Song learning in birds: diversity and plasticity, opportunities and challenges

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A common trend in neuroscience is convergence on selected model systems. Underlying this approach is an often implicit assumption that mechanisms observed in one species are characteristic of all related species. Although the model system approach has been extremely productive, it might not account for all of the mechanistic differences between species that differ behaviourally. Using the neural system that regulates song learning in songbirds as an example, we demonstrate how integrating model system and comparative approaches can lead to a more complete picture of neural mechanisms, and can resolve issues raised by a focus on selected species.

Introduction

The neural system that regulates song learning in songbirds has become a prominent model for studying the neural mechanisms of learning. This system offers several advantages. (i) In many species, song learning is characterized by well-defined sensitive periods. (ii) Song learning and production are controlled by discrete, well-defined neural circuits (Figure 1). (iii) Song is essential for the reproductive behaviour of birds and provides an opportunity to study the neural basis of a learned behaviour in a naturalistic context. Animals evolve and live in natural environments and studying the mechanisms of behaviour from this perspective can provide unique insights. (iv) There are >4000 songbird species and, as will be summarized here and discussed in detail in a companion paper [1], they show extensive diversity in different aspects of song learning.

Much of what we know about the song control system has come from studies of one particular songbird, the zebra finch (*Taeniopygia guttata*) [2] (Box 1). Zebra finches are domesticated, easily bred in captivity, and reach sexual maturity by 90 days post-hatch (PH). They rapidly learn a single, stereotyped song, which facilitates study of their song behaviour.

In this article, our goal is to demonstrate how specific hypotheses raised by studies of zebra finches can be tested by exploiting species song diversity in comparative studies of the neural mechanisms of song learning [2,3]. Comparative study should expand the picture presented by zebra finch studies, and could open new frontiers in the study of the neurobiology of song learning. We will first discuss interspecific diversity of song learning programs.

Second, we will describe examples in which species diversity has successfully been exploited to study mechanisms of various aspects of song behaviour. Third, we will propose particular species that could be used to address open questions about the neural control of song learning. A comparative approach is facilitated by the striking observation that, despite extensive species diversity in different attributes of song behaviour, the same neural song control circuits are present in every songbird species examined [4,5].

Diversity of song learning programs

A comparative survey reveals that among the >4000 species of songbirds there is extreme diversity of song learning programs, and that many of these programs are very different from that of the zebra finch [1] (Box 1). Diversity occurs along several dimensions of song
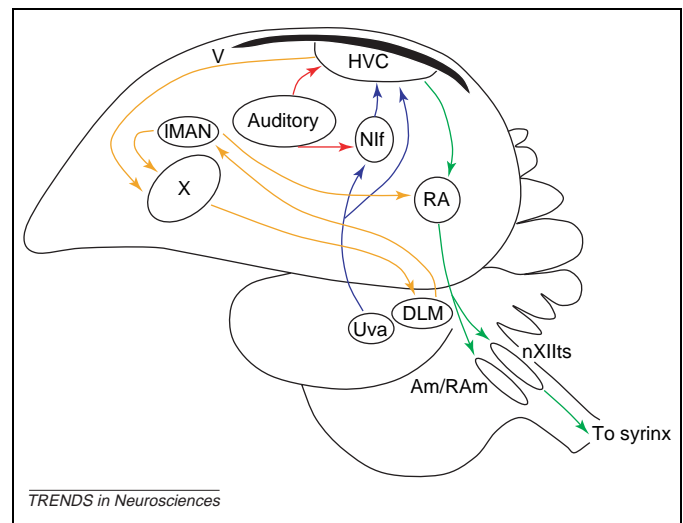

Figure 1. Projections of the major nuclei in the song control system. The motor pathway (green) controls the production of song and consists of descending projections from HVC (acronym used as the proper name) in the nidopallium to the robust nucleus of the arcopallium (RA), and thence to the vocal nucleus nXIIts (tracheosyringeal part of the hypoglossal nucleus), the respiratory nucleus retroambigualis (RAm) and the laryngeal nucleus ambiguus (Am) in the medulla. Motor neurons in nXIIts innervate the muscles of the syrinx, the avian vocal production organ. Blue lines indicate afferent inputs to HVC from the thalamic nucleus uvaeformis (Uva) and nidopallial nucleus interface (NIf). Red lines indicate auditory input to NIf and HVC from telencephalic auditory regions. Orange lines indicate the anterior forebrain pathway (AFP) that is essential for song learning and perception. It indirectly connects HVC to RA, via area X (X; thought to be a basal ganglia homologue), the medial portion of the dorsolateral nucleus of the thalamus (DLM) and the lateral portion of the magnocellular nucleus of the anterior nidopallium (IMAN). IMAN also projects to area X. Additional abbreviation: V, ventricle.

