



Developmental Plasticity in Primate Coordinated Song: Parallels and Divergences With Duetting Songbirds

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Homeothermic animals (birds and mammals) are prime model systems for investigating the developmental plasticity and neural mechanisms of vocal duetting, a cooperative acoustic signal that prevails in family-living and pair-bonded species including humans. This review focuses on the nature of this trait and its nurturing during ontogeny and extending into adulthood. I begin by outlining the underpinning concepts of duet codes and pair-specific answering rules as used by birds to develop their learned coordinated song, driven by a complex interaction between self-generated and socially mediated auditory feedback. The more tractable avian model of duetting helps identify research gaps in singing primates that also use duetting as a type of intraspecific vocal interaction. Nevertheless, it has become clear that primate coordinated song—whether overlapping or antiphonal—is subject to some degree of vocal flexibility. This is reflected in the ability of lesser apes, titi monkeys, tarsiers, and lemurs to adjust the structure and timing of their calls through (1) social influence, (2) coordinated duetting both before and after mating, (3) the repair of vocal mistakes, (4) the production of heterosexual song early in life, (5) vocal accommodation in call rhythm, (6) conditioning, and (7) innovation. Furthermore, experimental work on the neural underpinnings of avian and mammalian antiphonal duets point to a hierarchical (cortico-subcortical) control mechanism that regulates, via inhibition, the temporal segregation of rapid vocal exchanges. I discuss some weaknesses in this growing field of research and highlight prospective avenues for future investigation.

Keywords: antiphonal, brain-to-brain coupling, development, duet code, singing primates, songbirds, vocal flexibility

INTRODUCTION

“The development of communication is fundamentally embedded in social interactions across individual brains (Hasson et al., 2012).” Duetting, the coordinated sequences of acoustic signals exchanged between two individuals, has emerged as a remarkable phenotype of two brains wired to either cooperate or mitigate conflict (Fortune et al., 2011; Hoffmann et al., 2019; Okobi et al., 2019; Coleman et al., 2021). Whether this is a matter of hard or soft wiring remains an open question, but the diversity of mammalian and avian song duets holds great research promise for exploring how dyadic vocal interactions are shaped during ontogeny.

Here, I review the evidence for developmental plasticity in singing non-human primates¹, highlighting parallels and divergences with research on duetting songbirds. Collectively, these two phyla encompass tropical species that share similar socio-ecological characteristics, including putative sexual monogamy, family-living, and year-round territoriality with robust arboreal adaptations (Tobias et al., 2016; De Gregorio et al., 2022). However, they also differ in one key aspect, namely “vocal production learning,” which is the ability to produce novel sounds from auditory experience (Janik and Slater, 2000; Vernes et al., 2021). While oscine songbirds (passerines) stand out as fine vocal learners, evidence of this is limited in non-human primates [Snowdon, 2017a; Janik and Knörnschild, 2021; but see Lameira (2017) who makes a strong case of vocal production learning in the voiceless calls of great apes].

THE NUTS AND BOLTS OF SONGBIRD DUETTING

The considerable progress in research on avian duetting is marked by several influential reviews (Farabaugh, 1982; Hall, 2009; Dahlin and Benedict, 2014). Duetting patterns in songbirds range from loosely coordinated song (Benedict and McEntee, 2009; Tobias and Seddon, 2009) to synchronized or antiphonal song² uttered with exquisite temporal precision (Wickler and Seibt, 1980; Templeton et al., 2013; Kovach et al., 2014) and combining alternation and synchrony (Mann et al., 2006).

