

# THE ROLE OF FEEDBACK FROM THE VOCAL ORGAN

## I. Maintenance of Stereotypical Vocalizations by Adult Zebra Finches<sup>1</sup>

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### Abstract

The stereotypical vocal patterns of adult male zebra finches (*Poephila guttata*) were examined before and after elimination of auditory feedback and/or feedback from the vocal organ (the syrinx). Elimination of auditory feedback was accomplished via bilateral removal of the cochleae, whereas feedback from the syrinx was eliminated by cutting hypoglossal afferent fibers while leaving hypoglossal efferents intact. Very little or no disruption of song was observed in birds which underwent deafening as well as unilateral deafferentation of the syrinx. Control experiments showed that the minor deficits observed were not attributable to lesion of pulmonary fibers in the descending branch of the vagus. There was also little deficit in song behavior of birds that were deafened and subjected to bilateral deafferentation of the syrinx. These results are consistent with the hypothesis that stable song patterns in adult passerine birds are not dependent on peripheral sources of feedback, but may be governed by a learned central control program.

Male passerine birds learn a species-typical song during a "critical" period of development (e.g., Thorpe, 1958; Marler, 1970). One of the prerequisites for vocal learning is exposure to conspecific song during this period. For example, young zebra finches that are isolated from adult males never produce normal song (Immelmann, 1969). White-crowned sparrows that are acoustically isolated during early development produce highly abnormal songs, even if they receive extensive exposure to conspecific song at a later time, whereas juvenile white-crowns that are "tutored" with tape recordings of adult song later produce a close imitation of the tutor tape (Marler, 1970).

In addition, young birds must be able to hear their own incipient vocalizations in order for song development to proceed normally. For example, white-crowned sparrows exposed to conspecific song and then deafened prior to the time that they begin to vocalize themselves produce a greatly disrupted song pattern (Konishi, 1965). In contrast, deafening adult birds that have already acquired a stable ("crystallized") song pattern produces little or no change in song performance (Konishi, 1965; cf. Nottebohm, 1968; Price, 1979).

Because deafening adult birds does not disrupt singing behavior (whereas deafening juvenile birds severely disrupts song development), it has been hypothesized that learning to produce

a particular song pattern involves either (1) transfer of control from auditory feedback to proprioceptive (nonauditory) feedback or (2) the establishment of a central control program that controls vocal production independently of peripheral feedback (Konishi, 1965). Nottebohm (1967) attempted to test the role of proprioceptive feedback in song maintenance by sectioning motor innervation of the vocal organ (syrinx) in two adult male chaffinches. He reasoned that denervation of the syrinx would alter song-related proprioceptive feedback. Although the songs of these birds showed several structural abnormalities, their vocal patterns were stereotyped and were of normal length and complexity. This result suggested to Nottebohm that stable song patterns are controlled by a "motor tape" which is not dependent on patterned sensory feedback (Nottebohm, 1968). However, a direct test of the role of syringeal feedback was impossible since it was not known whether sensory innervation of the syrinx existed.

We have recently demonstrated the existence of afferent fibers originating in the syrinx and described the peripheral course of these fibers (Bottjer and Arnold, 1982). By selectively lesioning syringeal afferent fibers at various stages of development (leaving motor innervation intact), we can begin to assess their contribution to vocal learning, thereby providing a test of the first hypothesis referred to above—namely, that vocal learning is dependent on feedback from the syrinx. The experiments reported herein examine the role of syringeal afferents in the maintenance of crystallized song patterns by adult male zebra finches. Our prediction was that if there is a transfer of control from auditory feedback to sensory feedback from the syrinx, cutting afferent fibers from the syrinx to the brain would result in massive disruption of song behavior, similar to the effects obtained by deafening young birds. The results are not consistent with this prediction.

