Evolution of human language: duetting as part of prosociality and cognition

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The evolution of human language is a topic that has received undiminished attention. Numerous hypotheses for the origin of human language have been proposed, including gestural communication found specifically among apes. This study advances the hypothesis that human evolution, including human language development, is three-pronged: prosocial, cognitive, and collaborative. Duetting and turn-taking in primates are used as pivotal examples of how bonding leads to joint action and collaboration. It points out that such vocal behavior itself may be a crucial precursor of language evolution in the sense that it is explicitly focused on a conspecific. Some current hypotheses have acknowledged duetting as an important perceptual and behavioral example of synchronicity. Some forms of synchronized behavior, as found in duetting, synchronized dance, or even shared song, were perhaps crucial evolutionary steps preceding the evolution of human language. Duetting signifies more than that, however, because it is an observable and significant cognitive investment that signals attention toward a partner. This study also advances the hypothesis that affect and cognition would have needed to precede any form of duetting or signs of affiliation such as grooming. Hence, this study, asking what duetting in primates signifies in evolutionary terms, takes a multidisciplinary and multimodal approach to suggest important affective and cognitive steps in the evolution of human language and speech, the chief of which is prosociality. Prosociality, as an attitude and awareness of another, be this as a friend or partner for whom one can do favors or whom one can help, is a model for collaboration and cooperation, and also increased cognition.

KEYWORDS

prosociality, duetting, cooperation, synchronicity, cognition and emotions in primates, human language evolution, communication (vocal, gestural)

1. Introduction

Duetting exemplifies a significant step in the evolution of language for several reasons. It is usually a time-sensitive vocal activity performed by a pair of closely connected individuals. It further requires coordination of vocal production and a degree of vocal flexibility. In duetting, listening is a key element in the switch from self- to other-oriented and affiliative behavior that may signal cooperation on a broader scale (i.e., beyond duetting). Such behavior may be termed "prosocial". Prosociality has often been understood as a main facilitating driver of cooperation (Martin et al., 2021). Coordination in the sense of prosociality, unlike empathy, carries no direct cost to the actor but presupposes a positive attitude toward another and doing things together, even supporting others (Silk, 2007).

Accommodation of the behavior and even needs of others may then develop into a new awareness and affective sensibilities toward others for which a new cognitive framework may be needed. Since duetting is an exemplification of one of the most basic forms of joint vocal action of committed pairs, it will be discussed in light of prosocial tendencies.

The literature seems to agree that during the last 2 million years, hominins had become more and more socially complex animals in comparison to other primates (Dunbar, 2014). According to James Baldwin's insights (called the Baldwin effect) evolution by natural selection occurs in three stages: (1) the appearance of new environmental challenges, (2) the adoption of a new behavior through learning (natural selection favoring cognitive plasticity), and (3) new genetically based predispositions when natural selection favors individuals that exhibit a particular adaptive behavior (Podlipniak, 2017). Certainly, the first stage can be readily reconstructed, i.e., the changing physical environments in which early humans moved (Suzuki, 1970). Africa was drying, vegetation reducing, leaving a band of ill-equipped hominins surviving on the savannah exposed to formidable predators. Confronting such new environmental challenges, as Baldwin argued, would lead to the invention of new behavior and this might have forged how individuals acquired synchronizing behavior and collaboration and probably did so as the best or even only chance of survival (Klein, 1977; Caley et al., 2018).

Baldwin's third stage (new genetically based predispositions when natural selection favors individuals that exhibit a particular adaptive behavior), such as the shift to more prosocial, even verbal communication, may have been a step too far for chimpanzees and even bonobos. Chimpanzees, although many attempts were made, could not be taught, or made to speak (Gardner and Gardner, 1969; Gardner et al., 1989). Hence, acquiring the ability first to be able to articulate sounds in the sequence required physiological and cognitive changes (brain nuclei to process information), memory, and the ability to expand vocal expression. Vocal convergence, in which adjustments to one sound type result in similarities between individuals, occurs in a wider range of mammalian orders including primates, mole-rats, goats, and mice (Janik and Knörnschild, 2021). Duetting is part of these parameter adjustments. Learning for a purpose, most likely for cooperation, might well have been a crucial element that fostered the human species' survival and eventually might also have led to the development of human language.

I argue in this study that new environmental pressures forced the development and expression of innovative and new socio-psychological traits and that prosociality is a key characteristic as a driver for this change. Duetting is used as an example of one possible tipping point toward prosociality and eventually cooperation.

To develop these ideas, the study will first introduce the prosocial hypothesis along with hypotheses on human language evolution and then present duetting as a special case of vocal interactive behavior that leads to cooperation and cognitive expansion, and it finally shows why prosociality has an important place, or might well be the lynchpin, in the evolution of human language.

1.1. Background

The evolution of human language has been of undiminished interest and has been pursued by vastly different scholarly disciplines and, sometimes, these disciplines either do not read each other's conclusions and insights or their respective conclusions expose chasms. For instance, biology-based evolutionary theories and linguistic explanations concerning human language evolution have often been at loggerheads with each other (Hockett, 1959; Cadková, 2015). The alleged uniqueness of the human language proposed by 19th-century linguists was irreconcilable with evolutionary theory. Darwin (1859) certainly outraged Oxford University linguist Friedrich Max Müller who proclaimed that "language is the Rubicon which divides man from beast, and no animal will ever cross it" (cited by Fitch, 2013). Müller was not the only critic. Later, researchers adopted an *a priori* position arguing that primates were incapable of engaging in vocal learning (i.e., did not possess the ability to modify acoustic and syntactic sounds and were unable to imitate sounds and words) and hence primate communication was far inferior to that of humans, and to suggest otherwise was indefensible (Penn and Povinelli, 2007). As recently as 20 years ago, some linguists still expressed the belief that animals only produced sounds whose signal inventories "are limited and not subject to cultural modification" or, more precisely, animals were only able to produce innate sounds (Studdert-Kennedy, 2000). Studdert-Kennedy and Goldstein (2003) further argued that human language is defined by the dissociation of sound and meaning and has no precedence in animal vocalizations. Dissociation is seen as a critical discontinuity that separates human language from other primate systems of vocal communication (Studdert-Kennedy and Goldstein, 2003).

Not surprisingly, despite the controversies about primate linguistic abilities, comparative research into the origins of human language has focussed on the primate line, the closest extant relatives of humans (Fedurek and Slocombe, 2011; Wheeler and Fischer, 2012; Townsend and Manser, 2013; Levinson, 2016; Vonk, 2020). Some primates, particularly apes, actually show a great diversification of communicative acts, from gestures (Liebal and Call, 2012; Hobaiter et al., 2022) to body movements (Gasser and Arbib, 2019), from singular vocal acts to sustained vocal expressions (Liebal and Oña, 2018), and, finally, to joint vocal actions (Sekulic and Chivers, 1986; Baker-Médard et al., 2013) and even "song"; the latter largely limited to gibbons (Geissmann, 2000), Malagasy Indri, *Indri indri* (Maretti et al., 2010; De Gregorio et al., 2019), titi monkeys, of the following three genera: *Cheracebus*, *Callicebus*, and *Plecturocebus* (Adret et al., 2018; Aldrich et al., 2023), and Sulawesi tarsiers (MacKinnon and MacKinnon, 1980; Clink et al., 2022). These various and diverse examples of communicative behavior in primates have provided a rich canvas as starting points for human language origins, be they initially gestural or vocal (Deacon, 2003).

Indeed, theories of language evolution have proposed a vast range of different possibilities, be this via gestures, music, and rhythm (alternatives to be discussed later) but the puzzle remains how the switch from non-speaking great apes to speaking humans could have occurred. We know now that apes can form concepts and abstract ideas concerning the passage of time (Patterson,

1978). Through American Sign Language, ample evidence has been accumulated that apes use this means of communication to create new meanings, invent new signs, and combine words in ways that create a message (Miles, 1990, 1994). And Koko, a gorilla, showed that he was able to remember past events and plan or imagine the future (Patterson, 1978). Experience, memory, and learning produced new outcomes. Barton (1998) and later Barrett and Henzi (2005) explained that, as primates formed larger and socially more cohesive groups, their perceptual system needed to be enhanced to process details of dynamic social stimuli, such as facial expression, posture, gaze direction, and the like (Barton, 1998).

Significantly, research has shown that proto-language or gestures in great apes are mapped to specific areas of the brain used in human language such as Wernicke's and Broca's areas (Cantalupo and Hopkins, 2001). Interestingly though, the greatest expansion of the primate brain over evolutionary time apparently occurred in the visual cortex (in particular, area V1; Das and Gilbert, 1995), in the parvocellular region, which is associated with the analysis of fine detail and color in diurnal primates (Harting et al., 1973; Smaers and Vanier, 2019). Also largely located in layer V1 of the visual cortex are the recently discovered spindle cells, probably unique to great apes and the human brain (Banovac et al., 2021). There is some evidence that specialized spindle cells project to highly specific motor centers "controlling vocalization, facial expression, or autonomic function" (Nimchinsky et al., 1999). Perceptual abilities and the ability to discriminate vocal and facial expressions are certainly of benefit when subtleties in communication and an understanding of the emotions and intentions of others are increasingly important. Gesturing is a non-linguistic act but, as had been shown time and again, it can convey very specific meaning. Pointing, in particular, has often been identified as a key behavior for understanding the development of language and theory of mind (Camaioni et al., 2004). More of this later. Recent work has also identified a "primate mosaic brain evolution" (De Casien and Higham, 2019). The authors concluded that these were in the area of sensory and cognitive specializations that enabled effective communication even at a non-linguistic level (De Casien and Higham, 2019).

