Janik & Knörnschild, 2021; Patel, 2006, 2014, 2021). Parrots, for example, can be trained to synchronise their pecks with isochronous stimuli over different tempos and even spontaneously entrain their movements to human music (Hasegawa et al., 2011; Schachner et al., 2009; Seki & Tomyta, 2019). Simpler forms of entrainment can also be found in lower-order vocal learners, such as a bonobo (Large & Gray, 2015), and a chimpanzee (Hattori et al., 2013), which have been shown to be able to spontaneously synchronise tapping to an isochronous rhythm. However, both individuals were only able to entrain at a tempo range near their spontaneous tapping rate. Taking these findings into account, Merchant and Honing proposed the gradual audiomotor evolution hypothesis, suggesting that rhythmic entrainment is not necessarily linked to vocal learning, but developed gradually in primates, with humans showing the most advanced abilities in beat-based timing while sharing the ability of interval-based timing with non-human primates (Merchant & Honing, 2014).

Additionally, isochronic behaviour is also shown in vocal non-learners, such as frogs, and fish (e.g., Picciulin et al., 2024; Zelick & Narins, 1985). These findings may support the bootstrapping hypothesis by Ravignani (2021), which suggests that isochrony may be the basis for both advanced rhythmic and vocal capabilities, which in turn can bootstrap each other to further lead to vocal rhythms and, eventually, musicality.

Further insights into speech and music evolution could also be provided by a link between isochrony and emotional arousal. A musical protolanguage may have taken two routes: one leading to music, to mostly convey emotions, and the other to speech, to mostly convey meaning (Ma et al., 2019). In parallel, in the isochronous song of lar gibbons two tempos are prominent, one that corresponds to musical rhythms (~2 Hz) and the other corresponding to speech rhythms (~3-7 Hz; Raimondi et al., 2023). However, there has been no conclusive research on the link between isochrony and emotional arousal. In Cape fur seals, faster barks, associated with higher arousal (i.e., higher emotional intensity; Martin et al., 2022), lead to lower isochronous precision (Osiecka et al., 2024). Contrastingly, in crested gibbons faster call rates lead to more accurate isochrony (Ma et al., 2024), although the arousal levels during the production of these vocalisations cannot be inferred. Considering that, according to Filippi and colleagues (2019), communicating emotional arousal might be the evolutionary basis of temporal structures in vocalisations, further research is important to gain insight into how arousal affects isochronous precision.

Summary and Conclusion

In this review, we summarised the evidence for adaptive functions of isochrony in naturally occurring animal calls, highlighting three main possible adaptive functions of isochrony.

Firstly, there is evidence that isochrony can play a role in improving communication and conveying meaning to others. For example, vocal isochrony can provide adaptive benefits to both the sender and listener by improving auditory detection in noisy environments (Norton & Scharff, 2016) and better capturing the attention of others in urgent situations. Furthermore, isochrony can be associated with a particular context (De Gregorio, Maiolini et al., 2024; Osiecka et al., 2022, 2024) with individuals being able to learn to associate rhythms with certain circumstances (Ręk, 2013). In situations involving aggression, territorial defence and alarm calls, vocal isochrony providing effective transmission of signals can increase the survival of oneself, group members and offspring. Indeed, multiple studies find isochrony present in aggressive or territorial signals (e.g., Osiecka et al., 2024; Ręk, 2013). As such situations are often associated with arousal, isochrony might be the by-product of a lower limit of interval durations due to respiratory constraints, when an animal calls as fast as possible (De Gregorio, Maiolini et al., 2024). However, studies show that faster call rates can lead to both more isochronous (Ma et al., 2024) as well as less isochronous rhythms (Osiecka et al., 2024) and isochrony at different call tempi (De Gregorio, Maiolini, et al., 2024; Raimondi et al., 2023).

Secondly, isochrony can have an adaptive function in sexual selection. Studies show that isochrony is present in mate attraction calls (e.g., Norton & Scharff, 2016; Vieira et al., 2021) and although there are to our knowledge no studies directly investigating the preference for isochrony in a mating context, females have been found to be more attracted to temporally regular calls (Perrodin et al., 2023). Isochrony in vocal signals might indeed indicate mate quality (e.g., respiratory capabilities, higher energy reserves and genetic impairments; Amorim et al., 2010; Van den Broek & Todd, 2003, 2009; Vieira et al., 2021) and there seems to be a link between isochrony and reproductive success (Demartsev et al., 2023).

