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Bird Song Systems: Evolution

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Introduction

Bird song systems refer to specific neural systems found in those species of birds that produce learned vocalizations, usually learned songs. This vocal learning trait is rare, as it is found to date in only three distantly related groups of birds (parrots, hummingbirds, and songbirds) and at least four distantly related groups of mammals (cetaceans, bats, elephants, and humans). Vocal learning is a critical behavioral substrate for spoken human language. Brain pathways for vocal learning have been studied in the three vocal learning bird groups, where each appears to have seven similar but not identical cerebral vocal nuclei distributed into two vocal pathways: a posterior vocal pathway, which in songbirds is used for producing learned song, and an anterior vocal pathway, which in songbirds is used for learning song. These vocal pathways are not found in vocal nonlearning birds but are similar to brain pathways used for other types of sensorimotor learning in mammals. An auditory pathway that includes the cerebrum is present in all birds and is used to perceive the vocalizations and possibly for auditory learning. This article presents the organization and function of these pathways in vocal learning birds and discusses hypotheses about their evolution.

Vocal Learning Behavior

The unique aspect of bird song systems is that they are involved in vocal learning. 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 when a dog learns to associate the words 'sit' (English), *sientese* (Spanish), or *osuwari* (Japanese) with the act of sitting. The dog understands the word but cannot imitate the sound of the word. Vocal learners, such as humans, parrots, and some songbirds, are able to imitate noninnate sounds such as sit, *sientese*, or *osuwari*. Most vocal learners, however, imitate sounds of their own species that have been passed on through cultural transmission. Vocal learning depends on auditory learning, but auditory learning does not depend on vocal learning. Vocal learners must hear the sounds they will later imitate. They use auditory feedback to correct their vocal output by comparing the output with auditory memories of the sounds they are trying to imitate.

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 found experimentally to date only in the three distantly related groups of birds (parrots, hummingbirds, and songbirds, Figure 1(a)), and the four distantly related groups of mammals (cetaceans, bats, elephants, and humans). There is some suggestion that sea lions are also vocal learners. Each of the vocal learning avian (Figure 1(a)) and mammalian groups has close vocal nonlearning relatives. Thus, it has been argued that vocal learning has evolved independently of a common ancestor in the three vocal learning bird groups and presumably in the vocal learning mammalian groups. The question that thus arises is whether there is something special about the brains of animals that can imitate sounds.

Vocal Learning Song Systems

Only vocal learners – such as songbirds, parrots, hummingbirds, and humans – have brain regions in their cerebrums that control the acoustic structure and syntax of their vocalizations. In birds, these regions make up what are called song systems because they control learned song. Remarkably, in all three vocal learning bird groups, their song systems consist of seven comparable vocal brain nuclei: four posteriorly located nuclei and three anteriorly located nuclei (Figure 1(b); abbreviations in Table 1). These vocal nuclei have been given different names in each bird group because of the possibility that each group evolved its vocal nuclei independent of a common ancestor with such nuclei.

