

Selection for and against vocal learning in birds and mammals

Erich D. JARVIS[#]

Department of Neurobiology, Duke University Medical Center, Box 3209, Durham, North Carolina 27710, USA

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Abstract Vocal learning, the substrate for human language, is a rare trait found to date in only three distantly related groups of birds (parrots, hummingbirds, and songbirds) and four distantly related groups of mammals (humans, bats, cetaceans, and elephants). Brain pathways for vocal learning have been studied in the three bird groups and in humans, and they have a number of similarities. In addition, use of learned vocalizations is also similar among vocal learners. Together this suggests common selection pressures. Here I present hypotheses on what could have selected for or against vocal learning and associated brain pathways in birds and mammals. The brain pathways I suggest were selected from a pre-existing motor pathway. Selection for vocal learning behavior I suggest occurred by two factors: mating preference for varied vocalizations and a need for rapid adaptation to propagate sound in different environments. Selection against vocal learning I suggest occurred by predation, where varied vocalizations makes an animal an easier target for predators. Once predator selection pressure is overcome, then, I suggest, learned vocalizations can be used for other functions, such as abstract communication.

Key words Epigenetic constraints, Sexual selection, Song, Speech, Warble

Vocal learning is the ability to acquire vocalizations through imitation rather than instinct. It is distinct from auditory learning, which is the ability to make associations with sounds heard. Auditory learning occurs for example when a dog learns to associate the words ‘sit’ (English), ‘sientese’ (Spanish), or ‘osuwali’ (Japanese) with the act of sitting or learns the meaning of complete sentences such as ‘come here boy’. The dog understands the words, but cannot imitate them. Vocal learners, such as humans, parrots and some songbirds, are able to imitate non-innate sounds such as sit, sientese, or osuwali. Most vocal learners, however, imitate sounds of their own species that have been passed on through cultural transmission (Marler 1967).

Given the above definitions, most, if not all, vertebrates are capable of auditory learning, but few are capable of vocal learning. The latter has been experimentally found to date only in three distantly related groups of birds (parrots, hummingbirds, and songbirds) and four distantly related groups of mammals

(humans, bats, cetaceans, and elephants; Fig. 1) (Nottebohm 1972; Rendell & Whitehead 2001; Jarvis 2004; Poole et al. 2005); the finding in elephants was recently shown (Poole et al. 2005). Not all species in these groups have vocal learning abilities to the same degree. Humans, the most prolific vocal learners, can learn to produce a seemingly infinite number of learned vocalizations. While not as prolific, some parrots, corvid songbirds, and mockingbirds can produce hundreds to thousands of calls and/or learned warble/song combinations (Derrickson & Breitwisch 1992; Farabaugh et al. 1992; Boarman & Heinrich 1999; Pepperberg 1999). Finally, less prolific vocal learners, such as the Zebra Finch (*Taeniopygia guttata*) and Sombre Hummingbird (*Aphantochroa cirrochloris*), produce only one distinct song type with little variation (Zann 1996; Ferreira et al. 2006).

Each of the vocal learning avian and mammalian groups has close vocal non-learning relatives (Fig. 1). Because of this, it is thought that vocal learning in all seven groups evolved independently from a common ancestor that had this behavior or that their vocal learning cousins lost the behavior multiple independent times (Fig. 1) (Nottebohm 1972; Jarvis 2004). A

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[#] Corresponding author, E-mail: jarvis@neuro.duke.edu