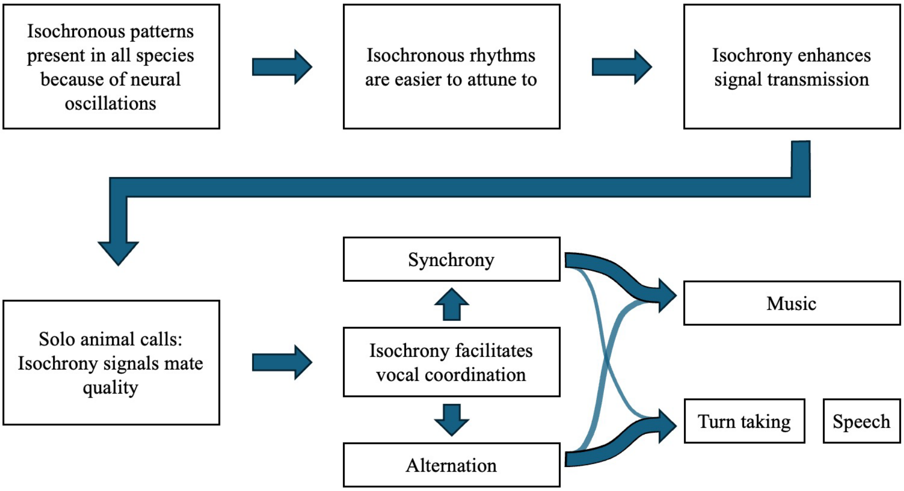
Lastly, the predictability of isochrony can aid in vocal coordination (i.e., synchrony and alternation), helping animals to more accurately predict the timing of the next call (Ravignani & Madison, 2017; Roeske et al., 2020). Recent research on singing primates shows better coordination between males and females when the male sings more isochronous (De Gregorio et al., 2022; Ma et al., 2022, 2024; Torti et al., 2013). Furthermore, isochrony is found in vocal coordination of dolphins and birds (e.g., Herzing, 2015; Ręk & Magrath, 2023).

The indicated adaptive functions of vocal isochrony are not exclusive but seem to be highly interrelated. Isochrony that may enhance auditory detection allows signals to reach listeners, including potential mates or vocally coordinating partners, better in noisy environments (Hersh et al., 2024; Norton & Scharff, 2016). Sexual selection and vocal coordination are probably also dependent. Synchrony could help to better attract mates by increasing the amplitude of attraction calls or by signalling habitat quality, whereas alternation is thought to have evolved to avoid the masking of mate attraction signals (Greenfield & Merker, 2023). These manifold benefits of isochrony raise the question why isochrony is not more often found in animals' vocalisation. Studies suggest that the production of stable rhythms might be subject to physiological constraints, such as body condition, respiratory ability and genetic predisposition (Demartsev et al., 2023; Van den Broek & Todd, 2003, 2009; Viera et al., 2021) and producing isochronic sequences could be energetically costly (Viera et al., 2021). Further research is needed to investigate whether there are direct links between isochrony and, for example, respiratory capabilities.

The interrelated functions of vocal isochrony can also give us clues into how both music and speech have evolved (Figure 1). We argue that, before vocal coordination came into play, solo animal calls initially influenced by sexual selection were central to the origin and persistence of vocal isochrony today, both in coordinated and non-coordinated vocalisations. Isochrony could have inherently been present in vocalisations performed solo due to the neural oscillators, from which potential mates could detect genetic impairment by detecting deviations from regularity (Van den Broek & Todd, 2003). From isochrony providing benefits in solo calls, vocal coordination could then have come into play. Vocal isochrony has likely facilitated both synchrony and alternation, leading to the development of music and turn-taking in speech, respectively, as also suggested by Ravignani and Madison (2017). While synchrony and alternation might have both played a role in the evolution of music and speech, we argue that synchrony was most important for the evolution of music and alternation for the evolution of speech. However, some questions remain open, such as why isochrony remains present in music to this day, while it seems to have disappeared in modern human speech, and how emotions and isochronous precision are linked. Thus, vocal isochrony in animals remains an intriguing research topic for investigating the possible adaptive function of isochrony in sound production.

Figure 1

A Representation of the Properties and Adaptive Functions of Vocal Isochrony and How They Might Have Evolved Into Music and Speech



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