# The evolution of gender dimorphism in the human voice:

# The role of *octave equivalence*

## Abstract

Humans exhibit what appears to be a unique vocal property: octave equivalence whereby adult male voices are, on average, an octave lower in pitch than those of adult females and children. The evolutionary significance of this seems largely to have escaped notice. While sexual selection might explain why male voices are generally lower, it cannot explain why they should be so much lower than what would be expected for body size, nor why the average difference should be exactly one octave. Nor does a generalised dimorphism convey why precisely tuned octaves feature so commonly in human vocal interaction.  The octave features strongly in the organisation of music. A consequence of this characteristic of human pitch perception and production is the capacity to share and respond to vocal pitches (and their instrumental equivalents) as if they are ‘the same’ irrespective of the difference in range, a phenomenon known as *octave equivalence*. We investigate the nature of octave equivalence from an adaptive perspective and propose a hypothesis for its evolution based on the importance of chorusing for social bonding and pitch-matching in inter-generational exchange.

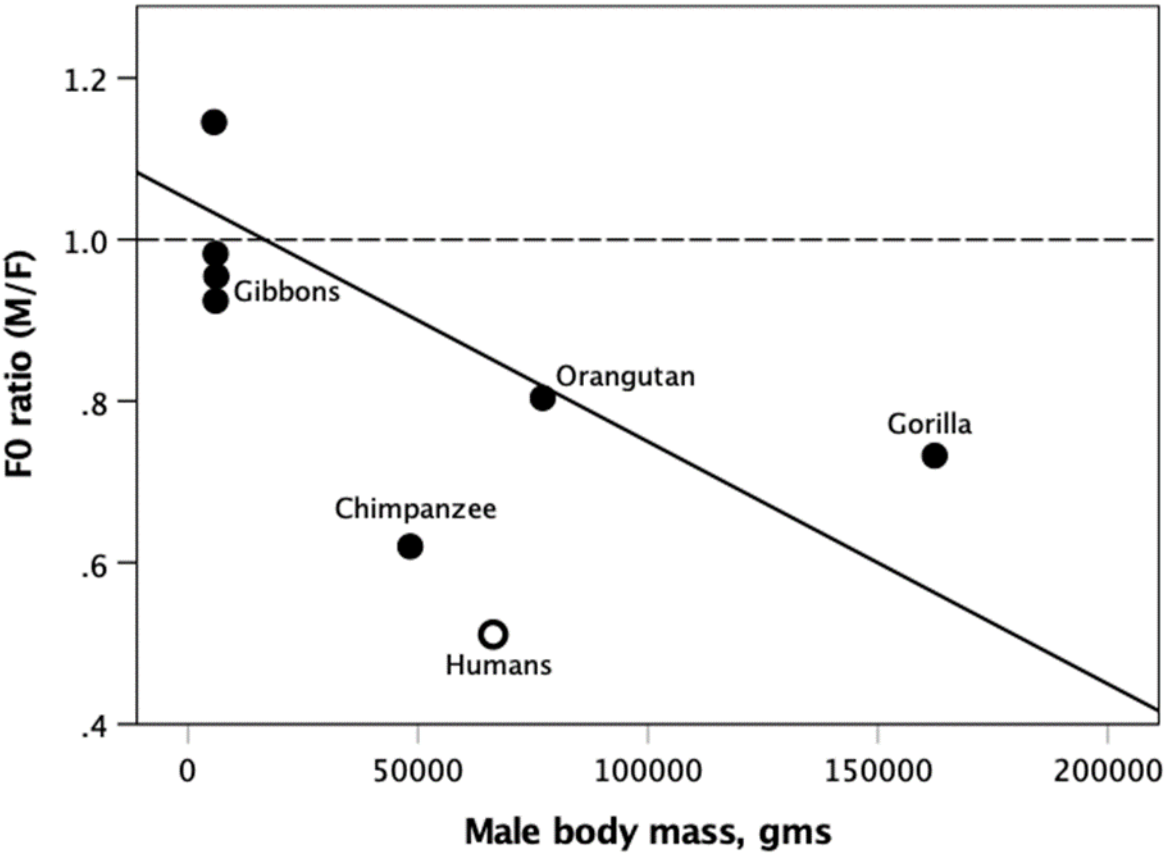
## Introduction: prevailing themes in the evolution of musical communication

An increasing body of research in a variety of disciplines (Bannan 2003, 2008, 2020; Dunbar 2012, 2014; Harvey 2017; Morley 2013; Savage et al. 2020; Wallin 1991) has converged on a position that presents the human capacity for music as adaptive and as representing the potential bridge between animal communication and human language. Features of proto-musical behaviour that contribute to this perspective include: the capacity, unmatched in any other species, to entrain to a beat, and to achieve this during both locomotion and work with the hands, as well as in dance (Larsson, Richter and Ravignani 2019); the unique capacity to match pitch precisely as a potentially meaningful interaction with others (Podlipniak 2016); the similar capacity to match timbre, and innately to perceive connections between the properties of timbre and frequency (Sethares 1993; Titze 2003); the capacity to share common purpose in utilising these abilities to communal benefit (Dunbar 1998), and to promote social bonding (Dunbar 2012; Tarr, Launay and Dunbar 2016a; Savage et al. 2020); the capacity to utilise these abilities to act on memory and set up expectations for subsequent events, through mediating the experience of the past in the present and shaping the response to the future (Druskin 1983: 120; Podlipniak 2020; Stravinsky 1962); and the capacity to affect, elicit and convey emotion (Belyk and Brown 2015; Scherer 1992; Snowdon, Zimmermann and Altenmüller 2015). Few of these behaviours are apparent in our closest primate relatives to the extent that they are in humans (Merker 2000, 2012; Harvey 2017), and some not at all.

Within this broad pattern, however, one observation stands out: in humans, the two sexes differ in their voice pitch, or fundamental frequency, both when speaking and when singing. Comparative cross-species studies of vocalisation frequency have noted a consistent negative relationship between fundamental frequency and body size. Larger species have both a lower fundamental frequency ($F_0$) and lower formants ($F\Delta$) on average than smaller species, a relationship which is particularly strong among the primates (Bowling et al. 2017a). In many mammals, the males have both a lower $F_0$ and $F\Delta$ than females (Charlton and Reby 2016; Fitch and Hauser 2003). This sexual dimorphism is more pronounced in highly territorial species and those with polygynous mating strategies (Charlton and Reby 2016; Puts et al. 2016). Studies of individual differences in humans suggest that certain traits (such as sex, size and upper body strength) may be predicted by the frequency profile of one's vocalisations (Pisanski et al. 2014; Pisanski, Raine and Reby 2020; Pisanski, Groyecka-Bernard and Sorokowski 2021). Crucially, listeners can infer these traits from hearing another's voice (Raine et al. 2019); they can, for instance, even predict the outcome of a tennis match by comparing the $F_0$ of grunts made by the players (Raine, Pisanski and Reby 2017). Low frequency vocalisations seem to predict dominance in human males, rather than attractiveness to females, suggesting that the function of vocal sexual dimorphism in humans may be for male-male competition (Puts et al. 2016). This has inevitably resulted in a widespread assumption that vocal dimorphism is simply a consequence of mating competition and, hence, sexual selection.