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**Materials and Methods**

The peripheral course of the hypoglossal nerve in zebra finches is diagrammed in Figure 1A. The main trunk of XII divides into two branches at the trachea. The ascending branch innervates the tongue musculature and is referred to as the lingual (l) nerve. The descending branch innervates the tracheal and syrinxal muscles, and is referred to as the tracheosyringeal (ts) nerve. Nottebohm (1971) has shown that bilateral section of the ts nerve completely eliminates song production in adult male chaffinches. Three efferent hypoglossal roots exit the brain ventrally and come together to join the main XII trunk at the point where XII anastomoses with the Xth cranial nerve. Motor axons from the caudal two-thirds of the hypoglossal nucleus exit the brain via the lower two hypoglossal roots, travel along the main XII trunk and the ts nerve, and innervate the syrinx. Motor axons from the rostral third of the hypoglossal nucleus exit the brain via the uppermost hypoglossal root, join the lingual nerve, and innervate the tongue (see Nottebohm et al., 1976; Bottjer and Arnold, 1982).

Afferent fibers from the syrinx travel along the ts nerve and main XII trunk, but join the vagus at the X-XII anastomosis, have cell bodies located in the vagal ganglion, and enter the brain dorsally with vagal fibers (Bottjer and Arnold, 1982). Afferent fibers from the tongue also

leave the main XII trunk and join the vagus. Thus, hypoglossal afferent fibers travel separately from motor axons of the hypoglossus proximal to the X-XII anastomosis. Therefore, it is possible to eliminate afferent feedback from the tongue and syrinx, while leaving their motor innervation intact, by sectioning the vagus above the X-XII anastomosis.

Zebra finches used in this study were hatched in our breeding colony or were purchased from a local supplier. All birds were sexually mature males (i.e., over 90 days old). There is considerable intraspecific variation in the songs of adult male zebra finches, but the song pattern of any one individual is extremely stable and does not change over time. Tape recordings of song patterns were made with a condenser microphone on a Tandberg series 3500X or 3600XD tape recorder using a tape speed of 3.75 inches/sec. Recorded songs were analyzed on a Kay Elemetrics Company sonograph (model 6061B or 7800) using the wide-band filter.

*Unilateral section of hypoglossal afferent fibers in hearing birds.* The song patterns of eight adult male zebra finches were recorded; a minimum of 50 songs were recorded for each bird. Each bird was then anesthetized via an intramuscular injection of 0.04 to 0.05 ml of Chloropent or Equithesin. All surgery was performed under a dissecting microscope. An incision was made through the skin lying directly over the caudalmost hyoid bone in the anterior ventral neck region on either the left or right side, and the hyoid bone and surrounding muscle were dissected free and retracted slightly. The X-XII anastomosis was then either wholly or partially visible; some retraction of the adjacent neck muscles was usually also necessary. In some cases access to the anastomosis was prohibited by its close proximity to the vasculature. This restricted access tended to be more of a problem on the right side than on the left, as the right X-XII anastomosis was frequently situated directly below a major blood vessel.

A pair of microscissors was used to cut through the vagus just proximal to the XII efferent roots (see a, Fig. 1A) on either the right (n = 4) or left (n = 4) side. This procedure entailed sectioning afferent and efferent fibers of the descending branch of the vagus in addition to hypoglossal afferent fibers from the tongue and syrinx; the ascending branch of the vagus joins the main vagal trunk proximal to the section and was not affected. In some birds the uppermost XII root was situated much more rostrally than the lower two XII roots; therefore, in these cases motor fibers which travel from the uppermost (lingual) XII root to the tongue were sectioned along with hypoglossal afferents as well as vagal afferents and efferents. The lower two XII roots contain motor axons which innervate the syrinx; these fibers were never disturbed. Because there was little or no change in song as a result of these nerve sections, we did not include controls for effects of sectioning fibers of the lingual branch of XII and the descending branch of X in these initial experiments. The skin incision was closed with Colloidion.

After a recovery period of 24 to 72 hr, the song pattern of each bird was recorded again. Within a week following the nerve section operation, each bird was killed with an overdose of anesthetic and subjected to a thorough postmortem examination to verify the nerve section. We attempted only unilateral section of the vagus rostral to the X-XII anastomosis in our initial experiments, since bilateral vagotomy resulted in death (but see below).