Duet Codes and Answering Rules

Duetting behavior occurs at both the individual and pair levels (Levin, 1996), while Logue (2006) studied duetting from an operational perspective in which two individuals establish a shared set of rules. This led to the notion of a “duet code”—a set of answering rules one individual uses to answer its mate’s song (Logue, 2006; Logue et al., 2008). While a duet is a pair-level property, a duet code is an individual attribute, and answers according to a duet code “adhere” to that code (Logue and Krupp, 2016). At its simplest, a single pairing rule, such as “answer F1 to M1,”³ generates the cyclical duet [i-n(M1-F1)]⁴ produced by many songbirds (Levin, 1996; Rogers, 2005). A more complex duet code, such as “answer F1 to M1, F2 to M2, and F3 to M3,” generates a non-repeated duet [i-(M1-F1-M2-F2-M3-F3)], as produced by an African weaver bird endowed with such a large syllable repertoire that both partners constantly switch between syllable types (Voigt et al., 2006; Lemazina et al., 2021). Logue’s duet code concept opened up new avenues for measuring how code complexity and adherence vary across species (Logue and Krupp, 2016), whether duet codes are pair-specific (Mennill and Vehrencamp, 2005; Templeton et al., 2013), whether one sex or

both adhere to these codes (Mann et al., 2003; Rivera-Cáceres, 2015), and whether duet codes emerge spontaneously in newly formed adult pairs or require vocal practice (Levin, 1996; Rivera-Cáceres et al., 2016). This begs the question: do young birds learn duet codes from their elders?

Duet Code Learning

Evidence that duet codes are learned from adults comes from observations of juveniles singing alongside their parents (Farabaugh, 1982; Hall, 2009). Such collective singing presumably allows juveniles to gain duetting experience, which not only requires learning what to answer and when but also mastering the duet rhythm in coordination with breathing given the rapid alternation (2–5 Hz) of male and female syllables (Hoffmann et al., 2019; Coleman et al., 2021). For example, song coordination in juvenile canebrake wrens improves over time via parental influence and independently of maturational effects, indicating a learning process (Rivera-Cáceres et al., 2018). Whether song acquisition results from copying a same-sex parent or integrating auditory information from both parental “tutors” remains unknown. There may also be alternative modes of code development with age. For example, a code might be retained throughout life (“close-ended”), whereby phrase-pairing rules remain constant regardless of partner identity (Levin, 1996); alternatively, mature individuals might re-learn a code each time they acquire a new mate (“open-ended”; Wickler, 1980). In the case of canebrake wrens, different pairs have distinct duetting rules, suggesting that learning in adulthood is likely. Indeed, removing and translocating individuals of well-established pairs confirmed that adult wrens re-learn pair-specific duet codes after re-mating, with males showing more flexibility in phrase-pairing rules than females (Rivera-Cáceres et al., 2016). Consequently, Rivera-Cáceres et al. (2018) proposed a three-step model for duet learning: (1) memorizing song material from auditory exposure, (2) rehearsing duet songs with both parents, and (3) re-learning to coordinate songs with a breeding partner (**Figure 1A**). Whether these two latter forms of sensorimotor learning share the same neural connections is the subject of future research (Nieder and Mooney, 2019).

Many songbirds co-sing in rapid turn on a syllable-to-syllable basis with sub-second latencies (Mann et al., 2009; Fortune et al., 2011; Rivera-Cáceres, 2015). To achieve such tight coordination, individuals rely on sensory information originating from two sources of auditory feedback—one generated by the bird’s own voice (autogenous) and the other from its singing partner (heterogeneous). Owing to the velocity of sound, the longer the distance between the duetters the longer the delay for both receivers. Duetting songbirds adapt to these delays by altering the timing of their singing (Fortune et al., 2011) or by using visual cues in open habitats (Rek and Magrath, 2016, 2020). How, then, is auditory feedback encoded in the brain?