The connectivity of the vocal nuclei has been studied best in songbirds (Figure 2(a)), but sufficient information exists about parrots and some about hummingbirds to make comparisons (Figure 1(b)). In all three vocal learning bird groups, the posterior nuclei form a posterior vocal pathway that projects from a nidopallial vocal nucleus (songbird HVC, parrot NLC, hummingbird VLN) to an arcopallial vocal nucleus (songbird RA, parrot AAC dorsal part, hummingbird VA), to the midbrain premotor (DM) and medulla vocal motor (nXIIts) neurons (Figures 1(b) and 2(a), black arrows). The nXIIts projects to the muscles of the syrinx, the avian vocal organ.
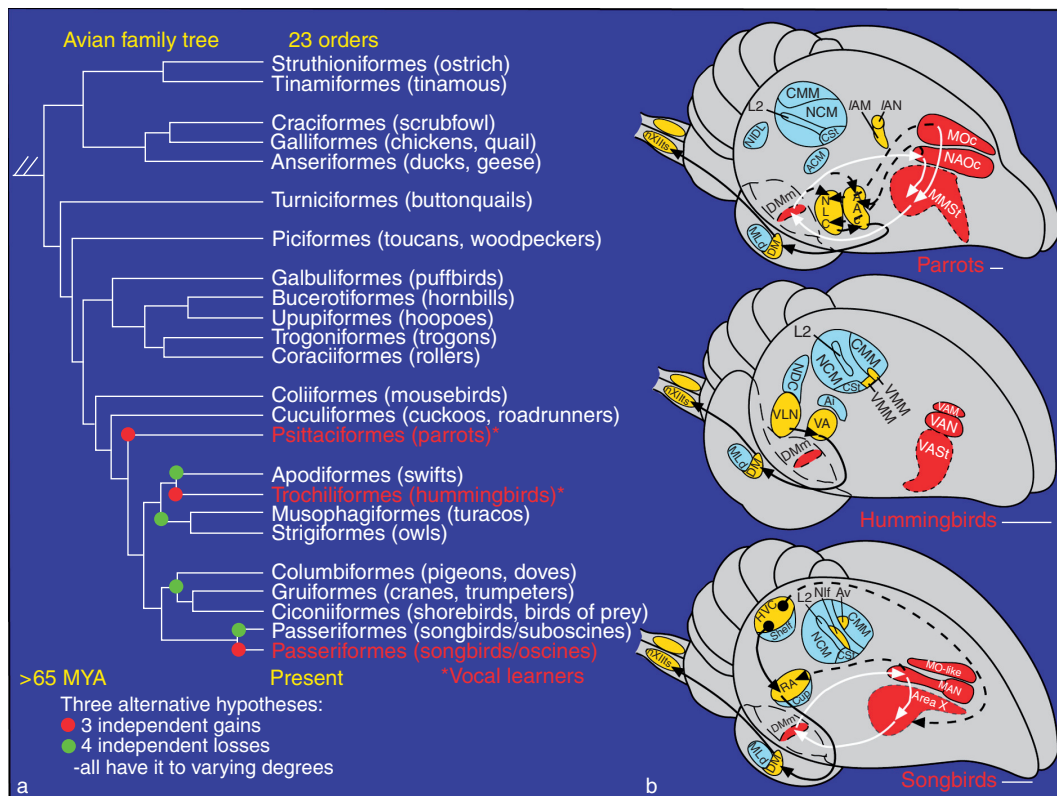
Figure 1 Phylogenetic relationship of birds and comparison of song pathways in vocal learners. (a) Family tree of living avian orders. The tree was derived from DNA–DNA hybridization analysis by Sibley CG and Ahlquist JE (1990) *Phylogeny and classification of birds: A study in molecular evolution.* New Haven, CT: Yale University Press. The Latin name of each order is given, along with examples of common species. Passeriformes are divided into two suborders: suboscine and oscine songbirds. MYA, millions of years ago. Red and green circles show the minimal ancestral nodes where vocal learning could have either evolved independently or been lost independently. Independent losses would have required at least one common vocal learning ancestor prior to parrots. The tree is not meant to present the final dogma of avian evolution, as there are differences of opinion among scientists. (b) Proposed comparable vocal and auditory brain areas among vocal learning birds. 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. For simplification, not all connections are shown. Basal ganglia, thalamic, and midbrain regions have broken-line boundaries to indicate that they are deeper in the brain relative to the anatomical structures above them. Scale bar = ~7 mm. Abbreviations are in **Table 1**. Adapted from Jarvis ED, Ribeiro S, da Silva ML, et al. (2000) Behaviourally driven gene expression reveals song nuclei in hummingbird brain. *Nature* 406: 628–632.

The connectivity of the other two cerebral posterior vocal nuclei in hummingbirds is not known, nor has it been well studied in parrots. In songbirds, one of these nuclei (NIf) projects to HVC, and the other (Av) receives a projection from HVC. The posterior vocal pathway is responsible for production of learned song and calls (determined only in songbirds and parrots); songbird HVC is thought to generate syntax and RA the acoustic structure of syllables. Vocal nonlearning birds have DM or nXIIts, but without projections from the arcopallium, for production of innate songs and calls. The posterior vocal pathway is also called the vocal motor pathway because of its role in song production.

The anterior nuclei (connectivity examined only in songbirds and parrots) are part of an anterior vocal pathway loop, in which a pallial vocal nucleus (songbird MAN, parrot NAOc) projects to a striatal vocal nucleus (songbird Area X, parrot MMSt), the striatal vocal nucleus projects to a nucleus of the dorsal thalamus (songbird DLM, parrot DMM), and the dorsal thalamus projects back to the pallial vocal nucleus (songbird MAN, parrot NAOc; **Figures 1(b)** and **2(a)**, white arrows). The parrot pallial MO nucleus also projects to the striatal vocal nucleus (MMSt). Connectivity of the songbird MO-like analog has not yet been determined. The anterior vocal pathway is responsible for learning song (determined mostly in songbirds); lateral MAN (LMAN) is thought to generate variability and Area X to generate stereotypy. Functions of the other nuclei of the anterior vocal pathways are not yet well studied. The anterior