While sexual dimorphism is most often associated with polygynous mating systems in primates, the sexual dimorphism for $F_0$ in humans is far greater than in most other primates (Puts et al. 2016), and is the greatest of any ape (Figure 1), despite humans not being strictly polygynous (Schacht and Kramer 2019) – and in contrast to humans' consistently intermediate position between monogamous and polygamous primates on most anatomical indices of mating system (including body size dimorphism, relative testis size and 2D4D ratio: Plavcan and van Schaik 1997; Harcourt et al. 1981; Wlodarski et al. 2015). More puzzling still is the fact that the voice pitches of the two sexes are, on average, *exactly* an octave apart in humans, especially when singing. More importantly, humans appear uniquely to possess and exploit a phenomenon in pitch perception known as *octave equivalence* (Hoeschele, Weisman and Sturdy 2012) – the ability to recognise when two notes are in harmony when an octave apart. Not only does this seem to have been little noticed by evolutionary scientists (though it is well known to musicologists), but there appears to be no obvious explanation for it. While we can accept that a lower male pitch is the result of sexual selection, as it is in other animals, some additional selection pressure is required to explain why the voice of the human male permits vocalisation exactly an octave below that of the female.

[place Figure 1 here]



[Caption]

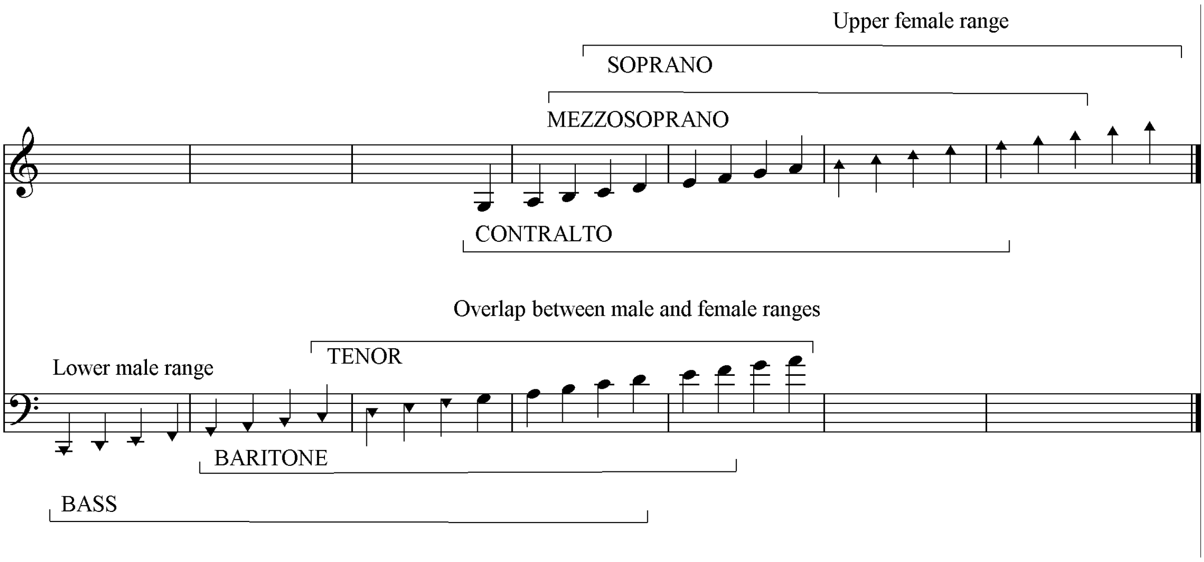
Figure 1. The relationship between body mass and vocalisation pitch in the higher primates. The dashed line indicates male $F_0$ = female $F_0$; the solid line indicates where the ratio would lie if it directly reflected sex dimorphism in body weight. Polygamous species have $F_{0\ \mathrm{male}} < F_{0\ \mathrm{female}}$. Within the great apes [non-gibbons], human males have much lower $F_0$ than females, notwithstanding their smaller body size compared to many other great apes. Adapted from Puts et al. (2016).

This effectively creates a three-stage explanatory structure (the evolution of musicality, the evolution of a sex difference in pitch, and the evolution of octave equivalence) that may each involve different historical selection pressures. Our concern here is with the third. We concur with the suggestion that musicality (and singing, in particular) evolved as a generic community bonding mechanism (Dunbar 2012, 2014, 2016; Dunbar et al. 2012; Savage et al. 2020), and likewise with the suggestion that the existence of a sex difference in pitch is due to sexual selection (probably as a correlated trait of divergent body sizes: Apicella, Feinberg and Marlowe 2007; Darwin 1871; Dunn et al. 2015; G. Miller 2000; Puts, Gaulin and Verdolini 2006). What remains to be explained is why the sexual dimorphism in pitch is exactly one octave. If sexual selection is the key driver for hyper-lowered pitch in males, why did male-male competition for access to females not drive it even deeper? Indeed, why has the sexual dimorphism in pitch not reduced since humans do not primarily have an obligate polygynous mating style? The fact that the difference is exactly one octave is too precise to be an accident, and instead implies that something else acted as a break on runaway selection. We will argue that the answer is group bonding during communal chorusing (with dyadic bonding as a secondary possibility). To make this claim, we first provide an overview of octave equivalence (OE) and its anatomical basis, and then make a case in the light of this for social bonding as the likely function. Finally, we ask whether this evolved early or late in hominin evolution, and offer some indirect evidence for a likely date.  We should be clear that, in terms of Tinbergen's (1963) "Four [biological] Why's", our main concern is with the why and when, rather than the mechanisms and ontogenetic how's, though we will comment on both of the latter in passing. We conclude by discussing how future research might illuminate and test this suggestion.

## Octave equivalence: ontogeny and phylogeny

Prepubescent children of both genders have almost identical vocal anatomy from before birth until the age of 10 or so (Fitch and Giedd 1999; Sergeant, Sjölander and Welch 2005; Weiss 1950). The vocalisation of these prepubescent children is achieved with close to identical anatomical configurations. Indeed, expert listeners are often unable to discriminate with certainty between the singing of individual boys and girls (Sergeant, Sjölander and Welch 2005), or between boys', girls' and mixed choirs (Welch and Howard 2002). Both sexes undergo a similar primary descent of the larynx within the first year of life, as the need simultaneously to breathe and feed evident in initial suckling gives way to growth within the vocal tract (Fitch 2002). However, there is a marked divergence early in adolescence.