Neural Mechanisms

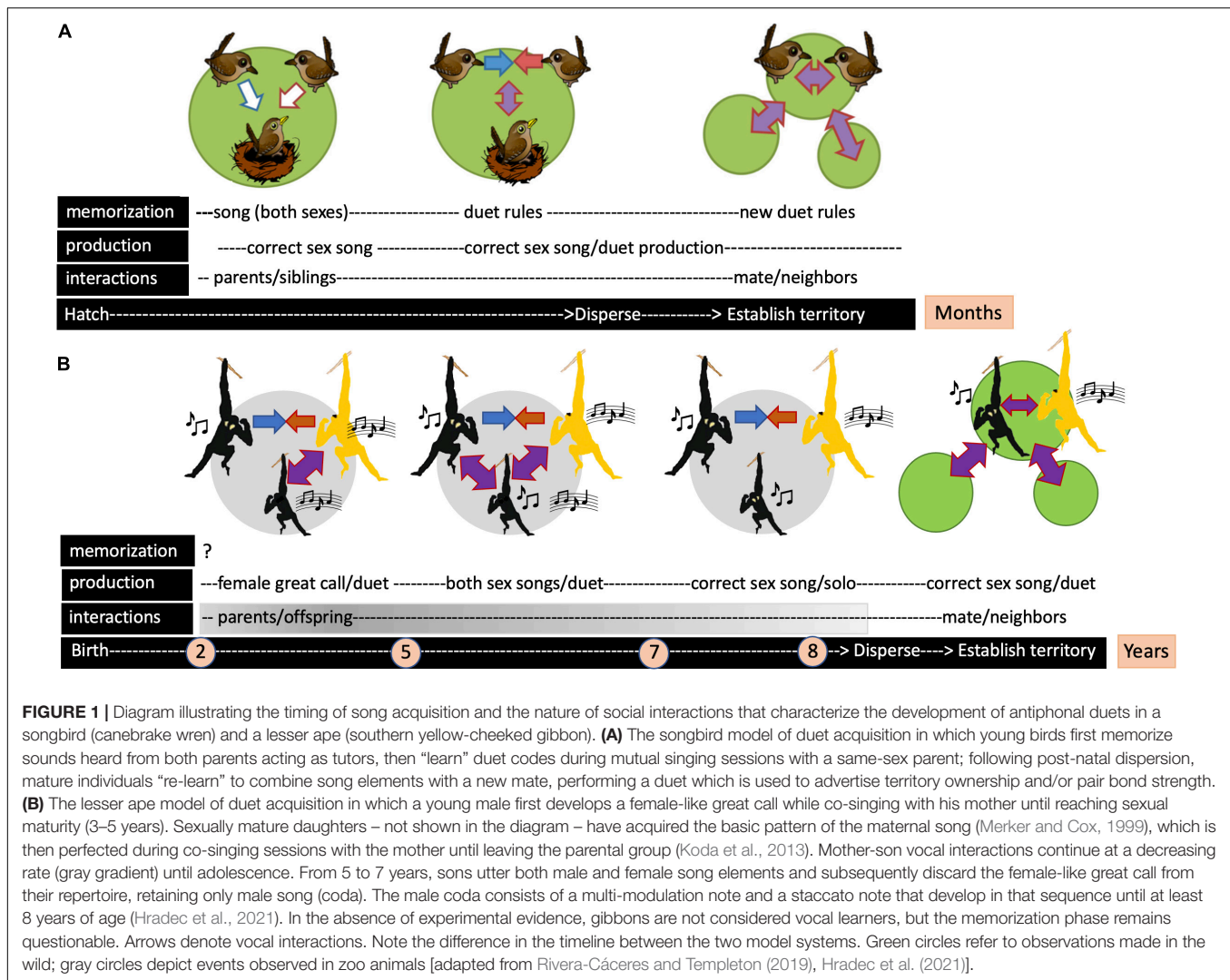
Neuroanatomical studies of duetting songbirds reveal the presence of well-developed brain nuclei dedicated to song production learning in both sexes, which contrasts with the females of species in which only males sing

¹Singing primates are distributed in Southeast Asia (e.g., gibbons, tarsiers, and the Mentawai langur), Madagascar (e.g., indri and Milne Edwards’ sportive lemurs), and South America (e.g., titi monkeys).

²A series of notes of different types, uttered following a hierarchical structure, and characterized by a frequency variation.

³Where F1 and M1 stand for female and male syllable types, respectively.

⁴Where “i” stands for the introductory notes, with $n > 1$.



