

# Where Is the Bird?

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**ABSTRACT:** Patterns of song perception, learning, and expression differ across species, sexes, and individuals. We can understand the neurobiology of song better by paying attention to these differences. I focus selectively on a few of the studies done in my lab over in recent years to illustrate this.

**KEYWORDS:** evolution; female choice; phylogenetic analysis; dendritic spines; *Acrocephalus warbler*; heritability

Although many of the papers in this volume are attempts to generalize their research results as broadly as possible, I would like to ask where the bird is in all this. I mean by this that patterns of song perception, learning, and expression differ across species, sexes, and individuals. We can understand the neurobiology of song better by paying attention to these differences. I will focus selectively on a few of the studies done in my lab over in recent years to illustrate this. More complete reviews both of our own work and of more general song system neurobiology can be found elsewhere.<sup>1,2</sup>

## RELATIONS BETWEEN SONG AND THE SONG SYSTEM ACROSS MALES

First, as even a casual observer of songbirds knows, species differ dramatically in all possible features of song—from the timing of learning, to contexts for its use, to the acoustic structure of individual sound elements, to the pattern in which elements are assembled into a song. Of particular interest is the observation that aspects of song are learned—and in this feature as in the ones mentioned above, there is immense variation across songbird species. For example, the songs of a nightingale and a black-capped chickadee differ immensely in the amount of learning that they incorporate. We have found that these differences are correlated with variation in gross morphology of the song system. Across a group of 41 very diverse species, the relative volume of HVC was positively correlated with the number of different songs typically produced by males in the species.<sup>3</sup> These findings suggest that essential functions of the song system evolved early in the songbird phylogeny and have persisted in many of the families of this group. However, only limited inferences can be drawn from studying such a wide phylogeny. The structure of song differs so widely

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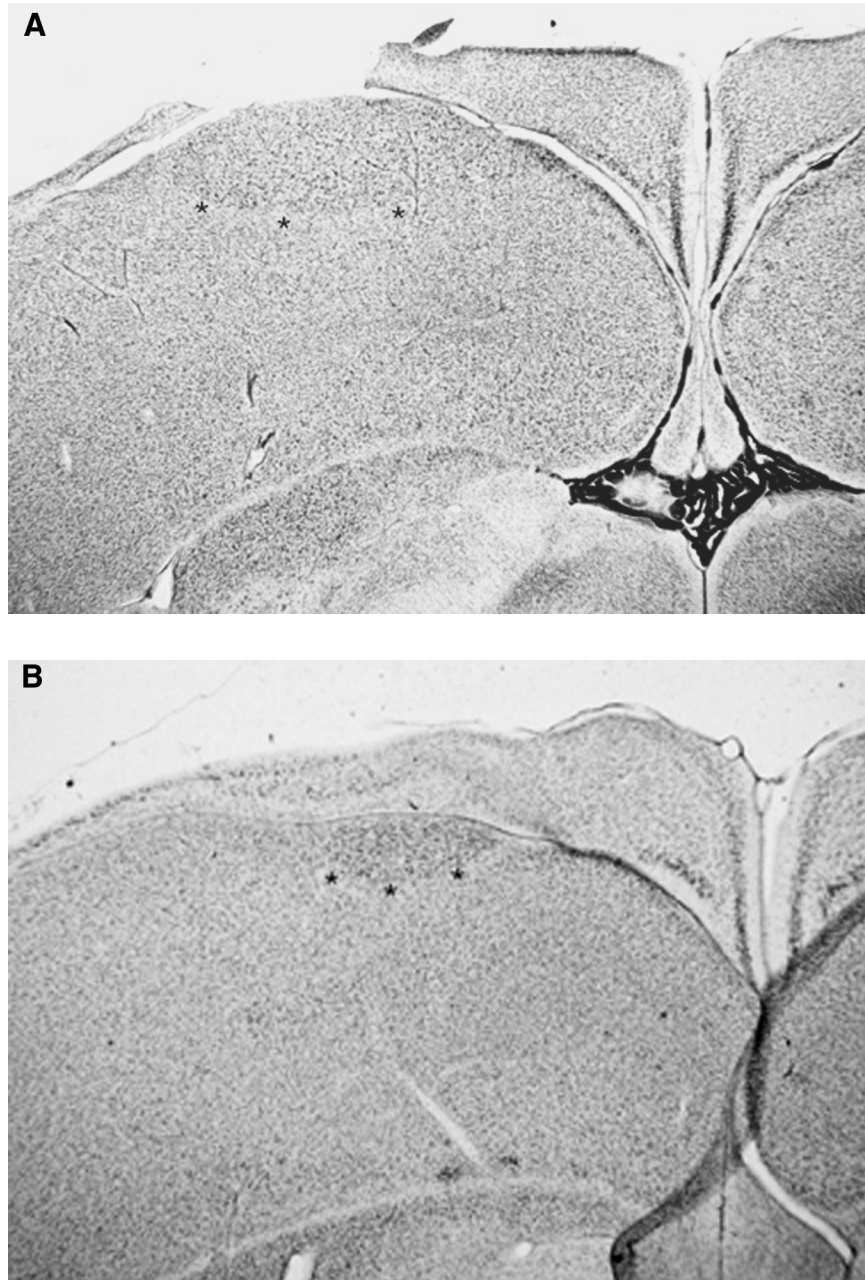
**Ann. N.Y. Acad. Sci. 1016: 778–786 (2004). © 2004 New York Academy of Sciences.  
doi: 10.1196/annals.1298.033**