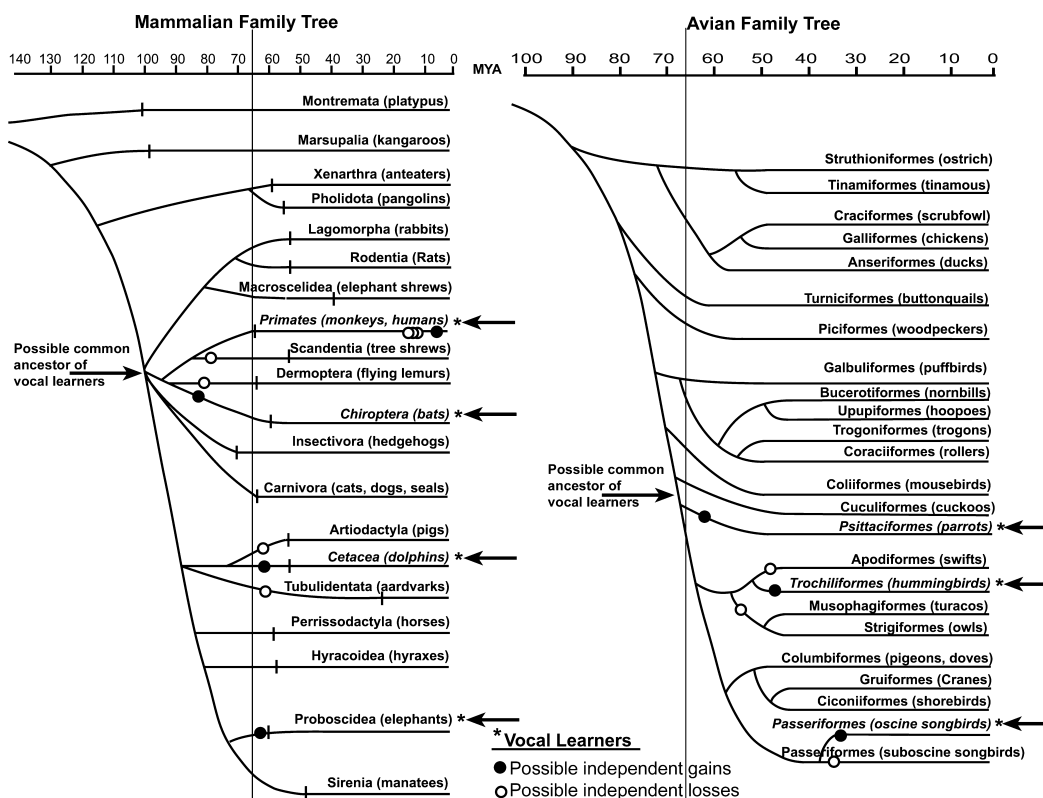


Fig. 1. Family trees of living mammalian and avian orders. The mammalian tree is derived from morphological analyses by Novacek (1992; 2001); horizontal lines indicate extent of geologic evidence from fossils. The avian tree was derived from DNA–DNA hybridization analysis by Sibley & Ahlquist (1990)(page 838). The Latin name of each order is given along with examples of common species. Passeriformes are divided into its two suborders: suboscine and oscine songbirds. The vertical line down each tree indicates the cretaceous–tertiary boundary, the time of the dinosaur extinction; MYA=millions of years ago. Open and closed circles show the minimal ancestral nodes where vocal learning could have either evolved independently or been lost independently. Independent losses would have at least required one common vocal learning ancestor, located by the right facing arrows. Within primates, there would have to be at least 7 independent losses (tree shrews, prosimians, new and old world monkeys, apes, and chimps) followed by the regain of vocal learning in humans (assuming that all non-human primates are vocal non-learners). The trees are not meant to present the final dogma of mammalian and avian evolution, as there are differences of opinion among scientist. Figure reprinted from Jarvis (2004) with permission.

question thus arises, is there something different about the brains of vocal learners.

BRAIN SYSTEMS FOR VOCAL LEARNING

Only vocal learners—songbirds, parrots, hummingbirds, and humans—have brain regions in their cerebrums (or telencephalon) that control the acoustic structure of their vocal behavior (Jurgens 1995; Jarvis et al. 2000). Vocal control brain regions have not yet been investigated in cetaceans, bats, and elephants. Vocal non-learners, including non-human primates and pigeons, only have midbrain and medulla regions that control innate vocalizations (Jurgens 1995; Wild

1997); the cingulate cortex in mammals controls the motivation to vocalize innate sounds, but does not control the acoustic structure or syntax of those sounds (Jurgens 2002).

