Functional Organization of Forebrain Pathways for Song Production and Perception

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ABSTRACT: **This article reviews the organization of the forebrain nuclei of the avian song system. Particular emphasis is placed on recent physiologic recordings from awake behaving adult birds while they sing, call, and listen to broadcasts of acoustic stimuli. The neurons in the descending motor pathway (HVc and RA) are organized in a hierarchical arrangement of temporal units of song production, with HVc neurons representing syllables and RA neurons representing notes. The nuclei Uva and NIf, which are afferent to HVc, may help organize syllables into larger units of vocalization. HVc and RA are also active during production of all calls. The patterns of activity associated with calls differ between learned calls and those that are innately specified, and give insight into the interactions between the forebrain and midbrain during calling, as well as into the evolutionary origins of the song system. Neurons in Area X, the first part of the anterior forebrain pathway leading from HVc to RA, are also active during singing. Many HVc neurons are also auditory, exhibiting selectivity for learned acoustic parameters of the individual bird's own song (BOS). Similar auditory responses are also observed in RA and Area X in anesthetized birds. In contrast to HVc, however, auditory responses in RA are very weak or absent in awake birds under our experimental paradigm, but are uncovered when birds are anesthetized. Thus, the roles of both pathways beyond HVc in adult birds is under review. In particular, theories hypothesizing a role for the descending motor pathway (RA and below) in adult song perception do not appear to obtain. The data also suggest that the anterior forebrain pathway has a greater motor role than previously considered. We suggest that a major role of the anterior forebrain pathway is to resolve the timing mismatch between motor program readout and sensory feedback, thereby facilitating motor programming during birdsong learning. Pathways afferent to HVc may participate more in sensory acquisition and sensorimotor learning during song development than is commonly assumed.** ***J Neurobiol* 33: 671–693, 1997**

Keywords: **chronic recording; awake behaving animals; hierarchical organization; singing; calling; evolution of song system; sensorimotor plasticity and learning; anterior forebrain pathway; auditory responses; anesthetic effect; modeling delayed feedback**

INTRODUCTION

To elucidate the neural mechanisms of birdsong production, perception, and learning, it is important to understand the functional organization of the song system in terms of behavior: i.e., song as a motor program, and the development of song under sensory and sensorimotor constraints. An important level of analysis is the response properties of single neurons. For the two forebrain song pathways, relatively little progress has been made in this direction. The major advance has been differentiation of forebrain pathways into a descending motor pathway necessary for song development and song production, and an anterior forebrain pathway necessary for song development but not immediately necessary for adult song production (for recent reviews, see Doupe, 1993; Margoliash, 1994; Vicario, 1994;

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Brenowitz and Kroodsma, 1996; Brenowitz et al., 1997). HVc appears to be a nexus for the flow of auditory information through both pathways and may serve as a site of sensorimotor integration during song learning. In anesthetized birds, auditory neurons in other nuclei throughout the forebrain song system have similar response properties to those of HVc neurons, being most responsive to the individual bird's own song (BOS). Beyond these generalizations, the specific roles played by the nuclei in the forebrain pathways and how these relate to behavior have generally not yielded to the lesion studies or physiologic investigations in anesthetized animals commonly employed. This article reviews recent progress emphasizing a new approach: recording single units and multiunits in the forebrain of awake behaving animals. Throughout, I stress theoretical implications of the results, identify future directions of research, and suggest experiments to resolve outstanding issues. Significant progress has also been made recently with complementary techniques to record peripheral activity during singing (Suthers, 1997).

HIERARCHICAL ORGANIZATION OF MOTOR PATHWAYS FOR SINGING

Functional Organization of HVc and RA

The original paper describing the song system emphasized the obligatory contribution of the forebrain nuclei HVc and robustus archistriatalis (RA) for song production (Nottebohm et al., 1976). Birds with bilateral HVc or RA lesions produced ''silent song'': Canary males vigorously courted females and adopted the characteristic singing posture but failed to make throat movements or produce sounds. Later, anatomical studies suggested connections between the auditory and song motor systems—a necessary condition for song learning (Kelley and Nottebohm, 1979), and auditory responses of HVc neurons were confirmed (Katz and Gurney, 1981). Auditory and motor modalities were shown to interact in HVc such that auditory responsiveness was absent when birds were singing, an interaction that presumably would arise during song learning (McCasland and Konishi, 1981). That study also reported that multineuronal recordings in HVc and RA of several species of birds exhibited activity preceding and time-locked to units of song. Ongoing multineuronal activity in HVc preceded that in RA, suggesting a hierarchical arrangement consistent with the unidirectional nature of the projections. Subsequent work showed that in RA neuronal activity could commence up to 40–50 ms preceding the onset of song, whereas in HVc activity could precede song onset by hundreds of milliseconds or even seconds (Yu and Margoliash, 1996, and unpublished observations; McCasland, 1987).

Experiments that directly assessed functional organization of the descending motor pathway have also been interpreted in terms of a hierarchical organization. Electrical stimulation of RA and HVc in anesthetized birds produced complex vocalizations with species-typical characteristics but failed to distinguish between the two nuclei (Vicario and Simpson, 1995). In contrast, Vu et al. (1994) stimulated HVc and RA while zebra finch were singing. Low levels of electrical stimulation in HVc ($<5\ \mu A$) resulted in birds terminating songs prematurely within motifs, then rapidly commencing to sing again at the start of a motif. In RA, similar manipulations resulted in disruption of the morphology of the ongoing syllable but did not disrupt the temporal pattern of song. Although the locus of the effects of electrical stimulation are difficult to determine in such experiments (e.g., it may be difficult to distinguish between effects on local circuits and effects on afferent input), the qualitative difference between effects of stimulation of HVc and RA clearly demonstrates that programming of the temporal sequence of song elements occurs only at higher levels of the pathway (Vu et al., 1994).

Direct evidence for hierarchical organization of the descending motor pathway has recently been obtained. Yu and Margoliash (1996) developed a technique for recording individual neurons in singing birds and were able to identify neural codes at different levels of the motor pathway. In the HVc of singing zebra finches, neurons exhibited relatively tonic patterns of activity throughout song that varied only with syllable identity but were independent of the position of the syllable within the song, and were independent of the identity of the preceding and following syllables. HVc neurons exhibited different activity profiles for syllables that were similar (e.g. shared some notes in common) [Fig. 1(A)]. Thus, at the level of HVc, single neurons apparently unambiguously code for syllable identity but not for note or motif identify. Production of syllables typically involves activity in many syringeal muscles in coordination with respiration, the vocal tract, and body posture (Suthers et al., 1994; Goller and Suthers, 1996; Westneat et al., 1994). Syllables are indivisible units of production: When a bird's song is suddenly interrupted, the bird tends to complete the syllable he is singing (Cynx, 1990). Thus, the

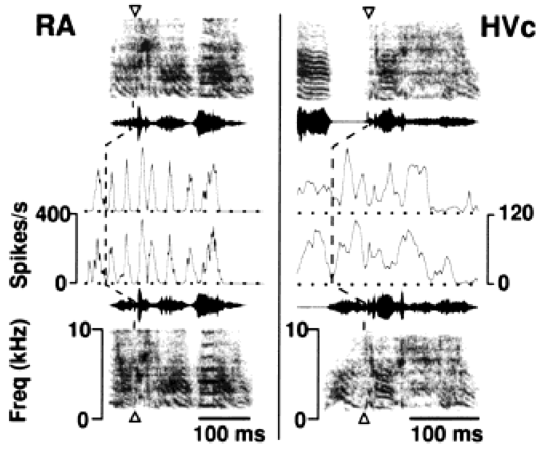

Figure 1 Premotor activity patterns of RA and HVc neurons. (Left) Recordings from an RA neuron when the bird produced two slightly different syllables (compare parts of the spectrographs and oscillographs on the top and bottom preceding and following the open arrowheads). Note that the activity of the neuron (middle traces) is very similar for similar notes of the two syllables and different for different notes of the two syllables. (Right) A comparable case for an HVc neuron. Note that the activity is different for all notes of the two syllables, even notes that are similar. Reprinted with permission from A. C. Yu and D. Margoliash, ''Temporal Hierarchical Control of Singing in Birds,'' *Science* **273:**1873. © 1996 American Association for the Advancement of Science.

syllable can properly be considered a motor program, probably the largest unit of vocalization meeting these criteria.

In contrast to HVc, during singing, RA neurons exhibited short phasic bursts of activity that varied only with the identity of subsyllabic vocal units (Yu and Margoliash, 1996). In cases where different syllables shared some notes in common, RA neurons would exhibit the same activity pattern for the similar notes but different activity patterns for the different notes of the syllable [Fig. 1(B)]. Thus, RA neurons may code for notes, and the activity of RA neurons may be related to individual syringeal muscles (see below).

Organization of Efferents and Afferents to HVc and RA

HVc and RA have complementary patterns of organization (Margoliash et al., 1994). HVc receives multiple inputs and has two outputs and is apparently not topographically organized, whereas RA receives two inputs and has multiple outputs and is topographically organized. The differences in these patterns of organization have functional consequences.