The apes' proven physiological inability to speak required morphological changes. Such changes included the dropping of the larynx before speech could occur and this led to humans' ability to speak (Lieberman, 1985). This theory had lost some traction in favor of suggesting different processes. Nishimura et al. (2022), for instance, have now shown that important physiological changes did occur but in an unexpected direction. The adaptations involved a process of *shedding* anatomical features of the vocal apparatus via structural simplifications: the laryngeal air sacs of great apes disappeared (Trenbeath, 2021) and as humans evolved, they also lost the standard primate laryngeal feature of thin upward projections of the vocal folds, and they considered these the crucial adaptations for speech (Nishimura et al., 2022).

As recent research has shown, however, some primate and avian vocal abilities are far more complex and varied than once thought (Kaplan, 2014), starting, in primates, with the discovery of referential signals in vervet monkeys, *Chlorocebus pygerythrus* (Seyfarth et al., 1980; Seyfarth and Cheney, 1986), continuing with the discovery of referential food grunts in chimpanzees, *Pan*

troglodytes (Watson et al., 2015), food calls in common marmosets, *Callithrix jacchus* (Rogers et al., 2018), and the vocal modifications found in pygmy marmosets, *Cebuella pygmaea* (Snowdon, 2018). Great apes and even new world monkeys (such as black-fronted titi monkeys, *Callicebus nigrifrons*: Caesar and Zuberbuehler, 2012; and white-faced capuchin monkey, *Cebus imitator*: Coss et al., 2019) have been shown to use referential gesturing and vocalizations. Indeed, the detailed linguistically based studies of the 1980s and 1990s confirmed that apes were able to learn American Sign Language (Gardner et al., 1989; Miles, 1994). They understood words, commands, and objects, even showed some sense of grammar (Greenfield and Savage-Rumbaugh, 1990), and were able to count (Boysen and Bernston, 1989). This was confirmed for all four great ape species (bonobos, *Pan paniscus,* and chimpanzees, *P. troglodytes*: Savage-Rumbaugh, 1984; gorillas, *Gorilla gorilla*: Patterson, 1978; orangutans, *Pongo abelii*: Miles, 1990). While some avian species trump some of the primate skills (from chickens being able to count (Rugani et al., 2011) to the ability to understand speech (Pepperberg, 2007), the point here is that there are many precursors to human language evolution, be this conceptually and semantically, and thus cognitively already present in primates (Lameira, 2017).

By the 1990s, experts in the field spoke openly about the "minds" of great apes, rather than about "cognition" (Russon et al., 1996). In primates, this abstract ability to be able to deal with symbolic representations of language and thus display complex cognitive processes led to a host of detailed investigations both of behavior and of the structure and function of the primate brain (Maestripieri, 1999; Reader and Laland, 2002). Such investigations and comparative studies between primates and humans continue to this day and have clarified differences (Palomero-Gallagher and Zilles, 2019) and similarities (Miller et al., 2021) between the brain of apes and the human brain. The discoveries of mental time travel (conceiving of past, present, and future) conveyed in sign language added depth to the view that apes are cognitively very advanced, can readily cope with abstract concepts, and imbue gestures with meaning (Leavens, 2004; Liebal and Call, 2012; Fröhlich and Hobaiter, 2018; Hobaiter et al., 2022). Cognitive features of primate behavior, such as cooperation, have also been identified as essential qualities for human language evolution (Williams et al., 2022).

2. The prosocial hypothesis

Prosocial behavior has long been of central concern and research interest in human psychology, partly because adolescents who show weakly developed prosocial behavior tend to display several behavioral problems (Card et al., 2008; Carson, 2013). The prosocial hypothesis proposed here is that human evolution and human language development depend on a three-pronged model of key pillars: prosocial, cognitive, and collaborative actions. It is not a combination of those three elements but a sequential development, i.e., of prosocial behavior leading to sharing of cognitive insights and eventually collaborative actions. These advances tended to offer or help solve a range of environmental and inter- or intra-group challenges. The argument of the prosocial hypothesis is well in line with other hypotheses of complex, often multilevel

social structures (Cronin, 2012; Sewall, 2015; Aureli and Schino, 2019; Kappeler et al., 2019; Morrison et al., 2020), communication, cognition (Sewall, 2015), and, importantly, cooperation (Jaeggi and Gurven, 2013) as drivers of evolution. They also fit well with the human self-domestication hypothesis (Hare et al., 2012). As Hare (2017) states: the human self-domestication hypothesis entails (a) selection for prosocial behavior linked to derived human cooperative-communicative abilities and (b) the domestication syndrome in human morphology, physiology, development, and cognition, as seen in other self-domesticated species (such as dogs).

However, there are some contradictory and unresolved problems between the studies of primatology and anthropology. The occurrence of prosociality in animal studies has spawned two main hypotheses, called the cooperative breeding hypothesis and the self-domesticated hypothesis. According to Amici et al. (2014), the cooperative breeding hypothesis, at least in primates, predicts *low levels of prosociality* when specific species are *non-cooperative* breeders, while the self-domestication hypothesis predicts high levels of prosocial behavior because self-domestication presumes high levels of tolerance of each other (Amici et al., 2014). Humans and callitrichid monkeys are the only primate species described as cooperative breeders, so they should show high levels of prosocial behavior and they do (Martin et al., 2021). All great apes should show *low* levels of prosocial behavior as Amici and colleagues found when they tested chimpanzees, bonobos, gorillas, orangutans, tufted capuchin monkeys (*Sapajus apella*), and Geoffroyi's spider monkeys (*Ateles geoffroyi*). Indeed, Amici and colleagues found little to no prosocial behavior in any of the great apes and New World monkeys they studied. This very much runs counter to other research results but, importantly, also to hominin evolution that has argued repeatedly that prosociality, indeed the human ability to support each other, is an essential precondition for the success of humans, perhaps the main reason why this species survived and thrived (Hare, 2017).

The results by Amici et al. (2014) showing little evidence of prosocial behavior especially in the four great ape species may be explicable by different circumstances and housing as well as gender. However, their results have been duplicated. Three years after the publication of their results, Verspeek et al. (2022) conducted experiments with bonobos and equally found no evidence of prosocial behavior, confirming the results and conclusion of Amici et al. (2014).

However, these results run counter to the prediction that self-domesticated primates should show *high* levels of prosocial behavior. The anthropological literature on human evolution from the Lower Paleolithic (ca 1.5 million to 200,000 years ago) to the Holocene Epoch (11,700 years ago to the present) periods strongly argues that later humans are self-domesticated (one hypothesis of prosociality) and, by the time of the Holocene, show strong prosocial behavior. The human self-domestication hypothesis (HSD) (Hare and Tomasello, 2005; Hare et al., 2012; Hare, 2017) seems very convincing and supports evolutionary trends also in other species, especially dogs (Hare, 2017). The assumption is, of course, that the nearest relatives to early humans, chimpanzees and bonobos, should share the same traits of prosociality and high levels of mutual tolerance or even spontaneous altruism, as has been described in humans, and certainly high levels of tolerance

were found in children and chimpanzees (Warneken et al., 2007; Warneken, 2015). Such incompatible results give at least pause for thought.

Equally, evolutionary theories, such as Darwin's and Baldwin's, suggest that environmental pressures led to the invention of a new behavior by means of learning (natural selection favoring cognitive plasticity) and gradually an increase in cognitive abilities in humans. However, more social pressure does not always require more cognitive ability but can lead to more subdivision of tasks and a lowering of individual cognitive ability (Fedorova et al., 2017).

The first imperative would seem to be that individuals had to bond with conspecifics in some social way. The social brain hypothesis Dunbar proposed in the late 1990s (Dunbar, 1998) was at first designed to explain why primates had unusually large brains for body size compared to all other vertebrates: He attributed this to their complex social system but later he extended this hypothesis to human evolution (Dunbar, 2014). The social brain hypothesis that Dunbar developed largely seemed to explain the expansion of cognitive abilities particularly in the primate line and chiefly in chimpanzees. It did not necessarily explain the evolution of complex communication and prosociality in humans until the human self-domestication hypothesis was developed and tested, showing that apart from the physical, physiological, and other changes, self-domestication selected for high prosociality (Cieri et al., 2014; Hare, 2017).

3. Hypothesizing the evolution of human language

The prosocial hypothesis advanced in this study does not conflict with the social brain hypothesis (Dunbar, 1998) or the hypothesis of a gestural origin of human language (Corballis, 2002, 2010). Both, as well as several others, rightly emphasize the gradual sequencing of psycho-social developments, including nuances of communicative behavior. The term "communication" is chosen deliberately here. In agreement with Fitch (2020), even sophisticated, vocalized (referential signaling), or verbalized (human speech) communication does not address the cognitive richness of concepts that may or may not be expressed in words and may not leave measurable behavioral evidence. Also, the multifarious, at times instantly changeable, and flexible interactions between environment and organism need to remain firmly in view. We know that extant apes are capable of distinguishing gestures, facial expressions, and vocal information and, presumably, so was the hominid and hominin brain.

Even gene expressions can change relatively quickly. Wiles et al. (2005) gave as an example the genetic ability of mammals to synthesize vitamin C in the body. But in primates, by a process called genetic redistribution, this gene expression was eliminated so that, from then on, the only way to acquire vitamin C had to occur exogenously. A second example, a purely morphological change, was provided by Darwin's Galapagos finches. Darwin concluded that consistent environmental differences in different habitats in the Galapagos promoted *directional natural selection* on resident finches for optimal beak morphology. This process has produced more than a dozen distinct species of finches, all unique to the

archipelago, further cementing Darwin's idea of natural selection (Grant, 2017).

