Neural Pathways for the Control of Birdsong Production

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ABSTRACT: As in humans, song production in birds involves the intricate coordination of at least three major groups of muscles: namely, those of the syrinx, the respiratory apparatus, and the upper vocal tract, including the jaw. The pathway in songbirds that controls the syrinx originates in the telencephalon and projects via the occipitomesencephalic tract directly upon vocal motoneurons in the medulla. Activity in this pathway configures the syrinx into phonatory positions for the production of species typical vocalizations. Another component of this pathway mediates control of respiration during vocalization, since it projects upon both expiratory and inspiratory groups of premotor neurons in the ventrolateral medulla, as well as upon several other nuclei en route. This pathway appears to be primarily involved with the control of the temporal pattern of song, but is also importantly involved in the control of vocal intensity, mediated via air sac pressure. There are extensive interconnections between the vocal and respiratory pathways, especially at brain-stem levels, and it may be these that ensure the necessary temporal coordination of syringeal and respiratory activity. The pathway mediating control of the jaw appears to be different from those mediating control of the syrinx and respiratory muscles. It originates in a different part of the archistriatum and projects upon premotor neurons in the medulla that appear to be separate from those projecting upon the syringeal motor nucleus. The separateness of this pathway may reflect the imperfect correlation of jaw movements with the dynamic and acoustic features of song. The brainstem pathways mediating control of vocalization and respiration in songbirds have distinct similarities to those in mammals such as cats and monkeys. However, songbirds, like humans, but unlike most other non-songbirds, have developed a telencephalic vocal control system for the production of learned vocalizations. © 1997 John Wiley & Sons, Inc. *J Neurobiol* **33**: 653–670, 1997

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INTRODUCTION

What may now be described as the classical vocal control pathway for song production (see Fig. 2 in Brenowitz et al., 1997) dates from the discovery of Nottebohm et al. (1976) of the projections from the high vocal center (HVc) to the robust nucleus of the archistriatum (RA) to the tracheosyringeal motor nucleus (nXIIts) in the canary (*Serinus canaria*). Although this pathway is unquestionably of central importance for the control of the syrinx, the bird's vocal organ, its frequent depiction in the past as the sole means of vocal control suggests that this is all that is required for vocalization. Nothing could be further from the truth, however, for if syringeal control were all there were to vocalization, the bird would never utter a sound. In fact, vocalization is as dependent on the respiratory system as it is on the syringeal system, and in ways that are not always fully appreciated. Thus, while it is generally recognized that the abdominal and internal intercostal expiratory muscles compress the associated air sacs to provide the necessary airstream for vocalization, this action is often described, and then summarily dismissed, as bellows-like, as if all the respi-

ratory system had to do was to provide a constant pressure head for use by the syrinx. That this is a totally inadequate conception of the role of the respiratory muscles in vocalization has been recognized by some workers for some time (e.g., Calder, 1970; Gaunt et al., 1982; Brackenbury, 1980, 1989), but more recently, it has become clear that the extremely precise temporal and modulatory control to which these muscles are subject by the nervous system rivals that of the syringeal muscles themselves, and includes control of inspiratory as well as expiratory muscles (Hartley and Suthers, 1989; Hartley, 1990; Goller and Suthers, 1996a,b; Suthers, 1997; Suthers and Goller, 1997; Wild et al., 1997a).

In addition, there is now evidence that supravocal structures such as the jaw are also involved in vocal production in songbirds (Westneat et al., 1993; Hoese and Westneat, 1996; Suthers et al., 1996) as they are in human speech and song, so that any consideration of vocal control systems in birds would be incomplete without some discussion of these structures.

There are thus three main systems for the control of vocalization: a vocal (syringeal) system, a respiratory system, and a supravocal system. In addition, since many birds often adopt characteristic postures during vocalization, especially those with a pronounced visual display during song, a case could be made for a fourth system involving general somatic musculature of the neck, body, and wings. These systems cannot, of course, function independently of each other during song without ensuing chaos. Therefore, the most important and essential requirement for effective vocalization in general, and song in particular, is coordinated neural control of these diverse sets of muscles, and it is a tenet of the present article that this coordination will be reflected in the organization of the nuclei and pathways subserving each of the effector systems, particularly of the vocal and respiratory systems.

The present article therefore attempts to present a more holistic view of vocal control in birds by describing the neural pathways mediating control not only of the syrinx but also of the respiratory apparatus, to a lesser extent that of the jaw, and to the least extent that of the body, since so little is known about the last with respect to vocalization.

NEURAL PATHWAYS FOR THE CONTROL OF SONG

These pathways (Fig. 2 in Brenowitz et al., 1997) have been reviewed in various contexts on several occasions (e.g., Konishi, 1985, 1989; DeVoogd, 1989; Arnold, 1992; Nottebohm, 1996; Nottebohm et al., 1990; Brenowitz and Kroodsma, 1996). They can be grouped into one set—the anterior forebrain pathways, primarily concerned with vocal learning (Doupe and Solis, 1997), and another concerned with vocal production, which this article will discuss.

The Classical Vocal Control Pathway: HVc–RA–nXIIts

The origin, course, and termination of this pathway will be described in reverse order, since an appreciation of what is being controlled is considered vital to understanding the system (Suthers, 1997).

nXIIts: The Tracheosyringeal Motor Nucleus. Since the syrinx is a uniquely avian structure, it follows that the hypoglossal nucleus (nXII) that supplies its motor innervation is in some ways also unique to birds: Only the rostral and slightly more ventral part of the nucleus supplies intrinsic tongue muscles, as nXII does in mammals. Approximately the caudal two-thirds innervates the syringeal muscles via a long descending nerve branch which traverses the length of the neck (NXIIts, or simply ts), a fact that would seem to suggest that the syringeal muscles are derivatives of occipital myotomes, which then migrate caudally. The ts also supplies en route so-called tracheal muscles such as tracheolateralis and sternotrachealis, but these can just as legitimately be thought of as extrinsic syringeal muscles, which in non-songbirds are the only muscles acting on the syrinx (King, 1989). Songbirds are usually said to have four to five pairs of intrinsic syringeal muscles, although the word ''intrinsic'' is, strictly speaking, a misnomer, since the attachments of none of them are confined to the syrinx (King, 1989).

Both the lingual and tracheosyringeal parts of nXII have typical multipolar motoneurons, although those of the former are slightly smaller than those of the latter. Their axons pass ventrally through the medial part of the inferior olive and exit the floor of the medulla in a series of rootlets, which immediately collect to form a rostral root carrying lingual efferents and two caudal roots carrying ts efferents (Bottjer and Arnold, 1982). These then pass through deep neck muscles to join a hypoglossal afferent-vagal anastomosis distal to the jugular ganglion. (Unlike the case in mammals, there is a major sensory component of the hypoglossal nerve in some avian species, including songbirds such as

finches) (Wild, 1981, 1990; Bottjer and Arnold, 1982.)

The dendrites of the tracheosyringeal part of the hypoglossal nucleus are more confined to the nucleus and its immediate surrounds than those of the lingual part, which extend a long distance into the ventrolateral medulla (Fig. 1) (Wild, 1993a). In songbirds, this is consistent with a different pattern of inputs to the two parts of the nucleus.