Nucleus HVc. The multiple inputs to HVc suggest that it may serve as a major site in the song system of integration of information, which is then provided to the two major pathways within the forebrain. HVc has at least four classes of projection neurons. Cells with thick dendrites and spherical or elongated dendritic arborizations project to Area X; cells with short dendrites and cells with furry dendrites project to RA (Nixdorf et al., 1989; Fortune and Margoliash, 1995). Additional cell types, including projection neurons and interneurons, have been tentatively described (Nixdorf et al., 1989; Fortune and Margoliash, 1995). To date, there is little information regarding functional differentiation of X-projecting and RA-projecting HVc neurons, leaving unresolved whether motor and auditory information flow through different channels within HVc (Katz and Gurney, 1981; Saito and Maekawa, 1989). Both X-projecting HVc neurons and RA-projecting HVc neurons extend dendrites ventrally into the shelf, however, which is thought to be a possible source of auditory information to HVc.

Three cytoarchitectonic regions have been identified for HVc, the commonly described central core that represents the bulk of the nucleus, a caudomedial subdivision, and a dorsolateral subdivision (Kirn et al., 1989; Fortune and Margoliash, 1995). The four morphological classes of HVc neurons are distributed throughout all three subdivisions, although X-projecting HVc neurons are the dominant class of cells in the caudomedial subdivision of HVc (Nordeen and Nordeen, 1988; Gahr, 1990). Using the same techniques that revealed topography of RA, no spatial organization has been determined for the projections of HVc onto RA or Area X, or the projections of other nuclei onto HVc (e.g., Nottebohm et al., 1982; Fortune and Margoliash, 1995). This evidence supports the concept of a spatially distributed representation at the level of HVc, which is consistent with the similarity of response properties throughout the nucleus observed both during singing and during playback of song (Margoliash et al., 1994; Sutter and Margoliash, 1994; Yu and Margoliash, unpublished results). Such an organization might obtain if there were no topography, and it also might obtain if what was mapped was represented in the time domain.

Inputs to HVc can be considered as organized into two major classes. The first represents nuclei that may be involved in song production (Uva and

NIf) and is considered here. The second represents auditory information reaching HVc that may be involved in sensory and sensorimotor aspects of song learning, and is considered in a separate section below. In addition, HVc receives input from the medial subdivision of MAN (mMAN) (Nottebohm et al., 1982; Okuhato and Saito, 1987; Bottjer et al., 1989). mMAN receives input from the dorsomedial nucleus of the posterior thalamus, which in turn receives input from the hypothalamus and from archistriatum, including RA (Foster et al., 1997; Vates et al., 1997). The function of mMAN is not well established and is not considered further here (see Foster and Bottjer, 1993).

The thalamic nucleus Uva was first identified based on its projection to HVc; Uva also projects to NIf (Nottebohm et al., 1982). In adult zebra finch, bilateral lesion of Uva results in disruption of the singing pattern but not loss of the ability to sing, and some multineuron recordings exhibit superbursts of activity associated with motif (supra-syllabic) boundaries of the song (Williams and Vicario, 1993). Such properties have not been observed for zebra finch HVc neurons. If this important result of Williams and Vicario (1993) obtains at the single neuron level [McCasland (1987) failed to find singing-related Uva activity in multiunit recordings], it would provide further support for the hypothesis of hierarchical organization of the motor system for song production. Uva neurons are sensory, receiving input from deep layers of optic tectum and from external cuneate and dorsal column nuclei, and responding to visual and somatosensory stimuli (Wild, 1994a). Uva additionally receives bilateral input from the nucleus of the rostroventrolateral medulla (RVL) and a lesser bilateral projection from DM (Striedter and Vu, in press). RVL receives input from RA and DM, and nucleus retroambigualis of the respiratory system (Wild, 1993a, 1994b). Thus, Uva has access to many inputs that might serve to gate or trigger singing while coordinating the song system bilaterally (Williams, 1989). Birds organize the singing pattern so as to take minibreaths in the longer silent intervals in song, such as between phrases in canary song (Hartley and Suthers, 1989). Perhaps the superbursts in Uva occasionally recorded by Williams and Vicario (1993) are associated with minibreaths zebra finch take between motifs.

NIf receives input from Uva and projects to HVc. Originally, NIf was thought to be essential for song production based on song deficits that followed gross knife cuts that transected NIf fibers projecting to HVc (McCasland, 1987). More recently, the zebra finch NIf was lesioned using the excitotoxin ibotenic acid, a technique that minimizes nonspecific effects and fibers-of-passage problems that confuse the interpretation of the previous knife-cut lesions. In a preliminary report, Vu et al. (1995) observed that song was initially severely disrupted, but even with complete bilateral lesions of NIf, birds recovered near-normal song within approximately 1 week. The disruption and subsequent recovery of song could potentially be explained if nearby Uva fibers projecting to HVc were partially compromised, or could be the result of recovery or plasticity at the level of Uva or HVc recruited by removal of the NIf input. McCasland (1987) showed multiunit activity in NIf preceding singing on a syllable-by-syllable basis. If so, it is fascinating that the first nucleus in the motor pathway to exhibit moment-to-moment neural activity associated with singing is not necessary for song production. It would be very interesting to conduct such lesion experiments in juvenile birds. If NIf lesions affect song development but not adult song production, this would be the first example of a nucleus outside of the anterior forebrain pathway with this property. The difficulty would be to make such lesions while sparing nearby Field L.

Nucleus RA. The organization of RA can be interpreted in functional terms. The bulk of RA is organized in a coarse topography, with regions of RA projecting in an ordered fashion onto the hypoglossal nucleus (Vicario, 1991a). Overlapping pools of neurons in the hypoglossal nucleus in turn project onto different muscles of the syrinx (Vicario and Nottebohm, 1988; Ruan and Suthers, 1996). Thus, there may be a myotopic organization at the level of RA. The ventral and dorsal RA ultimately project onto the two major muscle groups of the syrinx: dorsal and ventral muscles. These muscles have distinct functional roles during singing, either gating expiratory flow or controlling the frequency of vocalization (Suthers, 1990; Vicario, 1991b; Goller and Suthers, 1996). Thus, one may loosely consider RA as organized into separate streams of information, one for temporal control and the other for spectral control. The topography in RA is also present throughout the anterior forebrain pathway (Johnson et al., 1995; Vates and Nottebohm, 1995; Bottjer and Johnson, 1997), an observation which may help to refine hypotheses regarding the role of lMAN inputs in modulating or organizing synaptic connections between HVc and RA during sensorimotor learning (Johnson et al., 1995).

The multiple outputs of RA can be considered as organized into four functional sets of outputs. Each output receives information from both functional streams. One major set of RA outputs that have only recently been identified is to the brainstem nuclei involved in respiratory and laryngeal control (Vicario, 1993; Wild, 1993a,b; Reinke and Wild, 1996, 1997). In the context of RA myotopy, this pattern of outputs would provide moment-to-moment information about control of the configuration of the syringeal muscles to the respiratory and laryngeal systems, permitting tight coupling with syringeal control (Suthers, 1997). The second output is the well-known projection to the hypoglossal nucleus, controlling the syringeal muscles (Nottebohm et al., 1976). A third set of outputs is to thalamic nuclei that ultimately project back to HVc and RA (Okuhato and Saito, 1987; Bottjer et al., 1989; Wild, 1993b; Foster et al., 1997; Vates et al., 1997). These pathways are well suited to provide internal feedback during singing, which might be particularly important during sensorimotor learning. In adult birds the thalamic projections of RA are relatively sparse, but whether these pathways are more robust early in life during song development has yet to be examined. Finally, there is a thin dorsal ''cap'' region of RA that, along with the rest of RA, projects to the dorsomedial nucleus (DM) of the midbrain intercollicular complex (ICo) (Gurney, 1981; Vicario, 1991a; Wild, 1993b, 1994b). DM is also involved in motor coordination, projecting to the respiratory and laryngeal brain stem targets of RA, but with heavier contralateral and bilateral connections than shown by RA. In addition, DM may also be important for mediating interactions between forebrain and midbrain systems during singing and calling (Vicario and Simpson, 1995).

FOREBRAIN PREMOTOR ACTIVITY DURING CALLING—IMPLICATIONS FOR EVOLUTION OF SONG SYSTEM

A midbrain system for the production of innately specified calls has been extensively described for birds, but less is known about forebrain mechanisms of calling (Popa and Popa, 1933; Holst and St. Paul, 1963; Phillips, 1964; Phillips et al., 1972; Brown, 1965, 1971; Potash, 1970; Seller, 1980). Recently, Yu and Margoliash (unpublished results) observed that both HVc and RA are recruited during production of calls. In zebra finch males as in other oscine birds, some calls such as the long (contact) call are learned, whereas others are innately specified (Mundinger, 1970, 1979; Zann, 1985). Zebra finches commonly incorporate calls into song (Zann, 1984, 1985; Slater and Jones, 1995). In our experiments we categorized zebra finch calls as to whether they were sometimes incorporated into songs or produced exclusively outside of the context of song. Using chronic recording techniques, we observed that for HVc and RA neurons, calls that were sometimes produced in isolation and other times incorporated into song exhibited the same complex activity profiles in both behavioral contexts [Fig. 2(A)]. In addition, the long call was always associated with a complex pattern of activity. The timing and complexity of the activity patterns for these call types are similar to those observed in HVc and RA for other syllables during singing (Yu and Margoliash, 1996), suggesting direct, moment-to-moment forebrain control during calling. Calls that were exclusively produced independent of song, however, exhibited different patterns in the two nuclei. For HVc neurons, such calls exhibited a simple phasic excitation with a peak 0–20-ms preceding call onset followed by inhibition throughout the call. For RA neurons, such calls were associated only with inhibition, preceding and sometimes extending throughout the call [Fig. 2(B)]. This suggests that the forebrain does not exhibit moment-to-moment control over calls produced independent of song.