Thus, in psycho-cognitive developments, both behavioral synchronicity (the ability to match the behavior of another, be this in movement, sound, and mood) and prosocial inclinations need to *precede* the development of intentional acts toward conspecifics (see Table 1) and create a niche for enhancing cognitive abilities in what has been termed "emotional intelligence" (Salovey and Mayer, 1990). Communication is a very important part of this but so is finding a *reason for* extended communication, namely the emergence of "other-directedness", of the importance of a partner or a group for one's survival.

Table 1 should be read from left to right as a cumulative and dynamic development toward prosocial and affiliative behavior. Note that the Australian shingleback lizard (*Tiliqua rugosa*) is a monogamous lizard but the pair separates outside the breeding season. Only those species are included here with pairs also staying together outside the breeding season and that particular condition alone limits the number of species included in animal bonds. Table 1 also indicates that the life history data of species, including their reproductive strategies, are important variables.

The point of this study revolves largely around two main social characteristics of any form of cooperation (one is biparental care and the other is prosociality) as two imperative milestones in the evolution of human bonding (Launay et al., 2016) and human language. However, biparental care in humans has a slim evolutionary base. When, for instance, examining reproductive strategies in fish, reptiles, and amphibians (Andrew-DeWoody et al., 2000), or even mammals, the number of species across classes of animals remaining paired for years is very small indeed. While Table 1 has identified species from marine life to a broad range of land animals, pair bonds, let alone monogamous life-long bonds, are overall very rare in any vertebrates, except for birds. In birds, at least 95–97% of more than 10,000 avian species pair bond with a mate and jointly raise their offspring (Cockburn, 2006).

In mammals, according to Clutton-Brock (1991), only about 5%, including some primates such as marmosets (Burkart and van Schaik, 2020; Martin et al., 2021), meerkats, wild dogs, and certain species of mice, form lifelong pair bonds or even short-term pair bonds and practice biparental care. But the 5% of mammals that practice biparental care still tend to live in troops, groups, prides, or packs, in which the breeding pair typically consists of the alpha male and the alpha female. Hence, the social configuration of pair bonding of two humans and the evolution of complex communication systems, including language, in humans, have few direct evolutionary predecessors, and, with some exceptions, the various elements required for creating a prosocial context are often not in the one species together.

Birds and humans thus have in common that they both raise their offspring as pairs (biparental care) or raise offspring cooperatively and even join forces in group defense. Cooperation and bonding in hominin evolution may not be an innovation *de novo* but evidence of such social relationships and task coordination still offers challenges to our understanding of their developments, be this in humans or birds (Issa et al., 2023).

Great apes generally provide many variations in mating and alliance systems, however, making meaningful comparisons with human society more difficult. Of course, the mating system of a species does not always mirror its social system (Dixson, 2009). By and large, orangutans are solitary (Kaplan and Rogers, 2000), western lowland gorilla (*Gorilla gorilla gorilla*) groups with several females and offspring are usually ruled by a single silverback (Forcina et al., 2019), and, with some variations, mountain gorillas, *Gorilla beringei beringei*, although classified as one male group may be up to 40% multimale groups (Robbins, 1999; Morrison et al., 2020). Chimpanzees live in multimale and multifemale social groups and may strongly compete with and aggressively fight other groups, and bonobos have a matriarchal system (Sommer et al., 2011). At some stage, the human social organization may have been the closest to that of gorillas, living with them in forests (White et al., 2009) or having moved to savannahs (the oldest established hypothesis on human bipedalism; Senut et al., 2018) or, as has also been suggested, living largely near water and exploiting its resources (Stewart, 1994; Finlayson, 2014). As Schacht and Kramer (2019) noted recently, consensus on a human-typical mating system remains elusive. "While a simple classification would be useful for cross-species comparisons, monogamous, polyandrous, and polygynous marriage systems exist across contemporary human societies" (Schacht and Kramer, 2019).

In discussing various mating systems, respective benefits for offspring are worth mentioning here. For instance, there is evidence that stable, socially monogamous pairs or stable small family groups in whatever species or class of animal create a safe and largely stress-free emotional and learning environment (Raposa et al., 2016) strengthening survival and long-term health. In many species with these characteristics, there is also an extra social layer—that of socializing juveniles. As I have explored elsewhere (Kaplan, 2020a, 2023), such environments encourage extensive social play behavior that is intimate, communicative, and creative (Bateson and Martin, 2013), and this is usually regarded as beneficial for the individual concerned. Whatever one might call the effects of play: they are now recognized as generating positive emotions (rats: Panksepp, 2005; Pellis and Pellis, 2007; Vanderschuren et al., 2016; ravens: Osvath and Sima, 2014; primates: Loizos, 2017). Positive emotions are themselves reinforcing to seek similar contact in future. Hence, regardless of how social interactions proceeded to evolve into human language—be this via gestures, music (song and dance), drumming, whistling, or extension of referential vocal signals—it required motivation first to even get to a position of seeking expansion of any form of communication.

Second, Table 1 is meant to emphasize the centrality of evolving prosocial behavior in the formation and maintenance of strong affiliative bonds. "Prosociality", as already mentioned, has been highly topical in the field of psychology for some time (Luengo-Kanacri et al., 2021), especially in human developmental studies (Spataro et al., 2020). The social circumstances for the absence or presence of prosociality (which may be variable and flexible) continue to be explored, especially the consequences when a well-defined profile of prosociality is absent or weakly developed (Donald et al., 2021). However, its role in animal communication and bond strength (a) in flexibly functioning pairs, families, and animal communities and (b) as a trigger for the intentional sharing of goods, such as food (Feistner and McGrew, 1989; Jaeggi and Gurven, 2013; Güroglu et al., 2014), in communication and

TABLE 1 Types of animal bond.

Taxonomy		Species	Prosocial behavior								
			Pair-living breeding	Pair-living non-breeding	Maintain proximity	Joint territorial defense	Coordinated behavior	Biparental care	Affiliative behavior	Family defense (close-knit group)	Stress buffering
Invertebrates	Mollusca	Giant false limpet	*	*	*						
	Anthropoda	Snapping shrimp	*	*		*					
		Giant wood cockroach	*	*	*	*					
		Termites	*	*	*	*					
Vertebrates	Fish	Butterfly fish, Goby cleaner	*	*	*	*	*				
	Reptiles	Skinks	*	*	*	*	*	*			
	Amphibians	Poison dart frogs	*	*	*	*	*	*			
	Birds	Geese, Swans	*	*	*	*		*			
		Blue ducks	*	*	*	*		*			
		Cockatoos, Mackaws, Keas	*	*	*	*	*	*	*	*	
		Parrots	*	*	*	*	*	*	*	*	
		Song birds	*	*	*	*	*	*	*	*	
	Mammals	Prairie voles	*	*	*	*	*	*	*	*	*
		California mice	*	*	*	*	*	*	*	*	
		Wolves, Jackals	*	*	*	*	*	*	*	*	
		Marmosets/Tamarins	*	*	*	*		*	*	*	
		Titi monkey	*	*	*	*	*	*	*	*	*
		Great and lesser apes^	^	*	*	*	*	^	*	*	*
		Humans	*	*	*	*	*	*	*	*	*

Prosocial tendencies increasing.
^Great apes do not form pair bonds but are included here because they form long-term group bonds and males protect infants [what Wrangham (1979) called "permanent consortships"]. Gibbons (genera *Hylobates, Nomascus,* and *Hoolock*) and the siamang (genus *Symphalangus*), however, are the only hominoids to exhibit pair bonds and two-adult groups (Fuentes, 2000).
The double line is a demarcation line that indicates the emergence of prosocial behavior which is expressed as affiliative behavior.

ultimately in human language evolution is rarely considered. This is surprising, given the question: why are we the only primate that can speak? remains an open question.

I am suggesting a domino effect from joint action to prosocial tendencies, generating more detailed communication, leading in turn to an increase in differentiated acts of communication in both referential signals (vocal and gestural) as well as semantic content. Another point to be made here is that even the most occasional acts of prosocial behavior in great apes mean that prosocial behavior is, and most likely was, an option in primate culture.

Furthermore, prosocial behavior is causally linked to the evolution of human language because language is more than a linguistic manifestation. It is a tool for a *continuing motivation* to address a conspecific or partner. To achieve and maintain such motivation, both emotional and cognitive complexity needs to have developed and, if already present, increased further. In agreement with the dynamic systems paradigm (see Shanker and King, 2002; King, 2009), converging feelings and intentions among partners may continue to be enhanced in a dynamic of ongoing negotiation at inter- and intra-personal levels, leading perhaps to closer bonds. The latter is a claim of the involvement of emotions, recently discussed by Dukes et al. (2021).

Another point that at times seems to have been lost in debates between selfish and prosocial actions within pairs and groups of primates is to consider evolutionary principles: Whatever format of skills, communication, or affiliations is more sustainable, these traits are more likely to survive via natural selection. In some cases, they may even develop further, be this at the cellular level, in morphology, physiology, or even chemistry. Exhuberant morphological features are generally associated with food acquisition. Well-known examples are the elongated middle finger of one of the Madagascar's nocturnal lemurs, the Aye-Aye, *Daubentonia madagascariensis* (Sterling and McCreless, 2007), or the exaggerated beak length of the sword-billed hummingbird, *Ensifera ensifera* (Abrahamczyk et al., 2014), or, as Darwin described, the diversification of beak strength in finches in different environments. While the finch model of natural selection is well-known and can explain so many other variations in biology, it should be applied rigorously to behavior because the same evolutionary principles ought to apply.