Table 1 Abbreviations

AAC: central nucleus of the anterior arcopallium
AACd: central nucleus of the anterior arcopallium, dorsal part
AACv: central nucleus of the anterior arcopallium, ventral part
ACM: caudal medial arcopallium
Ai: intermediate arcopallium
Area X: area X of the striatum
Av: avalanche
B: basorostralis
CM: caudal mesopallium
CMM: caudal medial mesopallium
CSt: caudal striatum
DLM: medial nucleus of dorsolateral thalamus
DM: dorsal medial nucleus of the midbrain
DMM: magnocellular nucleus of the dorsomedial thalamus
E: entopallium
HVC: (a letter-based name)
L1: field L1
L2: field L2
L3: field L3
LLD: lateral lemniscus, dorsal nucleus
LLI: lateral lemniscus, intermediate nucleus
LLV: lateral lemniscus, ventral nucleus
LMAN: lateral part of MAN
MAN: magnocellular nucleus of anterior nidopallium
MLd: mesencephalic lateral dorsal nucleus
MMAN: medial part of MAN
MMSt: magnocellular nucleus of the anterior striatum
MO: oval nucleus of the mesopallium
MOc: oval nucleus of the mesopallium complex
NAOc: oval nucleus of the anterior nidopallium complex
NCM: caudal medial nidopallium
NDC: caudal dorsal nidopallium
NIDL: intermediate dorsal lateral nidopallium
NIf: interfacial nucleus of the nidopallium
NLC: central nucleus of the lateral nidopallium
nXIIts: tracheosyringeal subdivision of the hypoglossal nucleus
Ov: nucleus ovoidalis
PAm: nucleus parambigualis
RA: robust nucleus of the arcopallium
RAm: nucleus retroambigualis
SO: superior olive
St: striatum
Uva: nucleus uvaeformis
VA: vocal nucleus of the arcopallium
VAM: vocal nucleus of the anterior mesopallium
VAN: vocal nucleus of the anterior nidopallium
VAS: vocal nucleus of the anterior striatum
VA/VL: ventral anterior/ventral lateral nuclei of the mammalian thalamus.
VLN: vocal nucleus of the lateral nidopallium
VMM: vocal nucleus of the medial mesopallium
VMN: vocal nucleus of the medial nidopallium

vocal pathway is sometimes called the vocal learning pathway but is most often called the anterior forebrain pathway (AFP) because of its anterior location.

One major difference among vocal learning birds is in the connections between the posterior and anterior vocal pathways. In songbirds, the posterior vocal pathway sends input to the anterior vocal 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 (**Figures 1(b)** and **3(a)**). 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 (**Figures 1(b)** and **3(b)**). An important distinction in this regard is that the parrot posterior pathway vocal nuclei do not appear to send projections to the striatal nucleus of the anterior pathway. Another major difference is the relative location of the posterior vocal nuclei; in songbirds, they are embedded in the auditory regions; in hummingbirds, they are situated more laterally but still adjacent to the auditory regions; in parrots, they are situated far laterally and physically separate from the auditory regions (**Figure 1(b)**). At a minimum, the axons connecting the vocal and auditory systems would have to take different routes in the different vocal learners.

Cerebral Auditory Pathway

Vocal learning and vocal nonlearning birds have very similar auditory pathways. These similarities include projections from ear hair cells to cochlear ganglia neurons, to auditory pontine nuclei (CN, LL), to midbrain (MLd) and thalamic (Ov) nuclei, and to primary (L2) and secondary (L2, L3, NCM, and CM) pallial areas. A descending auditory feedback pathway from the dorsal nidopallium (vocal learners: songbird HVC shelf; parrot NIDL; vocal nonlearner; pigeon Nd) to the intermediate arcopallium (vocal learners: songbird RA cup, parrot ACM; vocal nonlearner: pigeon AIVM) to shell regions around thalamic (Ov) and midbrain (MLd) auditory nuclei (**Figure 2(b)**). An auditory region exists in the striatum (CSt) of all birds examined, but because of lack of detailed study of the connectivity of CSt in different species, it is not yet possible to make reliable comparisons for the striatal auditory region.

The source of auditory input into the vocal pathways of vocal learning birds is unclear. Various routes have been proposed. In songbirds, these include the HVC shelf into HVC, the RA cup into RA, Ov or CM into NIf, and from NIf dendrites in L2. In parrots, these include the NLC shell into NLC, and nucleus basorostralis, L1, and L3 into the comparable NIf-like nucleus LAN. More study is necessary to determine whether any of these regions truly brings auditory input into the vocal pathways.