A simple hypothesis to explain these observations proposes that all levels of the forebrain song system involved in motor coordination during singing are also involved in motor coordination during production of learned calls. The same system would be activated during calling, but only to initiate or interact with the midbrain calling system. Consistent with this hypothesis, forebrain lesions disrupt learned features of zebra finch male long calls (Vicario and Simpson, 1995). Determining whether other calls associated with zebra finch song are also learned or are innate will provide valuable information about the form of interaction between the forebrain and the midbrain. For innately specified calls—presumptively the calls exclusively produced independent of song—excitation in HVc produces inhibition of RA which commands or enables the avian midbrain calling. Thus, as for singing, the forebrain pathways for calling are hierarchically organized. The projection of RA to DM in the midbrain ICo may help mediate the interactions between forebrain and midbrain systems. Two functional hypotheses can be entertained. The midbrain calling system could be activated by release from inhibition when RA is inhibited, or the midbrain system could be activated by neurons in the dorsal cap region of RA. The latter hypothesis would addi-

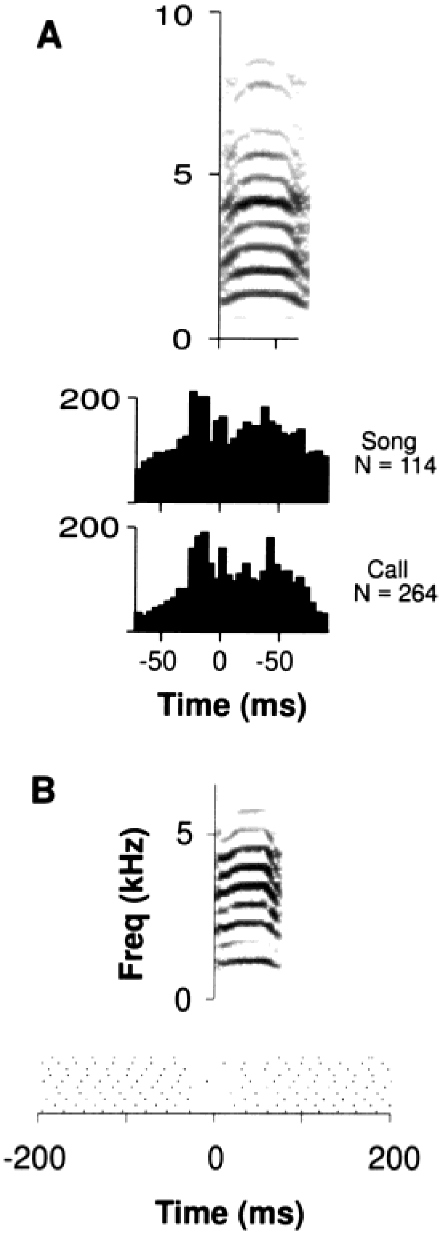

Figure 2 (A) Call-related activity of an HVc single unit. The histograms represent activity for two behavioral contexts. The top histogram is when the call was produced in the context of song, and the bottom histogram is when the call was delivered in isolation. Note that the activity patterns are very similar in the two cases. (B) Call-related activity of an RA single unit. This call was only produced in isolation. Inhibition of ongoing activity was associated with the call at this recording site, and at other recording sites for this bird (not shown).

tionally require that DM-projecting RA neurons of the dorsal cap have different properties during calling (i.e., excitation) from those observed for the rest of RA. If RA is functionally removed from the circuit by profound inhibition during production of innately specified calls, this can explain the absence of an effect of forebrain lesions on such calls (Nottebohm et al., 1976).

It is noteworthy that production of innately specified calls is an ancestral behavior associated with midbrain structures in all classes of vertebrates (Jurgens and Ploog, 1976; Ploog, 1981). The evidence that the forebrain nuclei of the song system are also associated with calling is the first evidence of direct forebrain involvement with innately specified calls. This also has implications for the evolutionary origins of the song system. The defining characteristic of the vocal behavior of oscine birds is a requirement for auditory feedback for normal song development (Kroodsma, 1982). In the context of the present data, parsimony suggests that the defining evolutionary step in the evolution of the song system occurred when a hypothesized ancestral avian forebrain system that influenced calling gained access to auditory input (Brenowitz, 1997). Birds call under a variety of situations which require assessment of acoustic, visual, and somatosensory cues. The ancestral system should have had access to these modalities.

Anatomical evidence provides support for this conjecture. The song system follows a general reptile–bird pattern of forebrain connections (Ulinski and Margoliash, 1990). Recent anatomical investigations of the forebrain nuclei have stressed the similarities in patterns of connections in songbirds (i.e., oscine passerines) and nonoscine birds. In nonoscines, the caudal subdivision of the dorsolateral posterior thalamic nucleus (DLPc) receives visual and somatosensory input, and projects to an intermediate neostriatal region and sends smaller projections to dorsal neostriatum (Kitt and Brauth, 1982; Gamlin and Cohen, 1986; Wild, 1987, 1994a; Funke, 1989a; Korzeniewska and Güntürkün, 1990). Wild (1994a) homologized the oscine Uva with the pigeon DLPc based on its position, connections, and cell types, and homologized the oscine NIf and ''shelf'' region ventral to HVc with the intermediate and dorsal neostriatal efferent targets of DLPc, respectively. Uva and NIf and their nonoscine homologs have visual and somatosensory responses (Güntürkün, 1984; Funke, 1989b; Korzeniewska and Güntürkün, 1990; Wild, 1994a). In oscines, most of the forebrain nuclei, which are cytoarchitectonically distinct, are also associated with nearby or surrounding indistinct regions (Kelley and Nottebohm, 1979; Wild et al., 1993; Fortune and Margoliash, 1995; Johnson and Bottjer, 1995;

Johnson et al., 1995; Vates et al., 1996). The indistinct regions associated with song system nuclei have patterns of connections parallel to the song system, suggesting that the song system arose as elaborations of areas within these indistinct regions (Margoliash et al., 1994). Thus, it may be possible to test the proposed evolutionary hypothesis by searching for call-related activity in Uva and NIf, in the homologous forebrain pathways in nonoscine species of birds that do not learn vocalizations, and by analyzing the indistinct regions in oscines.

AUDITORY RESPONSES IN THE FOREBRAIN

Auditory feedback–mediated learning dominates song development in oscine birds. Birds deafened early in life produce dramatically disrupted song as adults. Statistical analysis of the adult songs of early-deafened sparrows reveal some residual species-typical characteristics (Marler and Sherman, 1992). Species specificity in the songs of deaf birds potentially may reflect innate differences in central patterns of organization as well as species-specific characteristics of the periphery (e.g., the shape and musculature of the syrinx and the vocal tract). Nevertheless, the striking abnormality of these songs emphasizes the importance of sensorimotor learning for normal song development. The adult songs of deafened birds are disrupted at all levels of structural analysis. These songs lack stereotypy on a song-by-song basis, they lack normal temporal patterning such as cadence, and their notes and syllables have highly abnormal morphologies (Konishi, 1964, 1965a,b; Mulligan, 1966; Nottebohm, 1968; Marler et al., 1972; Marler and Waser, 1977; Price, 1979). These dramatic effects have been seen in all studies of early-onset deafening in oscine birds (and in psitticine birds such as budgerigars, which also learn vocalizations) (Dooling et al., 1987) and contrast sharply with the absence of effects of deafening that has been observed in nonoscines, including the suboscine passerine birds (Konishi, 1963; Kroodsma, 1982; Kroodsma and Konishi, 1991). The prominence of auditory feedback in regulating song development in oscines has focused attention on the organization of the forebrain auditory pathways in birds and their relation to the song system.

Organization of the Auditory Pathways up to HVc

Field L is the primary telencephalic auditory structure in birds, analogous to mammalian auditory cortex. The caudal forebrain including Field L receives input from the auditory thalamus, including nucleus ovoidalis in a complex arrangement with multiple parallel pathways (Karten, 1968; Bonke et al., 1979a; Kelley and Nottebohm, 1979; Brauth et al., 1987, 1994; Durand et al., 1992; Wild et al., 1993; Vates et al., 1996). The Field L complex is composed of four or five subdivisions (Fortune and Margoliash, 1992) which project to multiple targets within the forebrain (Bonke et al., 1979a; Kelley and Nottebohm, 1979; Brauth and McHale, 1988; Wild et al., 1993; Vates et al., 1996). There is an extensive literature on physiological properties of auditory neurons in Field L and its caudal forebrain targets. These demonstrate tonotopic organization and relatively simple neuronal properties within those subdivisions of Field L that receive the bulk of input from ovoidalis (Bonke et al., 1979b; Heil and Scheich, 1985; Müller and Leppelsack, 1985; Rübsamen and Dörrscheidt, 1986). In other subdivisions of Field L and in other parts of the caudal forebrain, neurons may have more complex properties (e.g., Leppelsack and Vogt, 1976; Scheich et al., 1979; Langner et al., 1981; Müller and Leppelsack, 1985). To date, there is no evidence that neurons in Field L are modified by song development (Leppelsack, 1983; Margoliash, 1986), but the size of Field L makes it possible to miss a particular site or subdivision, and thus precludes confidence in any such negative result.

The ascending pathways through Field L give rise to auditory responses in the oscine song system (see below). In parrots and allies (psitticines), a taxonomic group of birds distinct from songbirds that also learn vocalizations, different pathways through the thalamus and involving nucleus basalis, but not Field L, give rise to auditory input to the forebrain vocal control system essential for development and maintenance of vocalizations (Brauth et al., 1994). This is consistent with the observation that vocal learning evolved separately in various groups of birds (Nottebohm, 1972) and may have recruited different pathways. Thus, homologizing structures between oscines and psitticines should be approached cautiously (Striedter, 1994).

