Daniel Margoliash[a]
Eric S. Fortune[a]
Mitchell L. Sutter[b]
Albert C. Yu[c]
B. David Wren-Hardin[c]
A. Dave[a]

[a] Department of Organismal Biology and Anatomy, The University of Chicago, Chicago, Ill.;
[b] Center for Neuroscience, University of California, Davis, Calif.;
[c] Committee on Neurobiology, The University of Chicago, Chicago, Ill., USA

Distributed Representation in the Song System of Oscines: Evolutionary Implications and Functional Consequences

Key Words

Hierarchical
Parallel
Distributed
Redundant
Sensorimotor integration
Forebrain evolution
Bird song system

Abstract

This paper reviews the organizational principles and implications that have emerged from the analysis of HVc, a forebrain nucleus that is a major site of sensory, motor, and sensorimotor integration in the song control system of oscine passerine birds (songbirds). Anatomical, physiological, and behavioral data support the conclusion that HVc exists within a hierarchically organized system with parallel pathways that converge onto HVc. The organization of HVc is distributed and redundant, and its outputs exhibit broad divergence. A similar pattern of connectivity exists for neostriatum adjacent to HVc. This and other data support the hypothesis that the song system arose from an elaboration or duplication of pathways generally present in all birds. Spontaneous and auditory response activity is strongly correlated throughout HVc, with auditory responses exhibiting strong temporal modulation in a synchronized fashion throughout the nucleus. This suggests that the auditory representation of song is encoded in the synchronized temporal patterns of activation, and that the predominant selectivity for the individual's own song that is observed for HVc neurons results from interactions of auditory input with central pattern generators for song. Most, or all HVc neurons are recruited during singing. The auditory response and motor recruitment properties of individual HVc neurons have no simple relationship, and the spontaneous activity in HVc may build up in the seconds preceding a song. To the extent HVc participates in perceptual phenomena associated with song, production and perception are not tightly linked in adults but may be linked by shared developmental processes during periods of sensorimotor learning.

Dr. Daniel Margoliash
Department of Organismal Biology and Anatomy
The University of Chicago
1025 E. 57th St.
Chicago, IL 60627 (USA)

A	Archistriatum
Am	Nucleus ambiguus
AS	'Autogenous' song
cDLP	Nucleus dorsolateralis posterior thalami pars caudalis
CPGs	Central pattern generators
DIP	Nucleus dorsointermedius posterior thalami
DLM	Nucleus dorsolateralis anterior thalami, pars medialis
DLP	Nucleus dorsolateralis posterior thalami
DM	Dorsomedial subdivision of nucleus intercollicularis
DMP	Nucleus dorsomedialis posterior thalami
HV	Hyperstriatum ventrale
lMAN	Lateral magnocellular nucleus of the anterior neostriatum
mMAN	Medial magnocellular nucleus of the anterior neostriatum
N	Neostriatum
NC	Neostriatum caudale
NCM	Caudomedial neostriatum
Nd	Dorsal caudal neostriatum
NI	Neostriatum intermedium
NIDL	Neostriatum intermedium pars dorsolateralis
NIf	Nucleus interfacialis
NIVL	Neostriatum intermedium pars ventrolateralis
nXIIts	Nucleus nervi hypoglossi, tracheosyringeal component
OM	Tractus occipitomesencephalicus
Ov	Nucleus ovoidalis
RA	Nucleus robustus archistriatalis
RAm	Nucleus retroambigualis
SMS	Syllable of maximum synchronization
TCS	Temporal combination sensitive
TMS	Time of maximal synchronization
Uva	Nucleus uvaeformis
WTS	White-throated sparrows
X	Area X

Introduction

The richness of behavioral phenomena associated with song learning, production, and perception in oscine passerine birds [see Kroodsma and Miller, 1982] is supported by a richness of neurobiological complexity of the song control system. Although the analysis of song system circuitry at the cellular level is incomplete, for some nuclei there is now sufficient information to begin to relate neuronal struc-

[1] The HVc is a nucleus originally identified as ventral caudal hyperstriatum [Nottebohm et al., 1976] but is now thought to be in the dorsal caudal neostriatum [Nottebohm, 1987]. The suggested revision 'High (or Higher) Vocal Center' (HVC) retains the acronym for consistency with the substantial quantity of previous literature but is inadequate because it has funcitonal implications, and because it does not describe the position, shape, or size of the nucleus or its cellular constituents. We propose adopting the acronym as the proper name. This is not inconsistent with old terminology (e.g. field L) nor with some new terminology (e.g. area X).

ture with neuronal function. In particular, the nucleus HVc[1] is a major site of integration in the song system where sensorimotor transformations related to syllable and song structure probably occur. This paper will review recent data demonstrating a distributed, time-domain representation for song in HVc, including anatomical observations, physiological recordings in anesthetized preparations, and physiological recordings and lesion studies in singing birds. The analysis of HVc's anatomy and physiology has yielded insights into the organization of episodic behaviors, auditory temporal pattern processing, sensorimotor integration, and the relationship between production and perception of song. Additionally, we reinterpret the forebrain circuitry in and around HVc from an evolutionary perspective, concluding that the caudal forebrain components of the song system are an elaboration of a system which was probably present in ancestral forms.

HVc within the Context of the Song Control System

The motor system for song production comprises discrete forebrain, midbrain, and brainstem nuclei that subserve a limited set of discrete episodic behaviors (songs and calls) (fig. 1). The HVc is a major site of integration within the song system and participates in the two major song system forebrain pathways. One forebrain pathway includes nucleus interface (NIf), HVc, and the robust nucleus of the archistriatum (RA) in the caudal telencephalon and the caudal subdivision of the posterior thalamic nucleus (cDLP) in the thalamus – previously called nucleus uvaeformis (Uva); see below and Wild [1993a] – and ultimately projects to the brainstem hypoglossal nucleus, which innervates the syrinx, the vocal organ in birds. Lesion and chronic recording experiments demonstrate that these nuclei are involved in moment-to-moment control of song production [Nottebohm et al., 1976, 1982; McCasland, 1987; Williams and Vicario, 1993]. A second, more rostral pathway involves projections between HVc, area X (X), the lateral magnocellular nucleus of the anterior neostriatum (lMAN), and RA in the telencephalon and the medial division of the dorsolateral thalamic nucleus (DLM) in the thalamus. Lesion studies demonstrate X, lMAN, and DLM are not necessary for song maintenance in adult birds, but they implicate these nuclei in juvenile song development [Bottjer et al., 1984; Scharff and Nottebohm, 1991; Sohrabji et al., 1990]. Lesions of the rostral pathway may also result in song degradation in open-ended learners, such as canaries *(Serinus canarius)*, during seasonal periods of adult song development [Nottebohm et al., 1990], or in other species during experimentally induced periods of adult song plasticity [Morrison and Nottebohm, 1993].

Fig. 1. Schematic of the song system. Arrows indicate the direction of major projections. Subdivisions of nuclei (esp. Ov, Field L, and RA) are not represented. The projection of RA onto DLM [Wild, 1993b] is difficult to confirm with retrograde tracers. Note HVc is the major site of convergence, and RA is the major output structure [see also Wild, 1994].
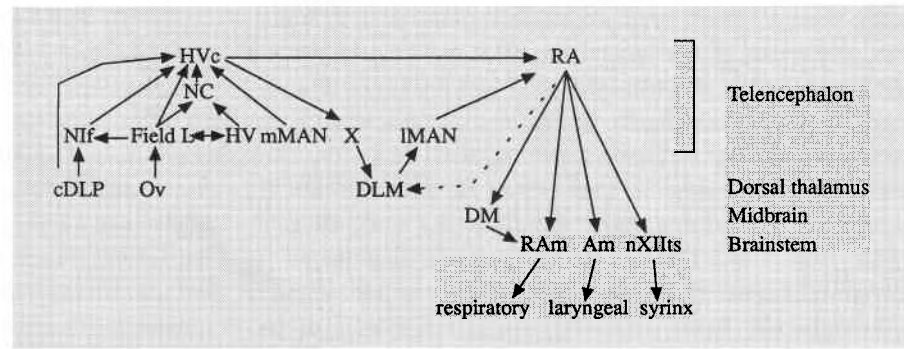
The unidirectional, and mostly unilateral connectivity of song system nuclei supports a hierarchical organization scheme, within which HVc has a special position. HVc is the major site of convergence in the telencephalon, and it gives rise to two efferent routes to RA, the major telencephalic output structure (fig. 1). One efferent pathway is the direct projection of HVc caudally and ventrally onto RA [Nottebohm et al., 1976]; the second pathway is the indirect projection to RA via the rostral pathway, HVc→area X→DLM→lMAN→RA [Nottebohm et al., 1976, 1982; Okuhata and Saito, 1987; Bottjer et al., 1989]. The indirect pathway has also been called 'recursive' [Williams, 1989; Nottebohm, 1991], however multiple but separate routes from the same source (HVc) to the same target (RA) does not constitute a feedback system. More recently Wild [1993b] presented preliminary evidence that RA may project to DLM, which would provide an anatomical substrate for possible feedback pathways within the forebrain, if not the highly specific form of feedback implied by recursion. The reinterpretation of nucleus Uva as homologous to the caudal division of DLP in non-oscines highlights a source of multimodal input to the song system, potentially including proprioceptive feedback [Okuhata and Nottebohm, 1992]. Multimodal activity in cDLP, which projects to HVc, may also help to explain visual flash evoked responses recorded in HVc [Bischof and Engelage, 1985].

Physiological and behavioral evidence also suggest that HVc acts as a major integrative site for sensory, motor, and sensorimotor processing in the song system. The auditory response properties of HVc develop during the sensorimotor phase of song learning [Volman, 1993], and it has been hypothesized that HVc neurons are actively involved during development in shaping the motor program for song via auditory feedback [Margoliash, 1987]. In adults, auditory neurons in HVc are selective for the individual bird's own song, exhibiting stronger responses to playback of own song than to conspecific songs [see Margoliash, 1987]. Such response selectivity implies hierarchical organization and a high degree of convergence, organizational principles generally observed in auditory systems [e.g. Konishi, 1991; Carr, 1992]. Furthermore, HVc is a nexus for auditory input to the song system: lesions of HVc abolish auditory song selectivity otherwise seen in both of HVc's efferent targets, area X and RA [Doupe and Konishi, 1991; Vicario and Yohay, 1993]. The concept of a hierarchical organization in the song system is also supported by motor properties of HVc. In zebra finches (*Taeniopygia guttata*), HVc stimulation during singing causes a re-setting of the pattern of song syllables, whereas stimulation in RA affects only the acoustic structure of the syllable being produced [Vu et al., 1993]. On average, there is a sequential recruitment of nuclei at the onset of singing, with earliest recruitment of the NIf neurons, followed in order by HVc, RA, and the tracheosyringeal subdivision of the hypoglossal nucleus (nXIIts) [McCasland, 1987]. This temporal order follows the caudal pathway's connectivity.

Multiple Pathways through HVc: Convergence and Divergence

We were interested in characterizing the anatomical organization of auditory input to HVc because it is an essential component for an understanding of the physiological properties of HVc. Neither field L, which was the presumptive source of auditory input to HVc, nor HVc itself, had been defined in cytoarchitectonic terms. Technically, such definitions are needed to determine the extent of tracer injections and the resulting patterns of labelling. Also, in the absence of such cytoarchitectonic definitions numerous authors have adopted a variety of definitions for field L and HVc, which has led to some confusion concerning bound-

aries, nomenclature, structure, and afferents of these nuclei. We attempted to resolve these issues in the zebra finch [Fortune and Margoliash, 1992, 1994, unpubl. observ.].