The cerebral auditory pathway is thought to be responsible for processing complex sounds, including species-specific songs, in a hierarchical manner. Auditory stimuli are relayed from the thalamus (Ov)
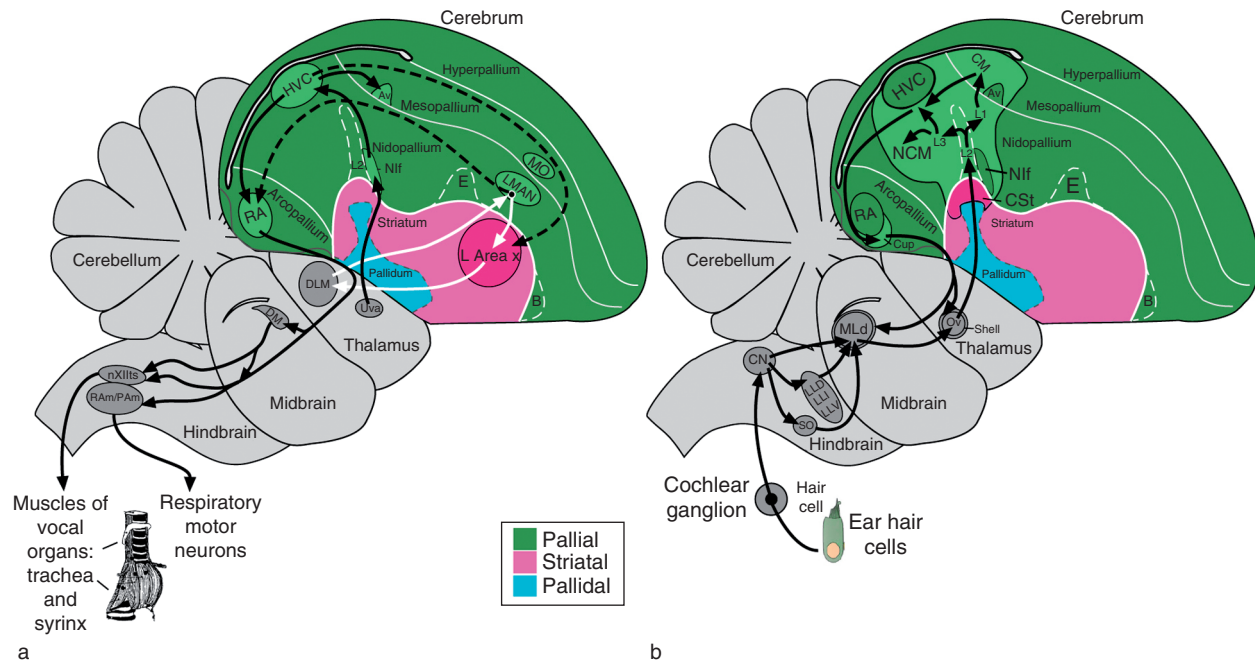
Figure 2 Comparison of vocal and auditory pathways of the songbird brain. Only the most prominent and/or most-studied connections are indicated. (a) Vocal pathway. Black arrows show connections of the posterior vocal pathway (or vocal motor pathway); white arrows, connections of the anterior vocal pathway (or pallial-basal ganglia-thalamic-pallial loop); and dashed lines, connections between the two pathways. (b) Auditory pathway. Most of the hindbrain connectivity is extrapolated from nonsongbird species. For clarity, reciprocal connections in the pallial auditory areas are not indicated. Colors denote major cerebral brain subdivisions of birds. Abbreviations are in **Table 1**. Adapted from Jarvis ED, Güntürkün O, Bruce L, et al. (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* 6: 151–159.

to the cerebrum, where L2 first performs a simple processing of the acoustic features of sounds, then L1, L3, and NCM process more-complex aspects of sounds, such as sequencing and discriminations, and finally CM, the highest station, processes the most complex aspects, such as fine discriminations. In this regard, NCM and CM are also thought to be involved in auditory learning for sound associations and discriminations, and have been proposed to be involved in auditory memory formation of songs used for vocal learning. This hypothesis still needs verification.

Evolution of Vocal Learning Pathways

In the simplest of interpretations, there are three alternative explanations of the way similar, although not identical, vocal learning brain pathways could have evolved among birds (**Figure 1(a)**): (1) the vocal systems in the three vocal learning bird groups evolved independently of a common ancestor. If this is true, then the similarities are remarkably coincidental. (2) In the common ancestor of vocal learning birds, there was a vocal learning pathway with seven cerebral nuclei, which were then lost multiple independent times in closely related bird 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 have vocal learning to various degrees, and songbirds, parrots, and hummingbirds independently amplified the associated brain pathways for their more highly developed vocal learning behaviors. If this were true, it would mean that many birds have at least primordial brain structures for vocal learning. So far, the evidence for this last hypothesis has been lacking.

One proposed answer is that different factors are dependent on or independent of a common ancestor. A proposed dependent factor is preexisting connectivity and function. The connections of the anterior and posterior vocal pathways resemble nonvocal motor pathways in mammals (**Figure 3(c)**), and the regions around the vocal nuclei form connections similar to those of the vocal nuclei and are active during production of nonvocal motor behavior. A proposed independent factor is that out of the proposed preexisting motor system, the vocal learning systems for song in the three bird groups evolved independently.