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Box 1. Song learning in the zebra finch

Zebra finches grow rapidly and reach sexual maturity by 90 days post-hatch (PH). They learn to produce a single stereotyped song by this age. Isolation from conspecific song during this early period results in grossly abnormal song. It is thought that an innate, crude 'template' guides zebra finches to memorize selectively conspecific song heard during an early sensitive period, and that exposure to conspecific tutor song converts the innate template into a more complex acquired template. The sensitive period for song memorization is ∼25–60 days PH [45]. Beginning ∼35 days PH, young birds convert the acquired template to a motor pattern in the sensorimotor phase of song learning by comparing auditory feedback from their initial poorly structured vocalizations to the memorized model. With practice, the bird's own song progressively improves in structure until eventually the bird produces a 'crystallized' (i.e. stereotyped) version of the memorized song by 120 days PH [45,46].

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learning (and on each dimension, the zebra finch lies at one extreme):

(i) Timing of song learning, from early sensitive period learners such as zebra finches to life-long learners such as European starlings (*Sturnus vulgaris*) and pied flycatchers (*Ficedula hypoleuca*).

(ii) How many songs a bird learns (i.e. repertoire size), from one song type in zebra finches to >1000 song syllables in brown thrashers (*Toxostoma rufum*).

(iii) Whether birds closely imitate conspecific song, as in zebra finches, or improvise by modifying song elements to create novel songs, as in sedge wrens (*Cistothorus platensis*).

(iv) Whether birds require early exposure to conspecific song, as in zebra finches, or can develop species-typical song even when raised in isolation, as in grey catbirds (*Dumetella carolinensis*) and sedge warblers (*Acrocephalus schoenobaenus*).

(v) Whether birds copy tutor material only if it fits tightly-constrained species-specific parameters, as in zebra finches, or will copy essentially anything they hear, as in northern mockingbirds (*Mimus polyglottus*) and marsh warblers (*Acrocephalus palustris*).

One implication of this diversity is that it is difficult to identify a single 'typical' songbird learning program, other than perhaps a general need to compare auditory feedback from self-generated song to an internal model (see also Ref. [6]). Thus, neural correlates of song learning observed in the zebra finch should not be assumed to be typical of all songbirds. Moreover, and this is our key point, the diversity of song learning patterns in the songbirds presents opportunities for testing the generality of the model of the neurobiology of song learning developed largely on the basis, so far, of studies of the zebra finch. A general question we can ask is whether the differences between patterns of song learning seen in songbirds are merely quantitative ones or are more significant, qualitative ones. For example, we might expect that the difference in neural encoding of one song type in a zebra finch and approximately ten song types in a song sparrow (*Melospiza melodia*) is quantitative. By contrast, the neural differences between birds that require early exposure to conspecific song and those that can develop normal song when raised in isolation might be qualitative.

Examples of the comparative approach

A superb example of the comparative method is found in studies of the peripheral mechanisms of song production [7]. Measurements of muscle contraction and airflow patterns in the sound producing organ, the syrinx, of different species show that song diversity evolved because individual species elaborated performance constraints in particular directions. This use of the comparative method has provided much insight into the proximate basis of species differences in vocal performance.

The comparative approach has also been used to explore the relationship between post-hatching neurogenesis and song plasticity [8–10]. Neurons are recruited to HVC (acronym used as the proper name) of juvenile zebra finches and island canaries (*Serinus canarius*) at a higher rate when they are actively learning to sing than when they produce crystallized (i.e. stereotyped) song. Canaries develop new song syllables as adults, and neuronal incorporation into adult HVC increases in the fall when song is variable and syllable addition is greatest. These observations together raised the hypothesis that neuronal addition to HVC is functionally related to song learning. In song sparrows, however, song learning is limited to the first year of life but seasonal changes in song variability and HVC neuronal recruitment are qualitatively similar to those seen in canaries [11]. This comparative analysis suggests that although neurogenesis might be necessary for song learning it is not sufficient, and provides a more complex picture of the relationship between these two processes.