In songbirds, nXIIts is strictly lateralized, i.e., each left and right nucleus supplies only the ipsilateral syringeal muscles. This situation is not present in non-songbirds, even in highly vocal species such as budgerigars (*Melopsittacus undulatus*), because there is a partial crossover of fibers from one ts nerve to the other via an anastomosis partway down the neck. In songbirds, the lateralization of nXIIts has particular implications for the anatomy mediating bilateral control of vocal production in songbirds, and this point will be addressed below.

A detailed description of nXIIts and its position, volume, size of constituent cells, cell density, sex difference, laterality differences, and of the effects of testosterone has been made for the canary by De Voogd et al. (1991) (see also Nottebohm and Arnold, 1976). In this species, in which song control is strongly biased in favor of left-sided peripheral structures, and in which males sing and females sing little or not at all (although this sex difference may be less in wild birds), nXIIts was found to be 6.4% larger on the left than the right in males (11.4% larger on the left in females), 83% larger in males than females, with individual neurons having a 13–18% larger area in males than females. However, the number of neurons does not differ on the left and right sides and does not differ between the sexes. This, suggests, of course, that the volume differences are largely accounted for by neuropil, although not necessarily by increases in synaptic density (Clower et al., 1989).

A possibility that has not been explored is whether there are synapses on the processes of nXIIts motoneurons outside the nucleus as defined by the cell bodies (DeVoogd et al., 1991). In normal Nissl-stained material, there is a pale, relatively cell-sparse region between the dorsal border of nXIIts and the dorsal motor nucleus of the vagus (nX), and having a characteristic protrusion that projects dorsomedially (Fig. 1). A narrower, pale region also surrounds the nucleus ventrally. The wider region dorsal to nXIIts was called suprahypoglossal (SH) by Wild (1993a), and includes the region of small cells dorsolateral to nXIIts that was noted by DeVoogd et al. (1991) in the canary. SH (and the

region ventral to nXIIts) can be seen to be completely filled with the retrogradely labeled processes (axons and presumably dendrites) of nXIIts motoneurons if the ts nerve is loaded with horseradish peroxidase (HRP) or cholera toxin conjugated to HRP (CTB-HRP) (Wild, 1993a). Furthermore, SH (and the region ventral to nXIIts) is completely filled with the fibers and presumptive terminations of descending projections to nXIIts, whether these originate from RA, the dorsomedial nucleus of the intercollicular complex (DM), or any of the other respiratory-vocal nuclei of the pons and medulla, such as the ventrolateral parabrachial nucleus (PBvl) (Wild et al., 1990, 1997b; Wild, 1993a) (see below), and frequently the apparent density of this labeling in SH is as high or higher than that within nXIIts itself, even after an injection of tracer into RA (Figs. 1 and 2). Furthermore, there are also neurons within SH and immediately ventral to nXIIts that project to the spinal cord (Wild, 1993b; Wild et al., 1997b), and these, too, could well receive projections from descending vocal control pathways. The SH area is likely to gain in functional importance in the context of the myotopic organization of nXIIts (Vicario and Nottebohm, 1988; Ruan and Suthers, 1996), our increasing knowledge of the function of particular syringeal muscles during song (Goller and Suthers, 1996a,b), and the realization that there are several inputs to nXIIts other than those originating in RA and DM (see below).

Nucleus Robustus Archistriatalis (RA). In terms of the control of song, the principal source of descending inputs to nXIIts is an encapsulated, ovoid to spherical ball of neurons located in the medial part of more caudal regions of the archistriatum (RA). Such a nucleus is not present in non-songbirds, including suboscines such as the phoebe, *Sayornis phoebe* (Kroodsma and Konishi, 1991; Brenowitz et al., 1997), although an analogous region of the archistriatum in budgerigars also projects upon nXIIts (Paton et al., 1981; Striedter, 1994; Brenowitz et al., 1997).

The cell types of RA are not homogeneous. De-Voogd and Nottebohm (1981) recognized four types in RA of the canary, including one with small, nonspiny dendrites (type I) and one with thick, very spiny dendrites (type IV), the latter being the most frequently stained in their Golgi material. Gurney (1981) recognized two cell types in RA of zebra finch, roughly corresponding to the two types of DeVoogd and Nottebohm (1981), but felt that both spinous and aspinous types were projection neurons.
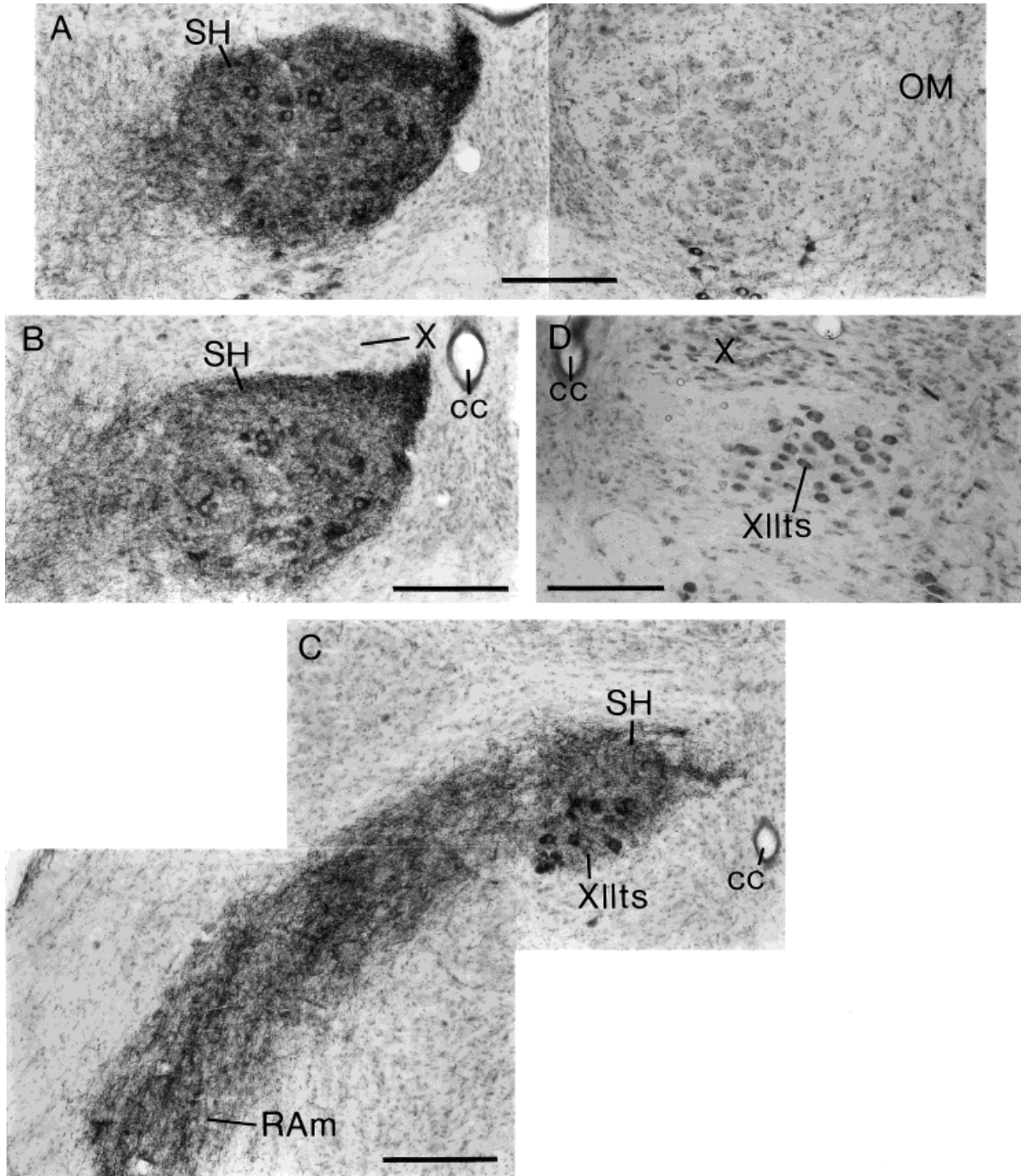
The axons of RA cells leave the nucleus at its