*Unilateral section of hypoglossal afferent fibers in deaf birds.* The song patterns of 16 adult male zebra finches were recorded; a minimum of 50 songs were recorded for each bird. Each bird was subsequently anesthetized with Equithesin, and both cochleae were removed according to methods described by Konishi (1964). Following a recovery period of 2 to 6 days, the song patterns of all birds were recorded again over a period of a few days. Next, each bird was anesthetized again, and the vagus was sectioned just rostral to the X-XII anastomosis (see a, Fig. 1A) on either the left (n = 4) or right (n = 4) side. As described above, this procedure left hypoglossal efferent fibers intact, but afferent and efferent fibers of the descending branch of the vagus were sectioned along with hypoglossal afferents. As a control for section of vagal fibers, as well as for possible effects of local irritation produced during surgery which could affect transmission in the efferent XII pathway, six birds underwent section of the descending branch of the vagus. In these control birds the anastomosis was exposed in exactly the same way as for experimental birds, and the descending vagus was sectioned immediately caudal to the X-XII anastomosis on either the left (n = 3) or right (n = 3) side (see b, Fig. 1A). Inspection of the X-XII anastomosis of two birds revealed that the XII afferent fibers coursed a sufficient distance alone (independently from other XII and X fibers) that they could be cut separately (see a, Fig. 1B). In these two cases the arrangement of the anastomosing nerves was identical to other

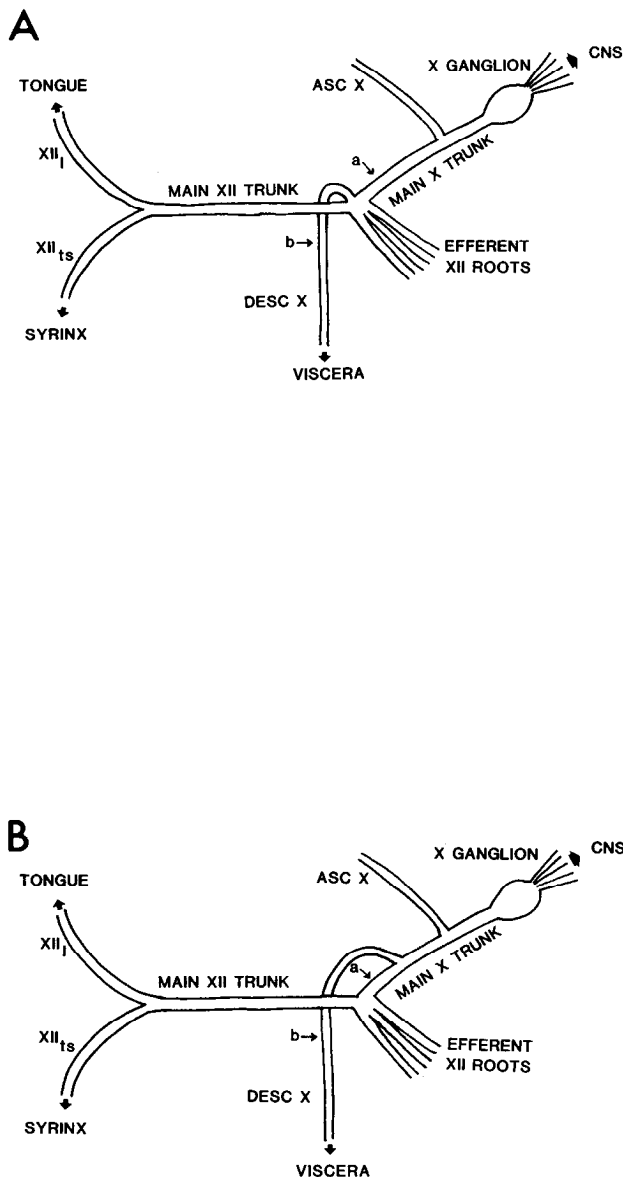


Figure 1. The peripheral course of the hypoglossal (XII) nerve and its anastomosis with the vagus (X) nerve. See the text for a full explanation.

birds, except that the descending branch of the vagus joined the main X trunk some distance proximal to the efferent XII roots (see Fig. 1B). Thus, that section of nerve traveling between the efferent XII roots and the descending branch of X contained only XII afferent fibers. Therefore, in these two birds, the hypoglossal afferents were cut (on either the left side or right side), while hypoglossal efferents and the descending branch of the vagus were left intact. Finally, the song patterns of these 16 birds were recorded again 2 to 11 (median = 3) days following the nerve section operation.