Field L is the primary thalamorecipient telencephalic auditory structure in birds, receiving input from ovoidalis and surrounding areas [Karten, 1968; Bonke et al., 1979a; Kelley and Nottebohm, 1979; Brauth et al., 1987; Häusler, 1988; Bell et al., 1989; Wild et al., 1990; Durand et al., 1992; Wild et al., 1993]. In oscines, we showed that field L is a complex of 4 or 5 subdivisions – L1, L2a, L2b, L3 and L, with the distinction between L2b and L uncertain [Fortune and Margoliash, 1992]. These subdivisions wrap around and insert into each other in a complex, three-dimensional organization. They can be differentiated by the morphology of Nissl stained cells and arrangement of cell clusters. Four types of Golgi-stained neurons occur in field L in the zebra finch and correspond to those described for the European starling *(Sturnus vulgaris)* [Saini and Leppelsack, 1981]. Types 1 and 2 neurons, which are the largest neurons in field L, are the major projection neurons.

We also showed that male HVc has 3 cytoarchitectonic regions, a ventral caudomedial region with densely packed small and medium-sized cells, a dorsolateral region with large oriented oblong or ovoid cells and cell clusters arranged into rows, and the commonly recognized central region with large, darkly staining cells and cell clusters [Fortune and Margoliash, 1994, unpubl. observ.]. The oriented cell region had not been previously described. All 3 regions of HVc in males project to area X and to RA, although the ratio of X-projecting to RA-projecting cells may vary across regions. Interestingly, all major cytoarchitectonic features of HVc's subdivisions may result from the action of hormones early in life: a female treated with hormones early in life (generously donated by M. Konishi) had all 3 subdivisions, whereas HVc in untreated females cannot be subdivided and is distinct from all the male subdivisions.

Originally, it was thought that field L projected to the 'shelf' ventral to HVc and that an area rostral and lateral to field L projected directly into HVc [Kelley and Nottebohm, 1979]. That report, however, was based on an incomplete cytoarchitectonic definition of field L – including L2a but probably excluding L1 and L3. Subsequently, the projection of NIf onto HVc was discovered [Nottebohm et al., 1982]. Since NIf is apposed to L1 and L2a, Nottebohm et al. [1982] postulated that the direct projections into HVc from rostrolateral field L described by Kelley and Nottebohm [1979] were the projections of NIf and not of field L. Thus, a direct connection between the auditory telencephalon and the song system had not been established.

Afferents of HVc

Our recent experiments using fluorescent and biotinylated dextrans injected into HVc have demonstrated a direct projection of field L into HVc, as well as other connections [Fortune and Margoliash, 1994]. All projections were confirmed with anterograde injections, although in some cases fibers-of-passage prevented final confirmation. Since structures ventral to HVc also receive inputs from field L (see below), it was necessary to make some small tracer injections that were confined to HVc. Injection sites that appeared to be restricted to HVc labeled axons within RA; injections that appeared to encroach upon the neostriatum ventral to HVc labeled axons around as well as within RA. This finding will be returned to later. We used the distribution of axons around RA as a second criteria for determining the extent of an injection site for our retrograde experiments.

Field L. Injections of biotinylated dextrans restricted to HVc labeled cells in subdivisions L1 and L3. Those cells that filled well enough to be classified were either type 1 or type 2 as defined in Golgi material [Fortune and Margoliash, 1992]. There was no apparent topography of labeled cells within L1 or L3. Labeled cells were distributed throughout L1 and L3, but more cells were labeled in L1 than in L3 in all cases. Injections of biotinylated dextrans restricted to HVc retrogradely labeled small numbers of cells in the field L complex (< 100), whereas injections of fluorescent dextrans restricted to HVc labeled somewhat more (> 100). Since field L is tonotopically organized (see below), the sparse labeling throughout L1 and L3 subdivisions implies that there is broad convergence of frequency information onto HVc. We found several types of Golgi-impregnated axons within HVc that have broad arborizations, but none that have small, dense spatially-restricted arborizations as would be expected in a topographically organized projection. This suggests that inputs to HVc project broadly throughout HVc.

Nucleus interfacialis. The NIf, which is apposed to L2a and L1 near the lateral edge of the field L complex, is a cytoarchitectonically distinct nucleus that projects to HVc [Nottebohm et al., 1982]. Restricted dextran injections of HVc densely labeled cells throughout NIf [Fortune and Margoliash, 1994]. The projection of NIf onto HVc also did not appear to be topographic. Small injections into HVc labeled fewer cells in NIf than did larger injections, but in all cases labeled cells were seen throughout NIf with a scattered distribution.

Most of the labeled cells in NIf had the morphological characteristics of type 5 cells as seen in Golgi material [Fortune and Margoliash, 1992], which have dendrites re-

stricted to NIf, but HVc injections also labeled cells along the rostral border of NIf that had extensive dendritic arborizations extending into adjacent L1. Such NIf cells had fusiform somata, not oblong as is typical for type 5 neurons. These cells may represent a separate morphological type of NIf neuron that receives auditory input from L1 and projects to HVc. Thus, L1 may modulate HVc activity indirectly through NIf.

Neostriatum Ventral to HVc. Caudal to field L and the ectostriatum there is a large, poorly characterized region known as the caudal neostriatum (NC). Various names have been applied to potentially overlapping parts of this region, including Nd (dorsal neostriatum) and NCM (caudomedial neostriatum). This area includes neostriatum ventral to HVc, and also includes the 'shelf', which we consider separately (see below). Ventrally located HVc neurons commonly have dendrites that extend outside of HVc, in some cases for hundreds of microns. Thus, axons synapsing near to but not within HVc may be potential sources of input to HVc. The neostriatum caudal to the field L complex and ventral to HVc is auditory [Scheich et al., 1979; Katz and Gurney, 1981; Müller and Leppelsack, 1985; Stripling et al., 1994; Margoliash, unpubl. observ.], and may form yet another pathway for auditory input into HVc.

Injections restricted to neostriatum ventral to HVc are difficult to interpret, because with the standard dorsal approach the pipette passes through HVc, and because the injection will interrupt fibers projecting to/from HVc. In our studies, we compared the pattern of labeling of injections restricted to HVc with the pattern of labeling of injections that encroached ventrally beyond HVc. We confirmed each putative projection with an injection of complementary (anterograde or retrograde) tracer into the putative projection target. The data support the conclusion that L1 and L3 of the field L complex project onto neostriatum ventral to HVc [Fortune and Margoliash, 1994]. This confirms Kelley and Nottebohm's [1979] result, although labeling is not restricted to the shelf (see below). Neostriatum ventral to HVc also receives inputs from the ventral hyperstriatum (HV), which is reciprocally connected with field L. Field L input to HV is primarily from L1 and L3 [Fortune and Margoliash, 1994], and HV projections terminate primarily within L2a [Bonke et al., 1979a; Wild et al., 1993]. The ventral hyperstriatum is auditory [Heil and Scheich, 1991; Müller and Leppelsack, 1985; Margoliash, 1986], thus neostriatum ventral to HVc may receive auditory input from field L directly and indirectly from HV. There are several parallel pathways, therefore, whereby field L may influence HVc.

Additionally, tracer injections centered in caudal HV retrogradely labeled cells in a shelf region that surrounds Uva [Fortune and Margoliash, 1994]. If Uva is homologous to caudal DLP of non-oscine species (see below), then the area surrounding Uva that projects to HV may represent a separate subdivision of DLP. We did not determine the positions and possible overlap of the regions of HV that receive from the area surrounding Uva, that are reciprocally connected with field L, and that project immediately ventral to HVc. All 3, however, are in caudal HV.

The Shelf. Some controversy surrounds the definition of the structure immediately ventral to HVc, the 'shelf'. The shelf was originally described as an area medial and posterior to ventral HVc, based on patterns of anterograde labeling in autoradiographs after injection of tritiated amino acids into field L of canaries [Kelley and Nottebohm, 1979]. The shelf as described by cytoarchitecture, however, is distinct along the lateral and anterior borders of ventral HVc but fades out medially and posteriorly [Fortune and Margoliash, 1994, unpubl. observ.]. That is, the pattern of labeling described by Kelley and Nottebohm [1979] is not co-extensive with the fiber-rich area just ventral to HVc. It is not uncommon in the literature to find the cytoarchitectonic and hodological definitions of the shelf used interchangeably.

There is also some question as to whether the shelf projects to HVc. In our restricted dextran injections of HVc, we did not label any neurons in the shelf, though we routinely labeled more distant cells in field L, NIf, Uva and the medial magnocellular nucleus of the anterior neostriatum (mMAN). The severe fibers-of-passage problem around HVc and apposition of the shelf to HVc make it particularly difficult to assess this putative projection with anterograde labeling from extracellular injections restricted to the shelf. Unfortunately, the intracellular data are also unclear. In vivo intracellular labeling showed that the axons of shelf neurons ramify within HVc [Katz and Gurney, 1981], but subsequent experiments using living brain slices, which permit direct visual guidance of the electrode, showed that axonal arborizations of shelf neurons avoid HVc [L. Katz, reported in Margoliash, 1987].

Intrinsic Connections and Outputs

Any injection site that impinged on any of the 3 regions of HVc labeled cells in all 3 regions of HVc. We probably labeled cells via their intrinsic projections because they are by far a larger component of axons within HVc than are HVc's extrinsic projections. In each case there were differences in the distribution of labeled cells in HVc, and there was no consistent topographical pattern across cases. In all cases, axons were also extensively labeled throughout HVc [see also Katz and Gurney, 1981]. This web of connections

could support considerable communication between all parts of HVc.

Injections of anterograde tracers into HVc demonstrated that the outputs of HVc exhibit massive divergence. Axons of HVc neurons ramify extensively throughout their target sites, either X or RA [Fortune and Margoliash, 1994; Bottjer et al., 1989]. Single axons from HVc extend over large parts of area X, giving rise to sparse terminations throughout. Single HVc axons appear to ramify extensively once they reach RA, although the extent of the arbors is difficult to estimate because even small extracellular injections labeled numerous axons. The projections of HVc onto area X and RA did not appear to be topographic [Fortune and Margoliash, 1994]. In contrast, there is some evidence for a topographic projection of RA onto the hypoglossal nucleus [Vicario, 1991], and the hypoglossal nucleus has at least some degree of myotopic organization |Vicario and Nottebohm, 1988]. This suggests that single HVc axons generally contribute to activation of all syringeal muscles. These data are consistent with a hierarchical scheme of organization of the motor system for song.

Summary

In summary, we find a massive convergence of inputs onto HVc, with multiple parallel pathways including the field L complex, NIf, cDLP, neostriatum ventral to HVc, and intrinsic HVc. Each of these projections may be sources of auditory input to HVc, and none of these inputs appear to be topographically organized. Additionally, the field L projection involves at least 2 subdivisions and 2 cell types from each subdivision, and there is evidence for 2 cell types in NIf that project onto HVc. These data support separate lines of inquiry, one regarding the functional implications of the convergence/divergence of information flow through HVc, a second regarding the evolutionary origins of this pattern of connections. We will address the second question first.