Figure 1 Transverse sections through the medulla of a male zebra finch showing fiber and terminal labeling in the left tracheosyringeal nucleus (XIIts) and suprahypoglossal area (SH) just rostral to the obex [(A) left side], just caudal to the obex (B), and further caudally at the level of nucleus retroambigualis (RAm) (C), following an injection of biotinylated dextran amine (BDA) in the ipsilateral nucleus robustus archistriatalis (RA). The left XIIts motoneurons were retrogradely labeled with unconjugated cholera toxin B-chain (visualized immunohistochemically) to show the extent of the nucleus as defined by the cell bodies. The smaller, retrogradely labeled neurons ventral to nXIIts are lingual motoneurons. In (A) (right side) and (D) (normal Nissl-stained section of catbird, *Dumatella carolinensis*), note the relatively pale surround to nXIIts, particularly dorsally, viz., SH. cc = canalis centralis; OM = tractus occipitomesencephalicus; X = nucleus motorius dorsalis nervi vagi. Calibration bars = 200 μm.
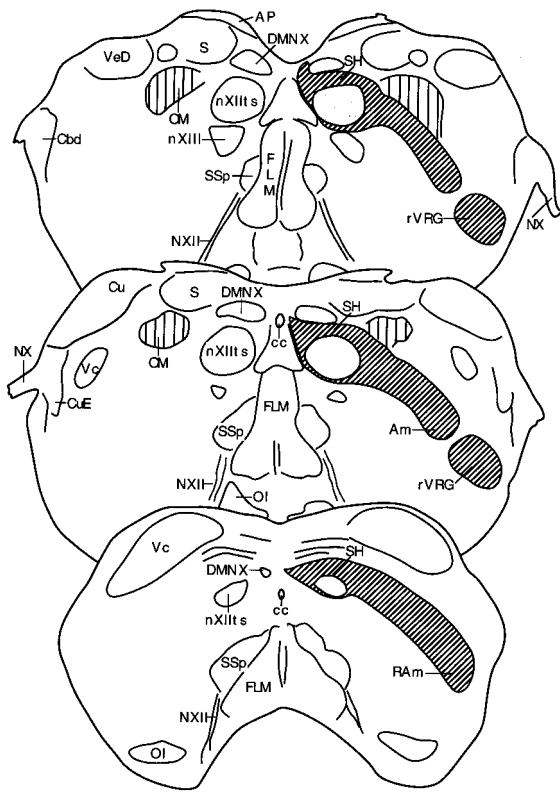
Figure 2 Schematic representation of fiber and terminal labeling (diagonal hatching, including nXIIts) at three rostrocaudal levels of the medulla in a zebra finch, such as results from an injection of biotinylated dextran amine (BDA) in the ipsilateral RA (Wild, 1993b). The relatively small contralateral projection is not shown. The top section is immediately rostral to the obex, the middle section just caudal to the obex, and the bottom section at the most caudal medulla. Note the extent of labeling surrounding the cell bodies comprising nXIIts, and in the ventrolateral medulla. The regions designated rVRG and RAm are the principal repositories of bulbospinal neurons projecting upon inspiratory and expiratory motoneurons, respectively, and of inspiratory- and expiratory-related unit activity (Wild, 1993a; Reinke and Wild, 1996, 1997). Am = nucleus ambiguus (where laryngeal motoneurons are located); AP = area postrema; Cbd = tractus spinocerebellaris dorsalis; cc = canalis centralis; Cu = nucleus cuneatus; CuE = nucleus cuneatus externus; DMN X = nucleus dorsalis motorius nervi vagi; FLM = fasciculus longitudinalis medialis; NX = nervus vagus; NXII = nervus hypoglossus; nXIIts = nucleus nervi hypoglossi, pars tracheosyringealis; OI = nucleus olivaris inferior; OM = tractus occipitomesencephalicus; RAm = nucleus retroambigualis; rVRG = rostral ventral respiratory group; S = nucleus tractus solitarius; SH = suprahypoglossal area; SSp = nucleus supraspinalis; Vc = nucleus descendens nervi trigemini, pars caudalis; VeD = nucleus vestibularis descendens.

rostral end and course rostroventrally into the floor of the hemisphere, where they form the most medial portion of the occipitomesencephalic tract (OM), which also carries fibers originating in other parts of the archistriatum (Zeier and Karten, 1971; Wild, 1993a). At the level of the anterior commissure, OM bends ventromedially into the diencephalon and passes caudally, ventral to the nucleus ovoidalis (Ov). Fibers in OM destined for nXIIts then traverse the whole length of the brain stem in the dorsal tegmentum and access the nucleus from its lateral side. Fibers and terminations are distributed throughout the whole length of nXIIts but as mentioned above, they are by no means confined to the cell bodies alone, but surround the nucleus, particularly on its dorsal aspect, where they are concentrated in the SH region (Wild, 1993a) (Fig. 2). The RA-nXIIts projection is very largely ipsilateral in the two songbird species so far examined, viz. canary and zebra finch, but the analogous projection in budgerigars is strongly bilateral and, unlike the case in songbirds, also terminates upon the lingual portion of nXIIts (Paton et al., 1981; Striedter, 1994).

In the adult zebra finch, axons of cell bodies in ventral and medial regions of RA preferentially terminate in caudal regions of nXIIts, where cells innervating the dorsal syringeal muscles are located. Axons of cells located in middle, and to a lesser extent ventrolateral, regions of RA preferentially terminate in rostral regions of nXIIts, where motoneurons innervating ventral syringeal muscles are located (Vicario, 1991b; Vicario and Nottebohm, 1988; Ruan and Suthers, 1996). Since we have only an inexact notion of the specific functions of the various syringeal muscles, it is not possible to identify categorically the control functions of the various parts of RA; but taking into account the activity of different syringeal muscles during song, as described for the brown thrasher (*Toxostoma rufum*) by Goller and Suthers (1996a,b), it may that the ventral part of RA is predominantly concerned with gating phonation via active adduction and abduction of the syrinx, whereas the middle regions of RA are concerned with the control of fundamental frequency, perhaps by their control of motoneurons innervating ventral syringeal muscles that may modulate the tension of the medial tympaniform membranes (Goller and Suthers, 1996b). It is also possible that there are species differences in the role of particular syringeal muscles, and hence in the role of different parts of RA. Vicario (1991a), for instance, attributed an abductive role to M. syringealis ventralis (VS) in the zebra finch, which would place

its control by RA in ventral, rather than middle, regions of the nucleus in this species.