Specifically, the songbird and parrot posterior vocal pathways are similar in connectivity to mammalian motor corticospinal and corticobulbar
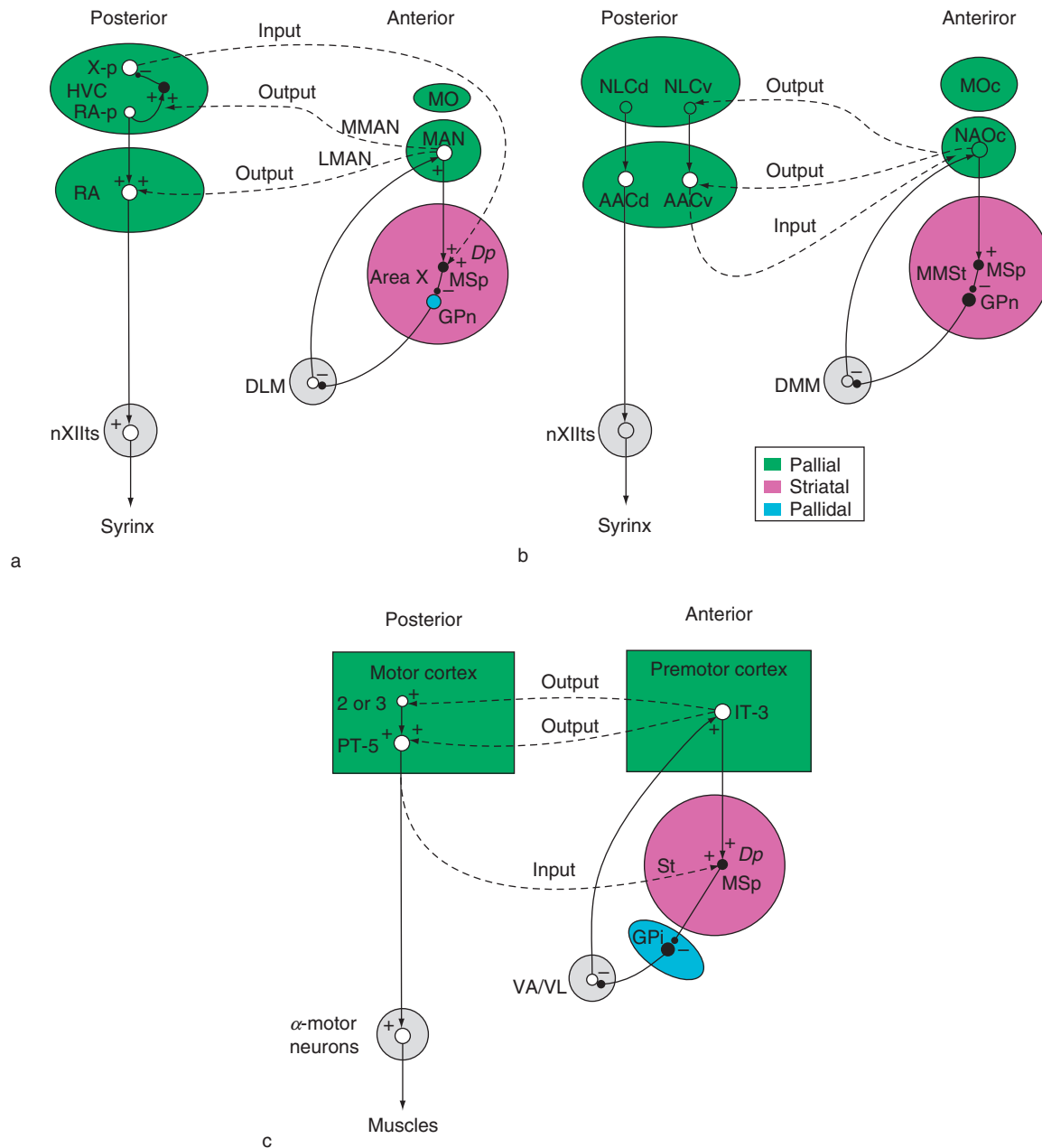
Figure 3 Comparative and simplified cellular connectivity of anterior and posterior vocal pathways in (a) songbirds and (b) parrots, and (c) motor pathways in mammals. Dashed lines: connections between anterior and posterior pathways; inputs and outputs are labeled relative to anterior pathways. Output from songbird MAN to HVC and RA is not from the same neurons; MMAN neurons project to HVC, and LMAN neurons project to RA. **O**, excitatory neurons; ●, inhibitory neurons; +, excitatory glutamate neurotransmitter release; −, inhibitory GABA release; MSp, medium spiny neuron; GPn, globus pallidus-like neuron in songbird Area X and parrot MMSt. Only the direct pathway through the mammalian basal ganglia (St to GPi) is shown as this is the pathway most similar to Area X connectivity (MSp to GPn). 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**. Adapted from Jarvis ED (2004) Learned birdsong and the neurobiology of human language. *Annals of the New York Academy of Science* 1016: 749–777.

pathways (**Figures 3(a)–3(c)**). Projection neurons of songbird RA and parrot AACd are similar to pyramidal tract (PT) neurons of lower layer 5 of mammalian motor cortex. The latter send long axonal projections out of the cerebrum through pyramidal tracts to synapse onto brain stem and spinal cord premotor and α-motor neurons that control muscle contraction and relaxation. The RA-projecting neurons of

songbird HVC and projection neurons of parrot NLC are similar to layer 2 and 3 neurons of mammalian motor cortex, which send intrapallial projections to layer 5 (**Figures 3(a)–3(c)**). Mammalian parallels to songbird NIf and Av are less clear. In mammals, sensory neurons from the thalamus project to layer 4 of cortex; motor feedback from the thalamus projects to layer 5 (in primary motor cortex) or layer 3 (in frontal cortex). NIf is directly adjacent to L2 and, like L2, similar to mammalian layer 4 neurons, it receives thalamic input from UVa, but like the mammalian thalamic input to layer 3, UVa has motor-associated activity, firing during vocalizing.