[place Figure 2 here]



[Caption]

Figure 2. The variety of ranges within human singing. Children's voices map on average onto the Mezzosoprano range. Note both the phenomenon of octave equivalence and the overlap between the upper range of male voices and the lower of females and children.
The onset of puberty introduces a phase in which maturation in girls is associated with relatively minimal change (Weiss 1950; Gackle 1991), while that of boys determines a period of descent and growth that, over time, leads to a drop in fundamental frequency of about an octave, and a related change in formant distribution (Cooksey 1997; Fitch and Giedd 1999; Harries et al. 1997). This is associated with a second laryngeal descent (Fitch 2002; Sergeant and Welch 2009; Weiss 1950) and enlargement of the vocal folds that commences in the mid-stage of puberty (Cooksey 1997), eventually conferring a voice sounding approximately an octave lower than its prepubescent form. It is worth noting in this context that young boys appear to adopt, quite instinctively and unconsciously, lowered formants when singing in the presence of girls (Keller, König and Novembre 2017).

From adolescence onwards, however, maturing males diverge progressively from male children, as well as all females, eventually achieving a pitch as adults that is approximately an octave lower – an expression of the phenomenon referred to as 'octave equivalence' (see Figure 2). These developmental changes are universal across human societies (Titze 2003, 1994), consequent on hormonal and anatomical causes that are determined by our genes, though there are slight differences in the age of onset of puberty due to environmental factors (de Muinck Keizer-Schrama and Mul 2001).

Concurrent with the acquisition of vocal fluency in speech and song is the development of *registers* (Henrich 2006): acoustic phenomena determined by varying discontinuities in the ranges within which the relationship between fundamental frequency and optimum resonance are available (Cooksey 1997; Gackle 1991; Story, Titze and Hoffman 2001). While experienced singers can learn both to overcome 'breaks' between registers (D. Miller 2000), and to exploit them in vocal styles such as yodelling (Echternach, Markl and Richter 2011), most adults remain constrained by their natural ('modal') vocal register. The principal developmental trait that requires explanation is the approximate octave difference between the modal voices of adult men on the one hand and, on the other hand, women and children (Aristotle, trans Forster 1927; Hoeschele 2017; Peter, Stoel-Gammon and Kim 2008).

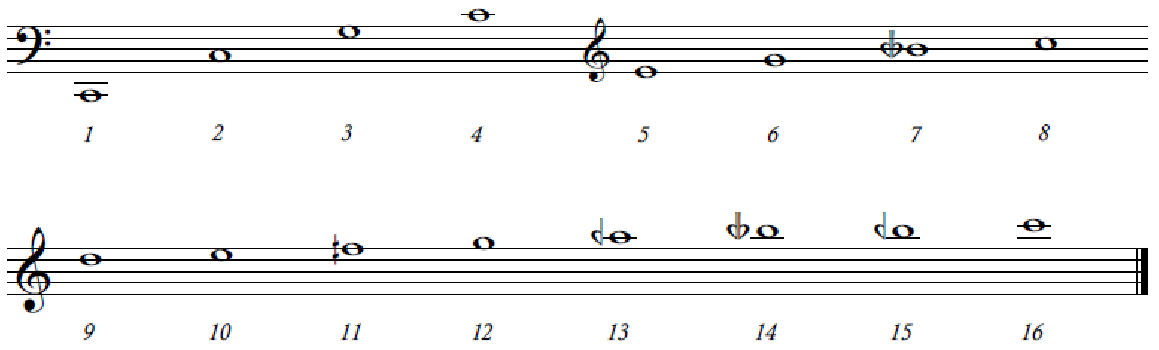
Importantly, vocal anatomy does not suggest that this developmental process occurs for purely physical reasons (Fitch and Giedd 1999; Titze 2003). The crucial factor in achieving this unique result resides in the neural control of production and perception without which it would fail (Harvey 2017; Titze 2017). Form may well have preceded function, but the latter relies upon brain development that enabled the otherwise unpromising engineering of the vocal tract (Titze 2003) to achieve song, language, and culture. Consequently, OE in humans embraces three related phenomena: the *perception* of octave equivalence; the ability to *produce* octaves vocally, in imitation as well as simultaneous performance; and *the average octave difference* between male and female voices. In sum, compared to species such as gibbons with similar vocal production across genders which permits equal duetting and turn-taking (Pika et al. 2018), a clear dimorphism evolved in humans. It is reasonable to assume that this represents a development whereby our species saw its males undergo change by stages, whereas female voices remained more or less as they were in childhood. At a point in this transformation, a new and beneficial factor was encountered. As male voices reached a range an octave lower than females, they became capable of interacting in octave unison (Bannan 2020), allowing them to leverage the perception of octave equivalence. At this point, we suggest, male voices became tethered to female voices – not in the same range, but in an equivalent range that permitted imitation and reinforcement that exploited the harmony made possible by the octave difference.

Octave equivalence has been detected as an aspect of auditory *perception* in species other than humans (e.g. rhesus monkeys, (Wright et al. 2000), white rats (Blackwell and Schlosberg 1943)), though only rarely in animal sound *production*. A dolphin learning to imitate synthesised pitch contours was able to achieve this through transposing its vocal production to a range it was able to access (Richards, Wolz and Herman 1984). Attempts to elicit octave equivalence in avian vocal mimics such as budgerigars (Wagner et al. 2019) and chickadees (Hoeschele et al. 2013) have, however, failed, suggesting that it may be an exclusively mammalian characteristic. Development of behaviours dependent on the perception of octave equivalence would thus appear to be a special human trait (Hoeschele, Weisman and Sturdy 2012) where perception and production represent a reliable feedback loop (Hockett 1960; Jones and Keough 2008). Doğantan-Dack (2013) concluded that '… the emergence of tonal encoding of pitch can be construed as a pre-linguistic stage … intimately related to the evolution of affective capacities'.

We provide further material concerning gender, vocal development and performance in Online Appendix S1.

Theoretical investigation of the phenomenon of OE and derivation of the frequency ratios of the Harmonic Series (Figure 3) have been known since Pythagoras (Hagel 2009) and, independently, the ancient Chinese (Falkenhausen 1992). Octave equivalence in the implicit practices of musical performance has been found all over the world (Hoeschele, Weisman and Sturdy 2012), and is viewed as salient in musical cognition (Borra et al. 2013; Deutsch and Boulanger 1984; Savage et al. 2020). Neural response to pitched sounds suggests that harmonic series relationships have shaped human hearing and aural engagement (Bowling, Purves, and Gill 2018; Foss, Altschuler and James 2007; Warren et al. 2003). Aristotle remarked (*Prob. Xix 39*) on the perceptual and developmental properties of octave equivalence, and the phenomenon has underpinned the construction of musical instruments and compositional techniques throughout modern history (Berlioz 1844; Mersenne 1636; Praetorius 1618; Rameau 1722), predominantly dependent on a 2:1 ratio in size.

[place Figure 3 here]



[Caption.]

Figure 3. The natural phenomenon of the Harmonic Series set out sequentially in music notation. The numbered pitches indicate the frequency ratios by which any two harmonics can be compared so as to derive the musical interval between them. Thus 2: 1 is the octave, whose equivalence is central to the argument of this paper (note that 2: 4, 3: 6 etc. also result in octaves, while 3: 4 results in a Perfect 4th, and so on.  Formants derived from harmonics sounding in relation to $F_0$ are perceived as distinct vowels. In *overtone singing,* the fundamental is sustained while oral filtering amplifies individual harmonics to produce melody.