Interspecific Comparisons: Evolution of the Song System

Our recent anatomical studies give some insight into the evolution of the song system. There is compelling evidence that vocal learning has evolved independently at least three times, in the oscines, psittacines, and in some of the hummingbirds [Nottebohm, 1972]. This implies the song system arose as an independent adaptation of oscine passerine birds. All oscines apparently have a song system [e.g. DeVoogd et al., 1993], including area X, HVc, lMAN, mMAN, NIf, and RA in the forebrain. (The distinction between the medial and lateral aspects of MAN may not be present in all songbirds.) This set of cytoarchitectonically distinct forebrain nuclei has been recognized only in the oscines, and similar nuclei are not readily visible in suboscine brains [Nottebohm, 1980; Kroodsma and Konishi, 1991]. The relationship of song system nuclei to forebrain structures in non-oscine birds is not well understood.

Parrots and allies, the other extensively-studied example of vocal learning [see also Baptista and Schuchmann, 1990], also have cytoarchitectonically distinct forebrain nuclei related to vocal production. Originally, it was concluded that the similarity in the connections of analogous nuclei labeled 'HVc' and 'RA' [Paton et al., 1981] implied a similar evolutionary origin for the forebrain structures involved in vocal control in psittacines and oscines. This view has been recently challenged by an analysis of the budgerigar *(Melopsittacus undulatus)* vocal control system, which showed that many details of budgerigar forebrain connections were different than those in oscines [Striedter, 1994]. For example, 'HVc' and 'RA' of the budgerigar do not receive direct or indirect input from field L [Hall et al., 1993; Striedter, 1994]. These significant differences between the vocal control system in songbirds and the budgerigar has motivated a change in the nomenclature of the budgerigar forebrain nuclei away from the implied homology [Striedter, 1994]. Some elements of the budgerigar telencephalic system involved in vocal control may be independent adaptations of non-homologous pathways, while others may be independent adaptations of homologous pathways also used for vocal control by oscines.

In our own studies, we noted that injections of HVc that included neostriatum ventral to HVc anterogradely labeled an area surrounding RA [Fortune and Margoliash, 1994]. Injections of X (possibly also involving tissue surrounding X) retrogradely labeled cells in neostriatum ventral to HVc as well as in HVc proper. Thus, the outputs of one or more areas immediately ventral to HVc are parallel to the outputs of HVc itself. Moreover, we established that field L projects both to HVc and areas ventral to HVc. The similarity of connections of HVc and neostriatum adjacent to HVc raises the possibility that HVc arose as an elaboration or duplication of an ancestral structure in the caudal neostriatum that is common to birds.

Forebrain

The song system follows the general pattern of reptile-bird forebrain organization [Ulinski and Margoliash, 1990] and the general architecture for the flow of sensory information in the forebrain of birds. Figure 2 shows this pattern
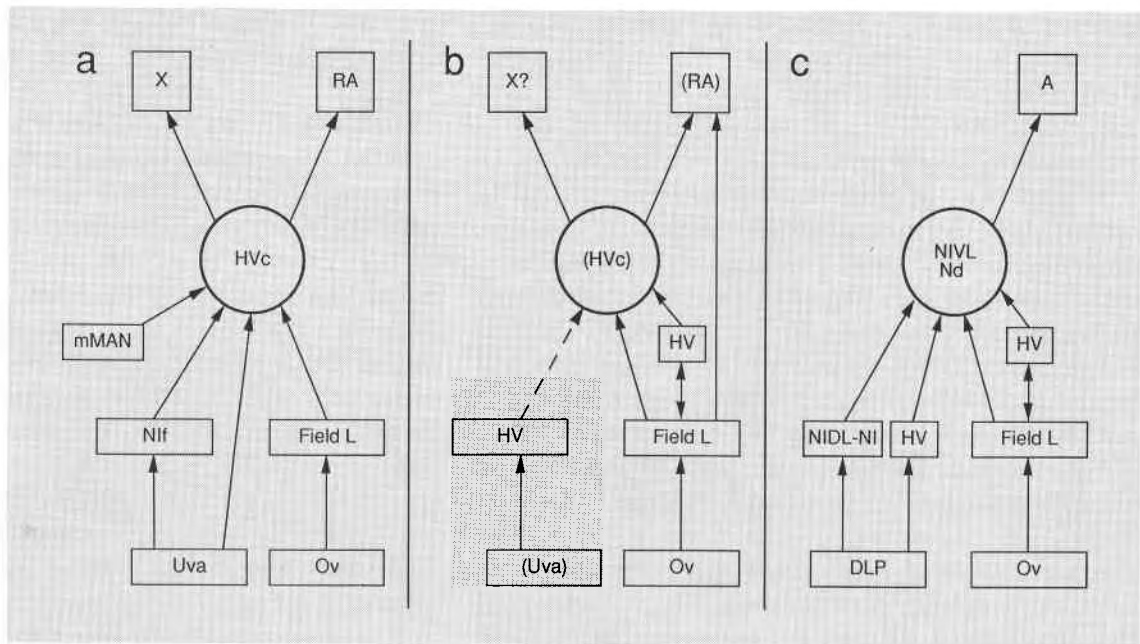
Fig. 2. Comparison of the connectivity of HVc (**a**), NC adjacent to HVc (**b**), and Nd/NIVL (**c**) in non-songbird species. **a** Afferents and efferents of HVc as demonstrated in the zebra finch. **b** Afferents and efferents of NC adjacent to HVc [see Fortune and Margoliash, 1994]. Parentheses indicate a region adjacent to a structure. The dotted line indicates that the (Uva) recipient area of HV may not be equivalent to the area of HV that projects to (HVc). **c** Connectivity of Nd/NIVL as demonstrated in non-songbird species (see text). The terms NIVL and NIDL are used exclusively in budgerigars.

for the auditory system by summarizing our recent results and those from previous studies of the ascending auditory pathways of non-songbirds. This general architecture begins with a projection of a dorsal thalamic sensory nucleus onto a structure between the intermediate and caudal neostriatum. This connection in the auditory system is the projection of nucleus ovoidalis (Ov) and associated areas onto the field L complex [Karten, 1968; Bonke et al., 1979a; Brauth et al., 1987; Durand et al., 1992], and in the visual system it is the projection of rotundus onto the ectostriatum [Karten and Hodos, 1970]. The somatosensory pathway is not as well described, though the emerging picture is that DLP, a multisensory nucleus [Korzeniewska and Güntürkün, 1990], projects onto a discrete area between the field L complex and the ectostriatum [Gamlin and Cohen, 1986].

The second projection in this general pathways is from the neostriatal structure onto the caudal neostriatum. Both the field L complex and the ectostriatal complex are known to project to the dorsal areas of the caudal or lateral neostriatum [Bonke et al., 1979a; Shimizu and Karten, 1991a]. The projections of the neostriatal somatosensory area are

not known. There is an overall topography, such that the efferents of the field L complex are medial to the efferents of the ectostriatum [Ulinski, 1982]. Topography within each of these projections has not been addressed, except the projection of field L onto HVc in zebra finches is non-topographic [Fortune and Margoliash, 1994].

The last projection in this general pathway is from the caudal neostriatum onto the archistriatum. In pigeons, the visual and auditory areas in the caudal neostriatum project onto the archistriatum [Shimizu and Karten, 1991a; Wild et al., 1993]. In the zebra finch, we have shown that the caudal neostriatum projects onto the archistriatum [Fortune and Margoliash, 1994].

The HVc, which resides in the caudal neostriatum, is situated in the middle of this topographical series of projections, apparently at the junction of all 3 sensory pathways. The visual projections from the ectostriatum are lateral to HVc, and auditory projections from the field L complex are medial and ventral to HVc. Since we expect the somatosensory projections to terminate between the visual and auditory projections, HVc may be near these inputs as well. In our laboratory, Mr. Peter Bell originally suggested that

nucleus Uva in zebra finches had similar position and efferents as did DLP (which is multisensory but primarily somatosensory) in other species.

Uva and DLP

We find that the morphology of cells in Uva, and the relationship of Uva to other dorsal thalamic nuclei, are similar in many respects to nucleus DLP in pigeons (Columba livia) [see also Wild, 1993a]. In pigeons, DLP projects onto the intermediate neostriatum [Kitt and Brauth, 1982; Gamlin and Cohen, 1986]. A reconstruction of figure 8A–D of Gamlin and Cohen [1986], which shows the projection area of DLP on the neostriatum, is similar in shape to NIf shown in figure 12 of Fortune and Margoliash [1992]. The area where DLP fibers terminate is also cytoarchitectonically distinct. The photomicrograph of the DLP projection area in pigeons (fig. 9A of Gamlin and Cohen [1986]) is similar to the appearance of NIf shown in figure 4E of Fortune and Margoliash [1992]. In addition, Gamlin and Cohen [1986] stated that injections of retrograde tracers into HV and more dorsal structures labeled a few cells in DLP. They did not describe the distribution of these cells, but the result is not dissimilar to that obtained from injections into HV of the zebra finch, where cells were labeled along the dorsal, caudal, and rostral edges of Uva.

Korzeniewska and Güntürkün [1990] showed that DLP in pigeons contains neurons that respond to somatosensory, visual, and auditory stimuli. If we assume that Uva is homologous to DLP, then this can help to explain auditory activity in Uva [Okuhata and Nottebohm, 1992]. The Uva could be a source of auditory input to HVc as well as the pathway for the visual responses in HVc described by Bischof and Engelage [1985].

We have been unable to determine the location of DLP in zebra finches. The position of DLP as shown in the Stokes et al. [1974] canary atlas is largely inconsistent with that shown in the pigeon atlas [Karten and Hodos, 1967]. In the canary atlas DLP is shown along the dorsal surface of the occipitomesencephalic tract (OM). In pigeons, DLP does not contact OM at all. Stokes et al. [1974] recognized this uncertainty – in their plate 21 DLP is shown in two locations, medial to OM and the dorsal intermediate posterior thalamic nucleus (DIP), and lateral to the dorsal medial posterior thalamic nucleus (DMP). In the pigeon atlas, DLP is lateral and caudal to DIP. In L3.00 of the pigeon atlas, there is a dark band which appears to be marked as DLP in the accompanying line drawing. This dark band is similar in appearance and position to Uva seen in zebra finches. Lastly, Wild [1993a] showed that the afferents of DLP and Uva are identical in several songbird and non-songbird species. Wild [1993a] concluded that Uva is homologous to the caudal subdivision of DLP (cDLP).

A Hypothesis for the Evolution of the Song System

Figure 2 shows a comparison of the pathways described in this report and those seen in previous reports, including those of Bonke et al. [1979a], Kelley and Nottebohm [1979], Brauth et al. [1987], and Brauth and McHale [1988]. The primary differences between the patterns seen in the zebra finch and those in other species are the projections of mMAN onto HVc, HVc onto area X, and field L onto a 'cup' surrounding RA. In other respects, however, the projections are similar. These similarities include the pathways from DLP through the neostriatum (N) to caudal neostriatum (NC), from Ov to NC through both the field L complex and HV, and the projections of dorsal NC and the field L complex onto the archistriatum (A). These pathways are parallel to those of the song system (fig. 2).

The song system itself is an autapomorphy of the oscine passerines [Kroodsma and Konishi, 1991], but the pathways that are parallel to the song system may be generally present in other species of birds (fig. 2). These data suggest the hypothesis that the song system of oscine passerines evolved from pathways that are plesiomorphic – specifically, that HVc and RA evolved as an elaboration or duplication of pathways that are common to birds [see also Brenowitz, 1991a]. For example, during evolution HVc may have arisen from a subdivision of caudal neostriatum that became cytoarchitectonically distinct with increased functional specialization, presumably associated with auditory-feedback mediated song learning.