Remarkably, in the cerebrum of all three vocal learning bird groups there are seven comparable vocal brain nuclei: four posteriorly located nuclei and three anteriorly located nuclei (Fig. 2A–C; abbreviations in Table 1) (Jarvis et al. 2000). These brain nuclei have been given different names in each bird group because of the possibility that each evolved their vocal nuclei independently of a common ancestor with such nuclei (Striedter 1994; Jarvis et al. 2000). In all three bird groups, the posterior nuclei form a posterior vocal pathway that projects from a

Table 1. Abbreviations

AAC-central nucleus of the anterior arcopallium	HVC-(a letter based name)
AACd-central nucleus of the anterior arcopallium, dorsal part	MOC-oval nucleus of the mesopallium complex
AACv-central nucleus of the anterior arcopallium, ventral part	L2-field L2
Ai-intermediate arcopallium	MMSt-magnocellular nucleus of the anterior striatum
ACM-caudal medial arcopallium	MAN-magnocellular nucleus of anterior nidopallium
aDLPFC-dorsal lateral prefrontal cortex	MLd-mesencephalic lateral dorsal nucleus
aCC-anterior cingulate cortex	NAOc-oval nucleus of the anterior nidopallium complex
aCd-anterior caudate	NCM-caudal medial nidopallium
aINS-anterior insula cortex	NDC-caudal dorsal nidopallium
Am-nucleus ambiguous	NIDL-Intermediate dorsal lateral nidopallium
aPt-anterior putamen	NIf-Interfacial nucleus of the nidopallium
aT-anterior thalamus	NLC-central nucleus of the lateral nidopallium
Area X-area X of the striatum	nXIIts-tracheosyringeal subdivision of the hypoglossal nucleus
Av-avalanch	Ov-nucleus ovioidalis
CMM-caudal medial mesopallium	PAG-peri aqueductal grey
VA/VL-ventral anterior/ventral lateral nuclei of the mammalian thalamus	preSMA-pre-supplementary motor area
CM-caudal mesopallium	RA-robust nucleus of the arcopallium
CSt-caudal striatum	Uva-nucleus uvaeformis
DLM-medial nucleus of dorsolateral thalamus	VA-vocal nucleus of the arcopallium
DM-dorsal medial nucleus of the midbrain	VAM-vocal nucleus of the anterior mesopallium
DMM-magnocellular nucleus of the dorsomedial thalamus	VAN-vocal nucleus of the anterior nidopallium
FMC-face motor cortex	VAS-vocal nucleus of the anterior striatum
	VLN-vocal nucleus of the lateral nidopallium
	VMM-vocal nucleus of the medial mesopallium
	VMN-vocal nucleus of the medial nidopallium

nidopallial vocal nucleus (HVC, NLC, VLN) to the arcopallial vocal nucleus (RA, AAC dorsal part, VA), to the midbrain (DM) and medulla (nXIIts) vocal motor neurons (Fig. 2A–C, black arrows) (Striedter 1994; Durand et al. 1997; Vates et al. 1997; Gahr 2000); nXIIts projects to the muscles of the syrinx, the avian vocal organ. This pathway is responsible for production of learned vocalizations (determined only in songbirds and parrots), where songbird HVC and NIf are thought to generate syntax and RA the acoustic structure of syllables (Yu & Margoliash 1996) (but see Hahnloser et al. 2002 for an alternative view). Vocal non-learning birds have DM and nXIIts, but without projections from the arcopallium (Wild et al. 1997), for production of innate vocalizations. The anterior nuclei (connectivity examined only in songbirds and parrots) are part of an anterior vocal pathway loop, where a pallial vocal nucleus (MAN, NAOc) projects to the striatal vocal nucleus (AreaX, MMSt), the striatal vocal nucleus to a nucleus of the dorsal thalamus (DLM, DMM), and the dorsal thalamus projects back to the pallial vocal nucleus (MAN, NAOc; Fig. 2A, C, white arrows) (Durand et al. 1997; Vates et al. 1997). The parrot pallial

MO nucleus also projects to the striatal vocal nucleus (MMSt) (Durand et al. 1997). Connectivity of the songbird MO analogue has not yet been determined. The anterior vocal pathway is responsible for learning vocalizations (determined mostly in songbirds), where lateral MAN (LMAN) is proposed to generate variability and AreaX to generate stereotypy (Scharff & Nottebohm 1991; Jarvis 2004; Kao et al. 2005). Functions of the other nuclei of the anterior vocal pathways are not yet well studied.