The songbird and parrot anterior vocal pathways are similar in connectivity to mammalian cortical-basal ganglia-thalamic-cortical loops (**Figures 3(a)–3(c)**). The projection neurons of songbird MAN and parrot NAO are similar to intratelencephalic (IT) neurons of layer 3 and upper layer 5 of mammalian premotor cortex, which send collateral projections, one to medium spiny neurons of the striatum ventral to it and the other to other cortical regions (**Figures 3(a)–3(c)**). Unlike mammals, the spiny neurons in both songbird Area X, and presumably parrot MMSt, project to pallidal-like cells within vocal nuclei Area X and MMSt instead of to a separate globus pallidus structure consisting only of pallidal cells. This striatal-pallidal cell intermingling may be a general trait of the anterior avian striatum. The projection of the pallidal-like cells of songbird Area X and parrot MMSt is similar to the motor pallidal projection neurons of the internal globus pallidus (GPi) of mammals, which project to the ventral lateral (VL) and ventral anterior (VA) nuclei of the dorsal thalamus (**Figures 3(a)–3(c)**). Mammalian VL/VA projects back to layer-3 neurons of the same premotor areas, closing parallel loops, like songbird DLM and parrot DMM projections to LMAN and NAO.

Because connections between the posterior and anterior vocal pathways differ between songbirds and parrots, comparisons between them and mammals will also differ. Input into mammalian cortical-basal ganglia-thalamic-cortical loops is from collaterals of PT–layer-5 neurons of motor cortex, one that projects to the brain stem and spinal cord and the other that projects into the striatum (**Figure 3(c)**). In the songbird, however, a specific cell type of HVC, called X-projecting neurons, projects to the striatum separately from those neurons (neurons of RA) that project to the medulla. Parrot vocal connectivity is even more different from mammalian connectivity. In parrots, AAC of the arcopallium has two anatomically separate neuron populations, AACd, projecting to the medulla, and AACv, projecting to anterior pallial

vocal nuclei NAO and MO. Output of mammalian anterior pathways are the collaterals of IT-layer 3 and IT-upper layer 5 neurons that project to other cortical regions (**Figure 3(c)**).

In terms of function, recent results suggest that vocal nuclei of vocal learning birds are embedded within at least seven brain areas active during the production of limb and body movements. The same movement-associated brain areas are found in vocal learning birds, such as ring doves. These and related findings have led to a motor theory for the origin of vocal learning whereby in the avian brain, a preexisting motor system in a vocal nonlearner ancestor is proposed to have consisted of seven brain regions distributed across mesopallial, nidopallial, arcopallial, and striatal brain subdivisions and separated into two pathways: an anterior premotor pathway that forms a pallial-basal ganglia-thalamic-pallial loop and a posterior motor pathway that sends descending projections to brain stem and spinal cord premotor and α-motor neurons. Then a mutational event or events might have caused descending projections of avian arcopallium neurons that normally synapse onto nonvocal motor neurons to instead synapse onto nXIIts neurons in vocal learners. Thereafter, cerebral vocal brain regions could have developed out of adjacent motor brain regions using the preexisting connectivity. Such a mutational event would be expected to occur in genes that regulate synaptic connectivity of pallial motor neurons to α-motor neurons. This hypothesis needs to be tested with more experiments before it can be accepted with more confidence. If it is true, then this hypothesis needs to account for how auditory information enters the vocal pathway during evolution of a vocal learning system.