The caudal neostriatum may generally exhibit integrative mechanisms involved in perceptual phenomena (for a related discussion, see Shimizu and Karten [1991b]). This is consistent with the general flow of sensory information in avian forebrains, in which NC receives input from primary sensory areas and in turn projects to archistriatum. Recent experiments support this hypothesis, implicating areas of NC other than HVc in conspecific song recognition in oscine birds [Mello et al., 1992]. In pigeons, the output of Nd, the part of NC that receives from L1 and L3, projects onto areas of the archistriatum that give rise to bilateral projections to areas surrounding thalamic and midbrain auditory structures [Wild et al., 1993]. This suggests the hypothesis that the ancestral caudal neostriatal structure that gave rise to HVc originally had an auditory function, and that part of the specialization involved acquiring projections to archistriatum involved in motor control.
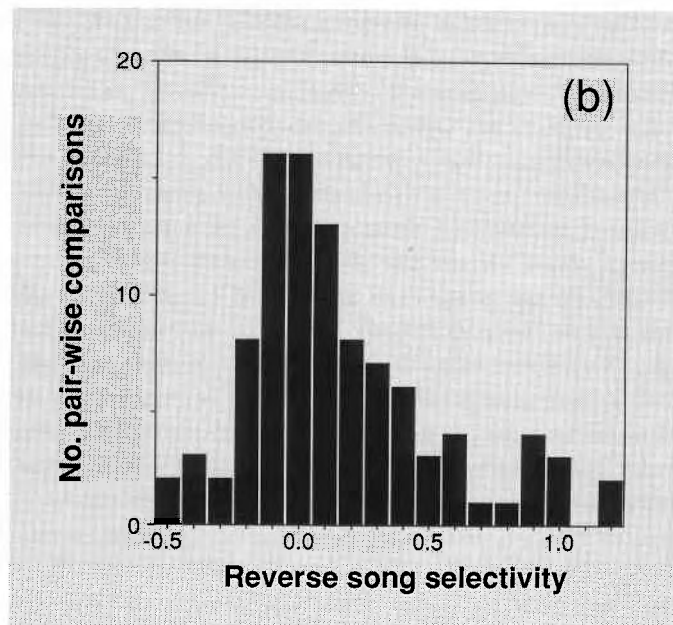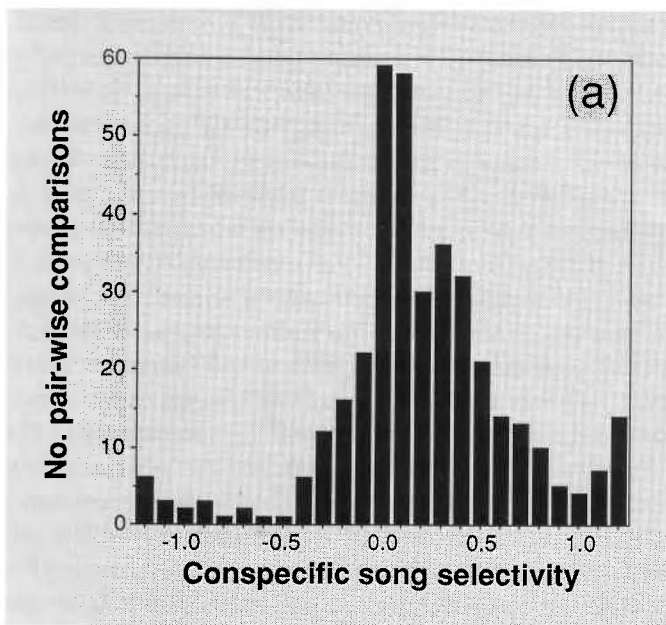
Fig. 3. Response selectivity of 329 zebra finch HVc single units recorded in 24 urethane-anesthetized birds. **a** One or more conspecific songs and the bird's own song (autogenous song – AS) were presented, resulting in 378 pair-wise comparisons. Response is defined as average spikes/s over an entire song minus spontaneous rate. Conspecific selectivity is the response to conspecific song/response to AS. For example, selectivity index = 1.0 implies same response to conspe- cific song and AS. Note that the average response to conspecific songs is close to the spontaneous rate (0.0); many conspecific songs elicit overall inhibition. **b** The response to forward and reversed AS was compared for 99 single units. Response is defined as in **a**. In almost all cases, forward song elicited a stronger response. For both **a** and **b**, extreme values are collapsed into the outermost bins of each graph. Songs were typically presented for 10 or 20 repetitions.

Selectivity for Autogenous Song: Distributed Representation within A Hierarchy

The unidirectional flow of information between most or all of the forebrain constituents of the song system, the position of HVc within those pathways, and the convergence and divergence of information flow through HVc suggests that HVc is relatively high within a sensory hierarchy and that information within HVc may be organized in a distributed fashion. The functional realization of these ideas is explored in the next three sections. First, auditory responses in HVc are compared with those in field L. In the second and third sections, auditory and motor data are presented that provide evidence for a distributed representation for song, and suggest that the distributed representation encodes song in the time domain.

Auditory Responses in HVc and in Field L

In several species the projection of ovoidalis onto field L has been shown to be topographic [Bonke et al., 1979a; Bigalke-Kunz et al., 1987; Brauth et al., 1987; Bell et al., 1989]. A tonotopic organization exists for field L, varying both with subdivision and species [Bonke et al., 1979b; Heil and Scheich, 1985, 1991; Müller and Leppelsack, 1985; Müller and Scheich, 1985; Rübsamen and Dörr-scheidt, 1986; Lim, 1993]. In general, L2a neurons have high spontaneous rates and robust responses to tone bursts, whereas neurons in L1 and L3 have lower spontaneous rates and, in some cases, weak responses to tone bursts [e.g. Bonke et al., 1979b; Scheich et al., 1979]. Neurons of L1 and L3 also tend to exhibit greater selectivity for species-specific vocalizations [Leppelsack and Vogt, 1976; Scheich et al., 1979; Leppelsack, 1983; Mori and Striedter, 1992], which may be based in part on broad tuning curves, requirements for several spectral peaks, or temporal requirements. Thus, the field L input to HVc is likely to exhibit some specialization for complex, species-specific sounds, although the physiology of the neurons that project to HVc has not been explicitly described.

In contrast, there is no evidence of tonotopic organization in HVc [Margoliash, 1987]. The HVc neurons tend to respond poorly to tone bursts (see below) but are selective for the individual bird's 'autogenous' song (AS) [Margoliash, 1986; Margoliash and Konishi, 1985], a property that

results from tuning to parameters of AS [Margoliash, 1983, 1986; Margoliash and Fortune, 1992]. In a recent analysis, 329 single units in the HVc of 24 urethane-anesthetized zebra finches were tested with AS, conspecific songs, tone and noise bursts, and other stimuli [D. Margoliash and E.S. Fortune, unpubl. observ.]. (The combination sensitive properties of a subset of these cells has been previously reported, where details of the experimental procedures are described; see Margoliash and Fortune [1992].) The responses to conspecific songs were almost always weaker than the responses to AS (fig. 3a). The responses to tone bursts were also generally quite weak. For only 13 of 69 neurons was the peak response (30 ms bin) to any tone burst stronger than the peak response to AS. (Since tone bursts are much shorter duration than songs, peak rates are a more meaningful comparison than average rates.) If anything, the actual distribution is even more skewed, since tone burst tuning is not rewarding in HVc and was not always attempted for weakly responding cells. Selectivity for AS may obtain generally in the HVc of oscine birds – similar results have been obtained in multiunit recordings in white-crowned sparrows *(Zonotrichia leucophrys)* [Margoliash and Konishi, 1985; Margoliash, 1986] and in preliminary single unit data in white-throated sparrows *(Zonotrichia albicollis)* [Margoliash, unpubl. observ.], and multiunit data in canaries and mockingbirds *(Mimus polyglottus)* [McCasland and Konishi, 1981].

The selectivity for AS apparently first emerges at the level of HVc – neurons with comparable properties are not recognized in field L [Margoliash, 1986; Lim, 1993], nor in preliminary data from Uva [Okuhata and Nottebohm, 1992] or neostriatum ventral to HVc [D. Margoliash, unpubl. observ.]. The auditory responses of NIf may exhibit some degree of song selectivity [M.L. Sutter, A. Dave, and D. Margoliash, unpubl. observ.]. The broad distribution of field L neurons that project to HVc make this conclusion particularly difficult to establish for field L. In perhaps the most direct comparison to date, Margoliash [1986] examined the multiunit properties of both HVc and field L in 3 adult white-crowned sparrows. The HVc recordings exhibited highly statistically significant stronger responses for AS compared to conspecific songs, reversed AS, frequency-shifted AS, and two other parametric modifications of AS. Two of the birds had been reared in the laboratory; HVc recordings in those birds exhibited stronger responses to AS than to the tutor songs. In contrast, the field L recordings in the same 3 birds with the same stimulus repertoires exhibited responses to AS that were weaker or comparable to the responses to other stimuli, with the exception that a weak preference for forward AS compared to reversed AS was observed.

Temporal Order Sensitivity of HVc Auditory Neurons. Stimulus selectivity can result from spectral specificity, temporal specificity, or both. Because frequency is mapped in the auditory periphery, spectral filtering has been emphasized as a mechanism for achieving selectivity. Recent computational work, however, has demonstrated that an auditory neuron's time-domain response property – for example, the phasic and tonic components of response – can more strongly affect the neuron's response to complex stimuli (in a least-squared-error sense) than static parameters of tone burst responses such as the frequency tuning curve [Bankes and Margoliash, 1993]. In HVc, there is evidence that analysis in the temporal domain is crucial. For example, HVc neurons systematically prefer forward AS compared to reversed AS, two stimuli with different time-varying features that share identical overall spectra (fig. 3b). The song selective properties of HVc units also suggest the importance of time-domain processing. Most single neurons in the HVc of zebra finches were highly selective for AS. When the response rate (spikes/s) of the population of HVc single units was corrected for spontaneous activity, the average response to conspecific songs was near zero, and many songs elicited overall inhibition (fig. 3a). If HVc contributes to song recognition [e.g. Margoliash, 1986; Brenowitz, 1991b], these data suggest that the temporal pattern of response to conspecific songs, rather than the absolute strength of response, is likely to be the most salient cue for recognition.

Studies of HVc temporal processing have focused on sensitivity to combinations of sounds. Temporal combination sensitive (TCS) neurons have been described in white-crowned sparrows [Margoliash, 1983] and zebra finches [Margoliash and Fortune, 1992; Lewicki and Doupe, 1993]. In general, non-linear summation of excitation to temporal sequences of notes [Suga et al., 1978; Margoliash, 1983; McKenna et al., 1989; Olsen, 1994] or to spectral components of a note [Fuzessery and Feng, 1982; Langner et al., 1981; Sutter and Schreiner, 1991; Margoliash and Fortune, 1992] is a widely recognized phenomenon in the auditory system used to generate higher-order response properties. In most cases, combination sensitivity is closely associated with processing for species-specific vocalizations.

In white-crowned sparrows, all TCS neurons responded to a sequence of two syllables but not to either syllable when presented in isolation [Margoliash, 1983]. The TCS neurons were highly selective, responding most strongly to AS, more weakly to other songs from the same dialect, and typically not at all to songs from other dialects or to simple artificial stimuli. Thus these neurons were termed 'song-specific'. The response selectivity of song-specific neurons

Organization of Song System:
Functions and Origins

was based, in part, on specificity to parameters of AS. This was best demonstrated in cases where it was possible to synthesize complex artificial sounds that mimicked the natural signal yet permitted parametric modification. In these cases, changing the frequency of either the leading or following element in the sequence reduced the response strength. The TCS neurons were quite insensitive to the duration of the first element of the sequence or to the duration of the interval between the elements. In general, these neurons had long integration times (up to 1 s), longer than field L neurons [Schafer et al., 1992].