4. Duetting

4.1. Characteristics

Duetting, a vocal manifestation of synchronicity, is one of the most studied vocal behaviors in mammals and birds and occurs in many forms, referred to as antiphonal singing, turn-taking, counter-calling, or counter-singing. Some of these exchanges are expressed between males. Whatever the dyadic composition, most interactions between two members of the same species are between male and female partners.

In the broadest sense, duetting and counter-singing are vocal behaviors that exist in many songbirds, in some primates, but also in Alston's singing mouse, *Scotinomys teguina* (Neff, 2019), Klipspringer antelopes, *Oreotragus oreotragus* (Tilson and Norton, 1981), the maned wolf (Ferreira et al., 2022), whales (sperm

whale, *Physeter macrocephalus*: Schulz et al., 2008; long-finned pilot whale, *Globicephala melas*: Courts et al., 2020; reviewed in Vanderhoff and Bernal Hoverud, 2022), amphibians (chorus frogs such as spring peepers, *Pseudacris crucifer*; Forester and Harrison, 1987; south African clawed frog, *Xenopus laevis*: Tobias et al., 1998; Legler's stream frog, *Ptychohyla legleri*: Etzel et al., 2020), toadfish, *Tetraodontidae* (Vieira et al., 2021), and even in a range of invertebrates (Bailey, 2003; Henry et al., 2013).

Duetting in the narrowest sense is defined as a temporally coordinated interactive vocalization between two adults, usually of established pair bonds. Such vocal exchanges tend to have specific temporal patterns and may overlap even substantially while, in birds, few or no overlaps occur. Taking turns, as Banerjee and Vallentin (2022) noted, requires a fast sensory perception of the sender's vocal output but also the precise control of the responder's vocal onset. During these interactions, participants simultaneously plan upcoming vocalizations while listening to respond as early as possible without interrupting the initiator of the duet (Levinson and Torreira, 2015; Banerjee and Vallentin, 2022). Many avian duets fit into this characterization. Duets consist of calls or syllables in rapidly produced vocalizations and even these can be void of specific meaning (Arriaga and Jarvis, 2013; Dahlin and Benedict, 2014; Barón Birchenall, 2016). Any of the turn-taking vocalizations can be defined as an orderly exchange of communicative vocal signals that may or may not overlap.

However, among those primates that are mated pairs in stable monogamous bonds and are in stable territories, duetting is a rare social phenomenon and involves clear-cut examples of closely temporally matched vocalizations. We know only of a few diverse primate families—Tarsiidae, Indriidae, Lemuridae, Hylobatidae, Cercopithecidae, and Pitheciidae—to which these conditions apply (e.g., Tarsius spp.; indri *Indri indri*; Mentawai langur, *Presbytis potenziani*; and gibbons, Hylobatidae). After studying the duetting and vocal behavior of some of these taxa Haimoff (1986) concluded that the occurrence of duetting in these primate species and the similarities found in the acoustical features of their vocal behavior, represented a case of functional convergence. Such convergence was possibly a result of their evolution of a common social organization or similar ecological niche (Haimoff, 1986). To my knowledge, this conclusion has not been challenged to date.

Duetting can have several functions, some of which might even be present in one single species (Dahlin and Benedict, 2014). These are mate-guarding (Dowling and Webster, 2018; Dolotovskaya et al., 2020), to signify and or strengthen partnerships (Mèndez-Càrdenas and Zimmermann, 2009; Smith et al., 2010; Singletary and Tecot, 2020), and may serve as an indicator of the presence of a well-versed territorial defense team that may send a warning to potential intruders (Adret et al., 2018; Amorim et al., 2022). In sperm whales, Schulz et al. (2008) studied the frequent exchanges of short sequences of clicks, termed codas. They found that the sequencing of exchanges into duet-like chains with overlapping and matching functions reinforced social bonds between whales, which is attributed to the same or very similar function to duetting as in primates or birds.

The act of duetting also seems to have some measurable, "feel-good" consequences for the participating partners, be this in hormonal changes in oxytocin and vasopressin and increased brain-to-brain synchrony in frontal and pre-frontal brain areas

(Amodio and Frith, 2006; Reindl et al., 2018), confirmed in bats (Zhang and Yartsev, 2019; Rose et al., 2021), primates (Smith et al., 2010), and human studies (Atzil et al., 2012; Bales et al., 2021).

We thus have some cumulative evidence that duets are largely partner and pair dependent and contribute to the bond, be this in inhibition driven by auditory feedback (Coleman et al., 2021: plain-tailed wrens, *Pheugopedius euophrys*) or in very precise timing but different frequencies (Hoffmann et al., 2019: white-browed sparrow-weavers, *P. mahali*). The evidence also suggests that, over time, coordination of duetting improves in timing and auditory adjustments to the partner's specific auditory characteristics of their part of the duet. In my research of duetting in wild free-ranging magpie larks (*Grallina cyanoleuca*), the duets I recorded of a local pair in coastal New South Wales, Australia (Coordinates 30.5869° S, 153.0001° E), were not just timed precisely but the segments of each partner were near identical (Figure 1). In one of the rare longitudinal studies of duetting, Hall and Magrath (2007) showed that, in magpie larks at least, duets in newly established pairs were not precisely timed and their vocalizations would even overlap. By contrast, in well-established pairs, timing became very precise in all measures. Presumably, a potential territorial invader can audibly ascertain whether a pair is well-established and has perfected the art of territorial defense or the pair was newly formed and relatively inexperienced in which case its territorial claims could be challenged. In this avian species at least, duetting has a dual function as a form of mate-guarding and as a warning for potential intruders that they are dealing with well-experienced pairs (Vanderhoff and Bernal Hoverud, 2022). In most cases, the coordination of a song tends to have a leader and a follower. The partner who maintains the rhythm becomes the leader and the partner who maintains the synchrony of the joint behavior becomes the follower, arguing that maintaining synchrony requires greater adaptation (Hoffmann et al., 2019).

Interestingly, in one of the larger nocturnal sportive lemurs (*Lepilemur edwardsi*) that Smith et al. (2010) studied, pair partners synchronized behavioral activities, especially *after* duetting. In other words, duetting is not an isolated skill but one that, in mammals and birds at least, is a well-evolved expression of social rules and bonds. The latter may readily lead to ever-increasing invention of sound symbols, i.e., sounds with semantic meaning (Vonk, 2020).

4.2. The relevance of duetting to human language evolution

Much has been made of the gestural origin of human language and for good reason. In apes, some 80 gestural referential signals have been identified (Leavens and Hopkins, 1998). As was mentioned before, apes trained in American Sign Language were able to show human researchers that they were capable of thinking of the past and the future (theory of mind), and of being linguistically innovative by making new combinatory words and even sentences (Corballis, 2002, 2010; Hobaiter et al., 2022). These discoveries were significant

in showing that concepts and theory of mind existed in apes before the evolution of human language and that these were applied intentionally and directed toward another individual or group.

One might argue (with some justification) that duetting is a very weak link to human language evolution especially when compared to the rich conceptual and symbolic range of ape gestures. With some exceptions (Clarke et al., 2006; Andrieu et al., 2020), duetting tends not to carry complex and personal messages as gestures can. But this is not the point. Lifting out any vocal behavior in extant species is providing a *static* snapshot of how and how far each species has taken its cognitive and affective abilities.

The question is why an expanded need for more communication arose in the first place, what its motivation was, and in what specific social context vocal communication eventually arose. Equally, the question remains as to why language as speech had to come about at all. A static snapshot may discover the extent of the cognitive achievements of a species, but it needs an evolutionary, dynamic perspective to address the question as to why and how vocal signals developed to the extent to which they did in humans.

It is generally agreed that biological changes can be due to mechanisms such as natural selection, random genetic drift (Santangelo et al., 2018; Miles et al., 2019), sexual selection (Kuijper et al., 2012), and other extraneous events or features (such as climate change: traditional food sources dwindling and changes in environmental topography; Veit, 2021). Such changes are responses and adaptations vital for enhanced chances of survival.

The changes that occurred in the hominin brain are structurally and functionally substantial. After investigating the differences in the brains of chimpanzees and humans, Ardesch et al. (2019) concluded, "…[our] findings suggest an evolutionary shift in the human brain toward investment of neural resources in multimodal connectivity facilitating neural integration, combined with an increase in language-related connectivity supporting functional specialization". The question is what possible internal or environmental factors could have made this happen? And how could language acquisition be achieved within the organisms' own biology and available social skills and resources?

In this regard, duetting is an important milestone, even if only shared by a few species among primates. This is not related to the less than frequent vocal displays of duets but for another reason: duetting can show the very point when adaptive behavior, that initially might have evolved for ecological reasons, can flip onto a cognitive and affective plane. First, unlike transitory mimicry of movement or sound, courtship dance rituals, or pre-copulatory synchronicity to *establish* a bond or common interests, this kind of synchrony investing in cooperative behavior means that such bonds have *already been established*. Such specific ongoing bonding practices may lead to further expressions of cooperative, prosocial, and even empathetic behavior (Hove and Risen, 2009). This is so because the partner has become a "significant other" and is given careful attention.