The two birds which had the selective unilateral section of hypoglossal afferents were subsequently reoperated on the contralateral side to section the vagus rostral to the X-XII anastomosis, and their song patterns were recorded again. Thus, hypoglossal afferents were sectioned bilaterally in these birds (and vagal efferents and afferents were sectioned unilaterally).

**Bilateral section of hypoglossal afferent fibers in deaf birds.** The discovery that section of hypoglossal afferents alone was possible in some birds (see above) prompted us to attempt simultaneous bilateral section of hypoglossal afferents in such birds. Our procedure was as follows: The song patterns of 10 adult male zebra finches were recorded. Each bird was then anesthetized with Equithesin, and the left X-XII anastomosis was exposed as described above. Inspection of the anastomosis revealed that section of the left hypoglossal afferents alone (leaving hypoglossal efferents and the descending vagus intact) was possible in 4 of these 10 birds. These 4 birds were immediately deafened via bilateral removal of both cochleae, as described above, and their song patterns were recorded again following recovery from surgery. Each bird was subsequently anesthetized again, and the hypoglossal afferents on the left side were sectioned alone, while the right vagus was sectioned completely just rostral to the X-XII anastomosis. Thus, hypoglossal afferents were sectioned bilaterally at the same time in these birds, and the right descending vagal efferents and afferents were sectioned unilaterally. The song patterns of the four birds were recorded again following this second operation.

## Results

**Unilateral section of hypoglossal afferent fibers in hearing birds.** Section of the left vagus rostral to the X-XII anastomosis had no effect at all on the song patterns of three of four birds (see *left half* of Fig. 2). The fourth bird (Y 107) exhibited some extremely minor changes in its song pattern postoperatively. The overall structure and tempo of the song did not change, but the form of one note (or of one note complex) changed somewhat (see *arrows*, Fig. 2). The lower frequency notes changed such that the same frequency was repeated three times in the postoperative note complex (compare with the more complex changes in this frequency range seen preoperatively). In addition, there was more noise present, especially in the higher frequencies (cf. Nottebohm et al, 1979).

Section of the right vagus rostral to the X-XII anastomosis had comparable effects. Three of four birds showed no change whatsoever in their song pattern as a result of the operation (see *right half* of Fig. 2). The fourth bird (LG 358) exhibited some slight changes in the form of one note or note complex (see *arrows*, Fig. 2). The frequency-modulated element seen in the beginning of the note complex prior to the operation was absent in the postoperative song, and the latter part of the note complex was noisier postoperatively. As in bird Y 107, the overall structure and tempo of the song were not affected. Overall, there was very little or no deficit in song behavior as a result of the nerve section operation. Nottebohm and Nottebohm (1976) also reported that section of the left vagus either caudal or rostral to the X-XII anastomosis had no effect on the song repertoires of two adult male canaries.

**Unilateral section of hypoglossal afferent fibers in deaf birds.** Neither deafening nor section of the left vagus rostral to the X-XII anastomosis affected the song patterns of three of four birds (see *left half* of Fig. 3). The fourth bird (DG 292) exhibited some minor changes in song as a result of being deafened. For example, the highly frequency-modulated note (marked by *arrows* in Fig. 3) was produced in a slightly more variable fashion

after the deafening operation. Following section of the left vagus, the song performance of this bird deteriorated further. The frequency-modulated note had completely lost the characteristic upsweep and downsweep seen in the preoperative song. In addition, the initial note of the song was changed to include a lower fundamental frequency not seen in the preoperative song. Interestingly, this bird was recorded again 13 days following the nerve section operation, at which time its song pattern showed substantial recovery to the point where it appeared to match the postdeafening song (not shown in Fig. 3).