The major differences among vocal learning birds are in the connections between the posterior and anterior vocal pathways (Jarvis & Mello 2000). In songbirds, the posterior pathway sends input to the anterior pathway via HVC to Area X; the anterior pathway sends output to the posterior pathway via LMAN to RA and medial MAN (mMAN) to HVC (Fig. 2C, 3A) (Foster & Bottjer 2001). In contrast, in parrots, the posterior pathway sends input into the anterior pathway via ventral AAC (AACv, parallel of songbird RA) to NAOc (parallel of songbird MAN) and MO; the anterior pathway sends output to the posterior pathway via NAOc to NLC (parallel of songbird HVC) and AAC (Fig. 2A, 3B) (Durand et al. 1997).

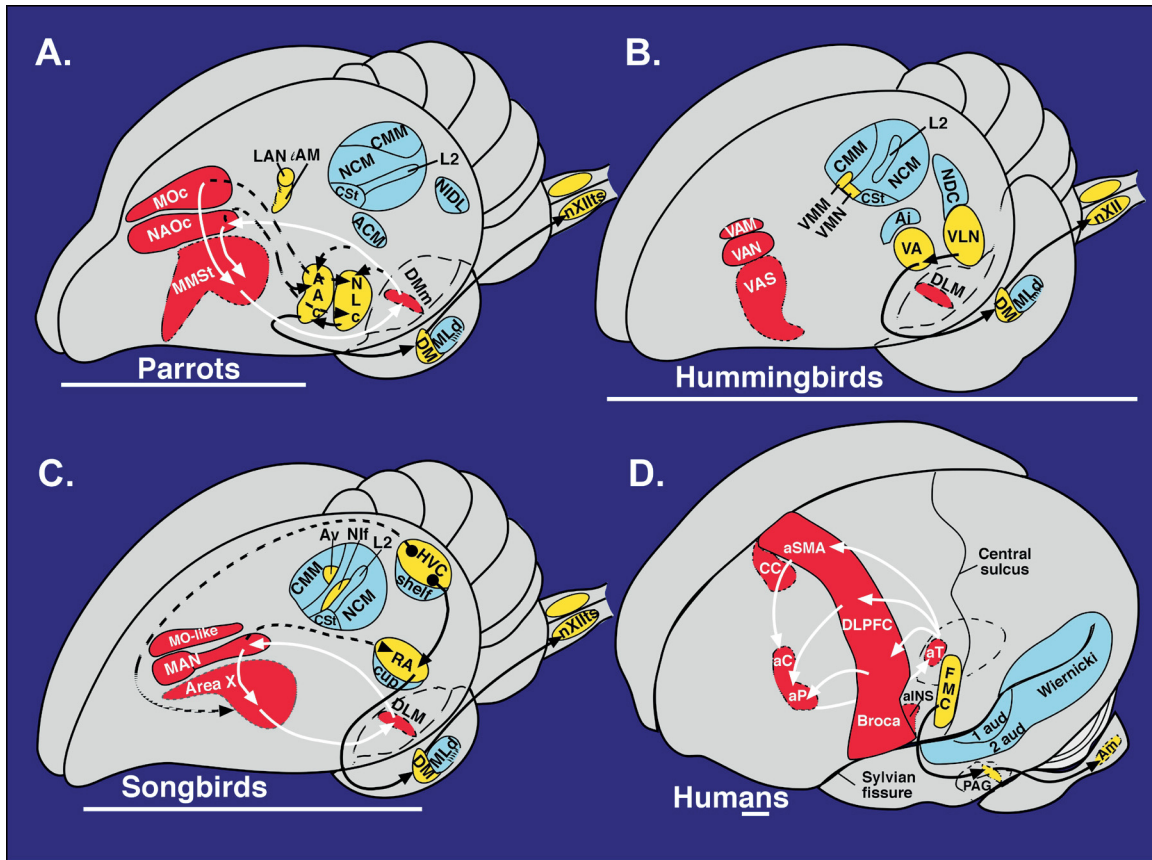


Fig. 2. Proposed comparable vocal and auditory brain areas among vocal learning birds and humans: **A.** Parrot, **B.** Hummingbird, **C.** Songbird, **D.** Human. Left hemispheres are shown, as this is the dominant side for human language. Yellow regions and black arrows indicate proposed posterior vocal pathways; red regions and white arrows indicate proposed anterior vocal pathways; dashed lines show connections between the two vocal pathways; blue indicates auditory regions, not discussed in this paper. For simplification, not all connections are shown. The globus pallidus in the human brain, also not shown, is presumably part of the anterior pathway as it is part of non-vocal pathways of mammals. Basal ganglia, thalamic, and midbrain (for the human brain) regions are drawn with dashed-line boundaries to indicate that they are deeper in the brain relative to the anatomical structures