that quantification with the same metrics is often impossible. Different avian families have experienced such prolonged and divergent selective pressures that the distribution of function within the song system may have diverged. Thus, to understand structure-function relations in more detail, it is necessary to study more closely related taxa.

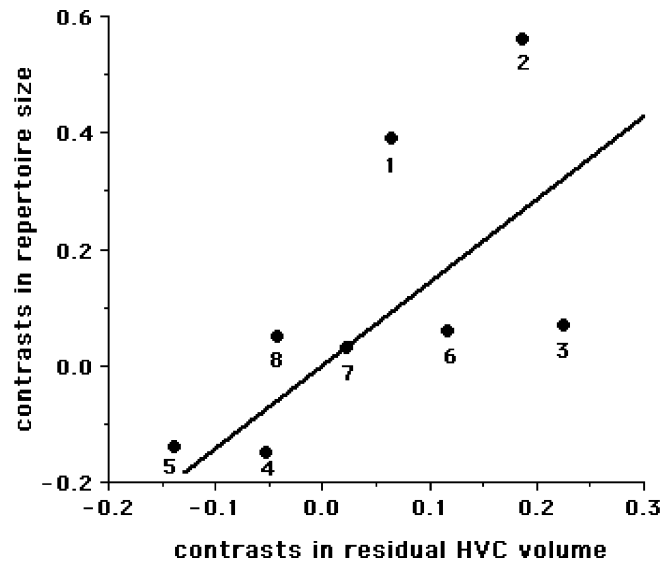
Even within avian families, there can be immense variation in song complexity. This can be observed within reed warblers, several closely related genera that are part of the sylvidae family. These species live in similar habitats, eat similar diets, and look very much alike. Marsh warbler (*Acrocephalus palustris*) songs consist of up to 100 different syllables.<sup>4</sup> In contrast, grasshopper warbler (*Locustella naevia*) songs consist of a single two-note syllable repeated scores to hundreds of times. Even this simple song contains features that are learned from models in a juvenile sensitive period.<sup>5</sup> HVC is several times larger in the marsh warbler than in the grasshopper warbler (FIG. 1). Across eight such warbler species, the relative volume of HVC is significantly related to the number of different song syllables typically found in a male's repertoire, once degree of relatedness is factored into the statistics (FIG. 2).<sup>6</sup>