Use of comparative studies to test song learning hypotheses

Sensitive periods for song memorization

The period of song learning in zebra finches correlates with changes in the structure and physiology of the song control system (for a comprehensive review, see Ref. [12]). Given the rapid maturation of zebra finches, there is much overlap between sensory learning, onset of singing, sensorimotor rehearsal, and development of auditory selectivity for a bird's own song (BOS) [13,14]. This has made it difficult to correlate a particular neural change with a specific aspect of song learning. Also, the song system is still developing during this time and some of the cellular changes observed could be related to developmental events independent of song learning. Comparative study of species in which the different phases of song learning are not compressed in time can help to clarify the roles of different neural mechanisms in specific aspects of song development, and can enable us to test the generality of specific hypotheses raised in studies of zebra finches.

The anterior forebrain pathway (AFP; Figure 1) is essential for normal song learning. In zebra finches, several anatomical changes occur in this pathway during the period of overlap between the sensory and early sensorimotor phases of song learning: in the lateral magnocellular nucleus of the anterior nidopallium (lMAN) shell, axon terminals from neurons of the medial dorsolateral nucleus of the thalamus (DLM) retract; dendritic spine frequencies and the number and density of synapses on lMAN shell neurons decrease; projections from the lMAN

core to the robust nucleus of the arcopallium (RA) are remodelled to develop topographic specificity; and new neurons are added in large numbers to area X [15,16]. There are also physiological changes in the AFP during the period of song learning. NMDA-receptor-mediated LTP can be induced by paired stimulation at lMAN synapses in birds sacrificed at an age before the onset of sensory learning, but the same stimulation produces synaptic depression in birds sacrificed at an age when the sensory learning phase normally ends [17].

The above observations raise two questions. First, are these anatomical changes functionally related to song learning or just part of a general developmental program [6]? This question can be addressed by studying species in which song memorization and rehearsal are delayed until late in the first year or early in the second year [e.g. song sparrows or indigo buntings (*Passerina cyanea*), respectively [1,18]], and species that memorize and rehearse new songs as adults (e.g. starlings [19–21]). If the anatomical changes described above are related to song learning, then we might predict that they would be delayed in species with delayed song learning. In species that memorize new songs as adults, a more 'juvenile' pattern of synaptic connectivity might be restored or maintained, depending on whether new songs are memorized seasonally or continually. If LTP at lMAN synapses is related to song memorization, then we might predict a delay in the shift from synaptic potentiation to depression in species that defer sensory learning (e.g. song sparrows and indigo bunting), and restoration or maintenance of LTP in species that memorize new songs as adults (e.g. starlings and mockingbirds).

The second question concerns which neural changes are functionally associated with song memorization versus song rehearsal. This can be addressed using swamp sparrows (*Melospiza georgiana*) reared in the laboratory [22]. Sparrows tutored with tape-recordings 22–62 days PH memorized song, but did not start to rehearse song until ~275 days PH. Neuron number in both area X and HVC increased sharply during the memorization phase, but did not increase during the sensorimotor phase. This same paradigm could be used to explore the relationship of the anatomical and physiological changes already discussed to song learning phases.

BOS-selective neurons, song repertoires and plasticity

Neurons in both the motor pathway and AFP are responsive to acoustic stimuli in zebra finches. Some neurons respond selectively to BOS under certain circumstances [17,23]. The functional significance of these BOS-selective neurons remains unclear [14]. They could provide an 'error signal' that promotes change in song production when a mismatch is detected between auditory feedback from self-song and the memorized song template, and could thus have a role in both song learning and maintenance [24,25] (but see Ref. [26]). A second function might be the perception of conspecific song [23,27–29]. These functions are not necessarily mutually incompatible and could be fulfilled by different populations of neurons [29,30].

Species diversity in song behaviour raises questions about the properties and function(s) of BOS neurons in other species. A zebra finch sings only one song type but most species have repertoires of multiple song types ranging from a few to >1000. In repertoire species, do individual neurons respond to single or multiple song types? Mooney *et al.* [31] investigated this question in swamp sparrows, which have small repertoires of 2–5 song types. They found that most single RA-projecting HVC neurons discharge selectively to playback of a single song type, whereas HVC interneurons respond to all song types of a particular male but not to heterospecific song. Swamp sparrow song types each consist of repetitions of a single song syllable and projection neurons could thus encode syllables rather than song types. A species such as the song sparrow, in which different song types consist of unique syllable combinations, could be used to determine whether these neurons encode syllables or whole song types (e.g. Ref. [32]). It would be interesting to determine whether the same pattern of selectivity seen in swamp sparrows occurs in species with large repertoires such as marsh wrens, mockingbirds and brown thrashers.