(Nottebohm and Arnold, 1976; Brenowitz and Arnold, 1986; Deng et al., 2001; but see Lobato et al., 2015). Research into the neural underpinnings of antiphonal duetting targets the HVC (used as a proper name), a high-order forebrain song nucleus involved in sensorimotor learning (Nieder and Mooney, 2019). Contrary to neurophysiological data obtained for songbirds in which only males sing, extracellular recordings in the HVC of anesthetized wrens show strong responses to auditory presentations of both male and female song when played in isolation (Fortune et al., 2011). Furthermore, experimental manipulation of song stimuli shows a sensitivity of HVC neurons to inter-syllable intervals. Importantly, the response strength of HVC neurons to duet stimuli exceeds the sum of neuronal responses to each individual’s song. This suggests that each participant not only knows what to sing but also develops an internal representation of the pair-specific duet (Fortune et al., 2011). Groundbreaking work in free-ranging African weavers further demonstrates the alternation of neuronal activity in each partner’s HVC, with bursts temporally locked to syllable onsets (Hoffmann et al., 2019). This “on-off” pattern appears to be

regulated by heterogeneous auditory feedback that reciprocally inhibits HVC premotor activity (Coleman et al., 2021). Such brain-to-brain coupling mechanisms ensure precise timing of dyadic vocal interactions, most likely through gamma-aminobutyric acid-ergic inhibition (Benichov and Vallentin, 2020). For comprehensive reviews on this topic, see Elie et al. (2019) and Rivera-Cáceres and Templeton (2019).

DUETTING STYLES IN SINGING PRIMATES

Worldwide, singing primates comprise 72 species, some of which are nocturnal and others diurnal; most share a family-living and territorial social system mediated by loud, coordinated calls emitted at predictable times, usually around dawn and/or dusk (De Gregorio et al., 2022). The gibbons’ “great-call sequence” combines the female great call and male coda, often repeated alternately [i-n(F1-M1)], with a pronounced sexual divocalism (Marshall and Marshall, 1976; Geissmann, 2002). Sexually

dimorphic species duet antiphonally, whereas in monomorphic taxa, singers tend to overlap (Deputte, 1982). The duet songs of lemurs, tarsiers, and the Mentawai langur overlap, except in *Lepilemur edwardsi* (Méndez-Cárdenas and Zimmermann, 2009) and *Tarsius niemitzi* (Shekelle et al., 2019). Sexually monomorphic indris advertise with duets and choruses⁵ in which the paired males and females overlap more than any other dyad while dominant and non-dominant individuals avoid overlapping (Gamba et al., 2016). In each of these lineages, sex-differentiated calls often occupy a different frequency register, making them readily distinguishable on spectrograms (Tilson and Tenaza, 1976; Nietsch, 1999; Torti et al., 2013). In contrast, Neotropical titi monkey duets overlap extensively, both in the time and frequency domains, with male and female contributions exhibiting an anti-phase-locked pattern of phrase coordination devoid of discrete turns (Robinson, 1979; Müller and Anzenberger, 2002; Caselli et al., 2014; Adret et al., 2018a; Clink et al., 2019, 2022). In each of these primate lineages, there is increasing evidence of vocal malleability for this trait, long thought to be subject to strong genetic constraints (Brockelman and Schilling, 1984; Tenaza, 1985; Hammerschmidt and Fischer, 2008).

FLEXIBILITY IN THE COORDINATED SONG OF SINGING PRIMATES

Vocal flexibility, the capacity for modifying vocalizations according to context, can affect call structure, amplitude, timing, duration, and rhythm. For duetting animals, this includes individuals adjusting their singing to either their partner's or neighbors' vocal outputs.

Interactive Group Singing

Neighboring groups of singing primates often call antiphonally (Kinzey et al., 1977; Marler and Tenaza, 1977; Raemaekers and Raemaekers, 1985) and counter-sung solos and duets are longer than solos and duets sung alone (Tenaza, 1976; Mitani, 1985). In support of the flexible timing of vocal output, active counter-singing and singing motivation have been experimentally corroborated (Chivers and MacKinnon, 1977; Mitani, 1988; Dooley and Judge, 2007). Studies of communication networks showing that siamangs are sensitive to their neighbors' group disruption (Morino et al., 2021) are likely to unveil further instances of vocal flexibility in the future.