Evolution of the Auditory Pathway

The auditory pathway described in birds has a number of similarities with auditory pathways in reptiles and mammals (**Figure 4**). Birds, reptiles, and mammals have ear hair cells that synapse onto sensory neurons, which project to cochlea and lemniscal nuclei of the brain stem, which in turn project to midbrain (avian MLd, reptile torus, mammalian inferior colliculus) and thalamic (avian Ov, reptile reunions, mammalian medial geniculate) auditory nuclei. The thalamic nuclei in turn project to primary auditory cell populations in the pallium (avian L2, reptile caudal pallium, mammalian layer 4 of primary auditory cortex). For connectivity in the cerebrum, detailed studies exist only for mammals and birds. It has been proposed that avian L1 and L3 neurons are similar to mammalian layers 2 and 3 of primary auditory cortex, the
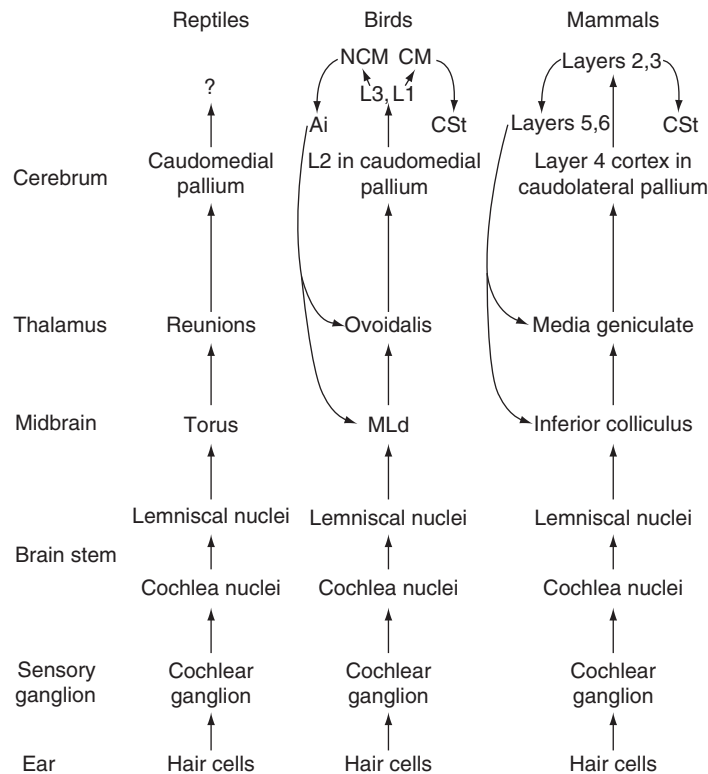
Figure 4 Comparative and simplified connectivity among auditory pathways in reptiles, birds, and mammals. The connectivity from CM to CSt in birds needs verification by retrograde tracing. Abbreviations are in **Table 1**. From Jarvis ED (2004) Learned birdsong and the neurobiology of human language. *Annals of the New York Academy of Science* 1016: 749–777.

latter of which receives input, like L2, from layer 4. Avian NCM and CM have been proposed to be similar to layers 2 and 3 in that they form reciprocal intrapallial connections with each other and receive input from L2. Neurons of the songbird RA cup, parrot ACM, and pigeon AIVM of the arcopallium are similar to mammalian layers 5 and 6, which send descending auditory feedback projections to the shell regions of mammalian thalamic and midbrain auditory nuclei. Avian CSt may be similar to an auditory region in mammals that is located caudally in the striatum. The connectivity of this region has not been verified in birds or mammals.

The similarities suggest that the auditory pathways of birds, reptiles, and mammals may be homologous. Further, since this auditory pathway exists in all birds studied, the auditory pathway in vocal learning birds was presumably inherited from their common avian ancestor, which inherited it from their common stem-amniote ancestor with other vertebrates, thought to have lived ∼320 million years ago. A cerebral auditory pathway would explain why birds and nonhuman mammals, including dogs, exhibit auditory learning, including learning to understand the meaning of simple human speech, although presumably with less facility than a human has. In this regard, when a vocal learning system evolves, it presumably uses the preexisting auditory pathway to bring auditory information into it.

Evolution of Vocal Learning Behavior

The previous sections discuss neural or genetic-based factors that may have influenced the evolution of bird song systems. This last section discusses the possible epigenetic, or environmental/behavioral factors. A number of hypotheses have been proposed to explain what selects for vocal learning. 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 it from others of its population. However, individual identification by voice is not a unique characteristic of vocal learners. As no two individuals look identical, neither do any two individuals within an avian or mammalian population sound identical, allowing vocal nonlearners to identify individual conspecifics by voice. It is true

that with vocal learning, individuals can be called by unique names. This, however, has so far been found among humans and maybe bottlenose dolphins but no other vocal learners. Thus, 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 vocal communication means that animate or inanimate objects have a specific vocalization or series of vocalizations associated with them. It contrasts with affective vocal communication, which means that vocalizations have emotional content associated with them. Despite this common notion, many vocal nonlearners, such as chickens and vervet monkeys, use innate calls to communicate semantic information, such as 'an eagle above,' 'a snake on the ground,' or 'a food source.' Vocal learning birds also use innate calls with such semantic information and only rarely have been found to use learned vocalizations for mainly semantic communication. Examples of the latter include the African Grey parrot's use of human speech words and the black-capped chickadee's use of calls to indicate predator size. Since this is not the common use of learned vocalizations among vocal learners, 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. These uses are found among the songbirds, parrots, and hummingbirds. Many vocal nonlearners use their innate calls and crows to defend territories and attract mates; examples include the crowing of male doves and chickens. There is, however, an additional feature of mate attraction that vocal learners use learned vocalizations for: variability. Vocal learners, but not vocal nonlearners, have the ability to produce more-varied frequency modulation (FM) and syntax, during vocal development and/or, in some species, after reaching adulthood. These variations in FM and syntax are preferred by females of the songbird species that have been examined. In addition, canaries have been shown to use their two voices, common among birds, to produce even greater FM variations, thought to stimulate estrogen production in the listening females; these are sometimes called sexy syllables or songs. In fact, in vocal nonlearners, such as ring doves, artificially increased computer-generated FM of innate sounds is more stimulatory for mating than are the innate coos. 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 maybe selected for. In this regard, mate attraction

was probably a major driving force in the selection for vocal learning.