Clearly, the longitudinal study of magpie lark duetting, cited above (Hall and Magrath, 2007), showed that learning was involved when the duetting signals matched more closely after a year
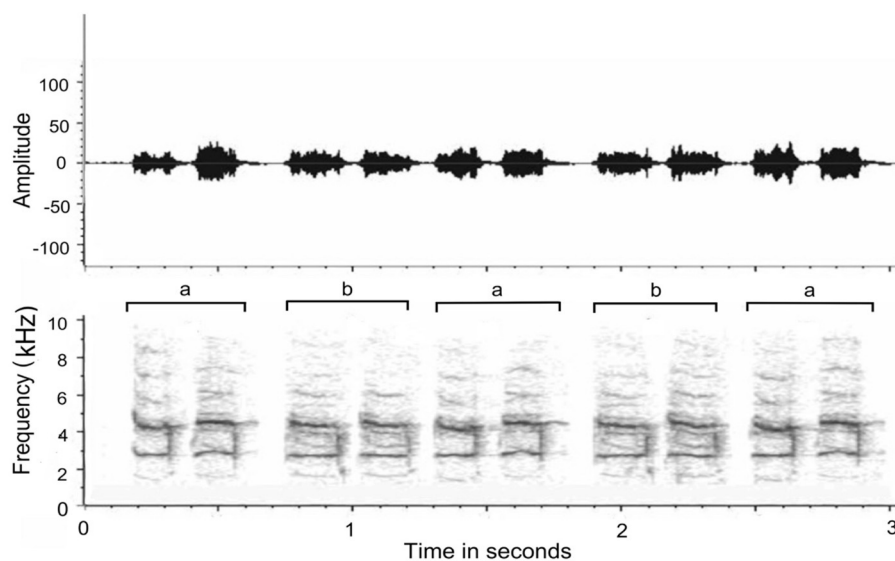
FIGURE 1
Waveform envelope **(Top)** and spectrogram **(Bottom)** of magpie lark duet (a) male; (b) female (author's recording). Note that the morphology of each call is matched almost exactly by the partner and the time intervals between initiated call and reply is reduced to split seconds. The miniscule time delay between a and b was not due to great distance or hesitancy by the replying bird but a function of the position of the remote-control microphone (closer to male) and wind direction (toward female).

than they did initially. Mastering precision requires close listening to and comprehending the other's rhythm, tempo, frequency, emphases, and even length of the duet. Nuances of duetting can vary substantially in terms of developmental plasticity (Adret, 2022), and calls can be sophisticated and distinct in expression (Clink et al., 2021) or may not seem sophisticated at all but are nevertheless significant as a collective behavior (Logue and Krupp, 2016).

This ability to create precise duetting is well-supported by identified brain mechanisms that allow such processes to occur. For instance, Okobi et al. (2019) pointed out that acoustic communication such as duetting often requires rapid modification of motor output in response to sensory cues. When they examined the vocal exchanges in Alston's singing mouse *Scotinomys teguina*, they found that males could modify their singing behavior on a sub-second time course that resembled "both traditional sensorimotor tasks and even conversational speech" in humans.

Two summary points about duetting can be made here in relation to the concept of synchronicity. First, duetting is just one manifestation of synchronicity, if a powerful one when the communication is intentional and practiced. Second, duetting is overwhelmingly found in stable and long-term relationships (Dahlin and Benedict, 2014). In pair duetting, "tuning in" to the bonded partner more than suggests that there is some flexibility both to innovate, learn, and adjust and to fit more directly with the vocal expressions of the bonded partner (Haraway and Maples, 1998; Oller and Griebel, 2008, 2021). Given these sustained observations, it becomes more plausible to suggest that some types of vocal behavior can lead to complex sociality and cognition (Roberts and Roberts, 2020).

5. Beyond synchronicity and toward cooperation

Synchronizing, as discussed above, denotes the precise timing and coordination of movements to coincide with those of another (Bernieri and Rosenthal, 1991). Coordination is socially not far removed from synchronizing behavior and thus plays a fundamental role in social interaction (Yu and Tomonaga, 2015), and such coordination can be a crucial step toward voluntary, intentional cooperation (Valdesolo et al., 2010; Michael et al., 2020). Unlike courtship dances or pre-copulatory synchronicity to *establish* a bond or common interests, this kind of synchrony investing in cooperative behavior presumes that such bonds *have already been established*. Past research has shown that synchronicity can also be tested behaviorally because it is interactional and observable (Hoehl et al., 2020).

5.1. Cognition and emotions

Results of many studies confirm that the brain of great apes and hominins, while expanding substantially from earlier primates (Smaers et al., 2017), did not do so uniformly, identifying some high-expanding areas within the forebrain (Sneve et al., 2019). According to Sneve et al. (2019), especially the brain of *Homo habilis* marked transverse expansion of the cerebrum and the frontal and parieto-occipital parts, and increases in the mass of the frontal and parietal lobes and the two major cerebral areas governing spoken language (Tobias, 1987). One notes also, that while brain mass increased, estimated body mass did not change appreciably (Table 2).

TABLE 2 Mean endocrinal capacity and body mass for select hominins.

Species	Mean endocranial capacity (cm^2)	Estimated body mass (kg)
Pan troglodytes (chimp.)	395.0	45.0
Homo habilis	640.2	48.0
Homo erectus	937.2	53.0
Homo sapiens	1,350.0	57.0

Data excerpted from Tobias (1987).

Such an increase in neocortical neurons comes with a high metabolic cost. Sneve et al. (2019) believed that the "capacity of high-expanding cortex to connect flexibly with various specialized brain 'networks' suggests an involvement in 'supramodal' cognition". Whatever is implied in this statement, it is clear that some of these expanding cortical areas are associated with language function in humans. For instance, both in humans and extant great apes, strong asymmetries are present at the population level in the frontal cortex, including a left hemisphere dominant asymmetry of the planum temporale, and in the brain region of Wernicke's area (Figure 2), which supports a critical component of speech production (Gannon et al., 1998; Hopkins et al., 1998; Spocter et al., 2010). Also, the sulci within the inferior frontal cortex, which contains Broca's area, displays left hemisphere dominant asymmetry in both humans and great apes (Sherwood et al., 2008; Hill et al., 2010). Both areas are specific to language and speech. Such patterns of select cortical expansions happened also during human evolution (Hill et al., 2010). In other words, the primate brain was already rather well-equipped to handle cooperation and coordinate activities in ways that required cognitive flexibility.

Those substantial expansions of some brain areas have come at a cost, however. The brain has been described as the most "expensive" part of the body (called "the expensive brain hypothesis", see Isler and van Schaik, 2009), demanding substantially higher energy input than the rest of the body. The "expense" is one of the nutritional requirement because neurons use up to 10 times more energy than body cells (Yu et al., 2014). We know from humans and mammals that energy consumption in the brain accounts for over 20% of total oxygen metabolism (Watts et al., 2018) and neurons consume 75–80% of energy produced in the brain (Hyder et al., 2013). The expensive brain hypothesis argues that the increased length and difficulties to raise an offspring usually lower the number of offspring that can be raised, which can lead to a creeping extinction, a process whereby replenishment of offspring falls below the death rate.

Such metabolic and cytoarchitectural changes in the brain would likely have occurred only if (a) there were substantial evolutionary pressures for new adaptations, (b) the "cost" could be offset by some external compensatory benefits and action, i.e., co-opt others to help protect and raise offspring, and (c) incurred benefits including higher survival rates of self and offspring. To have some negotiated position with a partner, family, or group to feed and care for an individual for a long period also raises the stakes as to the quality of social bonds and responsiveness to a partner—any close social bond or commitment thus involves the communication of some kind, creating a fertile social framework for the expression of emotions and the expansion of cognitive abilities.

Older theories of animal behavior tended to imply, influenced by the views of the French philosopher René Descartes (1596–1650), that animals were mere automata without minds, morality, language, or general intelligence (Thomas, 2020). In this instinct-dominated model, any behavioral expression by an animal was not based on choice but was elicited by a present stimulus that determined the frequency and form of the response. The behavioral form is the same from episode to episode of its elicitation and across animals of the same kind (Epstein, 1982; Miller, 2013). Against the affect-based theories, Richard Lazarus had argued from the 1960s onwards (Lazarus, 1982) that cognitive processes *precede* emotional ones, establishing a clear link between cognition and emotions well before neuroscience could confirm the brain processes involved. He argued that cognitive processes generate, influence, and shape the emotional response in every species that react with emotion.

According to the Lazarus doctrine, cognition is not a postscript to emotions, but for any species, no matter how limited its cognitive abilities may be, any event or encounter in the environment undergoes some evaluative process first. This suggested that most organisms, as far as tested, should come with an array of cognitive skills. This has since been confirmed experimentally. For instance, tests of young chicks have shown some abilities to form abstract concepts using geometrical cues (Vallortigara et al., 1990; Tommasi and Vallortigara, 2004). Indeed, young chickens were found to come equipped with a "package" of conceptual skills in geometry, physics, and mathematics (Vallortigara et al., 2010). Among non-vertebrates, similar cognitive skills were identified. For instance, bees can acquire the ability to deal with conceptual relationships such as "above" and "below", "same," "different," "larger than," and "better than," among others (Avarguès-Weber et al., 2011; Avarguès-Weber and Giurfa, 2013), and were recently shown to solve numerical cognition tasks (MaBouDi et al., 2021), but they may do so using quite different neural processes than birds or other vertebrates (Kaplan, 2015), and octopuses have multiple cognitive abilities that have now been identified (Amodio, 2019; Mather, 2022).

Hence, following several decades of research, it is now generally agreed that all of these elements described above—a basis in natural physics, mathematics, geometry, and natural psychology (for a review of these four pillars of animal cognition, see Vallortigara et al., 2010) is present in primates, many other mammals, birds, and even some insects so far tested.