Unlike middle and ventral regions of RA, a dorsal region of the nucleus has indirect, rather than direct, projections upon nXIIts, via DM and several other brain-stem nuclei (Vicario, 1991b; Wild, 1993a; Wild et al., 1997b). Some of the brain-stem nuclei are known to be involved in respiratory control, and thus the dorsal part of RA may be particularly concerned with the respiratory aspects of vocalization (Vicario, 1994). The projections to RA originating in lMAN, unlike those in HVc, are topographic, and those specifically to the dorsal region of RA arise from the most medial part of lMAN (Johnson et al., 1995; Perera et al., 1995; Vates and Nottebohm, 1995). This pattern of projections could therefore suggest a role for specific parts of the anterior forebrain circuit in learning the respiratory patterns associated with singing.

The HVc. Now known to occupy a dorsal part of the pallium known as the neostriatum (itself a misnomer, since it refers to no part of the basal ganglia, as it does in mammals), but once thought to lie in the hyperstriatum ventrale pars caudale (hence the abbreviation HVc, now referring to high vocal center), this nucleus, together with lMAN, provide the only known inputs to RA (Nottebohm et al., 1976; Bottjer et al., 1989). Of the two, HVc is the most directly involved in the control of song production (Vicario and Yohay, 1993) and, from the topographic point of view, at least, occupies the highest level of the descending vocal control pathway. The nucleus is fully discussed by Margoliash (1997).

Respiratory Control Pathways

Respiratory Muscles. The anatomy and what has been traditionally known of the physiology of the inspiratory and expiratory groups of muscles has been thoroughly reviewed by Fedde (1987), although most of the information pertains to non-songbirds, primarily the chicken. Although songbirds do not appear to possess different or more respiratory muscles than non-songbirds (cf. syringeal muscles), they are likely to require more refined control of their actions during song. This is because of the increased demand for dynamic modulation of subsyringeal air pressure in concert with rapid and variable amplitude changes in syringeal resistance as individual notes and syllables are fashioned on a millisecond time scale.

Figure 3 shows in highly schematic form some of the principal inspiratory and expiratory muscles. The designation of the respiratory muscles as inspiratory or expiratory usually refers to their action during quiet breathing, not necessarily to their action during vocalization, since many of them have never been recorded from in this context (Fedde, 1987; Reinke and Wild, 1997). Phonation occurs during expiration, which is brought about by compression of the abdominal and caudal thoracic air sacs by the abdominal muscles Mm. obliquus externus et internus abdominis, M. transversus abdominis, and M. rectus abdominis (when present), and presumably of the internal intercostal muscles. There are no data pertaining to the function of the internal intercostals during song, but the abdominal muscles are known to have pronounced phasic and modulatory activity during avian vocalizations in general and song in particular (Suthers, 1997). Of the inspiratory muscles, only M. scalenus and Mm. levatores costarum have been recorded from during singing. In zebra finch and cowbird, there is a pulse in M. scalenus correlated with every minibreath, and likewise for the levator in cowbird, but neither muscle in either species is active during any part of the actual phonatory period (Wild et al., 1997a). Thus, these muscles do not appear to brake expiration during phonation, in contrast to human intercostal muscles under certain circumstances.

Motoneurons Innervating Respiratory Muscles. These have been identified for the abdominal muscles in songbirds and pigeon (Wild, 1993a) and for M. scalenus, Mm. levator costarum, and Mm. intercostalis externi in pigeon, zebra finch, and budgerigar (Reinke and Wild, 1996, 1997). All the motoneurons are located at the tip of the ventral horn: those innervating the abdominal muscles in lower thoracic and upper lumbar regions, and those innervating inspiratory muscles in the lowest brachial and upper thoracic segments. These distributions are generally in accord with the origins and distribution of spinal nerves as described for the chicken (deWet et al., 1967). It is likely that there is substantial overlap in the rostrocaudal direction of motoneurons innervating internal and external intercostal muscles. There is no major difference in the morphology of motoneurons innervating inspiratory versus expiratory muscles. Both have two groups of widely ramifying dendrites: one directed dorsally and dorsolaterally into the lateral funiculus, and another directed medially toward the central canal (Fig. 4). This organization may be conducive
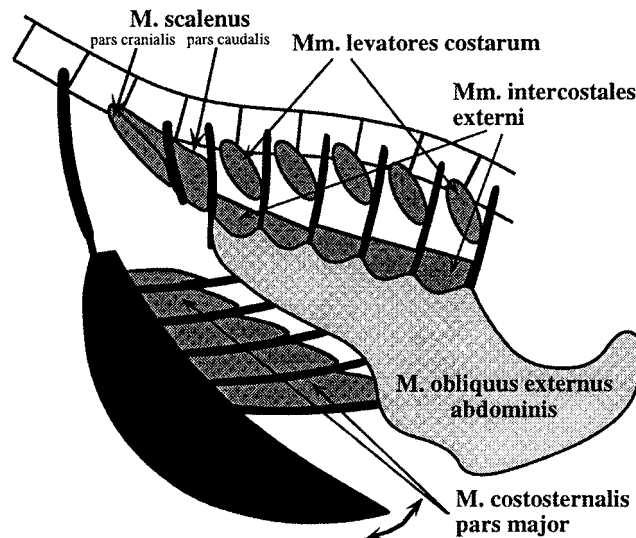
Figure 3   The location of some of the inspiratory and one of the four abdominal expiratory muscles in a non-songbird (Fedde, 1987; Reinke and Wild, 1997); similar arrangements are present in songbirds (Reinke and Wild, 1996). Rostral is to the left. Adapted from Reinke and Wild (1997).

to the reception of afferents having different origins or afferents traveling in different funiculi.

Premotor Neurons. The location of putative pemotor neurons for the respiratory system was determined using a combination of retrograde and anterograde tracing techniques combined with electrophysiologic identification of respiratory related neurons (Wild, 1993b; Reinke and Wild, 1996, 1997). Bulbospinal neurons with projections to regions of the spinal cord containing motoneurons innervating abdominal expiratory muscles are located in the caudal medulla and are concentrated ventrolaterally in nucleus retroambigualis (RAm) (Wild, 1993b), but also extend dorsomedially in an arc toward nXIIts and are found within the SH region (Wild, 1993b) (Fig. 2). Expiratory-related (ER) unit activity is most readily recorded in RAm (Wild, 1993b).

Bulbospinal neurons with projections to regions of spinal cord containing motoneurons innervating such inspiratory muscles as M. scalenus caudalis, Mm. levator costarum, and Mm. intercostales externi are rostrally continuous with the expiratory related neurons, and thus extend from levels caudal to the obex through the level of caudal pole of the descending vestibular nucleus (Fig. 2). Again, most are concentrated in the ventrolateral medulla, but some extend dorsomedially where they are found lateral to rostral levels of nXIIts and ventral to the nucleus tractus solitarius (nTS) (Reinke and Wild,

1996). Inspiratory-related (IR) unit activity is most readily recorded from neurons in the ventrolateral part of this distribution at levels straddling the obex.

The overall distribution of bulbospinal and respiratory related neurons in the avian ventrolateral medulla closely resembles that of the ventral respiratory group (VRG) of mammals (Monteau and Hilaire, 1991; Reinke and Wild, 1997). Expiratory-related neurons are located in the caudal part of VRG (cVRG) and inspiratory-related neurons are located in rostral VRG (rVRG).