We and other labs have found that the relations between gross morphology of the song system and aspects of singing can even be found across individuals within a species. Nottebohm and colleagues first observed that the number of syllables in the repertoire of male canaries is positively correlated with the volumes of HVC and of RA.<sup>7</sup> This observation extends to female canaries: the number of syllables they produce when induced to sing with testosterone implants is correlated with the volume of HVC.<sup>8</sup> There is no significant relation between HVC volume and size of the repertoire of song types sung by marsh wrens (*Cistothorus palustris*) that had been exposed to a restricted number of song types during rearing. However, if raised hearing a more normal number of song models, HVC volume and adult repertoire are correlated.<sup>9</sup> Even in laboratory-housed zebra finches, the number of notes comprising the stereotyped song varies between normal individuals. We have found that this variation in the overall content of song is positively correlated with the volume of the bird's HVC.<sup>10</sup> Ward and colleagues<sup>11</sup> have found a significant correlation between the number of learned elements in the zebra finch's song and HVC volume. This brain-behavior relation is present in wild birds too. In sedge warblers (*A. schoenobaenus*), HVC volume is significantly correlated with syllable repertoires recorded in individuals singing on their territories.<sup>12</sup> Thus, as Nottebohm observed in the early 1980s, learning literally requires brain space, and more learning requires more space. Together, these data suggest that learning makes use of the amount of substrate that is available, not that learning induces measurable changes in the overall volume of HVC.

These correlations should be viewed cautiously on the anatomical side. Clearly, volume is only an estimate of features like number of neurons or amount of neuropil that are in fact directly related to function. Furthermore, HVC by itself does not learn or produce a song. It is part of sensory and motor circuits that contain many brain regions, and it is the connectivity and interactions between these components that determines outcome. Indeed, in the study relating zebra finch song and song system anatomy, we found that the volumes of Area X and l-MAN also predict repertoire size. Interestingly, reduced size in Area X was associated with a larger repertoire. A statistical model in which HVC volume was a positive factor and Area X volume a



**FIGURE 1.** HVC is substantially larger in a marsh warbler (A) (which sings a large repertoire) than in a closely related grasshopper warbler (which sings a very small repertoire).



**FIGURE 2.** Across eight closely related warbler species, contrasts in the relative volume of HVC are positively correlated with contrasts in syllable repertoire, once degree of relatedness is factored out.<sup>6</sup>

negative factor accounted for nearly 90% of the variance in syllable repertoire.<sup>10</sup> A reanalysis of our comparative reed warbler data also indicates that including Area X volume together with HVC volume produces a stronger correlation with repertoire size. Across these species, as among the zebra finches, a smaller Area X is associated with a larger repertoire.<sup>13</sup> Perhaps Area X inhibits shifting from one motor pattern to another when the motor patterns of song are learned.

Correlations between song complexity and song system anatomy should be viewed cautiously on the behavioral side as well. It would be easy to conclude from these studies that a function of HVC is to encode vocal motor variety, permitting a male to learn and produce as many syllables as his HVC will accommodate. However, different aspects of song are correlated with each other, and our ability to readily measure one aspect like repertoire size does not mean that this is the factor that has been shaped by selection and learning. In our work on wild sedge warblers, we also measured song length and the number of unique syllables per song bout, and these values also were significantly related to HVC volume.<sup>12</sup> In our work with zebra finches, HVC volume was correlated with the length of song phrases as well as with the number of unique syllables.<sup>10</sup> Ultimately, resolving what the singer (and the song system) is designed to achieve may come from studying the receiver: if a male sings to a female, her reaction to songs may give the best indication of the song qualities that his song system is being optimized to produce.

In recent years, we have begun to look for cellular correlates of song learning, both in males in which the consequence of not learning is typically an inability to

produce a complex song, and in females in which it is still unclear whether song learning contributes to later song recognition and selection. In both sets of experiments, we have examined zebra finches that grew up with restrictions on their opportunity for song learning. We have chosen to do this by removing adult males from a colony before the chicks reached the sensitive period for song learning. While this eliminates some kinds of social interaction as well as exposure to stereotyped song, it seems the least disruptive means of depriving the young birds of song models.

Several components of the song system are affected by this treatment in male zebra finches. At 5 weeks, early in the sensitive period, neurons in I-MAN have elaborate dendrites with large numbers of dendritic spines. In normally reared birds, the number of spines per unit length decreases by more than 50% over the next two months.<sup>14</sup> However, rearing the birds in aviaries from which adult males have been removed, results in preserving high numbers of dendritic spines on these neurons, at least for an additional 3 weeks.<sup>15</sup> This is consistent with this rearing treatment prolonging the period during which song elements can still be learned from a tutor.<sup>16,17</sup> Perhaps large numbers of spines can reinforce many sorts of motor programs within RA, whereas practicing a particular song reinforces and preserves only a subset of these.