The evaluative processes that animals may undertake, as Lazarus (1982) had argued, however, did not imply anything about deliberate reflection, rationality, or awareness but suggested that responses are based on learning and recall of previous and similar situations (accessible memory). Social learning undoubtedly plays a key role, both in an ecological and a psychological sense (Whiten and de Waal, 2018). Part of that learning process is taking note of someone else and, if a partner, that someone else may even be openly acknowledged by signs of affection (preening, for instance), in responding to requests, or in simple forms, by just walking in step, mirror imaging movements.
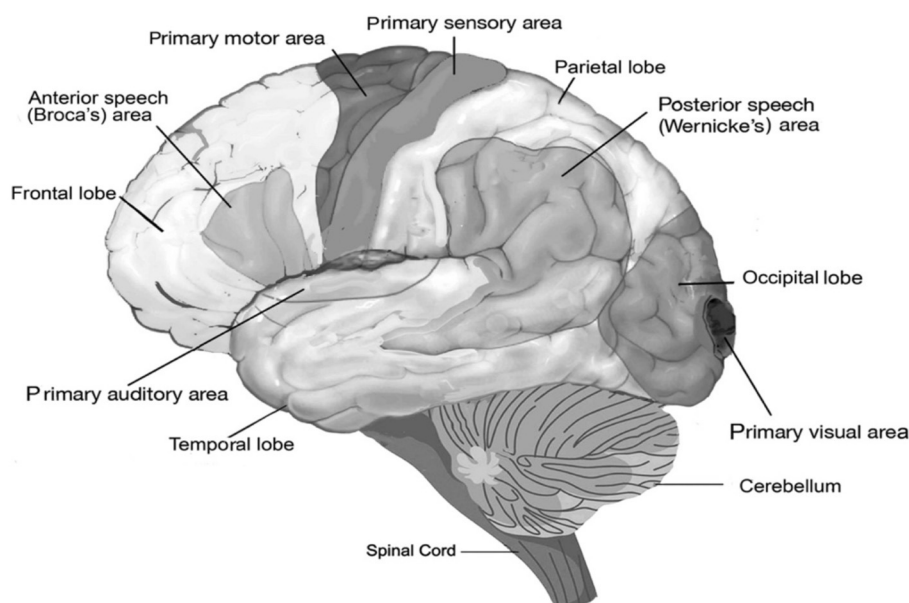
FIGURE 2
Functional areas of the human brain. The diagram shows the areas for speech and the location of basic perceptual areas (audition, vision, and primary sensory area) and motor area, as well as the anterior Broca's area and posterior Wernicke's areas, both of which are indispensable for speech and for which homologs have been found in non-human primates (Hopkins, 2022).

5.2. Multimodal perception, expression, and cognition

Both at functional levels and one that involves regulation of emotions in some way, duetting utilizes one single modality (audition), largely because individuals may be visually separated from one another (Smith et al., 2010). Duets may function as ways to reassure the two partners of their current location, be an example of mate-guarding or warn a potential intruder against invasion (Grafe and Bitz, 2004; Marshall-Ball et al., 2006). However, turn-taking in communication can happen in wider contexts and in visual contact with each other. Animals, be they diurnal or nocturnal, operate in a multi-sensory world (Partan and Marler, 1999; Hiramatsu et al., 2009). In addition to auditory information, individuals may simultaneously be exposed to and respond to visual and olfactory cues that may either confirm and strengthen the information received or contradict or annul information received in another modality (there is food but there is also a predator—a negative sensory input). Such stimuli combined may produce very different outcomes in behavior (Zhou et al., 2010). New World monkeys, such as the common marmoset (*Callithrix jacchus*), have a well-developed olfactory system and display a range of olfaction-based social behavior (Epple, 1993; Lazaro-Perea et al., 1999). As yet, however, there are too few studies that address the effects on the behavior of multi-modal signaling or incidental information on the response choices.

In our laboratory, we tested the idea of whether predator-naive marmosets (*Callithrix j. jacchus*) would show aversion to and withdrawal from fecal odors of predators and curiosity (approach) to food-based odors and found that marmosets perceive and respond to specific olfactory information and that olfaction may be more important for a broad range of functions not previously considered (Kemp and Kaplan, 2012). Although the importance of olfaction gradually declined in the primate line, it is worth remembering that olfaction has played an important role in perception apart from vision and audition (red-bellied tamarins: Caine and Weldon, 1989; cotton-top tamarins: Buchanan-Smith et al., 1993; wild mousse lemurs: Kappel et al., 2011). In the few research projects in which multimodal perception and responses have been investigated in detail, performance and success (whatever the measure might have been) tend to be enhanced by multimodal signaling. Rek and Magrath (2020), for instance, showed that visual display *enhances* vocal duet production in Australian magpie-larks, *Grallina cyanoleuca*.

Facial expressions, as visual stimuli, belong to another form of non-verbal communication that is shared by many primates, all apes, and humans, because we share the same facial musculature with the apes (Burrows, 2008). These expressions have been studied extensively, starting with Richard Andrew's first very detailed account (Andrew, 1963) and followed by an unbroken plethora of research publications until now, be this of great apes, some other primates, or humans (apes: van Lawick-Goodall, 1968; Parr and Waller, 2006; Kret et al., 2020; macaques: Hinde and Rowell, 1962; Partan, 2002; marmosets: Epple, 1967; Stevenson and Poole, 1976). We were interested to see how well marmosets could "read" the facial expressions of their cage mates and devised video footage, played back on large screens behind a food dish, and then tested whether

specific facial responses to food and predator-related stimuli might act as social signals to conspecifics (Kemp and Kaplan, 2013). We recorded two contrasting facial expressions (fear and pleasure) as separate sets of video clips and then presented food together with these images of cage mates. Results showed that the expression of a fearful face on the screen significantly reduced time spent near the food bowl compared to the duration of staying near the food bowl when a face showing pleasure was screened.

These multifarious non-verbal forms of communication in addition to gestural signals (Fröhlich and Hobaiter, 2018) remind one that all these aspects of primate and human social life act in unison, in one body and often simultaneously, providing a rich palate of possible emotions, messages, and intentions to be interpreted by the recipient (Kret et al., 2020).

The central cognitive task lies in the ability of the partner, offspring, or wider group to read these signals correctly and in conjunction with one another (Fröhlich and van Schaik, 2018). Waller's objection to viewing these communicative acts together is that they may have different underlying cognitive processes (Waller et al., 2013). Processing simultaneous signals can be far more challenging than one might suspect. The combinatory signals allow for strong messages in the negative and positive sense (Crivelli and Fridlund, 2018) by providing tools for deception (Gyger and Marler, 1988), contradictions, ambiguities, and misunderstandings—a possibility that does not improve with the evolution of speech (Herman et al., 2022). The understanding of non-verbal messages is supported by the brain's mirroring system that is shaped by individual experience. Tight links, therefore, exist between action and perception, both within an individual and between several individuals (Roelfsema et al., 1997; Dinstein et al., 2007; Schippers et al., 2010).

Michael Corballis has been particularly persuasive over the years in his argument that gestural communication was the forerunner of human language evolution (Corballis, 2002, 2010). Many have agreed with him, and they have been supported by further evidence, as already mentioned, showing homologous areas of the human brain for speech production (Broca's area) and for language comprehension (Wernicke's area) are found in great apes and macaque brains (Cantalupo and Hopkins, 2001; Gil-da-Costa et al., 2006). Infants make pointing gestures spontaneously from an early age (Liszkowski et al., 2004), a key to understanding the development of language and theory of mind (Butterworth, 2003; Camaioni et al., 2004). Others have argued that the act of pointing is a complex cultural and cognitive behavior (Kita, 2003).

Undoubtedly, such evidence of referential gesturing adds to the duetting paradigm of coordinated action involving a conspecific. However, it is not enough to explain the substantial expansion of the hominin brain and the actual development of human speech because gesturing itself is already a clear sign of motivation to expand communication. The question is rather, what events, ecological and social circumstances, prompted and motivated the expansion of communication and cooperation in partners and groups.
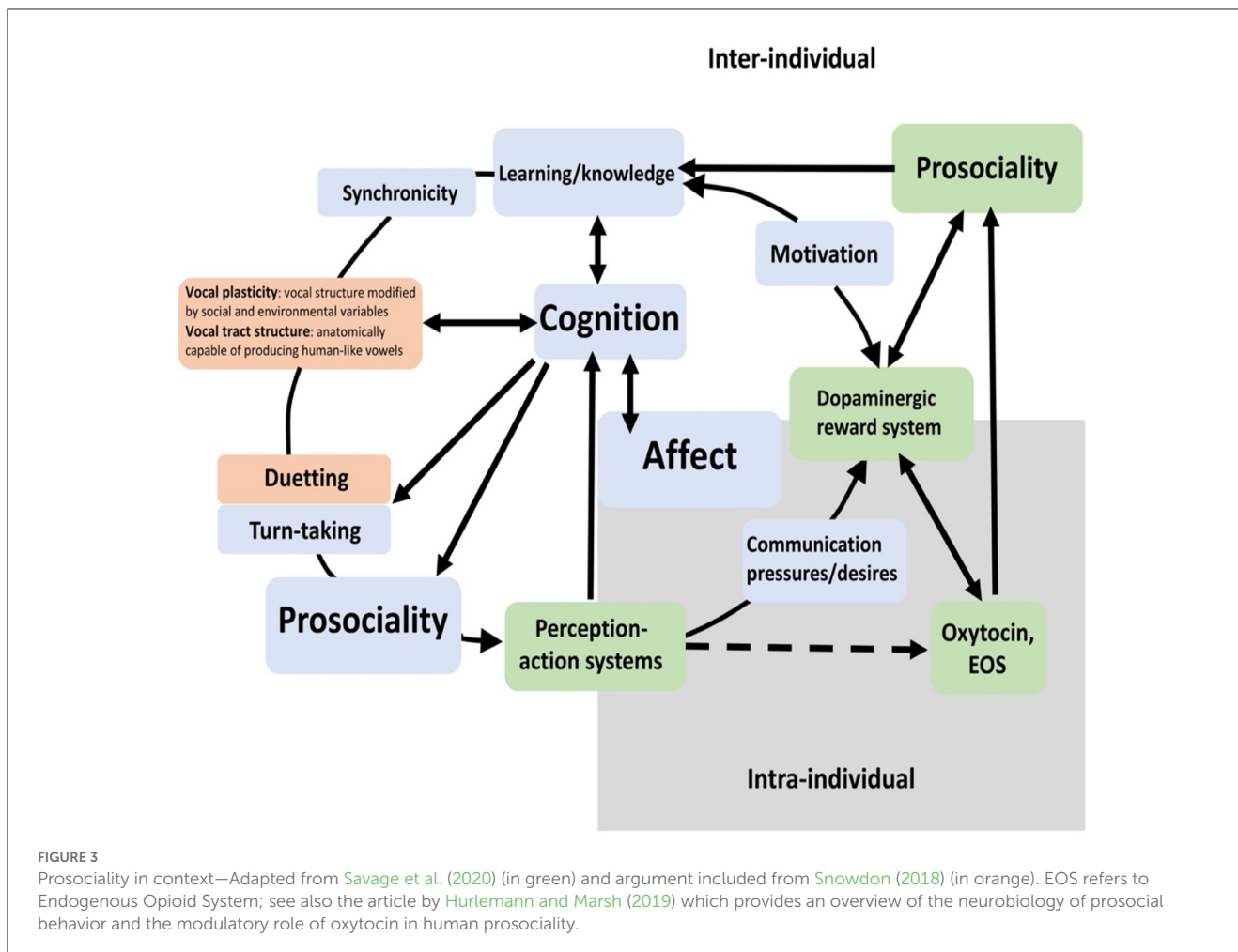
6. Prosociality and cognition