Within-Pair Vocal Coordination and Repair

Individual gibbons flexibly time their contributions relative to their mates' during the great-call sequence. Guided by subtle changes in female introductory notes that signal an impending great call, the male suspends phonation; cued by her post-climax descending notes, he resumes singing with a coda phrase according to a precise turn-taking pattern (Terleph et al., 2018a). Flexibility is needed given individual variability in the

female great call (Terleph et al., 2015, 2016). Adjustment made by hylobatids in response to a mate's vocal "mistakes" are termed "repairs," a universal principle of human conversation (Schegloff et al., 1977; Dingemanse et al., 2015). Repairs have been scrutinized for self-corrected, stalled, and aborted great calls (Haimoff, 1988; Haraway and Maples, 1998; Terleph et al., 2018a). Such studies confirm the existence of duet codes and answering rules in lesser apes. Non-adherence to the duet code (e.g., production of atypical notes or unexpected call timing) may result in duet interruption and song reset by the mate.

Vocal Accommodation in Call Rhythm

Coordinated singing and rhythm dynamics are not necessarily tied (Ravignani et al., 2014). For example, inter-onset call intervals extracted at each level of the indri's song organization (i.e., units and phrases), reveal music-like categorical rhythmicity (De Gregorio et al., 2021a). Both in adults and young individuals, females exhibit more flexibility than males, with a sensitivity to chorus size (Gamba et al., 2016; De Gregorio et al., 2019, 2021b). Sex-related "divergence" in indri song rhythm contrasts with titis and tarsiers. In a cross-sectional study of duetting pairs of titi monkeys, partners were found to adjust pulse rate and phrase duration to one another, showing call "convergence" (Clink et al., 2019). A longitudinal study with newly formed pairs of titis might establish whether vocal learning is involved through convergence in the spectral features of calls, as reported in marmosets (Elowson and Snowdon, 1994; Snowdon and Elowson, 1999; Zürcher et al., 2021). Likewise, male and female tarsiers flexibly adjust call rhythm relative to their partner through simultaneous accelerations and decelerations (Clink et al., 2020). Within-pair convergence in duet tempo might be achieved by entrainment, i.e., spontaneous responsiveness to a perceived rhythmic signal (de Reus et al., 2021).

Parental Influence

Immature individuals singing jointly with their elders have long sparked research attention (Deputte, 1982; Raemaekers et al., 1984; Pollock, 1986; Reichard, 2003). A longitudinal study of mother-daughter vocal interactions in gibbons revealed the acquisition of correct note sequencing over time (5–30 months; Merker and Cox, 1999). In a cross-sectional study of free-ranging family groups, an inverse relationship was found between mother-daughter co-singing rates and call synchronization; less proficient daughters co-sang at higher rates. Interestingly, mothers adjusted their song to a more stereotyped pattern when co-singing than when singing alone, suggesting a "teaching role" of mothers (Koda et al., 2013). While sexually mature females sing an adult-like maternal song (Brockelman and Schilling, 1984; Merker and Cox, 1999; Koda et al., 2013), males master the multi-part coda phrase years later (Hradec et al., 2021) via an intriguing developmental trajectory (Figure 1B).

Production of Heterosexual Song

Spontaneous production of a female-like great call by immature males has been reported in several gibbon species (Koda et al., 2014; Hradec et al., 2016, 2017, 2021). A triggering role of the maternal call in young males, possibly associated with low

⁵Coordinated song uttered by more than two individuals within a family group.

androgen levels, has also been invoked (Koda et al., 2014). Immature individuals producing male calls potentially face aggression from the father (Hradec et al., 2021) and there is evidence that the stress hormone cortisol may negatively interact with testosterone in influencing the expression of secondary sexual traits (Puts et al., 2016). Close monitoring of hormone levels would be worthwhile in order to determine the impact of parent–offspring relationships on gibbon song development (Burns and Judge, 2016).