Section of the right vagus rostral to the X-XII anastomosis in deaf birds affected the form of individual song notes in two of four birds and caused little or no change in the song patterns of the remaining two birds (see *right half* of Fig. 3). The song of R 7 did not change as a result of deafening, but it did exhibit some changes following the nerve section operation. All of the notes produced were considerably noisier following the vagal section, especially for frequencies over 2 kHz, making it somewhat difficult to determine whether the harmonic frequencies had changed substantially. The fundamental frequencies of most notes appeared to be unchanged, with one exception (see note marked by *arrows*, Fig. 3). The initial part of this note began between 4 and 5 kHz preoperatively and immediately dropped to include frequencies in the 2- to 3-kHz range. Postoperatively, this note began between 2 and 3 kHz, followed immediately by a small frequency downsweep not seen in the preoperative song. This bird was recorded again 8 days following the nerve section operation, at which time song production had recovered almost completely. The only peculiarity observed in the song at this time was the production of an unevenly modulated note at the end of some song bouts.

The song of the remaining bird, DG 310, changed as a result of deafening, primarily in the production of the two highly frequency-modulated notes of its song (see *arrows*). Following section of the right vagus, these frequency-modulated notes were completely disrupted, and all notes were extremely noisy. The overall structure and tempo of the song did not change. This bird was recorded again 19 days following the nerve section operation; although its song was still greatly changed from its preoperative version, it showed some recovery. Eight weeks following the nerve section operation the song of this bird continued to be considerably noisier than it had been preoperatively, but the form of all notes appeared to be otherwise recovered, including the fundamental frequency.

Thus, only one of eight deaf birds exhibited substantial disruption of song production as a result of the nerve section operation. Two other birds showed rather minor changes in song (R 7 and DG 292). Interestingly, there was no correlation between age of a bird and effect on song. Birds that showed some change in song were all over 118 days old, whereas birds that showed no effect ranged in age from approximately 90 to 580 days.

None of the six birds which underwent deafening followed by section of the vagus just caudal to the X-XII anastomosis exhibited any change in song performance as a result of this latter operation (see Fig. 4). One of these birds (R 31) exhibited some changes in song as a result of deafening, but no further changes in the song pattern were observed following section of the right descending vagus. Four of these six birds subsequently underwent section of the vagus rostral to the X-XII anastomosis on the same side on which they had previously been operated. None of these four birds showed any changes in their song patterns as a result of this latter section, which included only hypoglossal afferent fibers.

Two deafened birds underwent section of the hypoglossal afferents while leaving the descending vagus intact. The bird that was operated on the right side (R 6) showed no changes in