Recent single unit studies of the zebra finch have confirmed and extended these results. In the zebra finch, approximately 15% (48/329) of the cells were strictly temporal-combination sensitive (TCS), responding with excitation to a sequence of sounds but not to the individual sounds presented in isolation [Margoliash and Fortune, 1992]. In all cases, TCS cells responded much more strongly to AS than to any conspecific song tested. It should be noted that the long periods of time needed to unambiguously establish the TCS property suggests that 15% is probably a significant underestimate of the size of the population.

Different classes of zebra finch TCS neurons required different temporal sequences of song elements. Some neurons required a sequence of 2 parts (notes) of a single syllable. Other neurons required a sequence of 2 discrete syllables of song. Most remarkably, other neurons required a sequence of 3, 4, or in some cases even 5 discrete syllables of AS in the proper order. Additionally, in some cases the TCS response at a given syllable of song required prior excitation 3 or more syllables preceding the TCS excitation, but the prior excitation itself did not require a temporal sequence of sound elements (i.e., was not TCS). In all cases tested, the interval between syllables could be extended by hundreds of milliseconds without compromising the TCS response. Thus, there was a broad range of types of TCS neurons in the zebra finch HVc, with individual neurons exhibiting integration times of up to 1 s and up to 5 syllables of AS.

Models of Temporal Order Sensitivity. Specific circuit models have been proposed to explain temporal order sensitivity in HVc. In no small way, these are of interest because they can potentially describe a neural circuit directly involved in song learning. For ease of exposition, we define cell C1 which projects to cell C2; C2 exhibits temporal order sensitivity to the stimulus sequence S1 followed by S2. Margoliash [1983] proposed an 'inhibitory-rebound' two-cell model for TCS neurons in white-crowned sparrow HVc based on extracellular data. In that model, C1 inhibited C2 such that rebound excitation of C2

from release of C1 inhibition at the offset of S1 combined with excitation of C2 by S2 to produce suprathreshold excitation of C2. Selectivity for autogenous song was proposed to result from unspecified mechanisms that tuned C1 selectively for S1 and tuned C2 selectively for S2. This model was one of potentially many that could account for all the known dynamical properties of TCS neurons in white-crowned sparrows, especially very broad tuning to the duration of S1 or the interval between S1 and S2, phasic response near the onset of S2, maintenance of the TCS property even in cases when S1 and S2 are identical, and lack of response if S1 and S2 were presented simultaneously [Margoliash, 1983]. It is noteworthy that the long integration times in HVc precludes the use of delay lines, as has been proposed for TCS neurons in bats [Kuwabara and Suga, 1993].

Recent intracellular recordings in zebra finch have extended the analysis of temporal order sensitivity in HVc. Lewicki and Doupe [1993] presented preliminary evidence for the 'inhibitory-rebound' model of Margoliash [1983] as well as for the two other mechanisms. In the 'long-short' model, long-lasting depolarization produced by S1 combined with a shorter-duration depolarization produced by S2 to achieve suprathreshold excitation. In the 'burst-firing' model, depolarization by S2 produced a burst if preceded by a hyperpolarizing potential produced by S1; S2 alone produced few spikes. Interestingly, the burst-firing model produces a stronger non-linear response than the two other models. Below we note that the bursting activity of HVc neurons is probably synchronized throughout HVc.

The models of Margoliash [1983] and Lewicki and Doupe [1993] propose possible mechanisms for the final (or non-linear) stage of various circuits that exhibit temporal order sensitivity, but they do not explain how specificity for syllables of autogenous song is achieved. From the perspective of circuit analysis of song learning, this limitation implies lack of insight into the neuronal elements modified during song learning. Each bird sings a different song; HVc neurons are tuned to the parameters of the bird's own song. Which elements of the circuit reflect the idiosyncratic properties of HVc auditory neurons? From a modeling perspective, this limitation is particularly significant in the zebra finch, where some HVc TCS neurons integrate a sequence of up to 5 complex syllables before exhibiting excitation [Margoliash and Fortune, 1992].

The logical extension of the Margoliash [1983] two-cell model that accommodates a requirement for multiple syllables to elicit the TCS response is to add more cells in series, with the last cell exhibiting the TCS response. This is an unattractive solution because: (1) it is not parsimoni-
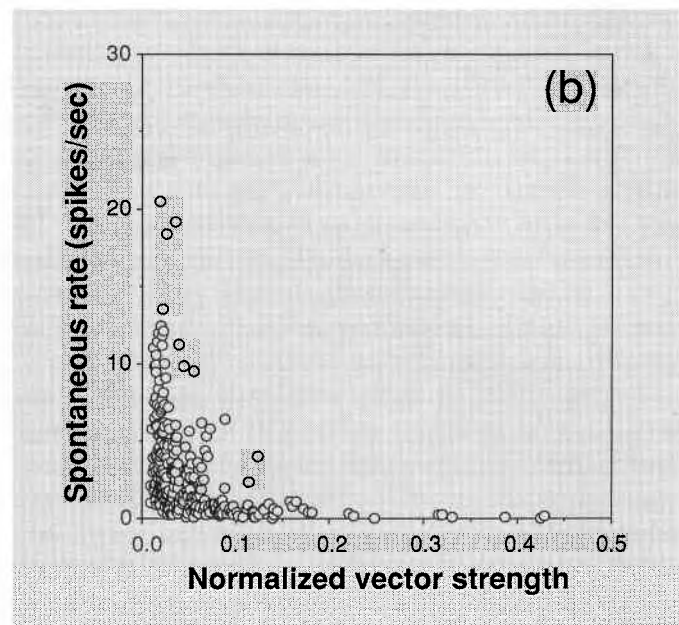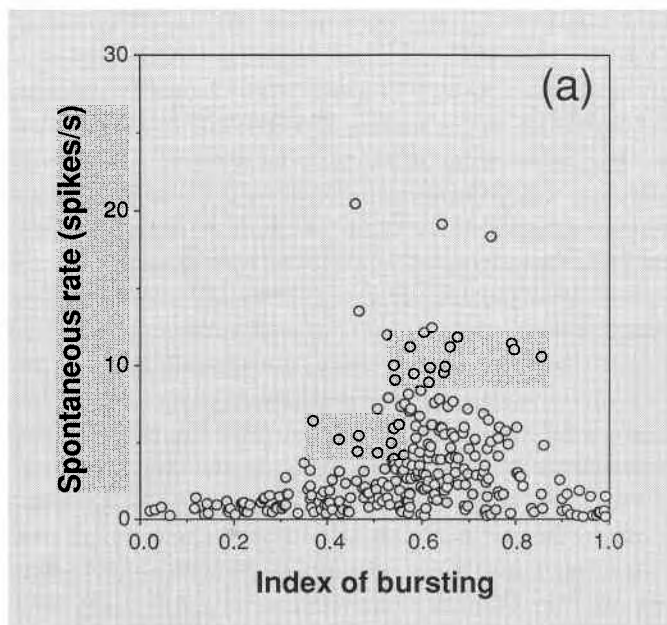
Fig. 4. Relationships between spontaneous and driven (response) properties of zebra finch HVc single units. The spontaneous rate is calculated over 30 s of spontaneous activity (whenever those data were collected) or over 1 s preceding each repetition of AS. **a** Spontaneous data for 267 units. The index of bursting measures spike 'clumping' in time: 0 implies equal inter-spike intervals for all spikes; 1 implies all spikes occurred simultaneously (a limit condition). High spontaneous rate neurons tend to be bursty whereas a clear pattern does not emerge for low spontaneous rate neurons. **b** Stimulus is AS, presented to 293 units. The vector strength (phasicness) of spontaneous-corrected response was calculated over duration of each syllable. Normalized vector strength is the average of the vector strength of responses to all syllables weighted by the number of spikes each syllable elicited. Most temporal combination sensitive neurons (see text) have low spontaneous rates and respond in a phasic manner to song.

ous; (2) it predicts the numbers of TCS neurons should go down with sequence length (more 2-syllable than 3-syllable TCS neurons, etc.), but the data indicate there are roughly equal numbers of TCS neurons in all different classes, and (3) such an extension still does not predict many other salient features of HVc activity. For example, in HVc high spontaneous rate neurons (> 2.5 spikes/s) exhibit a bursting pattern of spontaneous activity (fig. 4a). When stimulated by AS, these neurons respond tonically throughout song (fig. 4b). In contrast, virtually all TCS neurons are low spontaneous rate neurons (< 2.5 spikes/s; Margoliash and Fortune [1992]). The TCS neurons may or may not burst spontaneously (fig. 4a), but they almost always have phasic responses to song (fig. 4b). Presumably, phasic TCS neurons derive their response properties by convergence from the more numerous tonic/bursting neurons.

The spontaneous bursting of individual HVc neurons reflects greater complexity (more time constants) than the highly regular spontaneous activity commonly seen in RA [Mooney, 1992]. One possible interpretation of this complexity is in terms of central pattern generators (CPGs) – HVc neurons participate in circuits that encode 'higher-level' temporal features of song. This is consistent with the hierarchical organization of the motor system as judged by electrical stimulation of HVc and RA during singing [Vu et al., 1993]. The intrinsic properties of these sensorimotor HVc circuits are exhibited, in part, during spontaneous bursting. From this perspective, the analysis of TCS and other song-selective properties in HVc relates to how auditory input modulates CPGs.

Global Synchrony of Spontaneous and Auditory Activity. The properties of HVc neurons are influenced by correlated activity observed throughout HVc. This can be visualized most easily in multiple electrode experiments. Simultaneous recordings from two electrodes demosntrate that spontaneous bursting in HVc is remarkably similar throughout the nucleus. For example, figure 5 shows 30 s of spontaneous activity in two sites in HVc, separated by 850 μm that were recorded in a urethane-anesthetized zebra finch. The pattern of multiunit bursting is highly correlated, although not all bursts are well correlated (compare traces at 14–16 s). This degree of correlation occurs regularly throughout HVc, although we have yet to analyze it systematically or at the single unit level.