Acoustic analysis of large corpora of vocal utterance (Schwartz, Howe and Purves 2003; Chiba et al 2019; Kuroyanagi et al. 2019) confirms that human vocalisation, especially singing, maps with considerable accuracy onto Harmonic Series properties and the contours of melodic intervals derived from them (Robledo et al. 2016). A single example of the phenomenon must suffice to illustrate this. The pentatonic scale (Do, Re, Me, So, La – in solfège notation) has been claimed as a human universal (Trân Van 1977). In Tuvan overtone singing, it can be heard as deriving from (or mapping onto) harmonics 8, 9, 10, 12 and 13 above a sustained fundamental or *drone* (Trân Quang 2002) (see Figure 3). Melodies performed over a drone are also a near-universal (Gabisonia 2015; Jordania 2006; Nikolsky 2015; van der Merwe 1989; see also Parncutt 2012), according with Podlipniak's (2016) definition of *pitch centricity* that implies it is the oldest and most robust form of harmonic accompaniment. This suggests that human singing is well characterised by the use harmonics, and has been so for a long time.

A potential role for octave equivalence in language acquisition, in which children imitate the voices of both female and male ranges (Peter, Stoel-Gammon and Kim 2008; Peter, Larkin and Stoel-Gammon 2009) implies a more general, innate response than has hitherto been recognised. In parallel with this, traditional exploitation of Harmonic Series properties (i.e. not explicitly informed by theoretical understanding) has been found in sophisticated and varied forms in a wide variety of musical practices (Bannan 2008;  Dargie 2018; Ikhtisamov 1988; Trân Quang and Bannan 2012). Perceptual octave equivalence that may represent an adaptive response to the properties of the harmonic series would seem to have shaped human productive capacity to accurately map vocalisations onto those an octave higher or lower.

We summarise additional evidence for the phenomenon of octave equivalence in human vocalisation in Online Appendices S2, S3 and S4.

## Conventional explanations for the evolution of human vocal development

Body size alone would explain a lowered voice in males and the consequent vocal dimorphism between the two sexes. This would likely reflect the outcome of sexual selection driven by male-male competition and/or male attractiveness to females (Apicella, Feinberg and Marlowe 2007; Dunn et al. 2015; G. Miller 2000; Puts, Gaulin and Verdolini 2006). Low pitch in a variety of species has such functions (Fischer et al. 2002; Fitch and Reby 2001; Charlton and Reby 2016), and this may be selected for partly through the iterative preference of females for low voices as evidence of good providers with desirable genes (Saxton et al. 2016). This may well explain a developmental difference, but why in humans does the difference take the form of a precise octave that allows harmonic equivalence? Why not a runaway process (Zahavi and Zahavi 1999) resulting in a difference in range of *more* than an octave? Or, why, for that matter, would a smaller interval of difference not have been sufficient?

Cross-species comparisons (Honing et al. 2015; Ghazanfar and Rendall 2008) identify the allometric constraints for range and vocal character that illuminate the anatomical and acoustic features which characterise modern human vocality and its pathology (Titze 1994: Sundberg 1987). Even allowing for possible differences in size between males and females as a factor in human survival that was selected for by non-sexual drivers such as defence or hunting, the average bodily size difference of c. 10-20% (Ghazanfar and Rendall 2008) does not correlate with the 2:1 ratio of the difference in average fundamental pitch ($F_0$) and the corresponding average size difference in vocal fold length (2cm in males versus 1cm in females (Titze 2003). For it to do so, human males would need to be some three metres tall.

An alternative possibility is the use of song in male-male bonding – probably a near-universal cross-cultural phenomenon. Such a function for chorusing was proposed for archaic human males by Merker (2000), and the harmonic potential of mutual reinforcement that universally characterises human vocal interaction has been identified and explored by Bowling and Purves (2015). However, patterns of exclusively male/male cooperation in musical vocalisation (Faulkner 2012) clearly differ from those associated with female/female relationships (Garnett 1999) and the activities exhibited as anthropologically proper to each (Gaulin and Boster 1985; Dàvid-Barrett et al. 2015; Knight and Lewis 2017). While male collective and competitive chorusing on the lines proposed by Merker (2000) surely represents a potential stage in the development and function of human vocalisation, the instrument required to perform it – the deep male voice – had its anatomical origins in one originally pitched higher, within the female range, from which it departed under sexual selection. However, this does not explain while male voices have the pitch they do: if male bonding was the sole issue, any pitch would do. More importantly, perhaps, focussing solely on male voices simply leaves us bereft of any reason why women and children should have voices too – let alone why they are clearly different. It is essential therefore to account for the contributory role of the voices of females and children in any model of vocal evolution.

An alternative possibility that might circumvent this difficulty is that vocal exchanges might underpin pairbonding. Outside the obligately monogamous gibbons, humans are unusual among the apes in exhibiting a strong (albeit usually temporary) form of pairbonding (i.e. facultative, as opposed to obligate, monogamy). Coordinated dancing, for example, is known to facilitate pair formation in at least some human communities (Pitcairn and Schleidt 1976). Hughes et al. (2004, 2010) analysed the relationship between opposite-sex vocal attractiveness ratings in adults, indices of bodily dimorphism, and self-reporting of sexual behaviour to propose that voice difference may have been an important parameter of mate choice in human evolutionary history. Weustoff et al. (2013) interpreted the reproductive stage in the human lifecycle not only in terms of the role of the voice in mate attraction in adults, but also on the maintenance of paired relationships. They reviewed five available studies of the role of vocal $F_0$ in the vocally encoded emotional arousal of interactions between couples – what leads to friction in relationships, and how this can be considered as a component of relationship therapy. Their findings suggest that the means by which $F_0$ acts as an index of emotional arousal and of the intensity of emotional reaction are influenced by both basic biological processes and socially learned communication behaviours stemming from a similar evolutionary basis. At the same time, the achievement of precise tuning might, of course, represent (or be exploited to represent) an investment of stability, authenticity and salience in vocal signals intended to convey credibility (Mehr et al. 2020) , which could be underpinned by the achievement of precise tuning at the unison or octave. Such rich acoustic information carried by the varied timbral content of vocal signals would represent one of the means by which Theory of Mind (Livingstone and Thompson 2009) would have developed and contributed to human social culture.

Plausible as this might seem, in fact most animal species where pairs call to each other to reinforce the pairbond (or maintain contact with each other) typically have vocal registers that are very similar (e.g. the African bell shrike whose two-note duets are so tightly timed and individually indistinguishable as to sound like a single individual: Thorpe 1973). Moreover, in all these cases, the species are monomorphic and the two sexes do not differ in vocal range, making this an unlikely explanation for humans. More importantly, if duetting did evolve to facilitate bonding, we would expect duet singing ‘in the home’ rather than the communal singing that is so characteristic of human societies.