In birds, the predominant projection of respiratory-related bulbospinal neurons is contralaterally into the lateral funiculus (Fig. 4). Here, the axons are concentrated dorsolaterally and descend in a peripheral location until they reach an appropriate level of the cord. They then turn ventromedially and approximate the dorsolaterally directed dendrites of motoneurons innervating either inspiratory or expiratory muscles. The axons have varicosities suggestive of synaptic contacts on these dendrites and also appear to terminate on the cell bodies of the motoneurons themselves (Fig. 4). This pattern of input to respiratory motoneurons is entirely consistent with the direct control of respiratory muscle activity that seems to be required during song. Some descending fibers, however, extend across the intermediate gray and terminate in the region of the medially directed dendrites of respiratory motoneurons, and in ventral parts of the column of Terni, the avian sympathetic preganglionic cell column. The
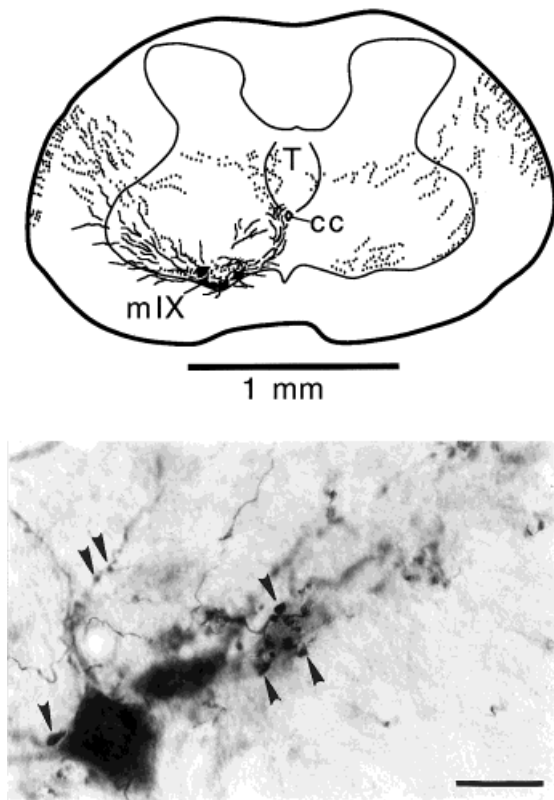
Figure 4 (A) Motoneurons in medial lamina IX (mIX) that innervate the principal inspiratory muscle, M. scalenus in a zebra finch, and bulbospinal axons in the periphery of the lateral funiculus bilaterally (strings of dots) that approximate the dorsolaterally and medially directed dendrites of the motoneurons. The axons were labeled following an injection of BDA at an inspiratory recording site in the ventrolateral medulla (Reinke and Wild, 1996). T = column of Terni. (B) BDA-labeled fibers and terminations (arrow heads) in relation to M. scalenus motoneurons retrogradely labeled with CTB. Calibration bar = 20 μm.

functional significance of this arrangement is presently unknown, but is consistent with a role in cardiorespiratory integration.

Injections of retrograde tracers into the spinal cord that label the groups of medullary neurons described above, also label several other groups of neurons in the medulla, some of which may also be involved in either respiratory or respiratory-vocal control. One of these is the raphe nucleus, known to be involved in respiratory modulation in mammals (Holtman et al., 1984; Lindsey et al., 1992; Hosagai et al., 1993), and another is the ventrolateral nucleus of the rostral medulla (RVL) (Wild, 1993a,b) located at the level of the nucleus magnocellularis cochlearis, slightly rostral to the rostral end of the inspiratory premotor cell column.

Sensory Input from the Respiratory System. In birds, inspiration is not monitored by pulmonary stretch receptors, as it is in mammals, but by intrapulmonary CO_2 receptors, which are innervated by vagal afferents whose central processes terminate in the nucleus parasolitarius lateralis (lPs) (Katz and Karten, 1983; Wild, unpublished observations in songbirds; Gleeson, 1987; Gleeson and Moloney, 1989; Fortin et al., 1994). Although pulmonary inputs are assumed to access the brain-stem respiratory-vocal network—via the projections of lPs to the ventrolateral parabrachial nucleus (PBvl)—it is not known whether these inputs have a role in respiratory-vocal control (Wild and Arends, 1987; Wild et al., 1990; Reinke and Wild, 1996). Neither is anything known about possible mechanosensory inputs from the respiratory apparatus in birds.

Respiratory-Vocal Control Pathways

Projections of RA to Brain-Stem Structures Other Than nXIIts. It was known from early reports that the dorsomedial nucleus (DM) of the midbrain intercollicular region was a distinct target of RA projections, but possible projections of RA to other parts of the brainstem were only hinted at (Nottebohm et al., 1976; Gurney, 1981; but see Paton et al., 1981). More recent tracing studies in songbirds, however, have revealed major projections of RA to several nuclei in the pons and medulla (Wild, 1993a,b; Vicario, 1993; Reinke and Wild, 1996), some of which have already figured in the previous section. The general pattern is one of descending projections upon the ventrolateral rhombencephalon, with distinct terminal fields in nucleus infraolivaris superior [(IOS), between the superior olive and the spinal lemniscus], the RVL, the inspiratory premotor cell group (called the rVRG by Reinke and Wild, 1997), and the expiratory premotor cell group (RAm) (Fig. 5). Nuclei IOS and RVL are little known, but may be comparable with the mammalian retrotrapezoid nucleus and Bötzinger complex, respectively (Reinke and Wild, 1997). The RA projections upon all these cell groups are very largely ipsilateral, and are just as dense as those upon nXIIts (Figs. 1 and 2).

This pattern of projections from a single telencephalic nucleus is very remarkable, and strongly reinforces the notion, emphasized here, that the neural control pathways for song are truly respiratory-vocal in terms of their functional organization, not just vocal (Suthers, 1997).
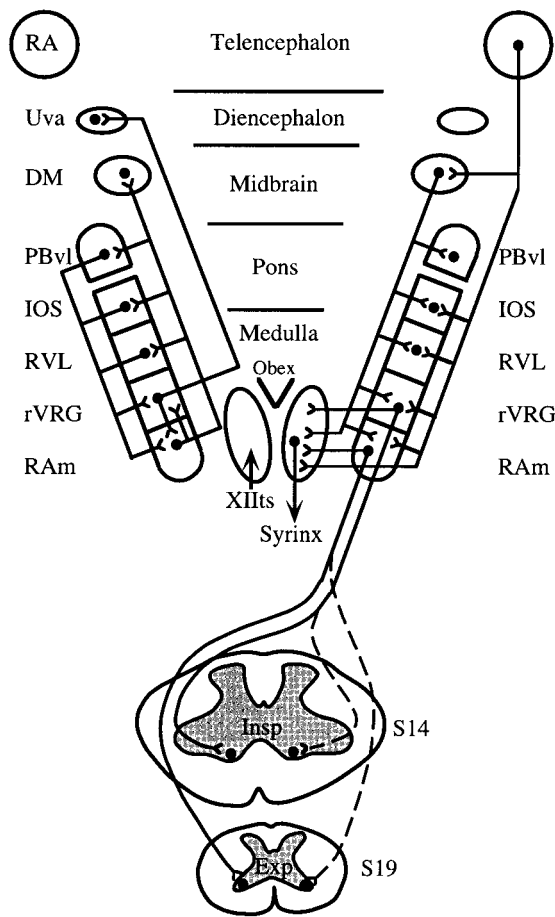
Figure 5 The descending cascade of respiratory-vocal nuclei and pathways in the brain of a songbird such as a zebra finch or canary. All the brain-stem nuclei except nXIIts form a more or less continuous ventrolateral column, PBvl (ventrolateral parabrachial nucleus; Wild et al., 1990) being slightly more separated in the lateral pons. Projecting upon this column are RA and DM, whose descending projections are very similar, except that RA also projects upon DM itself and does not project upon PBvl. Crossed descending projections from RA and brain-stem nuclei are not indicated. Single neurons in RAm and rVRG are shown projecting upon both nXIIts and the respiratory motoneurons, but this has yet to be verified experimentally. Bulbospinal projections to motoneurons innervating respiratory muscles are predominantly contralateral (unbroken lines). Only one of the recurrent pathways is shown: namely, that originating in the region of rVRG and projecting (bilaterally) upon nucleus uvaeformis (Uva). S14, S19 = segments 14 (lowest brachial) and 19 (lower thoracic) of the spinal cord.