Margoliash/Fortune/Sutter/Yu/Wren-Hardin/
Dave

Organization of Song System:
Functions and Origins

Fig. 5. Correlated spontaneous activity in HVc. Spontaneous activity from two recording sites in HVc separated by approximately 750 μm. The first 15 s of data are shown in the top panel, the following 15 s of data are shown in the bottom panel. Note that many bursts of activity occur in synchrony.
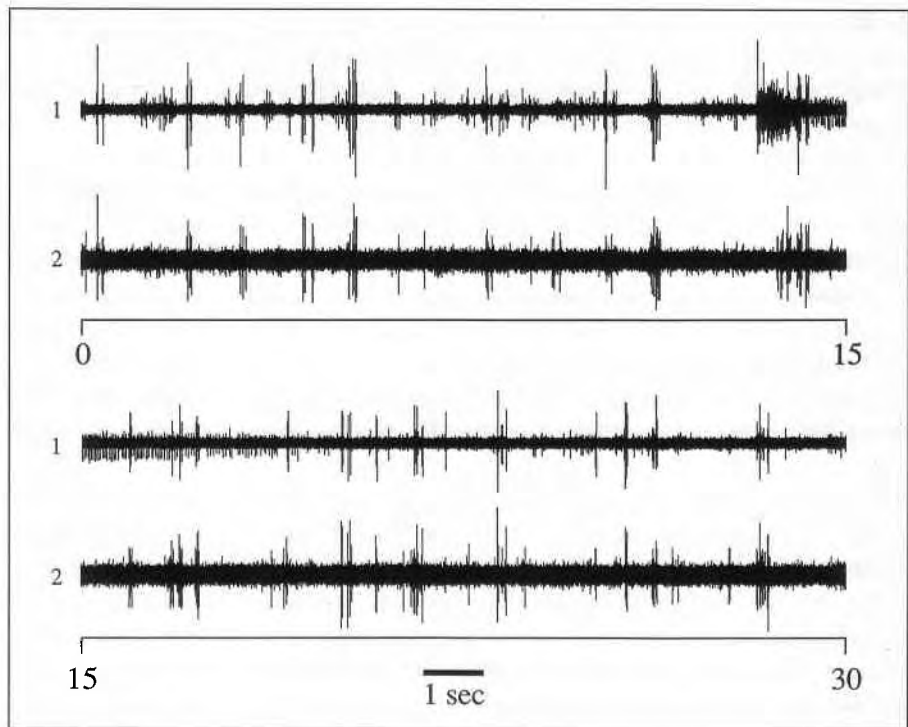
The global temporal correlation of spontaneous HVc activity suggests that stimulus-driven activity might also exhibit temporal correlation. This suggestion was confirmed in an investigation of the spatial distribution of extracellular responses to AS in the HVc of zebra finches [Sutter and Margoliash, 1994]. Within each of 7 urethane-anesthetized birds, multiunit and single unit responses to AS were similar across the entire spatial extent of HVc (up to 1.3 mm). This effect was not apparent in an 8th control bird with recordings just outside of HVc. For each bird, a narrow range of times elicited the strongest peak responses (calculated with 25 ms bins), called the time of maximum synchronization (TMS). Within a bird, 34–75% of recording sites exhibited the same TMS. The position of the TMS was generally unchanged as the window of integration was varied from 10–150 ms, demonstrating the TMS effect was robust. Each TMS was associated with a syllable of maximum synchronization (SMS). The positions of the SMS varied considerably across birds. In 4 birds, the SMS was in the first motif (a motif is a temporal sequence of syllables that is repeated one or more times to form a song); in 2 birds, the SMS was the introductory note of song, and in 1 bird the SMS was the second syllable of the last (third) motif. There were no apparent acoustical features of the SMS or the preceding syllable (morphological type, duration, amplitude) that could account for the global synchronous response to song. Typically, syllables of the same type as the SMS occurring in other motifs elicited much weaker responses, and some syllables of different type than the SMS elicited strong responses but only in non-SMS motifs. Thus, there was strong and consistent temporal modulation of the auditory response throughout HVc that was not predicted by any obvious local acoustical features.

The intra-individual similarity of response properties throughout HVc provides a logic for examining the aggregate activity of HVc [Sutter and Margoliash, 1994]. A measure of the aggregate (population) response of the nucleus was derived by summing multiunit data across all recording sites of each bird ('group PSHT' – post-stimulus time histogram). The aggregate response exhibited phasic excitation at most syllable onsets and offsets. Additionally, a recovery process after the end of response to AS was observed with a long inhibitory component. The duration of the recovery varied more than an order of magnitude across individuals (300 ms–6 s). Features of the temporal modulation of the response were related to the duration and relative strength of the recovery. This implies a long-time course process across the nucleus helps to shape the response to AS, and that the duration and magnitude of the process varies from bird to bird. Thus is consistent with the view that oscillators or other pattern-generating circuits that are broadly distributed help shape HVc auditory responses.

We conclude the auditory representation of song in the zebra finch HVc is distributed and redundant [Sutter and Margoliash, 1994]. The pattern of excitation and inhibition in response to AS is strongly temporally modulated, and is globally similar because of strong correlation of activity across HVc. A temporally-encoded representation may provide a useful reference framework for difference detection in relationship to conspecific songs or for error detection in relationship to auditory feedback.

The Organization of HVc during Singing

Studies of HVc as a motor structure provide further evidence for distributed representations in HVc. In one study, we examined the effects of small lesions on the songs of white-throated sparrows (WTS) [Hardin and Margoliash, 1992, unpubl. observ.]. Songs in white throated sparrows comprise simple descending or ascending whistles particularly amenable to detailed analysis, typically three long introductory whistles ('notes') followed by a series of short whistles organized into triplets. In the wild, the absolute frequency of notes and frequency ratio of successive notes is very stable across songs [Borror and Gunn, 1965; Lemmon and Harris, 1974; Hurly et al., 1991]. We focused our analysis on the first three notes of song. Bird's songs were extensively recorded prior to and 6–28 days after lesions, which were made by small injections of ibotenic acid to minimize damage to fibers-of-passage. The extent of damage was calculated by comparing HVc volumes of lesioned and control sides of the brain in transverse sections. Birds submitted to left HVc lesions (size: 2–100%, n = 14), right HVc lesions (size: 29–79%, n = 3; this species is left lateralized [Lemmon [1973]]), and 3 controls spared HVc. Lesions from ≤ 26% of HVc (13 birds total) produced permanent effects including a change in the frequency of song; lesions of 10% or smaller (4 birds) produced only temporary effects, or no effects. Postoperatively, the variability in the duration of notes also increased, although the mean durations did not change.

With a single exception (a bird singing an abnormal song), birds sang all notes of song after the lesions. In 2 of 13 birds with permanent frequency shifts, all notes of songs were equally effected, and in 11 of 13 birds there were significant changes in the frequency ratios of successive notes (p < 0.01). The magnitude of frequency shift for each of the first three notes of song was strongly (and significantly) positively correlated with the size of the lesion. Different parts of song were not affected differently by the location of lesions within HVc, although a unique effect of mediocaudal lesions on the initial note of song cannot be ruled out. This suite of observations is consistent with a distributed representation of AS within the level of resolution of the lesions.

Most birds exhibited a downward frequency shift, but 3 of 4 birds with the lowest frequency songs exhibited an upward shift in frequency. We hypothesize the population activity of HVc provides 'drive' to RA. Loss of drive results in lower tension of syringeal muscles (and internal tympaniform membranes), which produces downward frequency shifts when the song is above natural modes of vibration of the syringeal internal tympaniform membrane, but upward frequency shifts when song is below the natural modes of membrane vibration. This implies a remarkably simple code – the output of HVc is distributed throughout the part of RA that projects to the hypoglossal nucleus, with the total output of HVc being a meaningful parameter. Of course, many codes that have time-varying characteristics could exhibit such a global behavior.

Some songs of lesioned birds were distorted. The number of distorted songs significantly increased with the size of the lesion ($R^2 = 0.666$, p < 0.01). Distortions were characterized as a loss of fine control of the frequency of whistles – an increase in frequency variability within a whistle. Typically, for individual whistles the effect was all or none – either a whistle was distorted or it was not. Although distortions could begin with any of the first 3 notes, with the exception of 1 bird, the notes following a distorted note were very likely to also be distorted (p < 0.01, binomial test). The degree of distortion tended to increase in a sequence of distorted notes. Songs were more likely to terminate with distorted notes. Thus, the temporal dynamics of the population of HVc neurons is resistant to loss of large parts of the population, but once an abnormal dynamic state is achieved, the system has difficulty recovering. The abnormal state increases the probability of complete loss of coordination. Such behavior would be expected from a system that achieves and maintains its population dynamics through a high degree of correlated activity, although other explanations cannot be ruled out.

The Behavioral Significance of Auditory Responses in HVc: Functional and Evolutionary Links Between Production and Perception

In the previous section we described the organization of HVc, concluding that there is a distributed representation for song both for auditory and motor states, that this representation is redundant (similar throughout), and that the principal code for song is in the temporal rather than the spatial organization of neuronal activation. In this final sec-

tion we examine some of the implications of auditory responses in HVc.

The Process of Song Perception

The HVc auditory neurons exhibit exquisite selectivity for the individual bird's own song – the one song the bird is most unlikely to hear a neighbor sing. Auditory activity in HVc is inhibited during singing [McCasland and Konishi, 1981], and in any case most adult birds do not rely on auditory feedback to maintain song [Konishi, 1965; Nottebohm, 1980; Marler and Sherman, 1982; Price, 1979; Nordeen and Nordeen, 1992]. What then is the functional role of highly selective auditory responses in the adult HVc? Birds can recognize individuals on the basis of song alone [Falls, 1982]. In almost every species tested to date, the bird's own song has a special status as an external stimulus, releasing a level of territorial behavior that is intermediate between the effects of established neighbors and unknown conspecific strangers [e.g. Brooks and Falls, 1975; McArthur, 1986; see Falls, 1982]. In playback experiments in species with repertoires of different song types, individuals match song type most consistently when challenged with one of their own songs, a behavior thought to increase information exchange between singers [e.g., Falls et al., 1982; Falls, 1985]. These data support the hypothesis that adult songbirds perceive conspecific songs by comparing them to an internal 'reference' of their own songs or other known songs [Morton, 1982]. Further evidence to support this hypothesis exists in the form of playback experiments with acoustically degraded songs. Birds distinguished better between degraded and undegraded songs when they were familiar with those songs than when the songs were novel [McGregor et al., 1983; McGregor and Falls, 1984; McGregor and Krebs, 1984].

With these considerations in mind, Margoliash [1986, 1987] proposed that the representation of AS in HVc acts as a reference against which conspecific songs are compared. Support for a role of HVc in song recognition has come from a few laboratory studies that show adverse effects on discrimination following HVc lesions [Nottebohm et al., 1990; Brenowitz, 1991b]. In general, these effects are not strong or the results are somewhat ambiguous; for example, the lesions of female canary HVc that resulted in loss of discrimination between conspecific and heterospecific songs [Brenowitz, 1991b] may have also involved more medial aspects of NC. Thus, the role for HVc in song perception has not been well established.

If the motor system for song production is also involved in song perception then this demonstrates a linkage between production and perception but does not explain the form of that linkage. In humans, a motor theory of speech perception generally asserts that the articulatory mechanisms recruited during speech production are also recruited during the perception of like speech, with the pattern of recruitement being similar if in a somewhat vaguely defined fashion [Liberman et al., 1967; Liberman and Mattingly, 1985]. A parallel motor theory of song perception has been proposed based on the claim that playback of different types of song components selectively activates pools of motor neurons in different parts of the hypoglossal nucleus [Williams and Nottebohm, 1985]. That observation, however, results from a very small data set for a mapping study (14 recordings in 4 animals). It is difficult to understand how a topographic arrangement of syllables based on acoustics is consistent with the myotopic organization of the hypoglossal nucleus [Vicario and Nottebohm, 1988], especially when there is evidence that at least some syringeal muscles are involved in producing most syllables of song [Vicario, 1990]. Also, to date there is no known pathway that leads from the hypoglossal nucleus back into the brain, as would be required for auditory-related activity in the hypoglossal nucleus to have perceptual significance.

An alternative view of the relationship between production and perception arises from considerations of song learning. During development, HVc auditory response properties are shaped during motor learning [Volman, 1993]; this result had been predicted and hypothesized to contribute to the process of matching the memorized song model with auditory feedback during the trial-and-error phase of song development [Margoliash, 1987]. How does auditory feedback become decoupled from singing during development? In a recent set of experiments [Yu and Margoliash, 1992, 1993, and unpubl. observ.], we were able to achieve direct recording of multiple and single HVc units in singing zebra finches, which is technically challenging because of the small size of songbirds and because of movement artifacts during singing. In our small sample (11 multiunit clusters and 13 single units extracted using spike waveform classification techniques recorded from 8 sites in 7 birds), the neuronal recruitment PSTHs when the bird sang its song were completely different from the auditory response PSTHs when the bird heard its song. In many cases the change from auditory to motor properties occurred over a period of about 5 s prior to singing, during which the 'spontaneous' rates of neurons increased by 5–10×. This suggests that auditory and motor systems act over different spatiotemporal regimes of neuronal populations – have different state properties. This is not consistent with the suggestion that a linkage between production and perception of song results from closely related states [cf.