Acquisition of a Pair-Specific Duet Code

To reproduce outside their natal groups, mature individuals must coordinate their song with a prospective mate “having both different genetic parentage and a different history of developmental experience than their own” (Haraway and Maples, 1998). In indris, spectral-temporal features of descending phrases correlate with genetic distance in males, whereas females are less constrained (Torti et al., 2017). Thus, indri choruses may inform conspecifics about individuals’ genetic relatedness. Such an effect is less apparent in titi duets (Clink et al., 2022). Consistent with vocal flexibility and duet code learning, the duets of long-term mates are better coordinated than those of newly formed pairs (Geissmann, 1986, 1999; Maples et al., 1989; Müller and Anzenberger, 2002).

Conditioning

Robust conditioned responses are obtained in lesser apes via reinforcement and extinction procedures in which song presentation is contingent upon an individual’s own vocalization (Haraway et al., 1981; Maples and Haraway, 1982; Maples et al., 1988). Moreover, both in lemurs and gibbons, phonation can be brought under volitional control in response to an arbitrary visual signal (Wilson, 1975; Koda et al., 2007), thus demonstrating voluntary control over call timing.

Innovation

Captive siamangs can alter their calls using various “tricks,” including the production of hand- modulated and echoing calls (Badraun et al., 1998). Geissmann (2009) observed one female gibbon who amplified her duet contribution by slamming the sliding door of her sleeping quarters at the climax of her great call.

Causal Mechanisms

As renowned “soprano singers” (Koda et al., 2012), gibbons produce pure-tonal melodious song that requires appropriate hormonal and neural machinery for pitch control. Contrasting with humans, however, higher androgen levels result in calls with a higher pitch (Barelli et al., 2013; Puts et al., 2016). Experiments in a helium-oxygen atmosphere revealed that the unshifted call fundamental frequency is strongly attenuated and the first harmonic is emphasized, suggesting that the sound source (larynx) operates independently of the supralaryngeal vocal tract (Koda et al., 2012). Thus, call flexibility can be achieved by controlling laryngeal function and/or the resonance filter configuration (Gamba et al., 2011, 2017; Fitch et al., 2016), but the challenge is to account for the larynx development (Zhang et al.,

2020). Importantly, bipolar excitation in the inferior portion of the precentral gyrus in the left hemisphere yields adduction of the vocal folds (Mott et al., 1911). This suggests that, in the gibbon brain, a direct pathway exists from the laryngeal representation in the primary motor cortex to the laryngeal motoneurons of the nucleus ambiguus, which controls the muscles of the larynx for vocal production (Simonyan, 2014). This might explain why gibbons can be trained to call on command (Koda et al., 2007; but see Hage and Nieder, 2013).

DISCUSSION AND FUTURE DIRECTIONS

From strepsirrhines to lesser apes, the duetting patterns of singing primates provide compelling evidence of developmental plasticity extending into adulthood. This is consistent with the view that non-human primates exhibit more flexibility in their vocal behavior than is generally acknowledged

TABLE 1 | Parallels and divergences in vocal plasticity between duetting songbirds and singing primates.

	Acronym	Duetting songbirds	Singing primates
Parallels	COS	yes	yes
	CTS	yes	yes
	CTXL	yes	yes
	HET	yes	yes
	NFP vs. WEP	yes	yes
	REP	yes	yes
Divergences	CONV	?	yes
	CDT	?	yes
	INN	?	yes
	VPL	yes	?
	MEM	yes	?
Strengths and weaknesses	TDA	months	years
	ONT	weak	strong
	RIP	strong	absent
	NEULAB	strong	weak
	NEUTEL	strong	absent
	VOCTEL	strong	absent