Repertoire species also provide the opportunity to ask whether neurons are specialized not for particular songs of the bird but for particular song types, whether sung by that bird or another. In most species examined, neighbouring males and group members share song types [1]. In these species, do neurons in one male respond to rendition of a shared song by another male? If so, we can speculate that this stimulation by the song of a neighbour provides a mechanistic explanation for why males of so many species do share songs and use them in aggressive interactions; shared songs might be particularly effective in evoking auditory neuronal responses in competitors (see also Ref. [31]).

Species with plastic adult song structure pose another interesting question for BOS selective neurons. Sedge warblers rearrange their repertoire of ~50 song syllables to produce long, unique songs. Brown thrashers seem to continually improvise songs to produce huge repertoires (>1000) [1]. Are song system neurons in such species selective for BOS and, if so, do individual neurons continually modify their selectivity to match changing song structure? Yaki-Sugiyama and Mooney [33] tutored zebra finches with one song 0–30 days PH, and a second song 60–90 days PH. They found that lMAN neurons apparently altered their response selectivity under these conditions. lMAN receives auditory input indirectly via HVC, and 'mature' HVC neurons could retain their selectivity to the same song throughout their lives, whereas newly recruited neurons become 'tuned' to new song types [10]. Comparative studies of species that naturally modify their songs as adults will further contribute to our understanding of this topic.

Plasticity, diversity and the evolution of adult song learning

In addition to testing mechanistic hypotheses, comparative analysis can provide insights into the evolution of song learning by adult birds. In zebra finches, song learning is restricted to the first year and they are therefore referred to as 'age-limited' or 'closed-ended' learners. Other species, such as the island canary, go

through a similar song learning process during their first year but are also able to develop new songs in subsequent years as sexually mature adults; they are described as 'open-ended' learners [10]. It is often difficult to determine from field studies of open-ended learning species whether songs developed as adults involve memorization of new song models or production of previously memorized models [34]. The neural mechanisms underlying adult song memorization (e.g. in starlings) versus adult production without memorization (e.g. in sedge wrens) could be qualitatively different.

It has been implicitly assumed that closed-ended and open-ended song learning represent two distinct strategies, perhaps reflecting a dichotomous evolutionary divergence from a common ancestral pattern (but see Refs [35–37]). This apparent dichotomy, however, results from focus on a small number of species [1]. The lack of adult song learning had been assumed to result from a lack of plasticity in the song control system of closed-ended species. It is now clear, however, that adult song circuits are characterized by extensive plasticity in both closed-ended and open-ended species [38] (Table 1; Figure 2). Furthermore, a comparative analysis indicates that these two song learning strategies are not separated by clear boundaries (Figure 3). Instead, if we look at the diversity of song learning programs across species, we find a continuum in the extent of plasticity of adult song behaviour. Also, adult song learning is far more prevalent than we originally thought [1]. Together, these considerations suggest that closed-ended and open-ended song learning species can be regarded as differing quantitatively in the degree of plasticity in adult song, rather than differing qualitatively in the presence or absence of plasticity.

It is likely that comparative surveys will also reveal continua for other aspects of song learning, such as how tightly constrained a song model must be for birds to copy it. Such continua provide rich opportunities for fine-scaled studies of neural mechanisms underlying these aspects of song learning.

Practical considerations

We recognize that investigators who pursue comparative studies of the neural mechanisms of song learning will encounter logistical difficulties. Many neurobiologists lack training in the methods required to capture wild birds in the field, but they could collaborate with behavioural colleagues who have these skills [22,31,39]. Another consideration is that many behaviourally interesting species

Table 1. Attributes of song system that change seasonally[a,b]

Volumes of HVC, RA, area X and nXIIts
Neuronal number in HVC
Incorporation of new neurons into HVC
Neuronal soma size in HVC, RA, area X and IMAN
Neuronal density in RA and area X
Synaptic and dendritic traits in RA
Metabolic capacity of neurons in HVC, RA and area X
Spontaneous neurophysiological activity of RA neurons
Song stereotypy, duration and rate of production