The considerable interest in the pathways leading from Field L to the oscine song system is matched only by a lack of certainty as to the organization of these pathways. Initially, Kelley and Nottebohm (1979) used tritiated amino acid tracer to investigate the anterograde projections of Field L. Medial injections of Field L labeled a projection zone ventral to HVc (the shelf), but not within HVc itself, whereas more lateral injections also labeled fibers within

HVc. Subsequently, other nuclei that project to HVc were discovered (Nottebohm et al., 1982). These include NIf, which abuts the lateral aspects of Field L, and Uva in the thalamus. NIf fibers and Uva fibers both course through Field L, causing a severe fibers-of-passage problem that greatly complicates interpretation of anterograde patterns of projections onto or near HVc based on injections into Field L. Using retrograde techniques, some workers have tentatively concluded that Field L projects directly onto HVc (Fortune and Margoliash, 1995); others have disputed these claims but also failed to resolve the issue (Vates et al., 1996). Ultimately, the question of the projection of Field L onto HVc will be resolved only by examining the morphology of single Field L neurons. Using Golgi staining in starlings, Saini and Leppelsack (1981) concluded that fibers from the auditory neostriatum traverse the dorsal neostriatum and terminate in HVc. Tracing single axons in densely impregnated Golgi material is challenging, so that it would also be valuable to label individual Field L cells with intracellular injections, which has yet to be reported.

There is a complex of areas in dorsal neostriatum ventral to HVc that has yet to be fully described. The shelf, an area ventral and primarily medial to HVc is one such structure. It is commonly accepted that the shelf is a major source of auditory input to HVc. The close proximity of the shelf to HVc has hindered studies using lesion techniques, however, and evidence for the flow of auditory information through the shelf to HVc is purely anatomical and circumstantial. Axons of shelf area neurons apparently ramify extensively within the shelf but do not project to HVc, a preliminary result that has yet to be elaborated (L. Katz, reported in Margoliash, 1987). HVc neurons near the HVc ventral border extend their ventrally directed dendrites into the shelf (L. Katz, reported in Margoliash, 1987; Fortune and Margoliash, 1995; Vates et al., 1996). It is presumed that axodendritic synapses between shelf fibers arising from Field L, shelf neurons, or ventral hyperstriatum, and HVc dendrites form the auditory pathway into HVc via the shelf (Fortune and Margoliash, 1995). Surprisingly, there is little information regarding the physiological activity of neurons in the shelf. Extracellular single-cell techniques cannot easily resolve the location of a recorded cell with regard to shelf, HVc, or below shelf, and *in vivo* intracellular techniques have yet to be applied. One possible approach would be to use correlation analysis to compare the timing of activity of different neurons, one in HVc and the other nearby, which could give some insight into their relative connectivity. This approach would be facilitated by the considerable correlation of ongoing activity observed throughout HVc (Margoliash et al., 1994).

Multiple additional sources of auditory input to HVc have been implicated. One possible source is NIf. Neurons on NIf 's rostral border have dendrites that extend well into L1; these may access auditory neurons in L1 (Fortune and Margoliash, 1995). NIf also receives input from clHV, one of several forebrain regions which are reciprocally connected with the Field L complex (Vates et al., 1996). The study of Vu et al. (1995) casts doubt on original conclusion of McCasland (1987) that NIf is essential for singing (see above), focusing attention on other possible roles for NIf in sensory and sensorimotor aspects of song and song development (Williams, 1989). Nottebohm et al. (1982) originally named NIf (interfacialis) on the assumption that a structure embedded within Field L that projects to HVc must serve as an interface between the auditory and motor systems. The pathways that have been described over the years imply a more complicated interpretation involving multiple modalities (Wild, 1994a), but recent data lend support to the original speculation. Unfortunately, to date, auditory response properties of NIf neurons have not been unambiguously described.

Song-Selective Auditory Responses in HVc

Neurons in HVc are auditory, with response properties that result from the song-learning experience (Volman, 1993). HVc neurons exhibit selectivity for the bird's own song (BOS), responding preferentially (more spikes) to that song than to conspecific songs, including songs of the same dialect (Margoliash and Konishi, 1985; Margoliash, 1986). The selectivity for BOS arises from specificity for time-varying acoustic parameters of the BOS. Thus, most HVc neurons exhibit a weaker response to reversed BOS or to less dynamic stimuli such as tone or noise bursts (Margoliash, 1986; Margoliash et al., 1994). Some HVc neurons are additionally sensitive to combinations of temporally discrete acoustic elements (e.g., syllables) or combinations of individual spectral lines of an acoustic element (Margoliash, 1983; Margoliash and Fortune, 1992). Temporal and spectral combination sensitivity has been implicated in higher-order processing in other vertebrate systems (Suga et al., 1978; Langner et al., 1981; Fuzessery and Feng, 1982; Sutter and Schreiner, 1991; Rauschecker et al., 1995).

Many acoustic properties of HVc neurons are enigmatic, probably arising from the distributed nature of the representation at the level of HVc. One surprising result has been the comprehensive nature of selectivity for BOS at the level of HVc. Auditory neurons in Field L lack such selectivity, yet virtually all auditory neurons in HVc exhibit selectivity for BOS (Margoliash, 1986; Lewicki and Arthur, 1996). BOS selectivity is observed in the postsynaptic potentials of many HVc neurons, and multiple mechanisms operate that give rise to temporal combination sensitivity (Lewicki, 1996). In some sense, the absence of selectivity for BOS elsewhere has hindered analysis (Lewicki and Arthur, 1996), excluding elucidation at multiple levels of a sensory hierarchy that has been so successful in other systems (e.g., Konishi, 1992; Suga, 1990; Heiligenberg, 1991). In this context, if shelf area or NIf neurons are indeed a waystation to auditory processing in HVc, then it will be very important in future experiments to examine the properties of these neurons.

Modulation of patterns of synchronous activity in populations of neurons in forebrain systems may encode dynamical features of behavior (e.g., Vaadia et al., 1995). Synchronous activity is seen in the activity of the population of HVc neurons, and is characterized by the idiosyncratic nature of activity patterns. Within each individual, there is a tendency for HVc neurons to exhibit the maximum firing rate in the same small window of time (Sutter and Margoliash, 1994). The time of maximum synchronization is associated with a specific syllable of song, but the position of the syllable varies considerably across individuals. One possible explanation is that auditory responses are closely tied to the motor (singing-related) activity of the same neurons. Most premotor HVc neurons are also auditory (Yu and Margoliash, unpublished results). It is our distinct impression that ongoing activity of HVc neurons is patterned so as to represent a good physiologic marker for identifying when electrodes are within HVc (Margoliash, 1983). It also appears that details of the pattern of ongoing activity vary far less within an animal than among animals, which is consistent with a role for song development in shaping synchronous activity in HVc. Modulation of synchronous activity of the population of HVc neurons may be a method to encode the dynamic attributes of song. This hypothesis has been difficult to assess in sequential recordings, so it will be valuable to repeat the experiments of Sutter and Margoliash (1994) in awake animals with multisite recording techniques.

Understanding the mechanisms of HVc auditory responses is a challenging problem that few laboratories have addressed. But this would seem to go to the heart of identifying circuitry modified during birdsong learning. Future efforts in this direction would be valuable.

The Puzzling Distribution of Auditory Responses in the Song System

Data from Anesthetized Animals. Song-selective auditory responses as described above for HVc have been broadly observed in RA (Doupe and Konishi, 1991; Vicario and Yohay, 1993), Area X and lMAN (Doupe and Konishi, 1991; Doupe, 1997), and even the hypoglossal nucleus (Williams and Nottebohm, 1985). The auditory responses in these nuclei has been interpreted as resulting from HVc input. For example, RA receives input from both HVc and lMAN; RA song-selective auditory activity is compromised only with HVc lesions but not with lMAN lesions (Doupe and Konishi, 1991; Vicario and Yohay, 1993). The auditory responses of neurons in the anterior forebrain pathway are also apparently dependent on an intact HVc, but this is not directly established. HVc derives its auditory input from the ovoidalis-Field L system. The absence of parallel inputs from alternate forebrain auditory pathways into the song system also supports this conclusion (Wild and Farabaugh, 1996).