In adult birds, spine density in HVC is related to the complexity of an individual male's song. For example, adult male marsh wrens that had experienced 45 different song types and acquired songs with similar numbers of song types have higher spine densities on HVC neurons than do adult males that heard only five song types and formed a similarly simple song.<sup>18</sup> The two groups did not differ in spine density in RA. In zebra finches, removing adult males from the colony results in young males forming an abnormally simple "isolate" song. When mature, these males also have fewer dendritic spines on neurons in HVC than do normally reared males.<sup>19</sup> In contrast, sedge warblers raised with either complex or simple models for song do not differ in HVC spine density. However, in spite of the differences in rearing, these warblers also did not differ in the complexity of their adult song repertoires. Birds reared hearing a simple song appear to have improvised a repertoire at least as large as that of the birds reared with more complex song.<sup>20</sup> Thus, the density of spine synapses in HVC seems to be related to the complexity of the song that a bird produces, and not to the complexity of the songs that he had experienced. These data imply that song learning acts at the level of individual synapses in HVC, not noticeably at the level of region size or number of cells within a region. One of the implications of this is that a larger HVC can accommodate more of the synapses and temporal modules that might be needed for a complex repertoire than can a smaller HVC.

#### RELATIONS BETWEEN SONG AND THE SONG SYSTEM ACROSS FEMALES

Song is interactive. In many species, males sing to attract or maintain pair bonds with females. And in many species, females not only discriminate conspecific song from heterospecific song, they use song to discriminate between individual conspecific males. For example, female great reed warblers (*A. arundinaceus*) pair with and have extra-pair copulations with the males they encounter whose songs are most elaborate.<sup>21,22</sup> In such lineages, males will have experienced a selective advantage if

they have been able to produce the sort of song that is most exciting to females. Motor processing within males can only really be understood in the context of female perception. More precisely, variation in the content of a male's song is only meaningful to the extent that it can be perceived by females. However, much less is known about how females perceive song than about how males produce it. A huge advance in studying the problem of perception has come with the discovery of novel brain areas that are activated similarly in both sexes by song perception.<sup>23–25</sup> In one of these areas, NCM, different song syllables evoke distinct patterns of immediate early gene activation,<sup>26</sup> consistent with NCM being involved in song discrimination.

Preliminary data from several experiments suggest that relations between the anatomy of NCM and aspects of song perception in females are parallel to the brain-behavior relations described above for males. We have presented conspecific song to female African Marsh (*A. baeticatus*) and Cape Reed (*A. gracilirostris*) warblers, two species of reed warblers from southern Africa. While closely related and similar in appearance, habitat, and diet, the two species differ widely in the structure of male song. After returning from migration, male African Marsh warblers sing prolonged elaborate songs with scores of different syllables, while trying to establish a territory and attract a female. In contrast, Cape Reed males have prolonged pair bonds and territories and sing a much less elaborate song, in which variety comes more slowly. Hearing conspecific song evokes much higher levels of expression of ZENK protein in NCM in the African Marsh females than in the Cape Reed females. Thus females of the species that customarily listens to a more complex repertoire and must respond to it quickly show a greater amount of activation than females of the species that normally listens to a less complex repertoire.<sup>27</sup>

Initial observation in zebra finches indicates that learning contributes to a female's ability to discriminate between male songs. Normally reared females readily choose to approach normal song over isolate song. However, females raised in colonies without adult males (i.e., without exposure to song) are as likely to choose the isolate as the normal song.<sup>28</sup> Such females have fewer dendritic spines on neurons in NCM than do normally reared females.<sup>19</sup> Perhaps females learn about song by modifying synapses within a brain region that will be activated by song perception when they are adult.