above them. The anatomical boundaries drawn for the proposed human brain regions involved in vocal and auditory processing should be interpreted conservatively and for heuristic purposes only. Human brain lesions and brain imaging studies do not allow one to determine functional anatomical boundaries with high resolution. Scale bar: ~7 mm. Abbreviations are in Table 1. Figure modified from Jarvis (2004).

Using the above knowledge we have gained from birds, I have proposed that humans also have posterior and anterior vocal pathways for production and learning of language (Jarvis 2004). According to this proposal, the human posterior vocal pathway consists of the face motor cortex and its projections to mid-brain (PAG) and brainstem (Am) motor neurons (Fig. 2D, 3C). This pathway is responsible for production of speech. Like in vocal non-learning birds, the PAG and Am in vocal non-learning mammals do not receive motor cortical (pallial) projections and they control production of innate sounds (Kuypers 1958a;

Kuypers 1958b; Jurgens 2002). The proposed human anterior vocal pathway consists of a loop (Lieberman 2002; Jarvis 2004) that includes projections from a lateral-to-medial strip of premotor cortex –the anterior insula (aINS), Broca's area, the anterior dorsal lateral prefrontal cortex (aDLPFC), the pre-supplementary motor area (preSMA), and the anterior cingulate (aCC)- to an anterior region of the striatum, to the globus pallidus, to an anterior portion of the dorsal thalamus, and then back to the cortex (Fig 2D, 3C). Jurgens (2002), however, argues that the striatal-basal ganglia regions have a more direct connection