Finally, Falk (2004) argued that language evolved out of mother-infant singing, and might thus have originated as a child-rearing strategy that allowed hairless females to free their hands for foraging and other work. Dissanayake (2008) built on this by suggesting that the origins of music as a parental response to infants rests on the acoustic and rhythmic features of mother-child bonding such that the game-like aspects of adult sexual love-making would have been a natural extension of this for sustaining relationships. She describes a process whereby the mother-infant dyad displays bonding based on vocal and physical processes that recapitulate in the adult female-male dyad:

> The kinesic actions of mothers — touching, stroking, patting, holding the hand, embracing, grooming, and hugging their infant, and with an open mouth poutkissing against its body — echo a large number of the affinitive social behaviours noted in wild and captive primates … as well as being common adult gestures in humans of sympathy and affection (Dissanayake 2008, 175).

Identifying the husband-father role in the human family as unique among primates, she continues:

> I suggest adding the hypothesis that in human courtship the evolved proto-musical capacities and sensitivities that enabled mother-infant interaction, especially as they promoted temporal coordination and contingent responsiveness, were exapted and transformed into the elaborated and prolonged loveplay that also distinguishes human sexual behavior from that of other primates (Dissanayake 2008, 185).

We consider some further implications of Dissanayake's model in Online Appendix S5.

## A role for octave equivalence in community bonding?

Most of these claims focus on aspects of dyadic relationships. In common with many analyses of human behaviour, they overlook one crucial feature of human and primate sociality, namely the fact that all anthropoid primate species live in bonded social groups (Dunbar and Shultz 2021a). Such effects are underpinned by mutualism (Wrangham 1982) or group-level, or group augmentation, selection (Kokko et al. 2001; Okasha 2006; Kingma et al. 2014), sometimes identified as a third component (social selection) of natural selection in addition to conventional survival-related and sexual selection (Hamilton 1971; Crook 1972; Rubenstein 2012; Lyon and Montgomerie 2012). For primates, the evolution of bonded social groups that are able to maintain spatial cohesion through time and space has been key to their evolutionary success, with the mechanisms that underpin group coordination evolving long before the evolution of the capacity to cooperate (Dunbar & Shultz 2021; Shultz & Dunbar 2022). Group bonding is not an end in itself, but a means to a fitness end (something that often seems to get overlooked in discussions of possible social functions: e.g. Mehr et al. 2020).

The central problem faced by all primates is the need to ensure that social groups remain coherent through time and space in the face of stresses that for all other mammals result in group fragmentation and dispersal (Dunbar 2020; Dunbar and Shultz 2021a). These stresses should not be underestimated: they have very significant effects on health and, in particular, on female fertility (Dunbar and Shultz 2021b). These latter effects are so strong that they make it impossible for mammals in general to live in *stable* groups larger than 15-20 individuals. Anthropoid primates have been able to breach this glass ceiling by building bonded relationships by means of social grooming that buffer individuals against these stresses and counteract the centrifugal forces that otherwise act on them (Dunbar and Shultz 2021b). It is important to appreciate that bonding has nothing to do with cooperation (though bonding may give rise to cooperation in other contexts). Rather, its sole function is to maintain the integrity and cohesion of the group, so that the group can provide the protection against external threats (principally predators and conspecific raiders) that would otherwise sink individuals' abilities to survive and reproduce in high risk habitats.

Because there is a limit on the time that can be devoted to social grooming and other forms of affiliative behaviour (Dunbar 2009) and relationship quality is directly related to the time invested in it (Dunbar 1982; Sutcliffe et al. 2012), there is an upper limit on the size of primate groups that can be bonded in this way at around 50 individuals (corresponding to the third layer of human social networks: Dunbar 2020, 2022). This time constraint is further limited by the fact that grooming is a strictly one-on-one interaction that, even in humans, cannot be extended to multiple recipients without a significant loss of intimacy and, hence, bonding effect.  Since early hominin time budgets were already overstretched (Dunbar 2016), the only way group size could increase beyond this limit was to find behaviours that, in effect, allowed more individuals to be “groomed” simultaneously without need for physical contact (Dunbar 2012, 2016). Vocal mechanisms (laughter and, later, chorusing or wordless singing) appear to have been the earliest of these to evolve (Dunbar 2012, 2016, 2022). Both laughter and singing trigger the same neuropharmacological bonding mechanism (the brain’s endorphin system) as social grooming and precipitate a sense of bonding to those with whom one does the activity (Manninen et al. 2017; Pearce et al. 2015a, 2015b). Singing together seems to be uniquely capable of bonding individuals whose previous experience of each other has been entirely one of rivalry and competition (Pearce et al. 2015b). In addition, singing appears to be uniquely scalable, allowing choirs of 200 or more to feel more bonded even than choirs of twenty (Weinstein et al. 2016). None of the other behaviours that we use in social bonding, including laughter, dance, feasting and storytelling, seem to be capable of working on such a large scale.

We suggest that, in this context, there is something especially engaging about singing in unison, as well as in other well-tuned intervallic ratios derived from Harmonic Series relationships, and that doing so enhances the sense of bonding as a result (see also Savage et al. 2020). Of the most clearly perceived intervals derived from the harmonic series, it is the octave that has driven the most common and adaptively significant acoustic difference between the voices of men and women, evident in both song and speech. In a species capable of collective synchrony, precise attunement both efficiently amplifies the signal and preserves its integrity, permitting it to be retained in memory and shared accurately over time, thus enhancing bonding between generations. Given that male voices had diverged away from female voices under the pressure of sexual selection acting on body size throughout pongid and early hominin evolution, there would, we suggest, have been a significant secondary selection pressure from social bonding to push male voices as fast as possible to the next nearest 'sweet spot' at the lower octave.

## Evidence for the instinctive achievement of harmonic interaction

What evidence do we have that harmonic singing of this kind enhances social bonding? Although this has not, as yet, been examined in any experimental studies, there is considerable circumstantial evidence from music practice that it is likely to do so and considerable experimental evidence that singing in general both influences social neurohormone titres and elevates the sense of belonging to a group. We summarise briefly some of this evidence here.

An intensified capacity for social bonding in complex *a cappella* harmony singing was reported by participants in Averill's (1999) study of barbershop quartet performance. The same relationship between 'just intonation'[1] and style in historically informed performance of European Medieval and Renaissance vocal music has been identified by Covey-Crump (1992) in the rehearsal practice associated with solo-voice consorts that specialise in this repertoire. Precise tuning arouses heightened responses both in audiences and in the performers themselves. In the folk style of Sardinian male-voice performance, Castellengo et al. (2001) report the phenomenon whereby four men singing together in precise just

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[1] i.e. derived from tuning achieved between practised singers adopting Harmonic Series relationships, rather than in answer to the referent of a keyboard tuning in equal temperament.

intonation can appear to elicit a ‘fifth voice’. In barbershop circles, this evidence of precise harmonic reinforcement is referred to as ‘the angels joining in’ (personal communication, Barbershop Pioneer’s Convention, Elk Grove Village, Illinois, 1992) and is experienced as a peak aesthetic sensation both by the performers themselves and by listeners.