DM and Its Descending Projections. DM has been, and still is, one of the most enigmatic nuclei of the respiratory-vocal system (Seller, 1980, 1981).

Gurney (1981) showed it to be retrogradely labeled from injections of HRP centered on nXIIts in the zebra finch, but its descending projections were not investigated in detail until recently (Wild et al., 1997b). This study showed that the general pattern of descending projections of DM very largely replicates that of RA (Fig. 5). Thus there are terminal fields in IOS, RVL, rVRG, and RAm, as well as in nXIIts. One difference, however, is that DM, unlike RA, projects to all these nuclei bilaterally, although still with a pronounced ipsilateral predominance. Another difference is that DM, but not RA, projects upon the ventrolateral parabrachial nucleus (PBvl), which is thought to receive information from the lung via the lPs (Katz and Karten, 1983; Wild and Arends, 1987; Wild et al., 1990, 1997b). However, the specific role of DM in song is far from clear. Because this nucleus seems to be at the head of the vocal control system in non-songbirds (Wild et al., 1997b)—which do not for the most part learn their vocalizations—and because electrical stimulation of DM in songbirds will elicit calls but not song (Seller, 1980; Wild et al., 1997b), it has generally been thought that DM is concerned with unlearned vocalizations (Seller, 1980, 1981; Simpson and Vicario, 1990). It seems also to have been assumed that DM is primarily concerned with the respiratory aspects of vocalization, an assumption supported by its pronounced projections upon respiratory premotor nuclei (Wild et al., 1997b), and its receipt of descending projections from the same part of RA that projects upon the ventrolateral medulla where these premotor nuclei are situated (Vicario, 1991b, 1993; Reinke and Wild, 1996, 1997). However, it also has substantial projections upon nXIIts, and thus appears to have, like RA, all the requirements for the complete control of respiratory-vocal activity during calling. Whether DM effects this control via single neurons that project upon both nXIIts and the respiratory premotor nuclei, or whether its neurons are partitioned into groups projecting upon one or the other of these targets, as in RA, is not known. It would also be interesting to know whether the activity of DM neurons is correlated with singing as well as calling in songbirds.

The Descending Cascade. Each of the nuclei upon which RA and DM project also projects upon all the more caudal structures of the respiratory-vocal complex, in cascade-like fashion (Fig. 5) (Wild, 1994a; Reinke and Wild, 1997). The functional significance of this pattern of descending control is unclear, particularly as the role of several individual nuclear components, such as IOS and RVL, is ob-

scure at the present time. One implication of the descending cascade is that the two most caudal brain-stem structures that are most directly involved in phonation, namely nXIIts and RAm, receive a particularly rich innervation from a variety of more rostral sources, each of which may modify and pass on information from yet a higher source. Even RAm appears to project upon nXIIts (Wild, 1993b; Vicario, 1993), which may account for the expiratory-related rhythm that may be recorded in nXIIts in some species, such as zebra finch and budgerigar (Manogue and Paton, 1982; Vicario, 1991a). In addition, there appear to be reciprocal connections between many of the respiratory-vocal structures of the brain stem (Wild, 1993b), including connections between the inspiratory and expiratory premotor neurons (Wild et al., 1997b; Reinke and Wild, 1997; and unpublished observations in songbirds). In songbirds, these latter could conceivably mediate an oscillatory pattern that controls the rhythmical relationship between expiratory/phonatory periods and inspiratory minibreaths.

Pathways for Bilateral Control of Vocal Production

The problem of controlling and coordinating the two sides of a bilateral sound source such as the songbird syrinx has traditionally seemed a particularly difficult one, partly because of the apparent lack of any crossed projections between any of the telencephalic vocal control nuclei. Birds do not possess a corpus callosum, and although there are contralateral hemispheric projections from each archistriatum through the anterior commissure, none of these originates in RA or terminates upon any of the telencephalic vocal control nuclei.

Feedforward Pathways. Although RA does have a very small descending contralateral projection to the brainstem (Wild, 1993a), it seems doubtful that this could account for the observed behavioral coordination of the two independently innervated sides of the syrinx during song. This is supported by the results of electrically stimulating HVc ipsilaterally and recording evoked potentials in the ts nerve bilaterally (Paton and Manogue, 1982). When this is done, in canaries or zebra finches, for example, potentials can be recorded in the contralateral ts nerve, but they are much smaller, have a longer latency than those in the ipsilateral nerve, and are observed only when high rates of stimulation are used, suggesting that the crossed response is dependent on the temporal summation of excitation (Paton and Manogue, 1982).

However, endoscopic viewing of syringeal action during vocalization driven by unilateral electrical stimulation of HVc (in anesthetised birds), shows that the syrinx is adducted on *both* sides, although there is usually more occlusion of the bronchial lumen on the ipsilateral than on the contralateral side (Goller and Larsen, unpublished observations). In awake singing birds, however, activity in both descending HVc–RA–nXIIts pathways seems more likely to be the rule than the exception, but the temporal coordination of this activity is crucial for vocal patterning, presumably requiring some form of cross-talk between the two sides. How this might be effected is still not clear, but recent evaluations of possible sources of contralateral projections have suggested several candidates at subtelencephalic levels of the neuraxis. For instance, DM has a substantial contralateral projection, both to the opposite DM and to the more caudally situated respiratory-vocal nuclei, including nXIIts (Wild et al., 1997b). In addition, IOS, RVL, and rVRG all appear to have crossed projections upon nXIIts, and particularly RAm (Wild, unpublished observations). However, the means of bilateral control of syringeal activity could be different in different species, since canary and white-crowned sparrow song, for instance, is heavily dominated by syllables produced on the left (Nottebohm and Nottebohm, 1976), zebra finch song is slightly dominated by syllables produced on the right (Williams et al., 1992), and brown thrasher song is not dominated by syllables produced on either side of the syrinx (Suthers et al., 1994). It should be realized, however, that even when one side of the syrinx is not producing sound, the dosal syringeal muscles on that side are still highly active, to keep the syrinx closed, and the ventral muscles are active on both sides, irrespective of which side is phonating (Goller and Suthers, 1996a,b).