Nottebohm et al., 1990]. Rather, production and perception may share developmental processes and thus exhibit linkages in the adult [Margoliash, 1987]. In this scheme such linkages result only from shared changes during periods of song learning.

References

Bankes, S.C., and D. Margoliash (1993) Parametric modeling of the temporal dynamics of neuronal responses using connectionist architectures. J. Neurophysiol., *69:* 980–991.

Baptista, L.F., and K.-L. Schuchmann (1990) Song learning in the Anna Hummingbird *(Calypte anna).* Ethology, *84:* 15–26.

Bell, P.M., D. Margoliash, and P.S. Ulinski (1989) Cytoarchitecture and differential projections of nucleus ovoidalis in the zebra finch. Soc. Neurosci. Abstr., *15:* 617.

Bigalke-Kunz, B., R. Rünsamen, and G.J. Dörrscheidt (1987) Tonotopic organization and functional characterization of the auditory thalamus in a songbird, the European starling. J. Comp. Physiol. A, *161:* 255–265.

Bischof, H.J., and J. Engelage (1985) Flash evoked responses in a song control nucleus of the zebra finch *(Taeniopygia guttata castanotis).* Brain Res., *326:* 370–374.

Bonke, D.A., D. Bonke, and H. Scheich (1979a) Connectivity of the auditory forebrain nuclei in the guinea fowl *(Numida meleagris).* Cell Tissue Res., *200:* 101–121.

Bonke, D., H. Scheich, and G. Langner (1979b) Responsiveness of units in the auditory neostriatum of the Guinea fowl *(Numida meleagris)* to species-specific calls and synthetic stimuli. I. Tonotopy and functional zones. J. Comp. Physiol., *132;* 243–255.

Borror, D.J., and W.W.H. Gunn (1965) Variation in white-throated sparrow songs. Auk, *82:* 26–67.

Bottjer, S.W., K.A. Halsema, S.A. Brown, and E.A. Miesner (1989) Axonal connections of a forebrain nucleus involved with vocal learning in zebra finches. J. Comp. Neurol., *279:* 312–326.

Bottjer, S.W., E.A. Miesner, and A.P. Arnold (1984) Forebrain lesions disrupt development but not maintenance of song in passerine birds. Science, *224:* 901–903.

Brauth, S.E., and C.M. McHale (1988) Auditory pathways in the budgerigar. II. Intratelencephalic pathways. Brain Behav. Evol., *32:* 193–207.

Brauth, S.E., C.M. McHale, C.A. Brasher, and R.J. Dooling (1987) Auditory pathways in the budgerigar I. Thalamo-telencephalic projections. Brain Behav. Evol., *30:* 174–199.

Brenowitz, E.A. (1991a) Evolution of the vocal control system in the avian brain. Neurosciences, *3:* 399–407.

Brenowitz, E.A. (1991b) Altered perception of species-specific song by female birds after lesions of a forebrain nucleus. Science, *251:* 303–305.

Brooks, R.J., and J.B. Falls (1975) Individual recognition by song in white-throated sparrows. I. Discrimination of songs of neighbors and strangers. Can. J. Zool., *53:* 879–888.

Carr, C.E. (1992) Evolution of the central auditory system in reptiles and birds. *In* The Evolutionary Biology of Hearing (ed by D.B. Webster, R.R. Fay, and A.N. Popper). Springer Verlag, New York, pp. 511–544.

DeVoogd, T.J., J.R. Krebs, S.D. Heady, and A. Purvis (1993) Relations between song repertoire size and the volume of brain nuclei related to song: comparative evolutionary analyses among oscine birds. Proc. Royal Soc. Lond., Series B: Biol. Sci., *254:* 75–82.

Doupe, A.J., and M. Konishi (1991) Song-selective auditory circuits in the vocal control system of the zebra finch. Proc. Natl. Acad. Sci. USA, *88:* 11339–11343.

Durand, S.E., J.M. Tepper, and M.-F. Cheng (1992) The shell region of the nucleus ovoidalis: A subdivision of the avian auditory thalamus. J. Comp. Neurol., *323:* 495–518.

Falls, J.B. (1982) Individual recognition by sound in birds. *In* Acoustic Communication in Birds, 2, Song Learning and Its Consequences (ed by D.E. Kroodsma, and E.H. Miller), Academic Press, NY, pp. 237–278.

Falls, J.B. (1985) Song matching in western meadowlarks. Can. J. Zool., *63:* 2520–2524.

Falls, J.B., J.R. Krebs, and P.K. McGregor (1982) Song matching in the great tit *(Parus major):* the effect of similarity and familiarity. Anim. Behav., *30:* 997–1009.

Fortune, E.S., and D. Margoliash (1992) Cytoarchitectonic organization and morphology of cells of the field L complex in male zebra finches *(Taeniopygia guttata).* J. Comp. Neurol., 325: 388–404.

Fortune, E.S., and D. Margoliash (1994) Parallel pathways and convergence onto HVc and adjacent neostriatum of adult male zebra finches *(Taeniopygia guttata).* J. Comp. Neurol., in press.

Fuzessery, Z.M., and A.S. Feng (1982) Frequency selectivity in the aunuran auditory midbrain: single unit responses to single and multiple tone stimulation. J. Comp. Physiol., *146:* 471–484.

Gamlin, P.D.R., and D.H. Cohen (1986) A second ascending visual pathway from the optic tectum to the telencephalon in the pigeon *(Columba livia).* J. Comp. Neurol., *250:* 296–310.

Hall, W.S., P.L. Cohen, and S.E. Brauth (1993) Auditory projections to the anterior telencephalon in the budgerigar *(Nelopsittacus undulatus).* Brain Behav. Evol., *41:* 97–116.

Hardin, B.D., and D. Margoliash (1992) Effects on songs of lesions in HVc. Proc. Third Int. Cong. Neuroethol., 344.

Häusler, U.H.L. (1988) Topography of the thalamotelencephalic projections in the auditory system of a songbird *(Sturnus vulgaris). In* Auditory Pathways, Structure, and Function (ed. by J. Syka, and R.B. Masterton), Plenum Press, New York, pp. 197–202.

Heil, P., and H. Scheich (1985) Quantitative analysis and two-dimensional reconstruction of the tonotopic organization of the auditory field L in the chick from 2-deoxyglucose data. Exp. Brain Res., *58:* 532–543.

Heil, P., and H. Scheich (1991) Functional organization of the avian auditory cortex analogue. I. Topographic representation of isointensity bandwidth. Brain Res., *539:* 110–120.

Hurly, T.A., R.G. Weisman, L. Ratcliffe, and I.S. Johnsrude (1991) Absolute and relative pitch production in the song of the white-throated sparrow *(Zonotrichia albicollis).* Bioacoustics, *3:* 81–91.

Karten, H.J. (1968) The ascending auditory pathway in the pigeon *(Columba livia).* II. Telencephalic projections of the nucleus ovoidalis thalami. Brain Res., *11:* 134–153.

Karten, H.J., and W. Hodos (1967) A Stereotaxic Atlas of the Brain of the Pigeon *(Columba livia).* Johns Hopkins Press, Baltimore.

Karten, H.J., and W. Hodos (1970) Telencephalic projections of the nucleus rotundus in the pigeon *(Columba livia).* J. Comp. Neurol., *140:* 35–52.

Katz, L.C., and M.E. Gurney (1981) Auditory responses in the zebra finch's motor system for song. Brain Res., *211:* 192–197.

Kelley, D.B., and F. Nottebohm (1979) Projections of a telencephalic auditory nucleus – Field L – in the canary. J. Comp. Neurol., *183:* 455–470.

Kitt, C.A., and S.E. Brauth (1982) A paleostriatal-thalamic-telencephalic path in pigeons. Neuroscience, *7:* 2731–2735.

Korzeniewska, E., and O. Güntürkün (1990) Sensory properties and afferents of the N. dorsolateralis posterior thalami of the pigeon. J. Comp. Neurol., *292:* 457–479.

Konishi, M. (1965) The role of auditory feedback in the control of vocalization in the white-crowned sparrow. Z. Tierpsychol., *22:* 770–783.

Konishi, M. (1991) Deciphering the brain's codes. Neural Comp., *3:* 1–18.

Kroodsma, D.E., and M. Konishi (1991) A suboscine bird (eastern phoebe, *Sayornis phoebe)* develops normal song without auditory-feedback. Anim. Behav., *42:* 477–487.

Kroodsma, D.E., and E.H. Miller (1982) Acoustic Communication in Birds. Academic Press, New York.

Kuwabara, N., and N. Suga (1993) Delay lines and amplitude selectivity are created in subthalamic auditory nuclei: the brachium of the inferior colliculus of the mustached bat. J. Neurophysiol., *69:* 1713–1724.

Langner, G., D. Bonke, and H. Scheich (1981) Neuronal discrimination of natural and synthetic vowels in field L of trained mynah birds. Exp. Brain Res., *43:* 11–24.

Lemmon, R.E. (1973) Nervous control of the syrinx in white-throated sparrows *(Zonotrichia albicollis).* J. Zool. (London), *171:* 131–140.

Lemmon, R.E., and M. Harris (1974) The question of dialects in the songs of white-throated sparrows. Can. J. Zool., *52:* 83–98.

Leppelsack, H.-J. (1983) Analysis of song in the auditory pathway of song birds. *In* Advances in Vertebrate Neuroethology (ed. by J.P. Ewert, R.R. Capranica, and D.J. Ingle), Plenum, N.Y., pp. 783–799.

Leppelsack, H.-J., and M. Vogt (1976) Responses to auditory neurons in the forebrain of a songbird to stimulation with species-specific sounds. J. Comp. Physiol., *107:* 263–274.

Lewicki, M.S., and A.J. Doupe (1993) Synaptic activity of neurons in zebra finch song nucleus HVc in response to auditory stimuli. Soc. Neurosci. Abstr., *19:* 1016.

Liberman, A.M., F.S. Cooper, D.P. Shankweiler, and M. Studdert-Kennedy (1967) Perception of the speech code. Psychol. Rev., *74:* 431–461.

Liberman, A.M., and I.G. Mattingly (1985) The motor theory of speech perception revised. Cognition, *21:* 1–36.

Lim, D. (1993) Auditory response properties of field L in the zebra finch. Soc. Neurosci. Abstr., *19:* 415.

Margoliash, D. (1983) Acoustic parameters underlying the responses of song-specific neurons in the white-crowned sparrow. J. Neurosci., *3:* 1039–1057.

Margoliash, D. (1986) Preference for autogenous song by auditory neurons in a song system nucleus of the white-crowned sparrow. J. Neurosci., *6:* 1643–1661.

Margoliash, D. (1987) Neural plasticity in birdsong learning. *In* Imprinting and cortical plasticity, (ed. by J.P. Rauschecker, and P. Marler), John Wiley and Sons, New York.

Margoliash, D., and E.S. Fortune (1992) Temporal and harmonic combination-sensitive neurons in the zebra finch's HVc. J. Neurosci., *12:* 4309–4326.