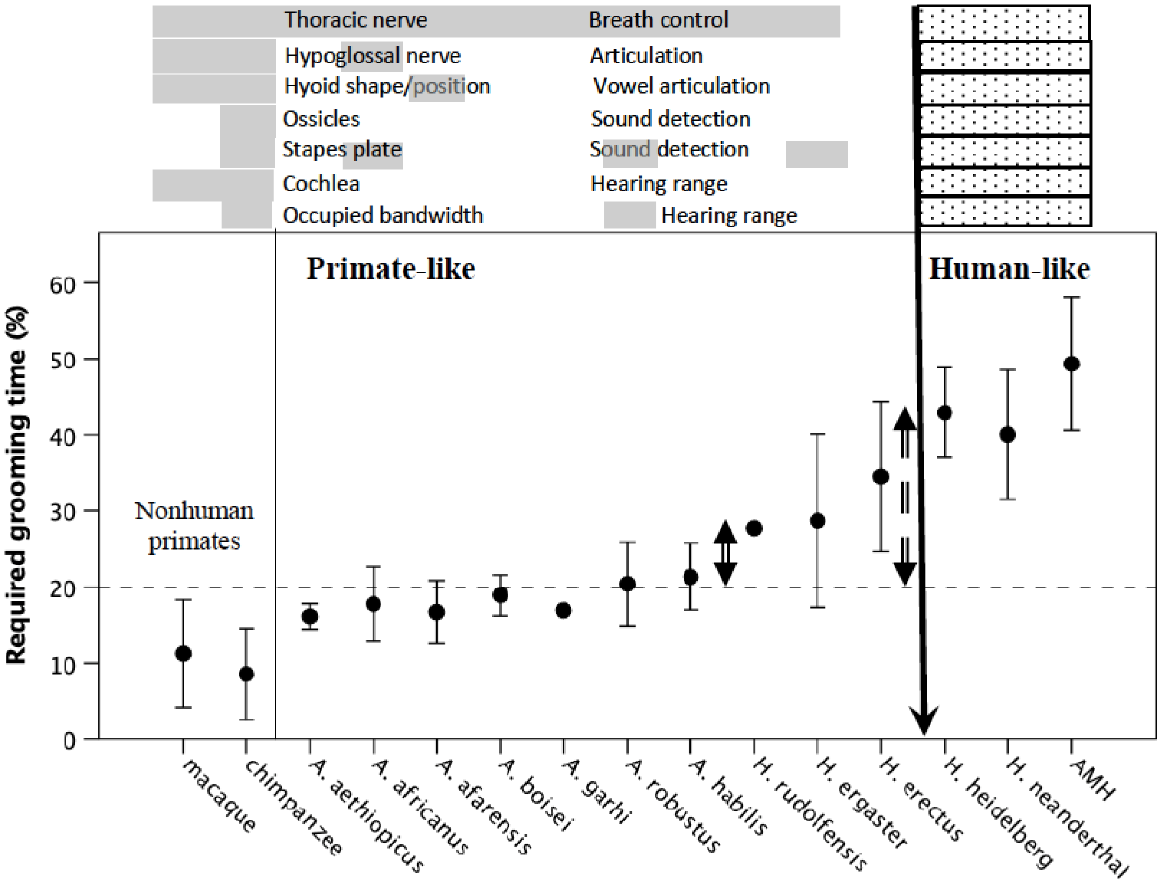
Singing in groups has been widely demonstrated to trigger the pleasure centres associated with endocrine expression (Harvey 2020), the release of endorphins (the principal bonding neuropeptide in primates) (Pearce et al. 2015a), the reduction of stress measurable in cortisol secretion (Fancourt et al. 2015) and an enhanced sense of bonding (Pearce et al. 2015a,b; Weinstein et al. 2016). Moreover, we know from studies of other group activities (including rowing and dancing) that synchronised performance in groups raises endorphin upregulation significantly above that achieved by individuals performing alone (Cohen et al. 2010; Tarr et al. 2015, 2016b; Lewis and Sullivan 2018). Such neural and limbic correlates of well-tuned singing cannot be mere side-effects of capacities that have evolved for other purposes. On the contrary, we argue that they are adaptive traits that are foundational to the complex social and anatomical achievement of human group singing, the part this plays in collective social cohesion as well as interpersonal bonding – both mate selection and mate retention – and the transmission of vocalisation between generations both in child-rearing and in fostering and upholding the identity of the wider family.

## Dating the Origins of Human Singing

Our claim, then, is that, because of the constraints imposed by time on the size of group that can be bonded by conventional social grooming, singing evolved to supplement grooming as a social bonding mechanism so as to enable humans to live in larger groups. If we could determine when a dramatic increase in grooming time became necessary, we might be able to estimate when in the course of hominin evolution the capacity to sing evolved. Since group size correlates closely with brain size (and especially neocortex size) in the hominids (Dunbar & Shultz 2021), we can use cranial volume to determine group size and, then, from this we can estimate the corresponding grooming time requirement (in each case using empirically determined equations: see Dunbar 2009, 2016, 2022). Figure 4 plots the estimated grooming time for each hominin species, along with equivalent estimates determined in the same way for the Old World monkey genus *Macaca* (macaques) and the ape genus *Pan* (chimpanzees). (Details for these calculations can be found in Online Appendix S6). These data suggest two likely points at which grooming time demand underwent a significant increase: a smaller increase around 2.5 Ma with the appearance of early *Homo* and a much larger one around 500 ka with the appearance of archaic humans (leading to a further small increase with the appearance of anatomically modern humans, *Homo sapiens*, around 250 ka). To decide between the two main options, we need to look for anatomical signatures of the kinds of voice control needed for language and/or singing.

No primate devotes more than 20% of its day to social grooming (horizontal dashed line), and Figure 4 suggests that none of the australopithecines would have exceeded this. Similarly, the pressure to evolve a novel bonding mechanism is at best modest in early *Homo*, but reaches serious proportions for archaic humans (compare the magnitude of the two dashed arrows in Figure 4). Singing (and speech) is dependent on a number of core features that include control over breathing (to allow for long exhalations without drawing breath), control over articulation (to vary pitch and timbre) and hearing (in order to match sounds between individuals). A number of relevant anatomical markers for speech-like vocal articulation are known to differ significantly between humans and other primates. Figure 4 plots, across the top of the graph, the known presence of nonhuman (grey boxes) and human (stippled boxes) forms for seven such anatomical markers. The appearance of archaic humans seems to coincide with an abrupt transition from a primate-like to the modern human form in all seven of the anatomical markers of vocal production and detection. The change in these markers seems to signal a new importance for a vocal channel that is very different from the conventional vocal communication of monkeys and apes. It is unlikely that this vocal channel involved fully-modern language since archaics did not have the *cognitive* mentalising capacity to support fully fledged human language (Pearce et al. 2014; Dunbar 2009, 2016). This is, hence, more likely to signal the appearance of singing in the form of chorusing. In other words, chorusing (wordless singing, or singing with limited verbal content) is most likely to have evolved around 500,000 years ago and functioned as an important supplementary bonding mechanism for archaic humans (see also Mithen 2005; Dunbar 2012)

[Insert Figure 4 here]



[Caption]
Figure 4. Mean (±2sd) for estimated grooming time requirement for the main hominin fossil species, compared to macaques and chimpanzees (for how these are calculated, see Online Appendix S6). Values for Neanderthals are corrected for their larger visual system (Pearce et al. 2013); those for *Homo erectus* are uncorrected. No primate species devotes more than 20% of its day to grooming (horizontal dashed line) (Lehmann et al.2007; Dunbar 2022). Double-headed vertical arrows indicate two major phase shifts in required grooming time that speech and/or singing could have evolved to fill a significant bonding gap. Mapped across the top are the presence of primate-like (grey) and human-like (stippled) anatomical indices of speech where these are known for individual taxa (with blank spaces indicating no data available). The seven anatomical indices are indicated on the left, and their functions on the right, of each line. The heavy vertical arrow marks the point where all the indices seem to switch together. AMH: Anatomically Modern Human (*Homo sapiens*) fossils.  Sources for anatomical data: see Online Appendix S6.