To be in synchrony with another individual on a specific task may be the beginning of some ongoing collaboration (Duguid and Melis, 2020) and thus create openings for entering into some level of the ongoing bond. When Heyes (2009) summarized her research interest in imitation and mimicry in human development, she might as well have spoken about prosociality in primates, birds, and humans. Heyes said: "Imitation is an important and intriguing neurocognitive process: a process that bridges the gap between one mind and another; that powers cognitive and social development in infancy and childhood; that promotes empathy, cooperation and well-being in our relationships with others" (Heyes, 2009). How these variables might interact is presented in Figure 3, showing that cognition is both shaped by learning or knowledge already gained and memorized and by perception-action systems (Savage et al., 2020). Evolving sociality, synchronicity of movement, body or facial expression, or synchronized vocalizations, such as duetting, increases the chances for further communicative acts, including the development of a gestural repertoire that is shaped and enhanced by cognitive abilities.

Note that, in Figure 3, prosociality is not featured as central to this diagram but it occurs two times: as part of the affective system and as part of the cognitive system. The cognitive system relies on perception and then relays its emotional response via a network of prefrontal nuclei for learning and memory to action a response. Figure 3 also shows that motivation is influenced and reinforced by emotions which in turn are regulated by a set of reward hormones: the dopaminergic reward system, the endogenous opioid system, and oxytocin (Savage et al., 2020). These systems also regulate moods and behavior in humans. However, they can only become active and functional if the individual has developed an ability to identify and respond to social cues, such as gaze and head or body orientation, clearly beneficial for the survival of any social animal, even in fish (Leadner et al., 2021).

Prosocial tendencies represent the next cognitive leap (post simple synchrony) in that a conspecific, or a group of conspecifics, come to constitute valuable "others" and are recognized as having their personalities, needs, moods, and demands. In addition, prosocial tendencies seem to require some basic form of bonding with another individual or a group beyond a mother–infant bond (that, in birds, can be achieved by imprinting, McCabe, 2019). Prosociality is sometimes referred to as "self-other resonance" to emphasize the interactive nature of this trait (Christov-Moore and Iacoboni, 2016) and is as much a social, emotional, and a cognitive process.

In human developmental psychology, prosociality has been a key topic for research into children's and adolescent behavior (Ferraro, 2019), but it is relatively rarely considered in animals. One of the reasons why it is so central in human developmental psychology is defined by the behavioral damage done to adolescent individuals in whom "prosocial" attitudes are missing or are poorly developed (Meehan et al., 2019).

However, de Waal and Suchak (2010) discussed prosociality in non-human primates at some length and emphasized the difference between empathy and prosociality, as is also used in this study. In brief, empathy is the capacity of the observer to

FIGURE 3
Prosociality in context—Adapted from Savage et al. (2020) (in green) and argument included from Snowdon (2018) (in orange). EOS refers to Endogenous Opioid System; see also the article by Hurlemann and Marsh (2019) which provides an overview of the neurobiology of prosocial behavior and the modulatory role of oxytocin in human prosociality.

feel with and indirectly experience the emotional state or even pain of the observed, while prosocial responses can be entirely unselfconscious, unaware, and consist of spontaneous helpful acts that demand no reciprocity. Prosociality and empathy have in common that either may be readily expressed within the social network of the observer or, in rare cases, may also be extended to strangers (Norscia and Palagi, 2011; Decety et al., 2016).

7. Human language evolution

In 2015, a specialist in evolutionary anthropology wrote an article that argued for human uniqueness on the grounds of three inherently human characteristics: an evolved advanced cognition, hyper-prosociality, and psychology for social learning (Marean, 2015). The narrative about human evolution and the development of human language as a set of linear prehistoric events seems to border on story-telling and certainly suggests an over-simplification, based on fossil finds that are possibly chronologically tens or even hundreds of thousands of years apart (de León et al., 2021). Nevertheless, fossil finds so far indicate that there was a modern human lineage in Africa (Templeton, 2002; Carotenuto et al., 2016; Husson et al., 2022), at least one

archaic African lineage (Hammer et al., 2011), and two archaic Eurasian lineages, Neanderthals and Denisovans (Mithen, 2006; Petr et al., 2020; de León et al., 2021). Certainly, the hypotheses of human evolution are getting more complex. The more fossil skulls are found and the more improved techniques of dating them in the 21st century, the less clear are the genetic and anatomical elements, involving consideration of admixtures and radiations which have made some evolutionary trajectories more confusing and unresolved (Lieberman, 2001). It is clear, however, that there was a substantial increase in brain volume from chimps and bonobos to *Homo habilis* and to *Homo erectus*, as shown in Table 2.

In between the estimated departure dates of hominins from Africa, there are long periods without any fossil evidence of any kind, in which various human groups would presumably have moved about, probably in small isolated bands. Genetically, socially and cognitively, much could have transpired. All hominin lineages eventually went extinct, leaving one single remaining homo member of the large family tree and perhaps its survival was contingent on precisely the qualities that were described in this study. From very different perspectives, the present paper and Marean's article have arrived at the same conclusion of the centrality of cognition, prosociality,

and the ability to work closely together, be these primates or humans.

Assuming the above is correct, the gap in explaining human language evolution is still large and might remain an open question. One can agree with Marean that the surviving branch was an "anomaly" in so far, as it was the only branch surviving despite tough climatic conditions and the species' very poor physical attributes. Humans, compared to other primates, had no fur to protect themselves from insects, from cold or heat, had poor climbing ability, only average speed in running, no claws, and little physical strength against any predators. But they did get one advantage: a large brain equipped for problem-solving and close cooperation, both enough to survive.

Human language is an arbitrary construct, and all bands of humans developed their own. One of the oldest living cultures in the world, Australia's Aboriginal culture, consisted of more than 250 nations and could boast as many languages, most of them bearing no similarity to each other (Blevins, 2001; Dixon and Dixon, 2011), except for the additional many dialects. There is no reason to think that all human communities developed language at the same time or had similar vocabulary sizes or even names for the same concepts or objects (Blevins, 2001; Dixon and Dixon, 2011).

An argument, rarely raised but possibly of substantial importance is to consider life histories in hominin species. Based on available evidence, John L. Locke and Barry Bogin did exactly that: they calculated the mean age of eruption of the first permanent molar and built the length of childhood around such available physical data. According to Locke and Bogin (2006), stages of childhood gradually lengthened from *Homo habilis* (3.8 years), early *Homo erectus* (4.5 years), and late *Homo erectus* (5.0 years) to *Homo sapiens* (6.2 years). Juvenile and adolescent stages also lengthened from 12 years in *Homo habilis* to 17 years in *Homo sapiens* (Locke and Bogin, 2006).

Lengthening childhood and juvenile stages over time suggests an increased biparental or family group commitment to protect and food-support their offspring for an ever-increasing period. We know from primates under group or biparental care, as well as from biparental care in avian species with protracted "childhoods", that the offspring seem to get three main benefits from this delay in maturation: 1, protection (low-stress levels); 2, long learning time; and 3, more play time with other juveniles fostering prosocial development. These social conditions, as I have shown elsewhere (Kaplan, 2020b), tend to correlate with growing large brains. In chimpanzees, offspring are typically weaned at ∼4 years of age, and thereafter the immatures of the western chimpanzees (*Pan troglodytes verus*), a subspecies of the genus *Pan troglodytes,* continue to associate with their mothers for up to 10 years beyond weaning (Samuni et al., 2020). From studies of both wild and captive gibbons, it is thought that gibbons reach sexual maturity at about 6–8 years of age, and the siamang (*Hylobates syndactylus*) at about 8–9 years (Geissmann, 1991). Similarly, in birds, some cockatoos reach sexual maturity when they are 6–8 years of age. To them and other avian species with similar life histories, the benefits tend to be identical to those in long-nurtured primates and hominin societies, such as longevity, cognitive complexity, and strong social bonds (Kaplan, 2019).