The broad distribution of song-selective auditory responses throughout the forebrain song system is somewhat puzzling. The most thorough analysis of song-selective auditory responses outside of HVc has been completed for Area X and lMAN neurons (Doupe, 1997; Doupe and Solis, 1997). Although some change in degree of neuronal song selectivity and responsiveness to noise bursts has been reported comparing HVc, Area X, and lMAN (Doupe and Konishi, 1991; Maekawa and Uno, 1996; Doupe, 1997; Doupe and Solis, 1997), what is striking is the similarity of auditory properties throughout the song system. Virtually every property observed for these neurons (specificity for acoustic parameters of the BOS; weak or no response to conspecific songs, reversed BOS, tone or noise bursts; temporal combination sensitivity; similarity of single neuron properties within individuals; and development of these auditory properties linked to song development) has also been observed for HVc neurons (Margoliash 1983, 1986; Margoliash and Konishi, 1995; Margoliash and Fortune, 1992; Sutter and Margoliash, 1994; Volman, 1996; Lewicki, 1996). The major difference observed is a progression of increasing selectivity for song from HVc to Area X to lMAN (Doupe and Konishi, 1981; Maekawa and

Uno, 1996; Doupe and Solis, 1997). It is difficult, however, to normalize selectivity indices across nuclei, especially if they have strikingly different spontaneous rates as do these nuclei. Also, comparing samples of HVc neurons with Area X or lMAN neurons is complicated by the fact that the HVc samples contain RA-projecting as well as Area X-projecting cells. This difficulty is compounded by the lack of information comparing auditory properties of RA-projecting and Area X-projecting HVc neurons. Thus, the striking feature that emerges from these analyses is the consistency of selectivity for BOS observed for HVc, Area X, and lMAN neurons. A similar conclusion obtains from comparisons of RA and HVc, although the RA data are not as extensive as are the data for the anterior forebrain pathway (Vicario and Yohay, 1993; Margoliash, in press; Dave et al., 1997). The absence of major differences in functional properties of HVc and post-HVc auditory neurons stands in contrast to the clear differences in functional properties described for properties of the ascending auditory pathways—for example, comparing Field L with HVc (Margoliash, 1986; Lewicki and Arthur, 1996)—and for properties of the hierarchically organized motor pathways (Vu et al., 1994; Yu and Margoliash, 1996).

Data from Awake Animals. The auditory response properties described above, however, have mostly derived from anesthetized birds. The interpretation of physiological properties in anesthetized, nonbehaving animals must be approached cautiously (Heiligenberg, 1991). In some cases, it has proven essential to assess physiological properties in awake animals whose behavioral state is well controlled (Kupfermann and Weiss, 1978; Eaton, 1983). One approach is to compare properties in anesthetized preparations (which have important technical advantages) with properties in awake preparations, where behavioral salience can be assessed.

There are relatively few examples in which the physiological properties of song system neurons were assessed in awake birds. In one case, the HVc of white-crowned sparrows was implanted with fixed multiunit electrodes. On days of experiments over the following 1–3 months, awake birds were restrained and auditory responses were assessed by presenting playback of conspecific songs and each BOS. For all days and recording sites, neurons gave vigorous responses to BOS, and weaker responses to conspecific songs (Margoliash, 1986). In another case, Vicario and Yohay (1993) demonstrated auditory responses in RA in an awake-restrained paradigm. Inexplicably, we have had great difficulty replicating the results of Vicario and Yohay (1993) (see below). There are no published data from awake-restrained recordings in Area X or lMAN.

The chronic recording technique of Yu and Margoliash (1996) offers a direct method to address this problem. Unrestrained birds in a quiescent but alert state were presented with playback of various songs. In the HVc, a small sample of units in awake birds ($n = 27$ single units, seven birds) had rates of ongoing activity similar to those observed for a much larger population of units in urethane-anesthetized birds (Dave et al., 1997; Margoliash et al., 1994). Most neurons in the awake birds showed auditory responses, and most auditory responses were excitatory (at three recording sites, all four units were inhibited by all stimuli presented). All excitatory neurons exhibited response to playback of the BOS (Dave et al., 1997). Without fail, weaker responses were observed when birds were presented with conspecific songs or with reversed BOS. Hence, these data indicate that for the sample of HVc neurons Yu and Margoliash (1996) recorded under chronic conditions, the auditory response properties were at least qualitatively similar to those observed in anesthetized birds (Margoliash and Fortune, 1992; Margoliash et al., 1994). There have been several reports that lesions of HVc may affect perception of conspecific songs (Brenowitz, 1991; Okanoya and Watanabe, 1995). Thus, it should be interesting in future experiments to have birds actively report their song preference using a behavioral paradigm while recording HVc neuronal responses.

In marked contrast to the HVc data, under the same chronic recording conditions we observed complete lack of auditory responses in RA neurons (Margoliash, in press; Dave et al., 1997). During playback of the BOS or any other stimulus, only the regular discharge typical for ongoing (spontaneous) activity in RA was observed. The same neurons exhibited strong activity when birds were singing (Yu and Margoliash, 1996). RA neurons also failed to respond when females in adjacent half-cages called to the males.

To explore this surprising result, we conducted further experiments using the awake-restrained paradigm. We have only very rarely observed auditory responses in RA when birds were awake but restrained, and those responses were weak (Dave et al., 1997; Vicario and Yohay, 1993). In four birds, all 14 single units and nine multiunits failed to exhibit auditory responses. Most units in the remaining bird (four of six single units, five of six

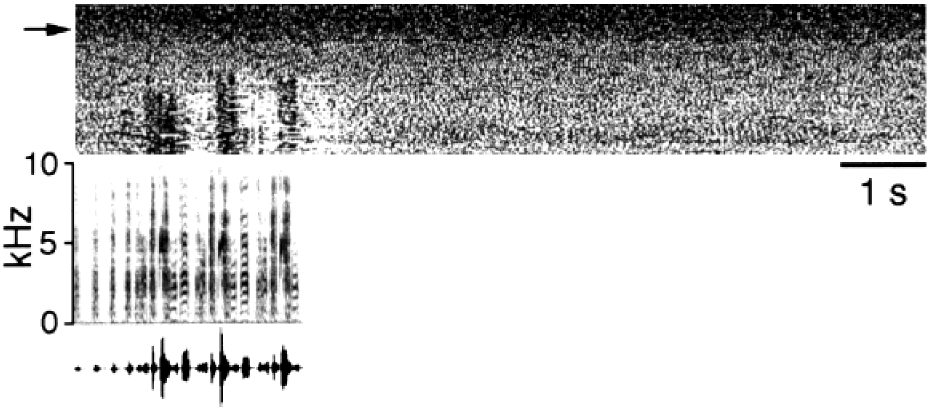

Figure 3 Raster plot of multiunits in RA. Each tick represents the time of a spike, and each row represents one repetition of the bird's song used as a stimulus (spectrograph and oscillograph at the bottom). Initially the bird was awake. At the arrow, the bird was injected with urethane. Note that the ongoing activity decreased shortly thereafter followed awhile later by emergence of a strong response to the song.

multiunits) showed weak auditory responses. These auditory responses were much weaker than those obtained in anesthetized birds (see below).

We have confirmed the previous reports that RA neurons exhibit strong BOS-selective auditory responses in urethane anesthetized birds (Vicario and Yohay, 1993; Doupe and Konishi, 1991). To directly assess the potential role of urethane in unmasking RA auditory responses, we conducted experiments where RA neurons were recorded prior to and after the bird was anesthetized. (As a control, we also recorded from HVc before and after the RA recordings to assess the viability of the preparation as measured by song-selective auditory responses in HVc.) We found complete lack of response to BOS in RA of awake-restrained birds, and clear auditory responses after birds were anesthetized. Particularly compelling were the cases where a recording was maintained while the bird was being anesthetized. For example, the multiunit recording depicted in Figure 3 did not respond to BOS prior to administration of the anesthetic (at the arrow), but began to respond shortly thereafter.

These results suggest that auditory activity normally does not access the descending motor pathway for song, at least in awake adult birds. Thus, these data cast serious doubt on the theory proposed by Williams and Nottebohm (1985), which was based on recordings in anesthetized birds, that auditory activity in the descending motor pathway in songbirds is involved in the moment-to-moment perception of conspecific songs (see also Margoliash, in press). These data do not exclude the possibility that auditory input to RA is available at special times: for instance, when an animal is stressed in the laboratory or when it is learning to sing. To address the latter point, it will be valuable to assess the auditory response properties of RA neurons in awake juvenile birds.

FUNCTIONAL ORGANIZATION OF THE ANTERIOR FOREBRAIN PATHWAY IN AWAKE BIRDS

Lesions of Area X or lMAN have little immediate qualitative effect on adult song production, yet disrupt song development (Bottjer et al., 1984; Nordeen and Nordeen, 1993). lMAN axons innervate RA early in life, whereas RA innervation by HVc axons is delayed (Gurney, 1980; Konishi and Akutagawa, 1985; Mooney and Rao, 1994). Coupled with the erroneous claim (see below) that there is no neuronal activity in Area X and lMAN during singing in adult birds (McCasland, 1987), these observations suggested a nonmotor (i.e., auditory) role for the action of the anterior forebrain pathway, perhaps exclusively during song development. This perspective has been the basis for much of the theoretical speculation regarding the action of the anterior forebrain pathway, but recent data challenge this perspective.

Two studies that investigated the long-term effects of lesioning lMAN described changes in song. Canaries that received lMAN lesions in the summer sang impoverished songs when they came into song the following spring (Nottebohm et al., 1990). In a preliminary report, adult white-crowned sparrows with lMAN lesions produced altered songs when they were induced to sing by manipulating the photoperiod, but only if the birds had failed to copy tutor models during song development. Most notably, the altered white-crown songs incorporated syllables previously copied during song development but subsequently dropped during song crystallization (Benton et al., 1994; T. J. DeVoogd, personal communication). This is the first evidence that syllables learned in plastic song but not committed to adult song are not irretrievably lost at the time of song crystallization. Since these syllables had been previously learned by the sparrows, it is difficult to conclude whether their reemergence following lMAN lesions was the result of a second round of auditory feedback–mediated trial-and-error learning. Chronic loss of lMAN input to RA may destabilize the RA network, resulting in expression of previously unfavored patterns of activity (i.e., the reemergent syllables). In juvenile birds, MAN lesions reduce the volume and number of RA neurons (Akutagawa and Konishi, 1994). A reduction in RA volume was not observed in the adult white-crowned sparrows with lMAN lesions, but this does not exclude other nonspecific effects on circuitry (T. J. DeVoogd, personal communication).