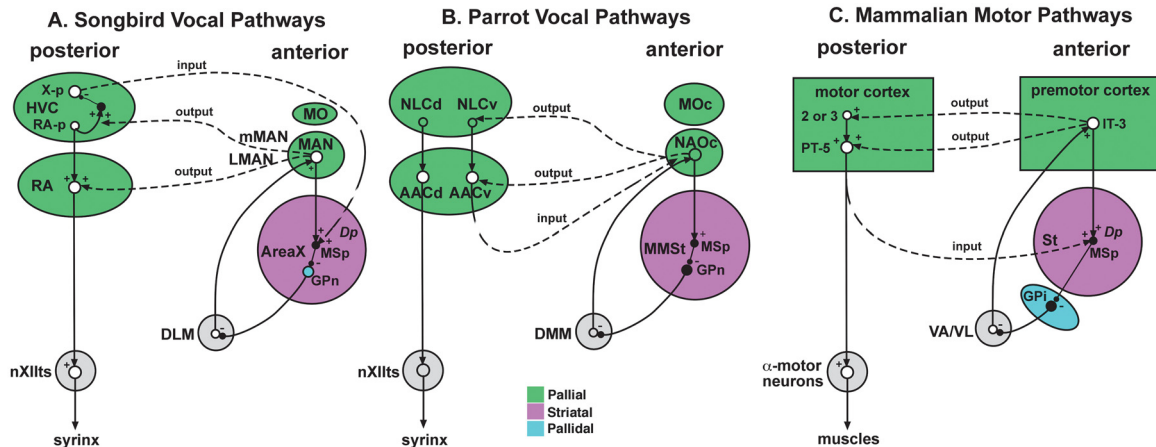


Fig. 3. Comparative and simplified connectivity of anterior and posterior vocal motor pathways in songbirds (A) and parrots (B), and motor pathways in mammals (C). Dashed lines: connections between anterior and posterior pathways; inputs and outputs are labeled relative to anterior pathways. Output from songbird MAN to HVC and RA is not from the same neurons; medial MAN neurons project to HVC, lateral MAN neurons project to RA. ○: excitatory neurons; ●: inhibitory neurons; +: excitatory glutamate neurotransmitter release; -: inhibitory GABA release. MSp: medium spiny neuron. GPn: globus pallidus-like neuron in songbird AreaX and parrot MMSt. Only the direct pathway through the mammalian basal ganglia (St to GPi) is shown as this is the one most similar to AreaX connectivity (MSp to GPn) (Reiner et al. 2004). X-p: X-projecting neuron of HVC. RA-p: RA-projecting neuron of HVC. PT-5: pyramidal tract neuron of motor cortex layer 5. IT-3: intratelencephalic projecting neuron of layer 3. Abbreviations are in Table 1. Figure modified from Jarvis (2004).

to premotor vocal neurons of the brainstem. These anterior brain regions in humans control the production of complex aspects of human speech, including learning to speak (Benson & Ardila 1996; Jurgens 2002; Lieberman 2002; Jarvis 2004).

Because connections between the posterior and anterior vocal pathways differ between songbirds and parrots, comparisons between them and mammals will also differ. Similar to the songbird posterior pathway, in primates, the face motor cortex (like songbird HVC and parrot AAC) makes a robust projection to the ventral putamen anterior to the anterior commissure (Jurgens 2002). However, in mammals, layer 5 neurons of motor cortex have axons collaterals, where one projects into the striatum and the other projects to the medulla and spinal cord (Fig. 3C) (Alexander & Crutcher 1990; Reiner et al. 2003). In songbirds, a specific cell type of HVC, called X-projecting neurons, projects to the striatum separately from neurons of RA of the arcopallium that project to the medulla (Fig. 3A). In parrot, AAC (the RA equivalent) of the arcopallium has two anatomically separate neuron populations, AACd that projects to the medulla and AACv that projects to other pallial vocal nuclei NAOc and MO (Fig. 3B) (Durand et al. 1997). Output of mammalian anterior pathways are proposed to be the collaterals of the layer 3 and upper

layer 5 neurons that project to other cortical regions (Fig. 3C) (Reiner et al. 2003; Jarvis 2004). Despite these differences, the similarities indicate that there must be some constraints on how vocal learning brain pathways can evolve.

EVOLUTION OF BRAIN PATHWAYS FOR VOCAL LEARNING

In the most simplest of interpretations, one can consider three alternative possibilities of how similar, although not identical, vocal learning brain pathways could have evolved among birds and mammals (Fig. 1) (Jarvis et al. 2000): 1) the vocal system in the three vocal learning bird groups and the proposed comparable system in humans all evolved independently of a common ancestor. If this were true, then the similarities are remarkably coincidental. 2) There was a vocal learning pathway in the common ancestor of vocal learning birds with seven cerebral nuclei, and a similar pathway in the common ancestor of vocal learning mammals, that were then lost multiple independent times in closely related bird and mammalian groups. If this were true, then the similarities are not as remarkable, but it would suggest that there is strong selection to extinguish vocal learning. 3) Most, if not all birds, mammals, and perhaps reptiles have

vocal learning to various degrees, and songbirds, parrots, hummingbirds, and humans (and perhaps bats and cetaceans) independently amplified the associated brain pathways for their more highly developed vocal learning behaviors. If this were true, it would mean that many birds and mammals, and maybe reptiles, have at least primordial brain structures for vocal learning.