## An integrated model

Our overview of the likely functions of singing yielded *prima facie* evidence in support of five different phenomena: singing as a mechanism for communal bonding, octave equivalence, mate choice/retention, mother-infant crooning and male bonding. This makes all of them correlates of singing, but not necessarily their causes. Statistically, one of these will have greater impact on fitness than the others, and so be the original cause, with the others being either secondary selection factors that reinforce the effect of the primary factor (but arise only because of the primary cause) or the consequence of windows of evolutionary opportunity (exaptations). In order to determine which of these is which, we need to determine the likely order in which the five elements appeared. There are 120 different possible sequences in which these five elements can be ordered. Evaluating all of these is beyond the scope of this paper, so we first seek to reduce the number of options by identifying the earliest likely dates for them. Figure 4 sets the benchmark by identifying 500 ka as a likely date for the evolution of the ability to articulate (and hear) sounds with sufficient precision to sing. Whatever function triggered the evolution of anatomical adaptations for vocal complexity (speech, but not necessarily language) at this point must thus be the original selection factor. Figure 4 specifically identifies the need to find behaviours that supplemented grooming for bonding large communities as an issue.

The other function that should be easy to date is mother-infant crooning (Falk 2004). In the light of contemporary human behaviour in all cultures, this almost certainly evolved in combination with rocking to sooth grizzling infants. Rhythmic rocking is known to sooth infants (Korner and Thoman 1972; Gursul et al. 2011), most likely because vestibular and/or cochlea stimulation caused by rocking triggers the endorphin system via SGN neurons whose sole function is to respond to head movements (Dunbar et al. 2021). Mothers singing to their infants might well have enhanced this endorphin effect because singing automatically entrains the rhythm of the rocking. Since monkey and ape infants do not exhibit the same level of grizzling (unlike tantrum behavior which has a very different form and does not attract a soothing response in either humans or other primates), the timing for this is likely to be the point at which human babies first began to have an extended period of helplessness through infancy and early childhood (Morley 2017). Human lachrymose crying – an honest visual signal of the need for comfort not exhibited by chimpanzees – might have reinforced this (Trimble 2014). If a rocking-and-crooning response is a response to very young, helpless babies, its origins would be at the time when reproduction switched from a generalised primate-like schedule to a modern human one in which babies are born approximately 12 months premature compared to their ape equivalents (Martin 1990; Rosenberg 1992). This transition appears to have a late origin, associated with the appearance of anatomically modern humans ca. 250 ka (Gruss and Schmitt 2015).

Dissanayke (2008) has argued that this kind of rocking and crooning to calm the infant down became co-opted to permit the emergence of intentional vocalisation and response to partner affection available to both genders. Later, males may have started joining in as part of the process of pair-bonding with a mate. If so, it must postdate mother-infant crooning and so also be associated with anatomically modern humans. This would fit with the anatomical evidence suggesting that a mating system based on pairbonded monogamy was not characteristic of either early *Homo* or archaic humans, and appears only with anatomically modern humans (Nelson et al. 2011; Shultz et al. 2014).

So far, then, we have a sequence which begins with communal chorusing and much later gives rise to maternal crooning leading on to crooning or singing as a possible mate choice and/or mate bonding mechanism. This leaves us with two final features to slot in: octave equivalence and male bonding.

It is implausible that the anatomical mechanisms required for male bonding would have evolved before communal bonding, since that would require males to have evolved a feature that females independently evolved only later. A common feature is likely to have evolved simultaneously in both sexes. This implies that the use of singing to bond males necessarily postdated the use of singing to bond groups. Whether it predates or postdates maternal crooning and/or pairbonding depends on whether male coalitions (most likely for raiding and defence against raiders) evolved early or late. It is not relevant to modern human hunting, since, ethnographically and archaeologically, this typically involved bow-and-arrow ‘stealth’ hunting that is best done alone or in very small groups of two or three individuals at most. A more plausible case could be made for Neanderthals who engaged in spear-based ‘confrontational’ hunting in which success depends on the (presumably male) hunters being sufficiently bonded to stand together in the face of very large-bodied dangerous prey (Gaudzinski-Windheuzer et al. 2018). In modern humans, group-hunting occurs only in the context of lion hunts by young warriors of the Nilo-Hamitic tribes of northeast Africa (e.g. Maasai, Galla) or raids against neighbouring tribes (the predominant form of warfare prior to settlement in villages post-12 ka); neither of these normally involve(d) singing, but are invariably initiated and executed in silence and considerable secrecy, often aided by drugs (Lehmann and Mihalyi 1982). Singing and dancing occurred in the celebrations on completion of an expedition or in men's groups as social contexts, but never as the prelude to such an expedition. Since other archaic humans (e.g. Heidelbergs) did not appear to engage in confrontational hunting to the same extent, this would imply that this function arose after 350 ka with the appearance of the Neanderthals as a distinct species in Europe, and that would necessitate a separate mutational event if this was also to be true for the anatomically modern human lineage. On the whole, that would seem implausible.

Lehmann, A. C., & Mihalyi, L. J. (1982). Aggression, bravery, endurance, and drugs: A radical re-evaluation and analysis of the Masai warrior complex. *Ethnology*, *21*(4), 335-347.

In contrast, if singing's original function was as a form of chorusing for group-bonding, then octave equivalence can probably be considered to have the same early origins as singing since there would likely be intense selection for harmonic convergence. This would have been necessary because all extinct fossil hominins, especially after the appearance of *Homo*, were sexually dimorphic in body size and the two sexes' vocal ranges would inevitably have been very different.

Taken together, this would suggest the following time course: chorusing as a social bonding mechanism evolved around 500 ka with the appearance of archaic humans, followed very soon afterwards by the evolution of octave equivalence; maternal crooning may not have evolved until around 300,000 years later with the emergence of anatomically modern humans, followed soon afterwards by the use of singing or voice-matching in mate choice and retention contexts. The use of singing for male bonding is less clear-cut; it might have evolved earlier among the archaic humans, but was perhaps more likely to have emerged with anatomically modern humans since the larger communities characteristic of this taxon will have had more males to bond than the smaller communities characteristic of archaic humans.