#### RELATIONS BETWEEN SONG AND THE SONG SYSTEM OVER GENERATIONS

The song system is present throughout the oscine phylogeny (the "songbirds") but not present in their closest relatives, the suboscines. Thus the nuclei and their interrelations develop in response to genetic instructions that differ from those present in the suboscines. Similarly, genetic differences must underlie the major differences in neural representation of the song system between families of oscines—the structures are relatively large throughout the Muscicapidae and quite small throughout the Paridae. As indicated above and elsewhere in this volume, females in many oscine species use song features in selecting mates. In *Acrocephalus* species, females appear to select males whose songs have many syllables (or other song features highly correlated with syllable number), a trait that usually is enhanced by learning. Over many generations, sexual selection like this can lead to increased expression of the

trait in the species and so shape evolution, but only if the selected trait is heritable. Or more specifically, capacity for learning should increase over evolutionary time if females select males with high levels of a heritable trait that depends on learning. While these theories have been developed over several decades, until recently, few experimental data have been available for assessing them.

The volumes of the nuclei comprising the song system vary between individual males. We have studied this variation in zebra finch families.<sup>29</sup> Two findings stand out. First, within individuals, variation in the volume of a song system nucleus is significantly correlated with variation in the volumes of the nuclei to which that nucleus is monosynaptically connected, as well as with the volume of the telencephalon as a whole. Thus, if an individual has a large HVC, he will tend to have a large RA and Area X as well as a relatively large telencephalon. Second, variation in the volumes of the caudal song system nuclei HVC, RA, and nXII is strongly heritable, whereas variation in the volumes of the rostral nuclei is only weakly heritable. Thus, fathers with a large HVC are likely to have sons with a large HVC.

These relations indicate that genetic variation contributes to individual differences in volumes of song system nuclei. Sexual selection for a complex song is likely to select for these genes, resulting in an increase in their representation and probably their effect as well. In evolutionary theory, sexual selection usually is associated with a benefit to the female's reproductive fitness, either related to a direct quality of the male, or an indirect feature that will be of benefit to the progeny. What could song tell a female about a male? Theories include information about his health, his age, his social experience, and his condition. To these, we can now add another. Elaborate song could tell a female that the male has a large HVC and so is likely to have a large telencephalon. It could also tell her that these traits are likely to be passed on to their sons.

Taken together, our findings suggest that if you want to increase the capacity for vocal learning in a species, you have to increase the volume of song system nuclei, especially HVC. If you increase the size of HVC, it is likely that RA and Area X will increase in size as well. However, our data suggest that increased volume in Area X is negatively correlated with song complexity, perhaps due to inhibition or gating motor programs encoded in HVC and RA. In a sense, this constraint against easy modification of the song system could keep a male honest—his song reflects qualities of his song system and his brain, and he cannot change the song without changes in his song system and, ultimately, more widely in his brain.

Our data on females suggest that the female side of the story may be just as interesting as that of the male, both in terms of perception and discrimination, and in terms of the evolutionary course that has given her these capacities. While much less is known of female abilities than of male abilities, it is likely that females have neural circuits dedicated to song perception. Neurons in these circuits are plastic and their anatomy is affected by auditory experience. This experiential tuning of perception then enhances the female's ability for fine discrimination. We do not know if this circuitry and the female's capacity for tuning and for complex discrimination differ between individuals. Data from our lab and others indicate that these features differ between species, which would suggest that they are genetically specified and may be subject to selective pressures as song production has been in males.

The identity of the bird is central to understanding the neurobiology of the song system. A zebra finch is not a prototypic songbird. Males and females have different

evolutionary goals in their use of song, and have neural circuitry likely to emphasize production and perception, respectively. In fact, different individuals of the same sex have differences in the neurobiology of their song systems that are reflected in individual differences in the amount or quality of song learning that is possible. Such differences are not annoyances in the path to a clear description of how the system works. Rather, they are the results of a grand evolutionary experiment, and provide an opportunity to understand the ultimate function of the song system as well as how it has been optimized for diverse goals across species, between sexes, and from one individual to another.

### ACKNOWLEDGMENTS

Supported by National Science Foundation—Division of Integrative Biology and Neuroscience (grant 0090963). Thanks to Zach Buchan, Michelle Tomaszewski, and Jordan Moore for suggestions and comments.

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