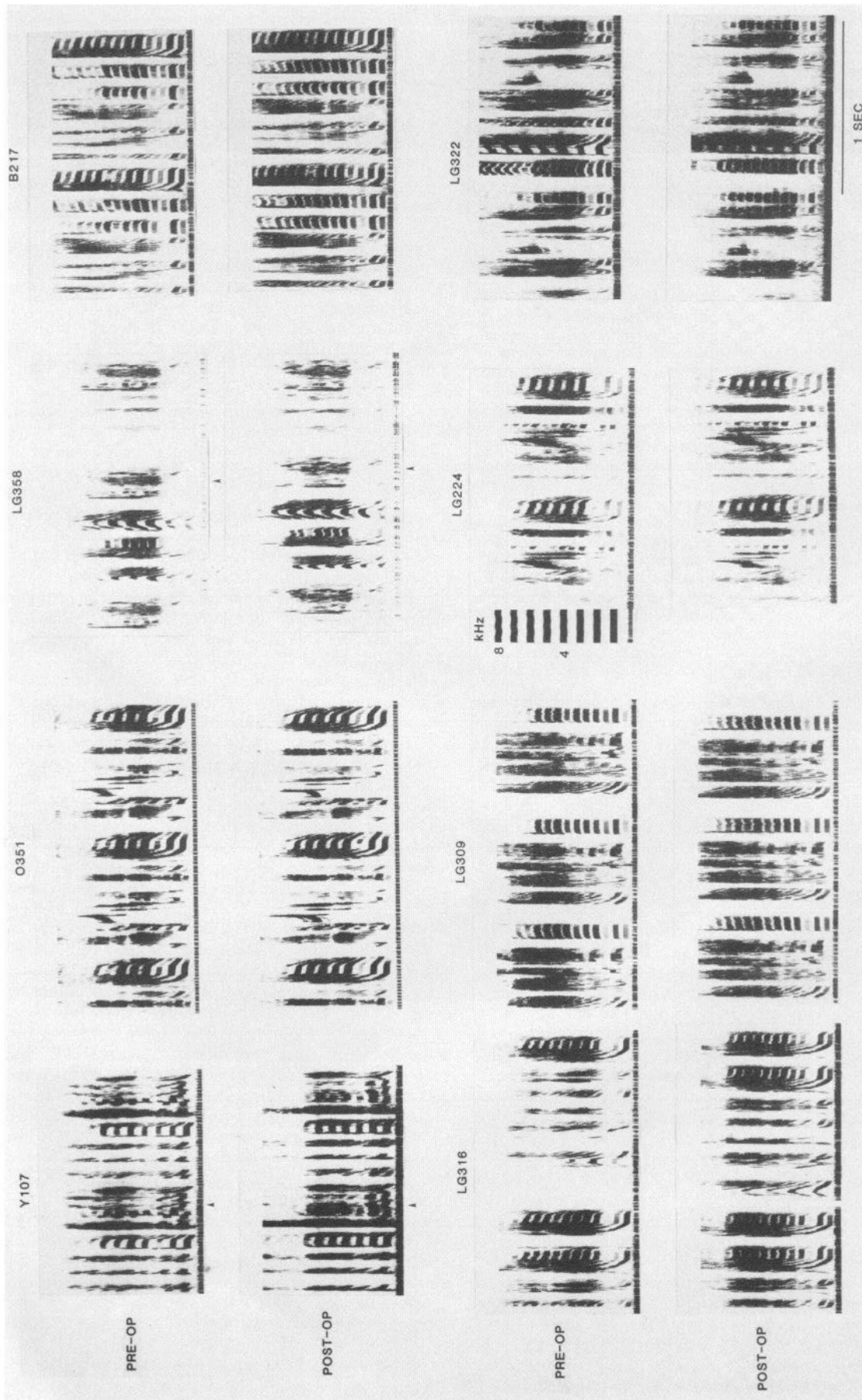


Figure 2. Pre- and postoperative sonograms for hearing birds which underwent unilateral section of hypoglossal afferent fibers. The four birds on the left underwent section of the left vagus rostral to the X-XII anastomosis; the four birds on the right had the right vagus sectioned. Arrows indicate notes which changed as a result of the nerve section operation; such notes are marked by arrows only the first time that they appear in the sonogram.