## Challenges

Our aim has been to offer an explanation for octave equivalence, rather than singing or music-making in general. We here briefly consider some potential challenges to this suggestion. We will not consider Pinker's (1997) claim that music has no adaptive significance but is instead simply a form of 'auditory cheesecake' that excites responses in neural substrates which developed for other purposes: this claim now seems irrelevant in the light of recent evidence that music does have an evolutionary function. A more serious alternative explanation, derivative of G. Miller's (2000) claim that musicality evolved as a sexually selected trait, is that OE evolved to support mate choice and, perhaps, mate retention. The strongest evidence against this claim is that pairbonding does not seem to have evolved before anatomically modern humans, whereas the capacity to sing is demonstrably considerably older.

An alternative challenge arises from the claim that musical preferences are shaped more by culture than by innate responses (List 1984), and hence that features such as octave equivalence are not human universals. This view has been most forcefully expressed in a series of studies of the Amazonian Tsimane' people. McDermott et al. (2016) studied the differences in musical perception (expressed as preferences for consonant and dissonant chords) between urban listeners in the USA and Bolivia compared to the Tsimane', and used this to reject the claim that the discrimination of harmonicity is a human universal. They argued, instead, that harmonicity is shaped by media experience not available to the Tsimane'. In a follow-up study intended to test for octave equivalence through requiring vocal imitation of synthesised sounds in a high range, Jacoby et al. (2019) found that Tsimane' tended to reproduce the *interval* of the fragment, but not in a manner that conveyed octave displacement. This is itself significant, however, since it suggests that the Tsimane' were executing a *transposition* of the stimulus, something that is actually more complex than simple octave mapping. The implication is that Tsimane' do in fact have a musical talent which allows them to preserve melodic frequency ratios rather than simply reproduce pitch chroma. In addition, Bowling et al. (2017b) have pointed out that the Tsimane' utilise the pentatonic scale in their own music, and doubted whether preference ratings represent the most suitable way of evaluating abilities. More importantly, perhaps, no report has been made of how these musical phenomena are transmitted from adults to children, nor, crucially, whether men and women can sing the same songs an octave apart. In short, it would seem that these studies are largely irrelevant to our present concerns.

Nonetheless, it may well be true, as Savage et al. (2020) have argued, that musicality arose as a consequence of some form of gene-culture co-evolution – although, in fact, this is probably more correctly described as the well-known Baldwin Effect (Baldwin 1896) whereby behaviour leads genetic change (Podlipniak 2017). However, this suggestion addresses the inheritance mechanisms that underpin evolutionary dynamics, and tells us nothing about the fitness functions that music or singing subserve. In contrast, our proposal is concerned only with the trait's evolutionary function. As is well understood, function, mechanism and inheritance are independent components of Tinbergern's 'Four Whys' (Tinbergen 1963) and, as Tinbergen pointed out, the answer to one has no implications for the answer to the other.

## Future Research

This paper aimed to provide an evolutionary explanation for the phenomenon of octave equivalence and the reasons why men's voices should be so much deeper than would be expected for body size compared to the voices of children and women. Future research that would illuminate the questions addressed includes:

1. The employment of Trân Quang Hai's model (Trân Quang and Bannan 2012; Online Appendix S1) of the dimorphic mapping of the four registers of the human voice (see also Henrich 2006; D. Miller 2000), testing a statistically significant number of child and adult human subjects in pairs as well as individually in response to a 'neutral' stimulus to ascertain the pitch and timbre of the most common responses cross-culturally when male and female voices interact; and when adult males interact vocally with children.
2. Acoustic analysis of the actual pitch of overtone sequences elicited by different modes of pitched performance, compared through same/different listener ratings. Such a project would help to discern the features of vocal production to which listeners respond, whether it be the distinct pitch (partial in relation to a fundamental) or a more general timbral perception. This kind of study could help to illustrate the frontier in perception between the assumed conditions of music and speech, and the common properties of both that evolved together as a consequence of human anatomy and auditory perception.
3. Listener ratings of vocal interaction with a measurable independent sound source that permits interval preferences to be elicited in practice, adopting an experimental method based on the studies of Arom (2010) and his laboratory.

4. Ethnomusicological evidence of how children learn songs from male and female models, and how paired and group singing illustrate patterns of harmonic interaction and their global distribution.
5. Quality and salience of listener and performer responses to the differences in terms of physical and hormonal reactions to measurably well-tuned and blended vocal unisons and harmonic reinforcements. [Since group vocalisation triggers the endorphin system, we would expect endorphin activation to be higher when singing is in well-tuned unison than when it is less accurate in its pitching, and to exhibit a similar peak in endorphin output when listening to men and women singing in approximate octave equivalence where the homophony lacks the reinforcement of harmonic coherence.]
6. Performer self- and group-report of the social bonding effects of group vocal participation, including more direct measures of the extent to which singers feel bonded to each other when singing in and out of melodic unison (both 1:1 and the 2:1 unison octave equivalence).
7. Some simple tests of the mate choice/maintenance hypothesis would be (i) to compare the voices of established couples, and (ii) to ask individuals to rate the pleasantness/unpleasantness of a set of target voices when they speak or sing with them.
8. The five key functions (motherese, mate choice, courtship, male bonding, communal bonding) could have emerged in 120 different possible orders: finding evidence to identify the correct order will provide deep insights into their relative importance in terms of fitness.

## Conclusions

Octave equivalence is the perceptual-productive mechanism, genetically endowed and released through vocal practice and imitation, that activates and refines the feedback loop between auditory and vocal processes during singing. It may have evolved from two competing pressures on males: the demands of sexual selection so as to exaggerate size in male-male competition through lower vocalisation frequency, and the need for harmonisation as a social bonding mechanism (both within groups and, perhaps, between sexual partners). The arrival at the octave represents a compromise that allows male voices to be lower in frequency, while still acoustically complementing female and juvenile voices.  It permits unison singing, which promotes social bonding, enhances group coordination, and may support mate retention through paired activity (Dissanayake 2008; Weusthoff, Baucom and Hahlweg 2013) as well as social bonding more widely; but also presents the best acoustic framework for vowel-matching that relates to adaptive human processing of the Harmonic Series as the determinant of social listening. Human capacity to match vowels in language learning depends on this, as do other interpretants of timbre – detecting age, health, state of mind, preparedness to interact (acoustic contagion), and level of perceived physical investment in communication (Bannan 2020; Snowdon, Zimmermann and Altenmüller 2015). These abilities indicate a role for pitch sensitivity in Theory of Mind (Livingstone and Thompson 2009) that is also consistent with Social Brain theory (Dunbar 2003; Savage et al. 2020). While these factors would inform natural selection and sexual selection models focused on reproductive success and survival, the plasticity of these sophisticated abilities also contributes to cultural manifestations such as ritual, play, and the marking of social milestones on which quality of life may also be built.

The communicative Rubicon was crossed when male voices reached a range at which they were as different as possible from those of children and adult females while being perceived acoustically as being ‘the same’, with all the benefits for musical and linguistic generativity that this confers.

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