Direct evidence of a role for the anterior forebrain pathway in singing has recently been described. In one approach, expression of immediate-early genes (IEG) in HVc and RA during singing has been demonstrated. The same IEGs exhibit little or no expression when the bird hears playback of his own song, and are strongly expressed when deafened birds sing (Rhea and Doupe, 1997; Jarvis and Nottebohm, 1997). The expression of the IEG ZENK was particularly interesting because it also exhibited high levels in Area X and lMAN (Jarvis and Nottebohm, 1997). The similarity of IEG expression observed in normal-hearing and deafened birds suggests that these patterns of expression are independent of auditory feedback, and hence reflect a motor component.

To directly address the physiologic properties of the anterior forebrain pathway in song production, we have begun to record from Area X and lMAN in singing birds, using the same techniques reported by Yu and Margoliash (1996). To date, two birds have been successfully recorded in Area X, resulting in a total of 13 single units while the birds sang a variable number of songs or while auditory stimuli were presented to the bird (Table 1). Although this data set is small, some patterns already emerge.

In awake birds, Area X neurons have very high levels of ongoing activity (126 ± 37 spikes/s, 13 units, range 66–164 spikes/s). This can be compared with data for urethanized birds, where ongoing rates of a large sample of Area X neurons are 19 ± 3 spikes/s in adults, and 30 ± 3 spikes/s in juveniles (Doupe, 1997). To what degree these differences in ongoing rates reflect differences in the two behavioral conditions or in the sample of neurons recorded under the two conditions (sampling bias) remains to be determined.

For five of the Area X recording sites (six single units), the bird sang three or more songs during the recordings. For all of these single units we observed activity during singing. Three units (three recording sites) were recorded in bird XX02. One of the neurons exhibited strong excitatory activity and was clearly premotor. The neuron exhibited time-locked activity starting prior to each element of song, including the initial introductory note [Fig. 4(A)]. The similarity of the activity pattern (histogram) for the different motifs (groups of syllables) is noteworthy, reminiscent of neuronal activity in HVc [Fig. 4(A)]. The neuron also exhibited premotor activity in relation to the long call [Fig. 4(B)]. The other two units from XX02 also exhibited premotor activity (Fig. 5). In contrast, the three single units (two recording sites) from Area X in bird Yu51 exhibited distinctly different patterns of activity during singing. For all three units, the activity patterns in relation to singing were dominated by inhibition, and were more modulatory in nature (less tightly locked to specific syllables) than observed in HVc (Fig. 5). These Area X neurons in bird Yu51 did not appear to be modulated with each and every syllable. Whether these neurons were responding to auditory feedback or in relation to motor activity during singing cannot be determined alone from these data. Recordings from deafened birds and other manipulations can address this issue. Obviously, in future experiments it will be valuable to examine the apparent differences between the two birds in relation to the topography of Area X.

Surprisingly, as with the RA data presented above, we have found very little evidence of any auditory activity in Area X when broadcasting song to quiescent birds. Neither the units that were excited during singing nor the units that were inhibited during singing exhibited strong activity to playback of BOS. The unit with the strongest activity to song playback exhibited only a very weak response, including slight excitatory and inhibitory modulations of its high level of baseline activity (Fig. 6). None of the other units showed evidence for modulation of spike rates in response to presentation of BOS (Fig. 6). This includes 10 additional units with 8–

Table 1 Number of Times a Bird Sang or a Song Was Broadcast While Recording from Area × Single Units

XX02			Yu51		
Site	Auditory[1]	Singing[2]	Site	Auditory	Singing
1	8	1	2	0	1
2	37	9–10	6	11	1
5	5	1	7/1	10	3
9	12	10	7/2	10	3
13	21	1	9	20	1
14	35	1	10	35	6
17	25	9			

[1] Number of presentations of BOS.
[2] Number of songs the bird sang.

37 presentations of BOS (Table 1). Thus, if the activity of these neurons during singing was indeed affected by auditory feedback, then the auditory feedback during singing must be gated to preclude auditory input from activating Area X neurons at other times.

The preliminary nature of the Area X data needs to be stressed. As well as the relatively small sample size and the heterogeneity of unit activity patterns, there is a topography in Area X that our recordings have barely begun to sample. In addition, in these preliminary experiments we have employed BOS exclusively as the auditory test stimulus. Area X neurons that do not respond to BOS might respond to other stimuli (e.g., other songs), although BOS is the most effective stimulus in anesthetized birds (Doupe, 1997). The shortcomings of the present data set notwithstanding, it is reasonable to tentatively conclude that during singing, many Area X neurons are likely to exhibit premotor activity, and that when the bird is not singing, auditory activity in these Area X neurons is likely to be weak or absent. This refocuses consideration of the role of the anterior forebrain pathway away from a purely sensory role to include a sensorimotor or motor role, as is discussed below.

CONCLUSIONS AND FUTURE DIRECTIONS: THE FUNCTIONAL ORGANIZATION OF LEARNING

Sensorimotor Learning Is Distributed

There is extensive evidence that functional changes associated with song development occur at multiple sites in the birdsong system. One line of evidence is the match between the hierarchical nature of the neural representation of the singing behavior and of song itself. All levels of organization of song are affected by learning, albeit to different degrees and with species differences (e.g., Marler and Sherman, 1985). In the zebra finch, the data support the hypothesis that nuclei in the motor pathway code for different levels of song organization (motif, syllable, and note). Organization at each level is apparently the result of interaction between input from the higher level and intrinsic circuitry (Yu and Margoliash, 1996). Thus, there is no one site where motor learning ‘‘takes place.’’ Rather, changes are seen at several loci. In the birdsong system, motor learning involves changes at synapses, but these changes cannot be meaningfully interpreted independent of the neural network and its relation to behavior.

Although the basic framework presented above is likely to be accurate, some caveats and extensions of the hierarchical organization hypothesis are noteworthy. The most direct data supporting this hypothesis are the neurophysiological recordings in singing birds (Yu and Margoliash, 1996). These recordings are conducted under extremely challenging conditions, however, so that incomplete data sets that result from sampling biases may be exacerbated. For example, there is no direct evidence that all the classes of HVc neurons or even both RA-projecting and X-projecting HVc neurons have been recorded under these conditions. The similarity in responses of multiunits and single units recorded at each site partially addresses this concern (Yu and Margoliash, unpublished data). In this context, also noteworthy are the electrical stimulation results of Vu et al. (1994), which provided strong evidence for a hierarchical scheme of organization.

More generally, oscine birds exhibit a wide variety of singing behaviors (see Fig. 1 in Brenowitz et al., 1997). Different species may exhibit different

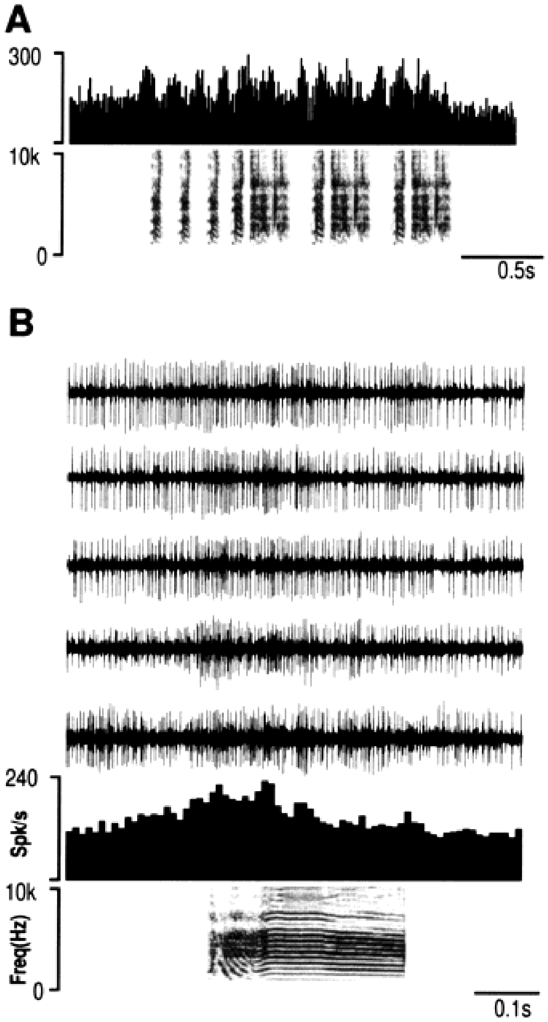

Figure 4 Premotor excitatory activity of Area X neuron XX02-09. (A) The top trace shows the extended activity histogram (EAH) and the bottom trace shows the spectrograph of the bird's song. The EAH is a composite of individual spike rate histograms, one per syllable in the spectrograph, which is a graphical device necessary to compensate for the slight differences in timing of syllables that occur each time the bird sings (Yu and Margoliash, 1996). Increases in the unit's rate of firing precede the first introductory syllable and most syllables of song. (B) Raw traces are shown from five of 39 times the bird produced the long call, with the spike rate histogram of all 39 calls and the spectrograph of the call on the bottom.

degrees of stereotypy, form phrases from few or many repetitions of syllables, sing continuously or in discrete songs, have one or many song types, and produce these song types with immediate or eventual variety (i.e., constantly switching between song types or singing a bout of one song type before switching to the next, etc.). In future work, it will be extremely fruitful to examine properties of the neural network in species chosen to represent such variation. Such analysis can help uncover the functional organization used at different levels of the birdsong motor system. Of course, the analysis of the motor system of laboratory-reared birds whose song learning has been manipulated by the investigator is an attractive and complementary approach.