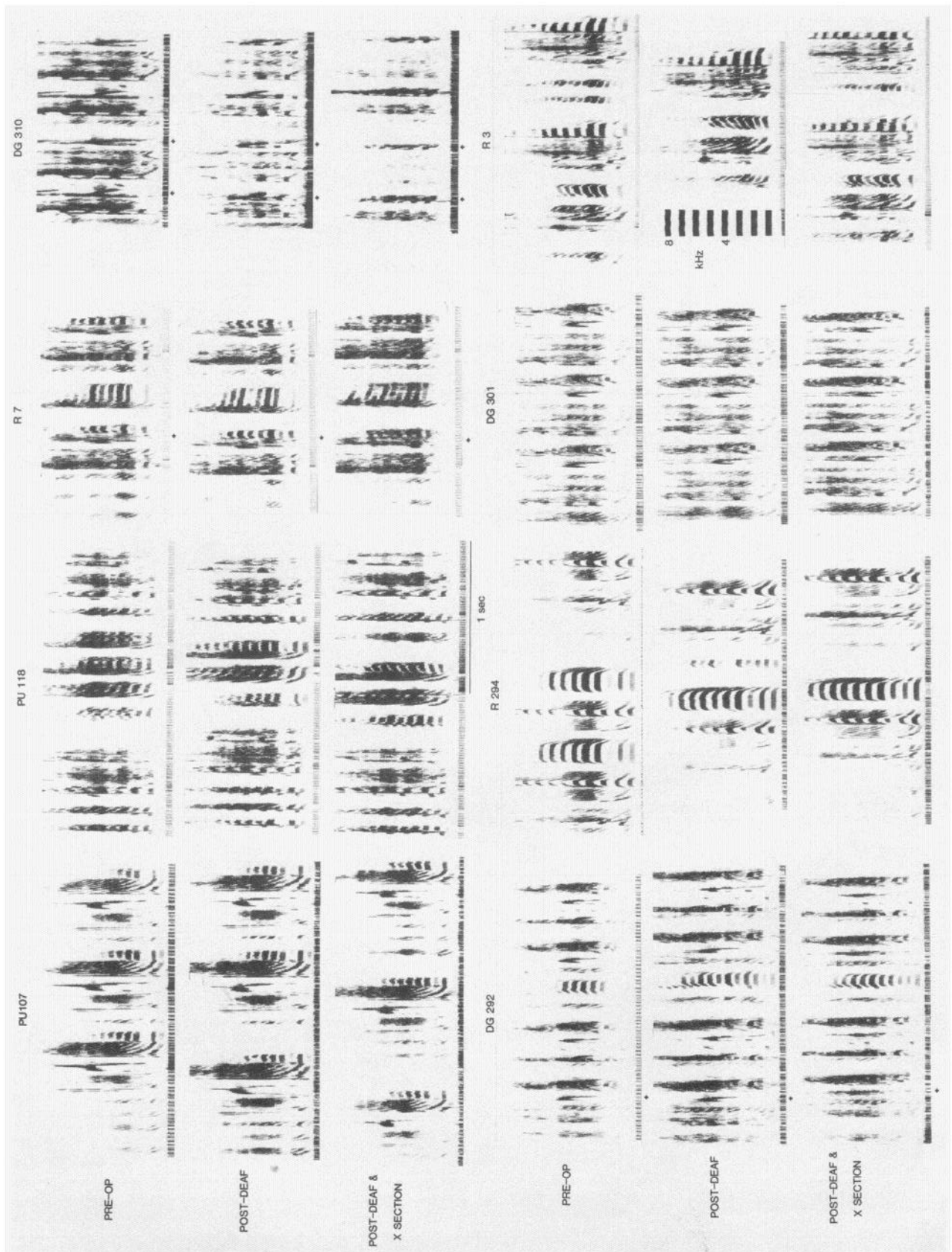


Figure 3. Sonograms for birds before they were operated, after deafening, and again following unilateral section of hypoglossal afferent fibers (point a, Fig. 1). All other details are as in Figure 2.