Recurrent Pathways. One way the vocal control nuclei of one side could coordinate with those on the other is via projections originating in some part of the motor pathway that cross the midline and ascend to higher centers. That such circuits are present is indicated by the fact that unilateral electrical stimulation of HVc during song ''resets'' activity in HVc bilaterally (Vu et al., 1994). There are now three candidates for the return of efferent information to the contralateral side. One of these is the thalamic nucleus dorsomedialis posterior (DMP), which receives a projection from RA and projects

bilaterally to mMAN (Vates et al., 1997). Another is a bilateral projection from DM to Uva (Striedter and Vu, personal communication), and yet another is a bilateral projection to Uva from the ventrolateral medulla (Reinke and Wild, 1996; Striedter and Vu, unpublished observations). However, whether these ventrolateral medullary neurons that project to Uva are also inspiratory premotor neurons, or whether they actually receive a projection from RA has not been determined, so it has yet to be shown that they are in fact the origin of a recurrent pathway, rather than of a straightforward ascending reticulothalamic pathway.

Possible Feedback Pathways to Vocal Control Circuits

Auditory Feedback. The importance of auditory feedback for vocal learning, and the role of lMAN in this process, are well documented (Konishi, 1965; Price, 1979; Marler and Sherman, 1983; Bottjer and Arnold, 1984; Bottjer et al., 1984; Sohrabji et al., 1990; Scharff and Nottebohm, 1991), but the role of auditory feedback in the control of vocal production in adulthood is more controversial (Nordeen and Nordeen, 1992, 1997).

The pathways by which auditory feedback may be mediated presumably include the classical auditory pathway to the telencephalon, which has been well described in both songbirds and non-songbirds (reviews in Wild et al., 1993; Margoliash et al., 1994; Vates et al., 1996). In songbirds, a point of contention has been whether Field L, the primary telencephalic auditory area, which is comparable to layer IV of primary auditory cortex of mammals, has direct or indirect access to HVc, the ''head ganglion'' of the vocal control system (see Margoliash et al., 1994; Fortune and Margoliash, 1995; Vates et al., 1996). This matter is more fully discussed by Margoliash (1997).

Birds have another auditory pathway to the telencephalon in addition to the classical pathway via the thalamic nucleus ovoidalis. This is the curious pathway originating in a nucleus of the lateral lemniscus (LLI), which projects without a thalamic relay directly to the caudolateral portion of nucleus basalis in the frontal telencephalon (Delius et al., 1979; Arends and Zeigler, 1986; Hall et al., 1993; Wild and Farabaugh, 1996). In the budgerigar, this pathway has been suggested to be the major source of input to the telencephalic vocal learning and production circuits (Striedter, 1994), but in a songbird (zebra finch), Wild and Farabaugh (1996) found no evidence for a similar linkage at telencephalic

levels. However, it is still possible that the extratelencephalic output of this system in songbirds accesses vocal control circuitry at lower levels.

Visual and Somatosensory Inputs. Visual cues may play a very important role both in song development and in vocal control during courtship and territoriality. It might be expected, therefore, that the vocal control system has access to visual information. Bischoff and Engelage (1985) showed, for instance, that visually evoked potentials could be recorded in HVc in songbirds, and Wild (1994b) suggested that this input could reach HVc via nucleus uvaeformis (Uva), since this nucleus receives bilateral projections from the major output layer of the optic tectum and projects ipsilaterally upon HVc (Nottebohm et al., 1982; Wild, 1994b). It also receives a mainly contralateral projection from the dorsal column nuclei, thereby potentially admitting somatosensory inputs to the vocal control circuitry (Wild, 1994b, 1997), although somatosensory responses have not been reported in HVc.

Proprioceptive Input. The notion that proprioceptive feedback from the periphery could play a part in regulating vocal output, particularly during song learning, has seemed an attractive and plausible one, especially in the light of the discovery of afferents in the syringeal nerve (Bottjer and Arnold, 1982). These workers showed, however, that removing the syringeal afferent input in adult zebra finches did not affect normal song production in any substantial way (Bottjer and Arnold, 1984); and further attempts to assess whether syringeal afferents are important during the development of song in zebra finches have had equivocal results (Bottjer and Arnold, 1986; Lohmann and Gahr, 1993). Readers interested in comparing the sensorimotor control of the mammalian larynx during vocalization, or of human speech in general, should consult Davis et al. (1993), Shiba et al. (1997), and Gracco (1991).

Pathways for Control of Suprasyringeal Vocal Tract Structures

The Larynx. The anatomy of the avian larynx was reviewed by McLelland (1989). The structure does not contain vibratable membranes and is not known to contribute to the generation of sound in any bird. Its role in sound modulation in song, if any, is therefore speculative. Avian laryngeal muscles are innervated by the glossopharyngeal nerve and their motoneurons lie in nucleus ambiguus in the ventrolateral medulla caudal to the obex. Here they lie in the

path of the descending vocal control pathways originating in both RA and DM (Fig. 2) (Wild, 1981, 1993a; Wild et al., 1997b; Manogue and Nottebohm, 1982; Grabatin and Abs, 1986), and so could be involved in the control of laryngeal aperture during song, and thus perhaps be involved in sound modulation.

The Tongue. The role of the tongue in birdsong, as opposed to other forms of vocalization (Warren et al., 1996), is not known. Like jaw motoneurons, neither those in the lingual portion of nXII (nXII1), which innervates the intrinsic tongue muscles, nor facial or glossopharyngeal motoneurons innervating tongue retractor and protruder muscles, respectively, receive a projection from RA. The tongue receives a sensory innervation from the facial and glossopharyngeal nerves in all birds and from the hypoglossal nerve in many seed husking/eating species (Wild, 1990) but there is no information in songbirds to suggest that these afferents may be involved in the sensory control of vocalization.

The Jaw. Westneat et al. (1993) were the first to show, using videographic analysis, that in some songbirds, e.g., song and swamp sparrows, there is a strong positive correlation between beak gape and fundamental frequency, i.e., there is a tendency for these birds to sing higher pitched notes with a wider gape (see also Hausberger et al., 1991; Hoese and Westneat, 1996). Using an on-line gape measurement system during singing, Suthers et al. (1996) showed that this relationship may also hold in other species, e.g., northern cardinals and brown thrashers, but only up to 3–4 kHz. Above those levels, the relationship between gape and fundamental frequency was much less predictable, and in fact, singing brown thrashers can sing the same syllable with quite different gapes. Moreover, the relationship between gape and fundamental frequency, subsyringeal pressure, and the side of the syrinx used to produce the syllable, or part-syllable, is far from invariant, indicating a complex control system for the coordination of beak movements with movements of other vocal tract structures during singing (Suthers, 1997).

This variable relationship between jaw movements and various vocal parameters is possibly reflected in the apparent separateness of the neuroanatomical control systems for the jaw and vocalization. Neither jaw motoneurons in the pons nor jaw premotoneurons in the medulla appear to receive direct projections from RA or DM in songbirds (Wild, 1993a; Wild et al., 1997b; Wild, unpublished

observations). Some medullary jaw premotor neurons that lie immediately ventrolateral to nXIIts and have specific projections to the contralateral facial and trigeminal motor nuclei are located within the terminal field of descending projections originating in the lateral, rather than the medial, part of the archistriatum, a region that receives a distinct projection from the more rostral nucleus basalis–neostriatal complex (Wild and Zeigler, 1980; Dubbeldam and Visser, 1987; Wild and Farabaugh, 1996; Wild, unpublished observations). This pattern of projections is therefore entirely consistent with a role in the sensorimotor control of jaw movements (Berkhoudt et al., 1981, 1982; Wild et al., 1985; Wild and Zeigler, 1996; Wild and Farabaugh, 1996), but how these movements are coordinated with those of the syrinx and respiratory apparatus during song is far from clear.