[a]See Refs [38,47] for reviews.
[b]Abbreviations: HVC, acronym used as the proper name; IMAN, lateral portion of the magnocellular nucleus of the anterior nidopallium; nXIIts, tracheosyringeal part of the hypoglossal nucleus; RA, robust nucleus of the arcopallium.
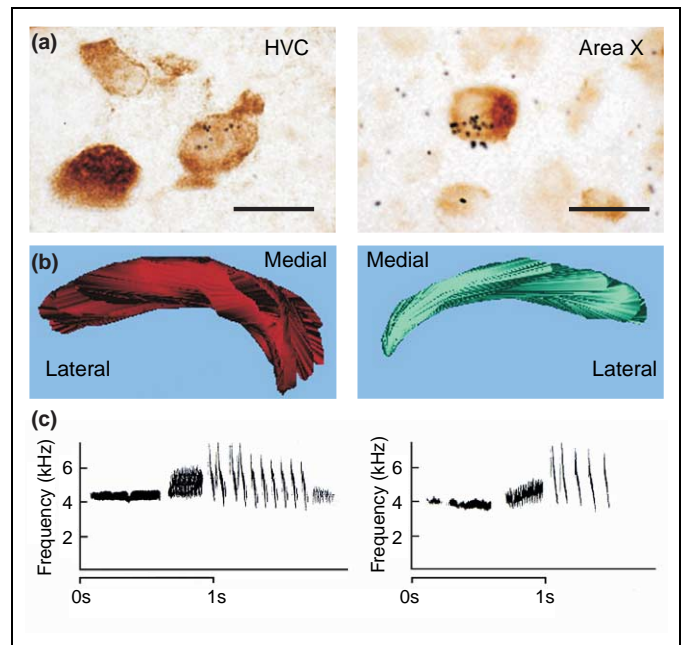
Figure 2. There is extensive plasticity of the song control circuits and song behaviour in both closed-ended and open-ended learning species. **(a)** New neurons continue to be recruited to HVC and area X in adults. Newly born cells in song sparrows (*Melospiza melodia*) that have incorporated ^{3}H-thymidine into their nuclei (indicated by silver grains) and that are immunoreactive for the neuron specific antigen Hu (brown) are shown. Scale bars, 15 μm. **(b)** In every seasonally breeding species examined, there is seasonal plasticity of the structure and physiology of the song system, regardless of closed-ended versus open-ended song learning [47,48] (Table 1). Three-dimensional reconstructions of HVC (caudal perspective) in breeding (left) and non-breeding (right) Eastern towhees (*Pipilo erythrophthalmus*) are shown [49]. **(c)** Seasonal plasticity of the song system induces plasticity of song behaviour regardless of the ability to develop new songs in adulthood [48]. Song becomes shorter and less stereotyped in structure outside the breeding season in canaries (*Serinus canarius*; open-ended) and in white-crowned sparrows (*Zonotrichia leucophrys*) and song sparrows (closed-ended) [50–53]. Songs recorded from white-crowned sparrows in the breeding (left) and non-breeding (right) seasons are shown. Note the quavering quality of the first and second syllables, and the shorter duration, of the non-breeding song.

live in remote areas of the paleotropics and neotropics [1]. Although anatomical, endocrine and even genetic studies can be conducted under such conditions [40–42], it would be extremely difficult to perform neurophysiological studies in the field. Many species of interest for such studies are, however, readily available in North America and Europe, where most birdsong neurobiology laboratories are located; all of the species that we have suggested using in specific studies in this article breed in these regions and can be brought into the laboratory. Our own experiences show that neurobiological studies of wild bird species are feasible and we hope that logistical concerns will not deter investigators from exploiting the rich diversity of song learning to be found among the songbirds.