Strengths and weaknesses identify several methodological approaches for which songbirds have proved to be more tractable experimentally. Note that, despite a protracted developmental period for duet acquisition, intensive studies have been carried out on the ontogeny of coordinated song in singing primates. CDT, conditioning; CONV, vocal convergence; COS, parent-offspring co-singing; CTS, inter-group counter-singing; CTXL, contextual learning; HET, production of heterosexual song in sexually dimorphic species; INN, vocal innovation; MEM, song memorization; NEULAB, neural investigations in captive animals; NEUTEL, neural telemetry in freely ranging animals, which is achieved, for instance, by trapping songbirds and implanting electrodes in a target brain nucleus to obtain chronic recordings of the neural activity via telemetry once the bird is released into the wild; NFP vs. WEP, newly formed pairs vs. well-established pairs; ONT, ontogeny of vocal duetting; REP, vocal repair; RIP, removal experiment and interactive playback in which one pair member is first captured; subsequently, the experimenter tries to elicit a duet with the lone, territorial individual by playing back his/her mate’s song contribution (unaltered or manipulated); TDA, timeline for duet acquisition; VPL, vocal production learning; VOCTEL, vocal telemetry in freely ranging animals equipped with a lightweight, backpacked miniature microphone (songbirds) or with the sensor fitted to the subject’s throat, in close apposition with the larynx (primates).

(Snowdon, 2009, 2017a,b, 2018). Promising areas of ongoing research include (1) vocal convergence as a learning process, linked to pair-bond strength (Clink et al., 2019, 2020), (2) sex-dependent mechanisms regulating “acquisition” of categorical duet rhythms (De Gregorio et al., 2021a), and (3) the potential for parental tutoring and vocal production learning in gibbons (Koda et al., 2013; Koda, 2016; Terleph et al., 2018b; Hradec et al., 2021).

Striking similarities have emerged in duet acquisition between songbirds and singing primates (Table 1). In both phyla, young individuals co-sing extensively with their elders, although timescales can widely differ (Figure 1). Furthermore, in species with sex-specific repertoires, males and females can produce heterosexual song (Geissmann, 1983; Chen et al., 2008; Rivera-Cáceres and Templeton, 2019; Hradec et al., 2021). The production of heterosexual song early in life suggests a pre-existing or learned auditory template (Adret, 2004; Cheyne et al., 2007), possibly engaging a mirror-neuron system (Newman, 2014).

Research currently tends to focus on antiphonal duets, given their potential as precursors of turn-taking conversations in humans (Levinson, 2016). At the same time, bio-acoustics research in titi monkey duets has been hampered by extensive call overlap (Caselli et al., 2014; Adret et al., 2018a; Clink et al., 2019); cracking the code will require radio-tracking calls with miniature voice detectors (Adret et al., 2018b), as has been elegantly demonstrated in songbirds (Hoffmann et al., 2019; Lemazina et al., 2021). Another solution is conducting studies in captive (or wild) populations for which high speed video of vocalizing animals can be paired with high quality audio to ensure caller identity (Haimoff, 1981). Performant computational methods also allow effective clustering of acoustic signatures at multiple levels within animal vocal repertoires (Sainburg et al., 2020). A machine-learning approach to acoustic stream segregation

might further help resolve the “cocktail party problem” (Elhilali, 2017). Developmental studies of duet acquisition in singing primates are also needed to investigate vocal flexibility in response to anthropogenic noise (Duarte et al., 2017).

While the neuroscience of pair-bonding in socially monogamous mammals is well documented (Bales et al., 2017; Potretzke and Ryabinin, 2019), a significant gap in knowledge concerns the neural mechanisms of duetting in singing primates. Integrating respiratory functions associated with coordinated song is also necessary to account for the generation of rhythmic patterns (Laje and Mindlin, 2003; Amador et al., 2005). Neuroimaging studies provide a powerful, non-invasive approach to mapping brain areas activated by antiphonal calling (Takahashi et al., 2021). Singing rodents, which offer a genetically tractable model system, produce antiphonal duets, which, much like duetting songbirds, reveals a hierarchical (cortico-subcortical) control mechanism that regulates the temporal segregation of rapid vocal exchanges via inhibition (Okobi et al., 2019). Emergence, deep in the evolutionary past, of an interlocking mechanism derived from sender-listener brain coupling (Hasson et al., 2012) may have been a key step in the evolution of human conversation.

AUTHOR CONTRIBUTIONS

PA conceived and wrote the article and approved the final version of the manuscript.

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