The answer may be that different factors are dependent and independent of a common ancestor. A dependent factor could be preexisting connectivity. The connections of the anterior and posterior vocal pathways resemble non-vocal pathways in both birds and mammals (Fig. 3) (Durand et al. 1997; Farries 2001; Lieberman 2002; Jarvis 2004). Further, preliminary results suggest that vocal nuclei of vocal learning birds are embedded within at least seven brain areas activated during movement behavior (Jarvis et al. 2005). In this manner, I argue that a mutational event that caused descending projections of avian arcopallium neurons to synapse onto nXIIIts or mammalian layer 5 neurons of the face motor cortex to synapse onto nucleus ambiguus may be the only independent major change that is needed to initiate a vocal learning pathway. Thereafter, other vocal brain regions could develop out of adjacent motor brain regions dependent on pre-existing connectivity. Such a mutational event would be expected to occur in genes that regulate synaptic connectivity of pallial motor neurons to α -motor neurons. If this is true, then it begs the question as to why vocal learning is not more common, and what selects for or against it?

SELECTIONS FOR AND AGAINST VOCAL LEARNING

A number of hypotheses have been proposed as to what selects for vocal learning, and thus language (Morton 1975; Aboitiz & Garcia 1997; Miller 2000; Okanoya 2002; Jarvis 2004). These include: 1) individual identification; 2) semantic communication; 3) territory defense; 4) mate attraction; and 5) rapid adaptation to sound propagation in different environments. For individual identification, the argument is that among vocal learners each individual can learn its own song and thus have a unique signature that differentiates that individual from others of its population. However, individual identification by voice is not a unique characteristic of vocal learners. As no two individuals look identical, so too no two individuals within an avian or mammalian population sound

identical, allowing vocal non-learners to identify individual conspecifics by voice. This includes vocal non-learning birds (Falls 1982), frogs (Shy 1985), deer (Reby et al. 1998) and macaques (Masataka 1985). It is true that with vocal learning, individuals can be called by unique names. This, however, so far has been found among humans and bottlenose dolphins (Tyack 1997; Janik 2000), but not other vocal learners. Thus, I argue that it is unlikely that individual identification was a primary driving force for the selection of vocal learning.

A common notion is that a selective advantage of language is semantic communication. Semantic communication is when animate or inanimate objects have a specific vocalization or series of vocalizations associated with them. This is in contrast to affective communication, where the vocalizations have emotional content associated with them. Despite this common notion, many vocal non-learners use innate calls to communicate semantic information, such as “an eagle above”, “a snake on the ground”, or “a food source”. These include alarm calls and food advertisement calls, such as those of chickens and Vervet Monkeys (*Cercopithecus aethiops*) (Seyfarth et al. 1980; Marler et al. 1986). Vocal learning birds also use innate calls with such semantic information (Zann 1996), and only rarely have been found to use learned vocalizations for mainly semantic communication. The later includes humans of course, as well as African Grey parrots (Pepperberg 1999) and possibly black capped chickadee calls in reference to predator size (Templeton et al. 2005). Since this is not the common use of learned vocalizations among vocal learners, I argue that semantic communication was probably not a major driving force for the selection of vocal learning.

Vocal learners use their learned vocalizations most commonly in affective contexts, to defend territories and/or attract mates (Catchpole & Slater 1995). These uses are found among the songbirds (Nowicki & Searcy 2004), parrots (Farabaugh & Dooling 1996), male hummingbirds (Ewald & Bransfield 1987; Ferreira et al. 2006), male whales (Guinee & Payne 1988; Tyack & Clark 2000), and I argue humans as well. We sing, and the singer’s voice is often an attractant leading them to become icons and sex symbols of human society. Many vocal non-learners use their innate calls and crows to also defend territories and attract mates. This includes the crowing of male doves and chickens (Marler et al. 1986; Slabbekoorn & Ten Cate 1998; Slabbekoorn & Ten