Finally, as Arbib (2013) rightly pointed out: "language" is not speech. Arbib (2013) and others before and since have seen song and dance as a bridge between music and language. The latter can exist as speech or in signs and can exploit voice, hands, and face (be this via voice utterances, whistles, drumming, clapping, and gesturing) using hearing and/or vision so that there is always a duality of patterning. To this day, there are sign languages, many whistled languages (Meyer, 2008), and also drum languages (Seifart et al., 2018; Ros, 2021). And there is dance combining rhythm, sound, and even song and movement. Laland et al. (2016) reminded us that dance has representational properties that "rely on the dancers' ability to imitate particular people, animals or events, as well as the audience's ability to recognize these correspondences." The beginnings of language might well have occurred via imitation and mimicry of animals and were expressed in music and dance. Both are ubiquitous among humans (Lewis, 2009; Knight and Lewis, 2017). Mimicry of sound (entrainment to a musical beat) or of body movement (dance) is suggestive of the capabilities of motor and vocal imitation (Fitch, 2016; Laland et al., 2016; Fink et al., 2021). Mimicry of sounds, songs, and dance may first have evolved from imitated movements (say of animals they have seen and might have hunted) to communicate socially relevant information about them accurately. Indeed, such information could have been conveyed in many ways, be this via gestures, pointing, sound imitation, or even dancing. These articulations may well be processed by a similar neural network as those responsible for vocal learning in songbirds (Schuppe et al., 2022). Darwin thought that different aspects of language were acquired *sequentially* and possibly over vast stretches of evolutionary time. Vocal actions needed partners, such as in duetting (Clink and Lau, 2020; Clink et al., 2020) or turn-taking (Takahashi et al., 2016), joint-calling as in choruses (Mitani and Gros-Louis, 1998; De Gregorio et al., 2021, 2022), and referential signaling addressed to a conspecific or a family group and groups (Seyfarth et al., 1980; Snowdon, 2020; Vonk, 2020). And in such partnerships in dyadic or group vocalizations and movements, coalitions and partnerships were forged that could solve problems and innovate.

Tobias et al. (2016) argued that communal signaling (which includes duetting and choruses) is perhaps the most complex and least understood form of communication in social animals. They used Bayesian phylogenetic models to test whether acoustic communal signals are explained by a range of life history and environmental variables across 10,328 bird species worldwide and estimated that duets and choruses occur in some 1830 (18%), and in these, evolutionary transitions between communal signaling and solo signaling were "not explained by latitude, migration, climate, or habitat, and only weakly correlated with cooperative breeding. Instead, they are most strongly associated with year-round territoriality, typically in conjunction with stable social bonds" (Logue and Hall, 2014; Tobias et al., 2016).

I suspect that in some cases, if not all, prosociality was a vital step toward communicating with others on a broader basis, be this out of necessity or to share information that was about matters not immediately visible. Beyond the speculative, the neurobiological and anatomical evidence and the behavior of extant vertebrates, especially primates, have provided mounting evidence of the

importance of the development of prosociality which makes its centrality in human language evolution very plausible.

8. Concluding remarks

In his treatise *The Expression of the Emotions in Man and Animals* (Darwin, 1872) and in chapters 2 and 3 of *The Descent of Man* (Darwin, 1871), Darwin talked about attention and imitation and he argued that if an individual can attend to something then it is possible for that individual either to imitate what it has seen or to be taught to do something (Kaplan and Rogers, 2004). Duetting and synchronized movements are both hallmarks of communication and group affiliations known in the primate line and particularly evident in many songbird species.

Furthermore, there is an ancestral social behavior network within the basal forebrain and midbrain that is common to all vertebrates from teleosts to birds and mammals and a mesolimbic reward system that forms a larger social decision-making network (Goodson, 2005; O'Connell and Hofmann, 2011). At the very least, one can say that a path to express and develop the ability for adaptive social behavior toward conspecifics has been in existence in ancient and well-preserved networks of the brain. Many research projects have also shown that interpersonal synchrony increases affiliation and increases cooperative behavior (Hove and Risen, 2009; Reddish et al., 2013). Note, however, that the social and vocal aspects of behavior can be mutually reinforcing. In a study of vocal behavior in bonobos, the researchers concluded that social bonds drive vocal exchanges (Levréro et al., 2019).

To have identified some potential sources for precursors of the evolution of human language should not be seen at the exclusion of many other evolutionary elements that might well have played into such a momentous innovation as speech. One might well speculate that any form of "language" in humans was evolutionarily a late development, suggested by complex activation of brain areas when such communicative acts occur. Kaan and Swaab (2002) found neuroimaging support for arguing that syntactical processing of multimodal information does not just recruit one specific brain area. Instead, a network of areas including Broca's area and anterior, middle, and superior areas of the temporal lobes are involved. Okobi et al. (2019) identified the neural control needed for duetting. Although this applied to Alston's singing mice, the model has been proposed as an emerging vocalization model also for duets in primates (Neff, 2019). Indeed, in primates, duetting happens to be one of the most convincing examples of vocal flexibility. How else would bonded couples achieve their voiced synchrony if it were not for the ability to adjust any specific features in vocal production, be they syntactical, rhythmic, or in frequency.

Anatomically, the road from pre-speech to speech in the hominid line was not blocked by the inability for vocal learning in primates or for lack of ability to form concepts, think of things past, and even plan a future. Primates and specifically great apes and some New World monkeys have shown remarkable cognitive abilities in solving problems and vocal learning.

Whether the gestural thesis of the origin of human language might explain the evolution of speech is not the point of argument here. The language might as well have developed via music and dance as said above. Moreover, "language" did not always result in speech as has also been pointed out above. These evolving systems of complex communication all reflect forms of self-expression as well as stable, communally agreed, unambiguous vocal labels for objects or concepts. While they well describe how rich in communicative abilities they may be, none of them show why any of them would have evolved in the first place.

The argument here has focussed on the possible motivators for the evolutionary precursors of such manifestations of communication.

First, in evolution, change tends to happen when an organism is stressed to fulfill its basic needs and/or when a small change in behavior or physiology gives one species a significant advantage over another. The hominid line had a poor record in meeting the challenges. All hominid ancestors eventually went extinct except *Homo sapiens*, suggesting that substantial innovations were needed to make this last hominin species viable. Studies on stress responses in modern humans interestingly found that stress triggers social approach behavior, which operates as a potent stress-buffering strategy, thereby providing evidence for the context and triggers in prosocial behavior, also referred to as the tend-and-befriend hypothesis (Von Dawans et al., 2012). How much speech has to do with it is yet another question.

Second, one constraint in the formulations of theories on human language evolution has been the need to remain focussed on one major variable, such as gestural origins, vocal synchronisations, and concept of musicality or dance. Hence, theories have tended to be single-focused on one singular candidate as a precursor of human language evolution. However, focus on any of these visual or vocal social expressions (and their expansions) is a focus on vocal expressions that are all, to varying degrees, *outcome*s in the communicative refinement of expressions of vocal and movement behavior.

Instead, this paper has posed the question of what impetus could have led to any of these impressive self-expressions and communicative complexities. It has been the contention of this study to ask why such outcomes occurred at all and which evolutionary steps had to precede these developments. As Hoehl et al. (2020) argued: Synchronizing benefits arise from an increased predictability of incoming signals and include many positive outcomes ranging from basic information processing at the individual level to the bonding of dyads and larger groups. Cooperative behavior, starting with specific vocal expressions such as duetting, fostered social cohesion (Launay et al., 2016). To achieve some synchronicity in duetting, as has been shown in many studies mentioned here, requires vocal flexibility. A recent study of lar gibbons, *Hylobates lar* (Raimondi et al., 2023), revealed not only substantial sophistication in the gibbon's rhythmic vocal expressions but showed that isochrony, at the core of human musicality, is present in lar gibbon duetting. Raimondi et al. (2023) found that gibbons are more isochronous when duetting than singing solo, achieving a higher-than-chance degree of synchrony in their duets because of this ability to rhythmically adjust their part of the duet and coordinate it (Raimondi et al., 2023).

In conclusion, the evolution of prosocial behavior may well be the vital precondition for, and the motivational link to, any

expansion of cognition and communication and ultimately causally related to the evolution of human language. Furthermore, evidence that has been provided in the duetting literature of primates and dolphins is the degree of flexibility in vocal exchanges. The remarkable vocal communication among dolphins has no bearing on human language evolution but is a case of convergent evolution. Their social behavior also showed consistency in some other social factors, comparable with primates (King et al., 2022). Indeed, in dolphins and some avian species, the same or very similar basic biological and social factors can be observed: high cognitive ability, strong social bonds, and a high degree of vocal flexibility and individuality as the vocal labeling of dolphins (King et al., 2018). Clink et al. (2022) discovered flexibility in vocal exchanges of Gursky's spectral tarsier, *Tarsius spectrum gurskyae*. They rightly argued that vocal flexibility (and individuality) is a precursor to human language, and it evolved early in the primate lineage and long before the emergence of modern humans (Clink et al., 2022).

It seems from the physical evidence on record that joint actions led to more cooperation, more communication, further brain growth, better problem-solving, and a more secure place for humans in the natural environment, despite the many physical inadequacies of the modern human species. The motivation to pursue shared goals and indulge in creative models of ever-expanding communication, eventually language, also has to do with the extensive reward system the brain provided. This probably came about because positive rewards accompanied acts and attitudes of prosociality and this, in turn, helped increase affiliative bonds.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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