Reassessment of the Role of the Anterior Forebrain Pathway in Sensory Acquisition and Sensorimotor Learning

Lesions of the anterior forebrain pathway nuclei severely disrupt song learning (Bottjer et al., 1984) but have less immediate effects on adult song; this may depend on species (Nottebohm et al., 1990; Nordeen and Nordeen, 1993; Benton et al., 1994). In juveniles, lesions of lMAN result in an overly simple, highly stereotyped song as if the bird crystallized its song too early in development. Lesions in Area X result in birds whose songs become variable in structure, similar to, though less severe than the effect of early deafening on songs (Sohrabji et al., 1990; Scharff and Nottebohm, 1991). By themselves, these lesion data do not distinguish between potential sensory, sensorimotor, and motor roles of the anterior forebrain pathway and its relation to the descending motor pathway. Recent data shed some light on this problem.

One hypothesis is that nuclei in the anterior forebrain pathway may serve as a site of modification during sensory acquisition and be involved in sensorimotor learning, ultimately with the lMAN projection to RA modifying the HVc to RA connections during song development (e.g., Mooney, 1992; Doupe, 1993; Doya and Sejnowski, 1995). Evidence for this hypothesis includes effects of lesions (Morrison and Nottebohm, 1993) and chemical blockade (Aamodt et al., 1996, Basham et al., 1996) of lMAN that have been interpreted in terms of sensory processing. One common problem in interpreting these results is the possibility that the effects arise from lesion or blockade of the surrounding shell of lMAN, which projects to archistriatum but not to RA (Johnson et al., 1995). Nevertheless, these studies stand as the best evidence to date demonstrating a sensory role for the anterior forebrain pathway during song development. It may also be interesting to pursue such studies in female birds (Williams, 1985). A recent study found a positive relation associating lMAN volume with female cowbird song perception (Hamilton et al., in press). Female cowbirds do not sing, so the properties of

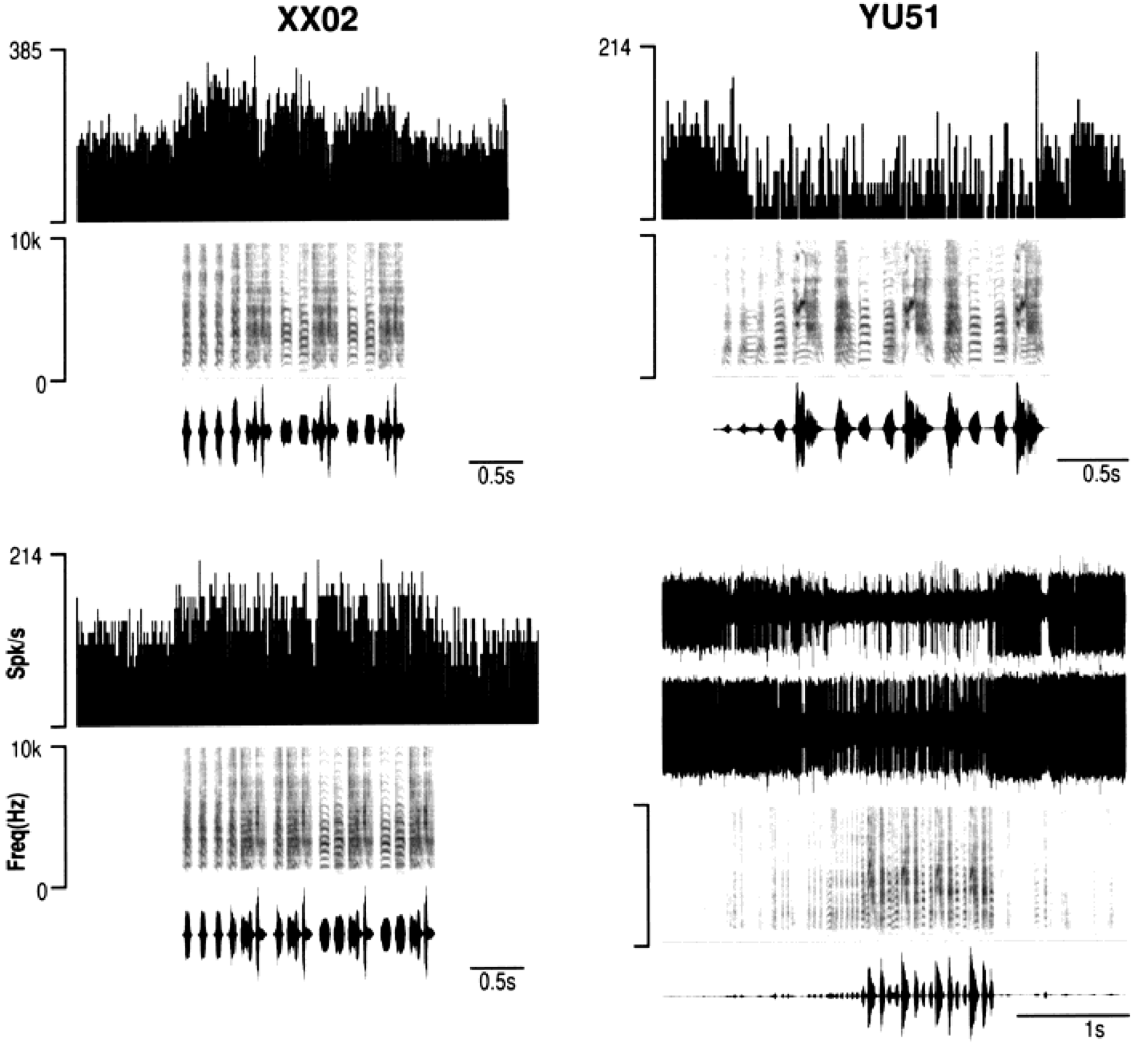

Figure 5 Five single units recorded from Area X. EAHs (Fig. 4) are shown for both neurons recorded from XX02, and for a neuron recorded from Yu51. Single traces are shown for two other neurons recorded simultaneously in Yu51. The XX02 neurons exhibited excitation and premotor activity during singing, whereas the Yu51 neurons exhibited inhibition during singing.

lMAN in those birds are presumptively related to an auditory task.

The sensory acquisition hypothesis has yet to find support in the physiologic data. Neurons in the anterior forebrain pathway are modified during sensorimotor learning, but the evidence that they are modified during the early sensory acquisition (song memorization) phase is equivocal, although it should be noted such experiments have only recently started and are technically difficult (Doupe, 1997; Doupe and Solis, 1997). The sensory acquisition hypothesis also suffers conceptual difficulties that have yet to be addressed. All nuclei in the anterior forebrain pathway are topographically organized (see above), a topography whose ultimate reference is the muscle groups of the syrinx. If a myotopic representation is established prior to the sensory acquisition phase of song development, this would seem to be inconsistent with a role of that pathway in sensory acquisition. This sequence of events would require the acoustic song stimulus to be mapped (memorized) in a motor coordinate framework prior to the bird developing such a mapping through the song-learning process.

A difficulty with the sensorimotor hypothesis of the role of the anterior forebrain pathway is that it is incomplete, failing to explain the development of response properties of HVc neurons. HVc neurons participate in direct motor control and are associated with the strongest evidence to date for sensorimotor