Concluding remarks

The birdsong system is as a valuable model for the study of several fundamental properties of the vertebrate brain, including adult neurogenesis, sexual differentiation and learning. The great diversity of song learning programs among songbird species provides superb opportunities for comparative studies of song learning mechanisms. Several questions stand out as benefiting especially well from a comparative approach:
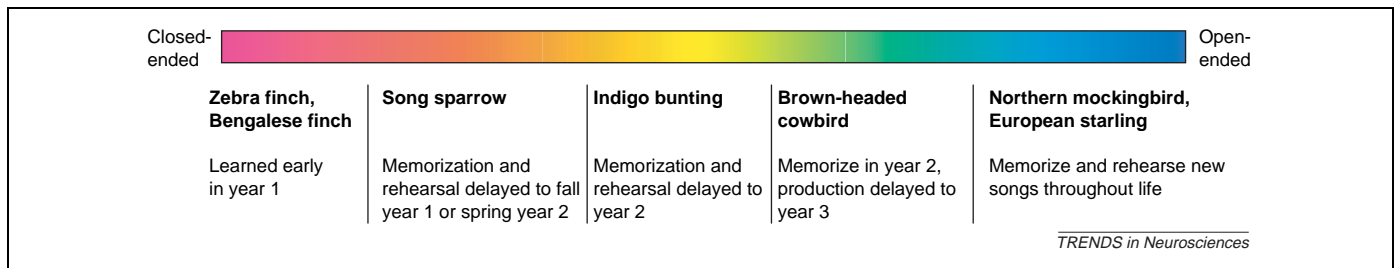
Figure 3. Diversity of song learning programs observed across species forms a continuum between closed-ended and open-ended learning strategies. 'Years' refers to calendar years. Zebra finches (*Taeniopygia guttata*) and Bengalese finches (*Lonchura striata*) are extreme examples of closed-ended learners: once song is crystallized in the first year, males sing the same song for the rest of their life (Box 1). A young male song sparrow (*Melospiza melodia*) learns song in the summer and fall of his first year, and perhaps in the following spring, when he memorizes songs of adult males in the area where he will subsequently establish his own breeding territory [54]. Indigo buntings (*Passerina cyanea*) typically delay sensory acquisition of song models until their first breeding season [18]. Male brown-headed cowbirds (*Molothrus ater*) memorize new songs in the first breeding season but do not sing them until the next breeding season [55]. At the opposite end of the spectrum from strictly closed-ended learners such as zebra finches are species that modify their songs throughout life, such as northern mockingbirds (*Mimus polyglottus*) and European starlings (*Sturnus vulgaris*) [19–21,56]. These species are presented to illustrate the concept of a continuum of temporal song learning programs, with no implication that they are closely related.

(i) What are the mechanisms of sensory versus sensori-motor song learning? Species in which the two phases are temporally dissociated are particularly amenable to this topic.

(ii) Are juvenile patterns of neural plasticity retained or seasonally restored in species that memorize and/or rehearse new songs as adults? To exploit fully the potential of species diversity in song for this question, it will be necessary to determine better for more open-ended species whether adult song learning involves new memorization of song models.

(iii) In species with large song repertoires, are single BOS-responsive neurons selective for single or multiple song types? Is the same song type sung by a bird other than the subject (i.e. a shared song type) as effective as the subject's own version at stimulating the subject's own neurons? In open-ended learners, do individual neurons modify their selectivity to match changing song structure, or do newly recruited neurons serve this function? The continuing development of chronic recording methods will facilitate such studies.

(iv) Are seasonal changes in neuronal recruitment to HVC common in seasonal breeders, and are they consistently associated with seasonal changes in behavioural song plasticity?

(v) What neural changes occurred over the evolution of closed-ended and open-ended song learning patterns? A phylogenetic approach is well-suited to such evolutionary questions.

(vi) Although space limitations have not allowed us to address molecular aspects of song learning, this is a burgeoning area of research that will benefit greatly from a comparative approach.

Focussing on neural mechanisms of song learning in a few selected species has been extremely productive. The practical benefits of working on a domesticated species such as the zebra finch are clear and of undeniable importance. Our understanding of this topic is, however, greatly enhanced by exploiting the extraordinary diversity of song learning programs found among the many species of songbirds. The song system is an example of how model system and comparative approaches can reinforce and augment one another. Although we have concentrated on the birdsong system, similar arguments apply to diverse neural systems in which there is a concentration of research on any one particular model species. For any model system, as the database of information obtained from study of one species increases, there is an ever greater incentive for future studies to use the same species. A focus on model systems, however, poses the risk of investigators coming to view the model species as typical of the taxon in general. Given the diversity observed within and between related species in neural and genetic mechanisms [43,44], making such an assumption is unwarranted. Embracing the diversity of neural mechanisms found through comparative study of different species is sure to deepen our understanding of fundamental aspects of brain function, as it has in the birdsong system.

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