For sound transmission, vocal nonlearners produce their vocalizations best in specific habitats, 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, whereas 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 explain why it is so rare. One proposed explanation 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 mammalian vocal learners have very few if any major predators (humans, whales, and elephants). Hummingbirds, because of their rapid flight and escape behavior, are also commonly known to be fearless of many animals. Various parrot species and ravens (a corvid songbird) are prey to hawks and large owls, like other birds, but they are said to be highly effective at mobbing behavior to evade such predators. A cautionary note: it is not known how valid the distinction is between vocal learners and nonlearners in terms of predation, as no systematic study has been done on prey and predatory behaviors across vocal learning and vocal nonlearning groups.

Some findings support this association. Okanoya and colleagues have shown that Bengalese finches that have been bred in captivity, without predators, for the past 250 years and without human selection for singing behavior show more-varied syntax than their white-backed munia conspecifics still living in the wild, from which they derive. Zann has shown that zebra finches bred in captivity show more variation in the songs learned among adults of a colony than do their wild-type conspecifics. For both species, females prefer the more varied songs. Given these findings, one

would expect to find more syntax complexity selected for in the wild than currently exists. Perhaps predatory pressure is selecting against it.

In summary, the investigations into the evolution of bird song systems are an active area of study, often leading to insights and to novel hypotheses about evolution of brain systems for complex behaviors, including spoken language. A great amount of knowledge has been obtained, but a great amount more is needed before various hypotheses can be rejected or new ones generated.

See also: Auditory System: Central Pathways; Bird Brain: Evolution; Birdsong Learning: Evolutionary, Behavioral, and Hormonal Issues; Birdsong Learning; Birdsong: The Neurobiology of Avian Vocal Learning; Signal Production and Amplification in Birds; Vocal Communication in Birds.

Further Reading

Brenowitz EA (1997) Comparative approaches to the avian song system. *Journal of Neurobiology* 33: 517–531.

Catchpole CK and Slater PJB (1995) *Bird Song: Biological Themes and Variations.* Cambridge, UK: Cambridge University Press.

Doupe AJ, Perkel DJ, Reiner A, and Stern EA (2005) Birdbrains could teach basal ganglia research a new song. *Trends in Neuroscience* 28: 353–363.

Farries MA (2001) The oscine song system considered in the context of the avian brain: Lessons learned from comparative neurobiology. *Brain Behavior and Evolution* 58: 80–100.

Janik VM and Slater PJB (1997) Vocal learning in mammals. *Advances in the Study of Behavior* 26: 59–99.

Jarvis ED (2004) Brains and birdsong. In: Marker P and Slabbekoorn H (eds.) *Nature's Music: The Science of Birdsong*, pp. 226–271. San Diego, CA: Elsevier-Academic Press.

Jarvis ED (2004) Learned birdsong and the neurobiology of human language. *Annals of the New York Academy of Science* 1016: 749–777.

Jarvis ED (2006) Selection for and against vocal learning in birds and mammals. *Ornithology Science* 5: 5–14.

Jarvis ED, Güntürkün O, Bruce L, et al. (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* 6: 151–159.

Jarvis ED, Ribeiro S, da Silva ML, et al. (2000) Behaviourally driven gene expression reveals song nuclei in hummingbird brain. *Nature* 406: 628–632.

Marler P and Slabbekoorn H (eds.) (2004) *Nature's Music: The Science of Birdsong.* San Diego, CA: Elsevier-Academic Press.

Nottebohm F (1972) The origins of vocal learning. *American Naturalist* 106: 116–140.

Okanoya K (2002) Sexual display as a syntactical vehicle: The evolution of syntax in birdsong and human language through sexual selection. In: Wray A (ed.) *The Transition to Language*, pp. 46–63. Oxford, UK: Oxford University Press.

Sibley CG and Ahlquist JE (1990) *Phylogeny and classification of birds: A study in molecular evolution.* New Haven, CT: Yale University Press.

Wild JM (1997) Neural pathways for the control of birdsong production. *Journal of Neurobiology* 33: 653–670.

Zann RA (1996) *The Zebra Finch: A Synthesis of Field and Laboratory Studies.* New York: Oxford University Press.

Zeigler HP and Marler P (eds.) (2004) *Special Issue: Behavioral Neurobiology of Birdsong. Annals of the New York Academy of Science* 1016.