Margoliash, D., and M. Konishi (1985) Auditory representation of autogenous song in the songsystem of white-crowned sparrows. Proc. Natl. Acad. Sci. USA, *82:* 5997–6000.

Marler, P., and V. Sherman (1982) Structure in sparrow song without auditory feedback: An emendation of the auditory template thesis. J. Neurosci., *3:* 517–531.

McArthur, P.D. (1986) Similarity of playback songs to self song as a determinant of response strength in song sparrows *(Melospiza melodia).* Anim. Behav., *34:* 199–207.

McCasland, J.S. (1987) Neuronal control of bird song production. J. Neurosci., *7:* 23–39.

McCasland, J.S., and M. Konishi (1981) Interaction between auditory and motor activities in an avian song control nucleus. Proc. Natl. Acad. Sci. USA, *78:* 7815–7819.

Mcgregor, P.K., and J.B. Falls (1984) The response of western meadowlarks *(Sturnella neglecta)* to the playback of undegraded and degraded songs. Can. J. Zool., *62:* 2125–2128.

McGregor, P.K., and J.R. Krebs (1984) Sound degradation as a distance cue in great tit song. Behav. Ecol. Sociobiol., *16:* 49–56.

McGregor, P.K., J.R. Krebs, and L.M. Ratcliffe (1983) The reaction of great tits *(Parus major)* to playback of degraded und undegraded songs: the effect of familiarity with the stimulus song type. Auk, *100:* 898–906.

McKenna, T., N.M. Weinberger, and D.M. Diamond (1989) Responses of single auditory cortical neurons to tone sequences. Brain Res., *481:* 142–153.

Mello, C.V., D.S. Vicario, and D.F. Clayton (1992) Song presentation induces gene expression in the songbird forebrain. Proc. Natl. Acad. Sci. USA, *89:* 6818–6822.

Mooney, R. (1992) Synaptic basis for developmental plasticity in a birdsong nucleus. J. Neurosci., *12:* 2464–2477.

Mori, K., and G. Striedter (1992) Neurons in field L of budgerigars prefer species specific calls to white noise. Soc. Neurosci. Abstr., *18:* 223.

Morrison, R.G., and F. Nottebohm (1993) Role of a telencephalic nucleus in the delayed song learning of socially isolated zebra finches. J. Neurobiol., *24:* 1045–1064.

Morton, E.S. (1982) Grading, discreteness, redundancy, and motivation-structural rules. *In* Acoustic Communication in Birds, Vol. 1, Production, Perception, and Design Features of Sounds (ed. by D.E. Kroodsma, and E.H. Miller), Academic Press, N.Y., pp. 183–213.

Müller, C.M., and H.-J. Leppelsack (1985) Feature extraction and tonotopic organization in the avian auditory forebrain. Exp. Brain Res., *59:* 587–599.

Müller, S.C., and H. Scheich (1985) Functional organization of the avian auditory field L. J. Comp. Physiol., *156:* 1–12.

Nordeen, K.W., and E.J. Nordeen (1992) Auditory feedback is necessary for the maintenance of stereotyped song in adult zebra finches. Behav. Neural Biol., *57:* 58–66.

Nottebohm, F. (1972) The origins of vocal learning. Amer. Nat., *106:* 116–140.

Nottebohm, F. (1980) Brain pathways for vocal learning in birds: a review of the first 10 years. Prog. Psychobiol. Physiol. Psychol., *9:* 85–124.

Nottebohm, F. (1987) Birdsong. *In* Encyclopedia of Neuroscience I (ed. by G. Adelman), Birkhäuser Boston, Inc., Boston, pp. 133–136.

Nottebohm, F. (1991) Reassessing the mechanisms and origins of vocal learning in birds. Trends Neurosci., *14:* 206–211.

Nottebohm, F., A. Alvarez-Buylla, J. Cynx, J. Kirn, C.-Y. Ling, M. Nottebohm, R. Suter, A. Tolles, and H. Williams (1990) Song learning in birds: the relation between perception and production. Phil. Trans. R. Soc. Lond. B, *329:* 115–124.

Nottebohm, F., D.B. Kelley, and J.A. Paton (1982) Connections of vocal control nuclei in the canary telencephalon. J. Comp. Neurol., *207:* 344–357.

Nottebohm, F., T.M. Stokes, and C.M. Leonard (1976) Central control of song in the canary, *Serinus canarius.* J. Comp. Neurol., *165:* 457–486.

Okuhata, S., and F. Nottebohm (1992) Single units in nucleus Uva respond to sound and respiration and are part of a motor loop in song production. Proc. Third Int. Cong. Neuroethol., 60.

Okuhata, S., and N. Saito (1987) Synaptic connections of thalamo-cerebral vocal nuclei of the canary. Brain Res. Bull., *18:* 35–44.

Olsen, J.F. (1994) Medial geniculate neurons in the squirrel monkey sensitive to intercomponent delays that categorize species-typical calls. Assoc. Res. Otolaryngol. Abstr., *17:* 21.

Paton, J.A., K.R. Manogue, and F. Nottebohm (1981) Bilateral organization of the vocal control pathway in the budgerigar, *Melopsittacus undulatus.* J. Neurosci., *1:* 1279–1288.

Price, P.H. (1979) Developmental determinants of structure in zebra finch song. J. Comp. Physiol. Psychol., *93:* 268–277.

Rübsamen, R., and G.J. Dörrscheidt (1986) Tonotopic organization of the auditory forebrain in a songbird, the European starling. J. Comp. Physiol. A, *158:* 639–646.

Saini, K.D., and H.-J. Leppelsack (1981) Cell types of the auditory caudomedial neostriatum of the starling *(Sturnus vulgaris).* J. Comp. Neurol., *198:* 209–230.

Schafer, M., R. Rübsamen, G. Dörrscheidt, and M. Knipschild (1992) Setting complex tasks to single units in the avian auditory forebrain. II. Do we really need natural stimuli to describe neuronal response characteristics? Hear. Res., *57:* 231–244.

Scharff, C., and F. Nottebohm (1991) A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: implications for vocal learning. J. Neurosci., *11:* 2896–2913.

Scheich, H., G. Langner, and D. Bonke (1979) Responsiveness of units in the auditory neostriatum of the Guinea fowl *(Numida meleagris)* to species-specific calls and synthetic stimuli. II. Discrimination of iambus-like calls. J. Comp. Physiol., *132:* 257–276.

Shimizu, T., and H.J. Karten (1991a) Central visual pathways in reptiles and birds: evolution of the visual system. *In* Vision and Visual Dysfunction, 2. (ed. by R. Gregory, and J.R. Cronly-Dillon), Macmillan Press, New York.

Shimizu, Z., and H.J. Karten (1991b) Computational significance of lamination of the telencephalon. *In* Visual Structures and Integrated Functions (ed. by M.A. Arbib, and J.-P. Ewert), Springer Verlag, Berlin, pp. 325–337.

Sohrabji, R., E.J. Nordeen, and K.W. Nordeen (1990) Selective impairment of song learning following lesions of a forebrain nucleus in the juvenile zebra finch. Behav. Neural Biol., *53:* 51–63.

Stokes, T.M., C.M. Leonard, and F. Nottebohm (1974) The telencephalon, diencephalon, and mesencephalon of the canary, *Serinus canaria,* in stereotaxic coordinates. J. Comp. Neurol., *156:* 337–374.

Striedter, G.F. (1994) The vocal control pathways in budgerigars differ from those in songbirds. J. Comp. Neurol., *343:* 35–56.

Stripling, R., S.F. Volman, and D.F. Clayton (1994) Electrophysiological responses to song presentation in caudiomedial neostriatum of zebra finches: links to ZENK gene induction. Soc. Neurosci. Abstr., *20,* in press.

Suga, N., W.E. O'Neill, and T. Manabe (1978) Cortical neurons sensitive to combinations of information-bearing elements of biosonar signals in the mustached bat. Science, *200:* 778–781.

Sutter, M.L., and D. Margoliash (1994) Global synchronous response to autogenous song in the zebra finch HVc. J. Neurophysiol., in press.

Sutter, M.L., and C.E. Schreiner (1991) Physiology and topography of neurons with multi-peaked tuning curves in cat primary auditory cortex. J. Neurophysiol., *65(5):* 1207–1226.

Ulinski, P.S. (1982) Dorsal Ventricular Ridge. A Treatise on Forebrain Organization in Reptiles and Birds. John Wiley and Sons, New York.

Ulinski, P.S., and D. Margoliash (1990) Neurobiology of the reptile-bird transition. *In* Cerebral Cortex (ed. by E.G. Jones, and A. Peters), Plenum, New York, pp. 217–265.

Vicario, D.S. (1990) Contributions of syringeal muscles to respiration and vocalization in the zebra finch. J. Neurobiol., *22:* 63–73.

Vicario, D.S. (1991) Organization of the zebra finch song control system: II. Functional organization of outputs from nucleus robustus archistriatalis. J. Comp. Neurol., *309:* 486–494.

Vicario, D.S., and F. Nottebohm (1988) Organization of the zebra finch song control system: I. Representation of syringeal muscles in the hypoglossal nucleus. J. Comp. Neurol., *271:* 346–354.

Vicario, D.S., and K.H. Yohay (1993) Song-selective auditory input to a forebrain vocal control nucleus in the zebra finch. J. Neurobiol., *24:* 488–505.

Volman, S. (1993) Development of neural selectivity for birdsong during vocal learning. J. Neurosci., *13:* 4737–4747.

Vu, E.T., M.E. Mazurek, and Y. Kuo (1993) Hierarchical organization of brain areas mediating zebra finch learned vocalizations. Soc. Neurosci. Abstr., *19:* 1015.

Wild, J.M. (1993a) Does the pigeon have a nucleus uvaeformis (Uva), or the songbird a nucleus dorsolateralis posterior thalami, pars caudalis (cDLP)? Soc. Neurosci. Abstr., *19:* 415.

Wild, J.M. (1993b) Descending projections of the songbird nucleus robustus archistriatalis. J. Comp. Neurol., *338:* 225–241.

Wild, J.M. (1993c) The avian nucleus retroambigualis: a nucleus for breathing, singing and calling. Brain Res., *606:* 319–324.

Wild, J.M. (1994) The auditory-vocal-respiratory axis in birds. Brain Behav. Evol., *44:* 192–209.

Wild, J.M., B.J. Frost, and H.J. Karten (1990) Some aspects of the organization of the auditory forebrain and midbrain in the pigeon. Soc. Neurosci. Abstr., *16:* 715.

Wild, J.M., H.J. Karten, and B.J. Frost (1993) Connections of the auditory forebrain in the pigeon *(Columba livia).* J. Comp. Neurol., *337:* 32–62.

Williams, H. (1989) Multiple representations and auditory-motor interactions in the avian song system. Ann. N.Y. Acad. Sci., *563:* 148–164.

Williams, H., and F. Nottebohm (1985) Auditory responses in avian vocal motor neurons: a motor theory for song perception in birds. Science, *229:* 279–282.

Williams, H., and D. Vicario (1933) Temporal patterning of song production: participation of nucleus uvaeformis of the thalamus. J. Neurobiol., *24:* 903–912.

Yu, C.-H., and D. Margoliash (1992) Recording of HVc in singing zebra finches. Proc. Third Int. Cong. Neuroethol., 342.

Yu, A.C.-H., and D. Margoliash (1993) Differences between motor recruitment and auditory response properties in zebra finch HVc neurons. Soc. Neurosci. Abstr., *19:* 1018.