Cate 1999). There is, however, an additional feature that vocal learners use for mate attraction –variability. Vocal learners, but not vocal non-learners, have the ability to produce more varied frequency modulation (FM) and syntax, either during vocal development, and/or after reaching adulthood in some species. These variations in FM and syntax are preferred by females of the songbird species that have been examined (Catchpole & Slater 1995; Tchernichovski et al. 1998; Okanoya 2002). In addition, canaries have been shown to use their two voices, common among birds, to produce even greater FM variations that is thought to stimulate estrogen production in the listening females (Vallet et al. 1998); these are sometimes called sexy syllables or songs. In fact, in vocal non-learners, such as in Ring doves, more FM of innate sounds has been shown to be stimulatory for mating (Slabbekoorn & Ten Cate 1999). Therefore, birds with the ability to produce more vocal variety are likely to be selected for this trait. Once the ability to produce variable sounds is selected for, then the ability of vocal learning is selected for. In this regard, I argue that mate attraction was probably a major driving force in the selection for vocal learning.

For sound transmission, vocal non-learners produce their vocalizations best in specific habitats (Marten & Marler 1977; Marten et al. 1977; Wiley 1978; McCracken & Sheldon 1997), which makes their vocal behaviors less adaptable to changes in the environment. For example, a pigeon's low frequency vocalizations travel best near the ground, while an eastern phoebe's higher pitched vocalizations travel better higher in the air. In contrast, vocal learners have the ability to change voice characteristics, either during the lifetime of an individual or through several generations, presumably allowing better group communication in different environments.

If mate attraction for varied sounds and a minimal mutational event to cause motor pallial areas to synapse onto α -vocal motor neurons is what it takes to evolve vocal learning, then this still does not answer why is it so rare. The answer, I argue, is that predation is a strong selection factor against vocal learning. If more varied syntax is attractive to mates, it may also be more attractive to predators. As innate vocalizations tend to be more constant, they may be naturally habituated to more easily, potentially becoming part of the background noise. Therefore, in order for a predator not to habituate to the sounds of his prey, he would have to evolve a neural mechanism to overcome the natural habituation at times

when he is hungry. If this were the case, then a species would have to overcome predatory pressure or have a relaxed predatory pressure before it could evolve vocal learning. In this regard, some vocal learners have very few if any major predators and are among the world's top predators. Humans are the top predator, which was thought to have come about at least 10,000 years ago (Walker & Shipman 1996), or possibly earlier with the development of stone tool use before the origin of our species over 200,000 years ago (http://anthro.palomar.edu/homo/homo_3.htm). Killer whales are the top predators of the ocean; predators of cetaceans generally are other cetaceans and large sharks, both, however, which hunt young, old, and sick animals (Heithaus & Dill 2002). Adult elephants do not have natural predators, besides humans, where lions, hyenas and crocodiles occasionally prey upon the young (Laursen & Bekoff 1978). Hummingbirds are also commonly known to be fearless of many animals, due to their rapid flight and escape behavior. Various parrot species and ravens (a corvid songbird) are prey to hawks and large owls, like other birds, but they are said to have highly effective mobbing behavior to evade such predators (Brightsmith 2002; Ferreira et al. 2006). On a cautionary note, though, besides the top predators, it is not known how valid is this distinction between vocal learners and non-learners, as no systematic study has been done on prey and predatory behaviors across vocal learning and vocal non-learning groups.

Some findings support this view. Studies of Kazuo Okanoya (2002), who has independently suggested selection for vocal learning through mate attraction and selection against it through predation, has shown that Bengalese Finches (*Lonchura striata* var. *domestica*) that have been bred in captivity without predators for the last 250 years and without human selection for singing behavior show more varied syntax than their White-backed Munia (*Lonchura striata*) conspecifics still living in the wild from which they derive (Okanoya 2002). Zann has shown that Zebra Finches bred in captivity show more variation on the songs learned among adults of a colony than do their wild-type conspecifics (Zann 1996). For both species, females prefer the more varied songs, including that wild munia females prefer the more varied songs of the domesticated Bengalese males (Tchernichovski et al. 1998; Okanoya 2002). Given these findings, we would expect to find more syntax complexity selected for in the wild than currently exists. Perhaps it is predatory pressure selecting against it. I argue that

once predation pressure has been overcome and mating selection for varied vocalizations proceeds, then learned vocal behavior can be used for more abstract communication, such as human language.

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