Pathways for the Control of Other Vocalization-Associated Movements

The songs of many species are frequently accompanied by patterns of movements that may collectively be called visual displays, that function in specific sexual and social contexts. For instance, the song of the brown-headed cowbird is frequently accompanied by a stereotyped ''pantomime'' in which the bird fluffs up its head and neck feathers, and spreads its wings and bows in a temporal sequence that is correlated to some extent with that of the various song components. How the neural control of such vocalization-associated movements is integrated with that of the vocal control system is not known. The control of head movements associated with crowing in quail, however, is known to be localized to specific segments of the lower brain stem, as Balaban (1997) showed using crowing quail-chick chimeras. Interestingly, the chicks receiving donor lower brain-stem somites from quail retained a chicklike call structure, despite adopting a quaillike pattern of head movement during vocalization, suggesting a separate and independent control of these behavioral components.

COMPARISON WITH VOCAL CONTROL PATHWAYS IN MAMMALS

The unique presence of the syrinx in birds and the direct projections to its motoneurons from a telencephalic nucleus in songbirds have tended to set the vocal control system in birds apart from that in mammals, including the human. These peculiarities

notwithstanding, the vocal control pathways of the brain stem in birds can be seen to be remarkably similar to those in mammals, especially when these are viewed, as they should be, in the broader context of respiratory-vocal control (Davis et al., 1993, 1996a,b).

The focus of this similarity is the nucleus retroambigualis (aka retroambiguus: RAm in birds, NRA in mammals), which in both birds and mammals appears to be nexus of the final common path for vocalization (Holstege, 1989; Wild, 1993b). Similar to the situation in birds, nucleus retroambigualis in mammals projects upon intercostal and abdominal expiratory motoneurons and upon many of the motoneuronal cell groups in the medulla that innervate larygeal and pharyngeal muscles involved in vocalization. Although Holstege (1989) initially felt that NRA also projected upon trigeminal and facial motoneurons innervating perioral muscles involved in vocalization, it now seems that the interneurons projecting upon the perioral motoneuronal cell groups are thought to lie adjacent to NRA rather than specifically within it (Holstege and Ehling, 1996; Davis et al., 1996a,b). This is exactly the pattern suspected to exist for the jaw premotor neurons in birds (Wild, unpublished observations), although there may also be a projection upon jaw motoneurons from inspiratory premotor neurons in birds (Reinke and Wild, 1997), a projection not yet investigated in mammals.

Nucleus retroambigualis in both birds and mammals receives a major projection from the midbrain; from the lateral periaqueductal gray (PAG) in mammals and from DM in birds (Jürgens and Pratt, 1979; Yoshida et al., 1987; Holstege, 1989; Gerrits and Holstege, 1996; Wild et al., 1997b). These nuclei may be homologous as the origin of vocalization-specific projections to the lower brain stem (Jürgens, 1994; Wild et al., 1997b). In both birds and mammals electrical or chemical stimulation of DM or PAG evokes distinct vocalizations that appear to be mediated via expiratory premotor neurons in RAm or NRA (Zhang et al., 1994, 1995; Wild et al., 1997b) and, in birds, via inspiratory premotor neurons in the rostral ventral respiratory group (rVRG) (Wild et al., 1997b; Reinke and Wild, 1997). A similar projection from PAG upon inspiratory premotor neurons may also exist in mammals (Davis et al., 1996a).

The similarities between the respiratory-vocal system of birds and mammals have been further reinforced by a recent analysis of brain-stem afferents to NRA in the cat (Gerrits and Holstege, 1996). As shown for RAm in pigeons and songbirds (Wild,

1993a,b; Reinke and Wild, 1997; Wild et al., 1990, 1997b), NRA in the cat receives descending projections from several brainstem nuclei, in addition to those originating in PAG (DM in birds), e.g., the ventrolateral parabrachial and Köllicker-Fuse nuclei, the retrotrapezoid nucleus, the Bötzinger complex, and the ventral respiratory group (VRG). All these nuclei in mammals are implicated in the control or modulation of respiratory and/or vocal activities (Gerrits and Holstege, 1996), and suggestions for similar functions have been made for birds (Wild, 1994a; Reinke and Wild, 1997).

The PAG-NRA projection system in mammals has been conceptualized as an emotional motor system having higher afferent projections originating in the limbic system (Holstege and Ehling, 1996). For the production of human speech and song, however, a second somatic motor system is required to provide both direct and indirect motor cortical projections to motoneurons innervating tongue, pharyngeal, mouth opening (jaw), and perioral muscles (Holstege and Ehling, 1996). Inputs to these motor cortical projection neurons arise in Broca's area.

The nuclei and pathways making up the emotional motor system described by Holstege and Ehling (1996) for mammals are clearly present in birds in the projections of DM to the respiratory-vocal nuclei of the brain stem, projections that perhaps comprise the basic vocalization system that all birds use for signaling emotional states by their calls. However, inputs to DM from the avian limbic system have yet to be identified (Wild et al., 1997b). In songbirds, as in humans, there has evolved a second somatic motor system originating in the telencephalon (RA) for the control of learned vocalizations (although it may also have some control over unlearned vocalizations, such as unlearned calls, as well) (Margoliash, 1997). The projections of this system in birds, however, unlike those in humans, not only include the origin of the emotional motor system itself (viz., DM), but also all the targets of DM, including the vocal motoneurons themselves. Thus, birds and humans have solved the problem of the control of learned vocalizations (speech in humans and song in songbirds) in ways that are in some ways remarkably similar, but which differ with respect to the extent to which the somatic motor system is superimposed on the emotional motor system, this apparently being greater in songbirds than in mammals. Thus, one and the same telencephalic nucleus (RA) can control the output of both the vocal and the respiratory systems—the necessarily coordinative and equal partners in song production. This may represent a unique evolution-

ary solution to the problem of coordinative motor control of vocal production, a problem that is also relevant to the control of human speech and song (Gracco, 1990).

DIRECTIONS FOR FUTURE RESEARCH

Such is the intricate involvement of the respiratory system in vocal production that the more is known about the central neural control of respiration in birds, the better we will be able to understand the nature of vocal control. We hope that some of the considerations of the present article will stimulate research in this area.

As a corollary, we feel it will be important to determine whether chemosensory or mechanosensory feedback from the respiratory system plays a role in vocal control.

Although some of the basic neuroanatomical circuits of the respiratory control system have now been worked out, the elucidation of the role of individual nuclei in respiratory and vocal control is now required.

Although RA can drive both the vocal and respiratory systems during song, the anatomical connections between them and the intricate coordination of syringeal and respiratory muscles that is so characteristic of singing suggest the presence of significant interactions between the two systems at brainstem levels. What is the nature of this interaction, and how is it effected at the cellular level?

The movements of the upper vocal tract, including the jaw, during singing are difficult to measure and analyze. Yet, anyone who has watched a canary sing will realize that such movements are obviously a highly important part of vocal behavior. Understanding how the neural control of these and other vocalization-associated movements during singing is integrated with that of the vocal and respiratory systems represents a significant challenge for future research.

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