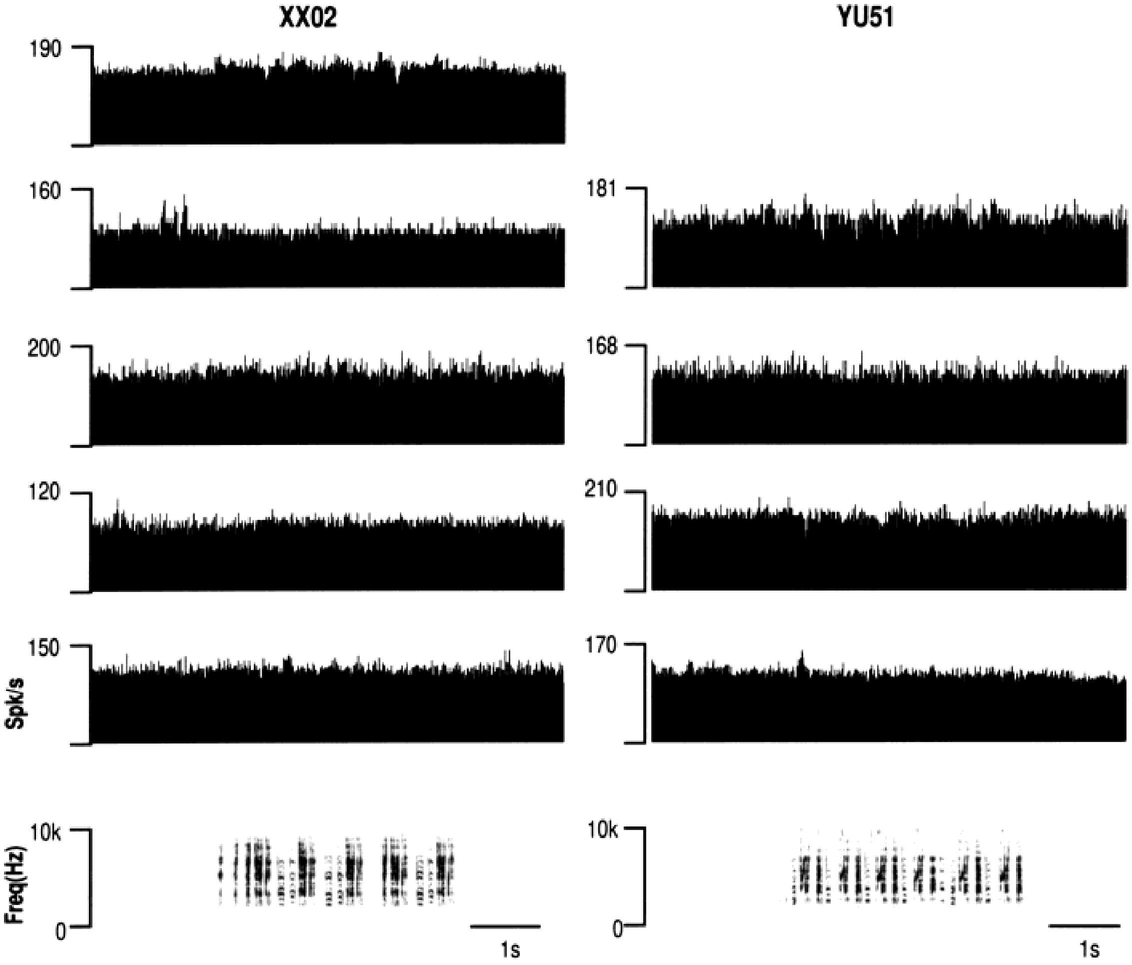

Figure 6 Nine peristimulus time histograms (PSTHs) of Area X single units responding to the bird's own song (BOS). Sonographs below each column indicate alignment of stimulus with histograms. The five units on the left are from bird XX02 (sites 2, 5, 9, 13, and 17); the four units on right are from bird Yu51 (sites 6, 7/1, 7/2, and 10). The small peaks in the PSTHs of XX02 site 5 (prior to stimulus onset) and Yu51 site 10 result from bursts that occurred only in one stimulus repetition, and do not reflect a consistent pattern of activity.

learning in the birdsong system. The anterior forebrain pathway is *not* recursive in the sense of Nottebohm et al. (1990)—it does not project back onto HVc. Other pathways that may provide feedback from RA to HVc or from RA back to RA have recently been described (Wild, 1993b; Foster et al., 1997; Vates et al., 1997). If the role of the anterior forebrain pathway is to store the acquired template and/or to provide an auditory feedback error signal, then what error signal shapes HVc neurons? If, on the other hand, the error signal is available to HVc, then it in turn can program RA. Certainly other possibilities may obtain, but they are complex, and accounts of birdsong learning emphasizing interactions between HVc and lMAN at the level of RA have tended to ignore this.

Distribution of Sensory and Motor Properties. The recent data on distribution of auditory responses within the adult song system also raises the question the behavioral significance of auditory activity in the anterior forebrain pathway. In considering these data, it is useful to compare HVc and post-HVc (RA, Area X, and lMAN) auditory responses. Most HVc neurons are premotor and also auditory, with the auditory responses exhibiting selectivity for specific parameters of the bird's song (Dave et al., 1997; Yu and Margoliash, unpublished results). Several lines of evidence indicate that HVc auditory response properties arise during song learning. The evidence includes the high degree of specificity of response properties in adults (Margoliash, 1983; Margoliash and Fortune, 1992), the fidelity of response to the BOS even in cases when that song is a poor match for the tutor song (Margoliash, 1986), selectivity in the adult for parameters of abnormal songs that result from laboratory manipulations (Margoliash, 1986), and the similarity of response properties throughout the HVc (Sutter and Margoliash, 1994). Indeed, the auditory response properties of HVc multiunits are apparently continuously modified during song development to match the bird's plastic song (Volman, 1993). Thus, the weight of the evidence suggests that auditory properties of HVc neurons are modified during song learning and help to modify the ongoing motor program for song (see Margoliash, 1987). Hence, HVc is a site of sensorimotor learning. Elucidation of the neuronal circuitry within the HVc and how it changes during song development is an exciting challenge for the future.

Auditory song selectivity similar to that described for HVc has been observed in all other song system nuclei examined (see above), and auditory properties of anterior forebrain pathway neurons also track developmental changes in song (Doupe, 1997). The significance of auditory responses in nuclei other than HVc, however, is not fully established. Three points should be noted.

The first issue concerns the patterns of auditory activity observed in the song system nuclei that receive input from HVc. In adult birds, virtually all auditory neurons throughout the song system are selective for BOS. This opens the possibility that auditory selectivity is not the principle response feature being modified in the post-HVc song system.

A second issue relates to the singing-related activity of Area X neurons. In our preliminary chronic/awake recordings from area X (see above), many neurons exhibited singing-related activity. These same neurons failed to exhibit strong auditory responses to playback of BOS. Thus, there exists a nonauditory, motor component in the activity of some Area X neurons. It should be noted that our data set of Area X neurons recorded in awake/chronic birds is small and may be biased to exclude low-spontaneous rate, irregularly firing units, so that the relative abundance of auditory and nonauditory neurons in awake birds has not been determined.

A third issue concerns the distribution of physiological properties of neuron in the anterior forebrain pathway of anesthetized birds. Preliminary experiments demonstrate that auditory responses are commonly observed in Area X neurons in awake-restrained adult birds (P. Rauske, unpublished data). The same experiments also demonstrate that auditory properties of Area X neurons are somewhat sensitive to the anesthetic state of the animal. Some Area X neurons acquire auditory activity and other neurons lose auditory activity when the bird is anesthetized. These results imply a far less severe anesthetic effect than what has been observed for RA neurons, but nevertheless suggest caution in interpreting the data from anterior forebrain pathway nuclei from anesthetized animals. Clearly, the same caution must be applied to recordings of anesthetized animals in other nuclei—especially HVc, where direct comparisons have yet to be made. It is possible that auditory activity in structures that receive input from HVc is highly sensitive to behavioral context. In non-singing birds attending to broadcast song, this might imply that familiarity with song, or the presence of male or female conspecifics under specific conditions may release auditory responses that are otherwise not observed. In singing birds, auditory feedback may be gated, permitting auditory activity to modify neuronal properties but only under conditions that have yet to be experimentally manipulated.

An Alternative Hypothesis for the Role of the Descending Motor and Anterior Forebrain Pathways

If the caveats concerning the preliminary nature of the present data are resolved, this would require rethinking the presumptive role of the anterior forebrain pathway in sensory acquisition and sensorimotor learning. Here we propose an alternative hypothesis.

1. We propose that structures afferent to HVc—for example, Field L, NIf, and/or caudomedial neostriatum—are sites where sensory acquisition modifies auditory properties (e.g., see Chew et al., 1996a,b). These sites would represent stored song memories acquired during song development (Konishi, 1978). Specifically, in this scheme the anterior forebrain pathway would not be the exclusive site of sensory acquisition (Doya and Sejnowski, 1995).
2. Song learning can modify all levels of song programming, but in sparrows has its principal effect on syllable and note morphology (Marler and Sherman, 1985). We propose that auditory feedback–mediated modifications of HVc neurons represent the changes in temporal patterning associated with syllables. These temporal patterns are read out at the level of RA to establish the individual notes

that comprise the syllable. We further propose that auditory feedback–mediated modifications of NIf and/or Uva serve to program song at higher levels of organization (larger units of vocalization). Thus, in this scheme, HVc and NIf and/or Uva would serve as the hypothesized comparitor (Konishi, 1978), receiving realtime auditory feedback via the auditory system up to Field L, and receiving input from the acquired sensory template via alternate pathways (see Margoliash, 1987, for an early description of this hypothesis).

3. A major problem that all sensorimotor systems face is the problem of compensating for delays in the feedback that is used to compute the error signal that reinforces motor programs. This is called the temporal credit assignment problem, and has properly occupied the attention of song system theoreticians (Doya and Sejnowski, 1995; Troyer et al., 1996). For example, in adult birds, neurons in HVc are active in relation to a specific syllable starting approximately 50 ms prior to that syllable (Yu and Margoliash, 1996), and the minimal delay of an auditory signal reaching HVc is about 20 ms (Margoliash, 1983). Additional time may be necessary if song-selective HVc neurons are activated (selectivity implies integration time). Thus, a sensory feedback error signal may reach HVc potentially only after the motor program for that signal has substantially played out or even been completed. This presents a difficult problem in assigning credit or reward to a correct motor gesture, since synaptic plasticity is assumed to rely on temporal correspondence between the activity of presynaptic and postsynaptic elements. The problem may be further compounded in juvenile birds if synchronous activity of nuclei are more variable than in adults.

In view of this problem, we propose that the major role of the anterior forebrain pathway is to resolve the temporal credit assignment problem. The long pathways and feedback projections of lMAN onto Area X are suitable for the required memories or delays. The input from HVc would provide a copy of the motor program at the syllable level, and would also represent an error signal—an acoustic difference signal—computed at the level of individual syllables. Possible feedback signals could also arise from the thalamic projections of RA. Ultimately, the output of lMAN onto RA would represent a reward signal that biases RA to produce correct output, assuming correct input from HVc in future bouts of singing. The reward signal could perhaps be modulated ballistically during singing, but not in realtime by auditory feedback. Perhaps the inability to use feedback to correct motor output in realtime is why song learning is an extended ontogenetic process. Each correct or incorrect output may be rewarded or punished appropriately, but because the temporal resolution of the reward signal is poor, the correction term can have only a small influence to bias the network on any given attempt at singing.

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