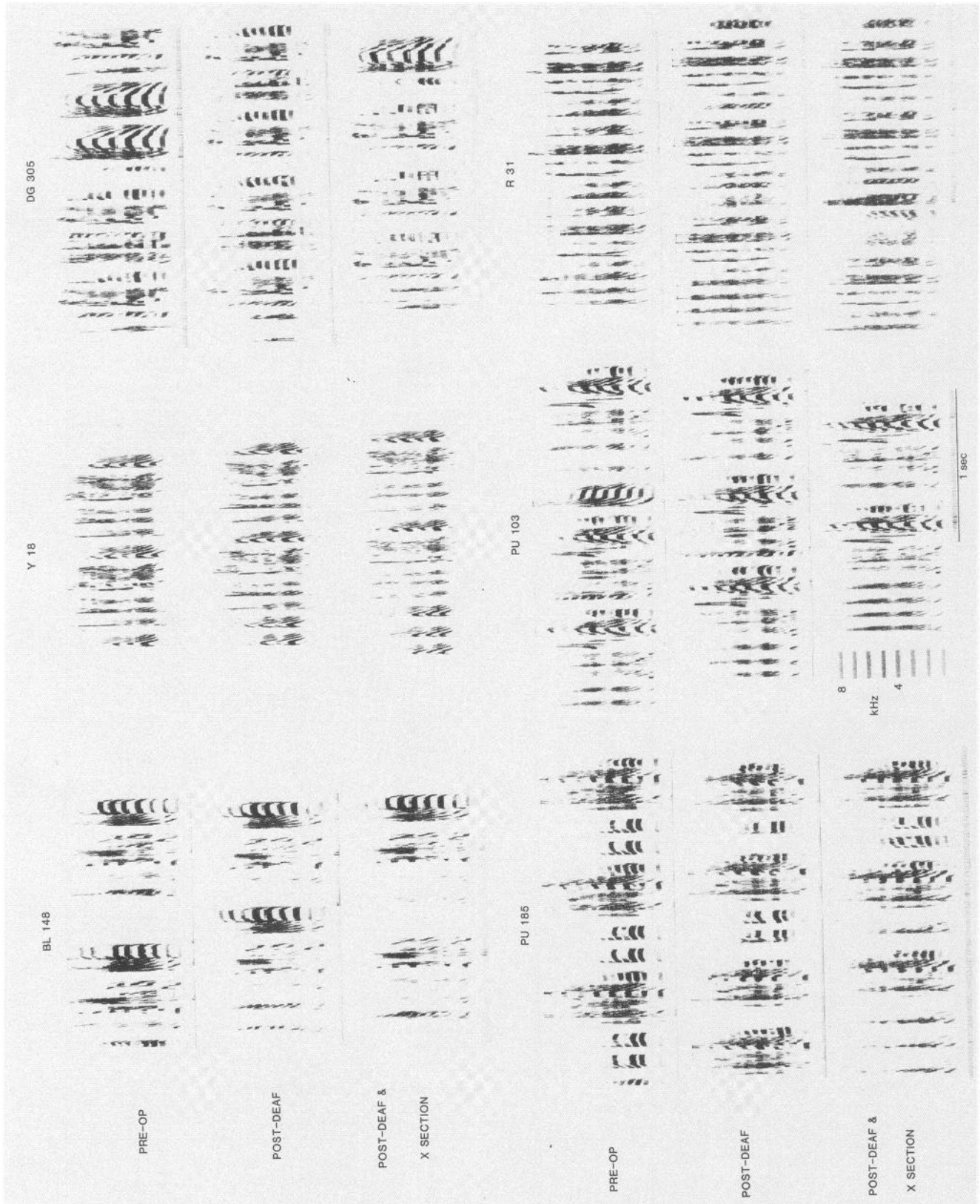


Figure 4. Sonograms for birds before they were operated, after deafening, and again following unilateral section of the descending branch of the vagus (point b, Fig. 1).

song performance as a result of deafening or unilateral nerve section (see Fig. 5). The song pattern of the other bird (R 18) did not change following the deafening operation, but the form of one note changed slightly following section of the left hypoglossal afferents (see *arrows*, Fig. 5). Preoperatively this note began between 4 and 5 kHz and quickly dropped to include frequencies between 2 and 4 kHz; postoperatively this note started at around 2 kHz (cf. description for bird R 7 and Fig. 3, above).

Both of these birds were subsequently reoperated to section the vagus rostral to the X-XII anastomosis on the opposite side, so that the hypoglossal afferents were bilaterally lesioned. R 6 continued to produce a good match of its preoperative song

pattern following this operation. Interestingly, R 18 showed some *improvement* in song performance despite the fact that hypoglossal afferents on both sides had been sectioned.

*Bilateral section of hypoglossal afferent fibers in deaf birds.* Each of the four deafened birds which underwent simultaneous bilateral section of hypoglossal afferents showed some minor changes in their song pattern (see Fig. 6). There were no changes in the song of R 58 after deafening, but following section of the afferents this bird was not able to produce a highly accurate copy of its song pattern. Almost all notes contained both higher and lower frequencies which were not seen prior to the nerve section operation. One note complex in particular was affected (see Fig. 6, *arrows*); the high frequency-

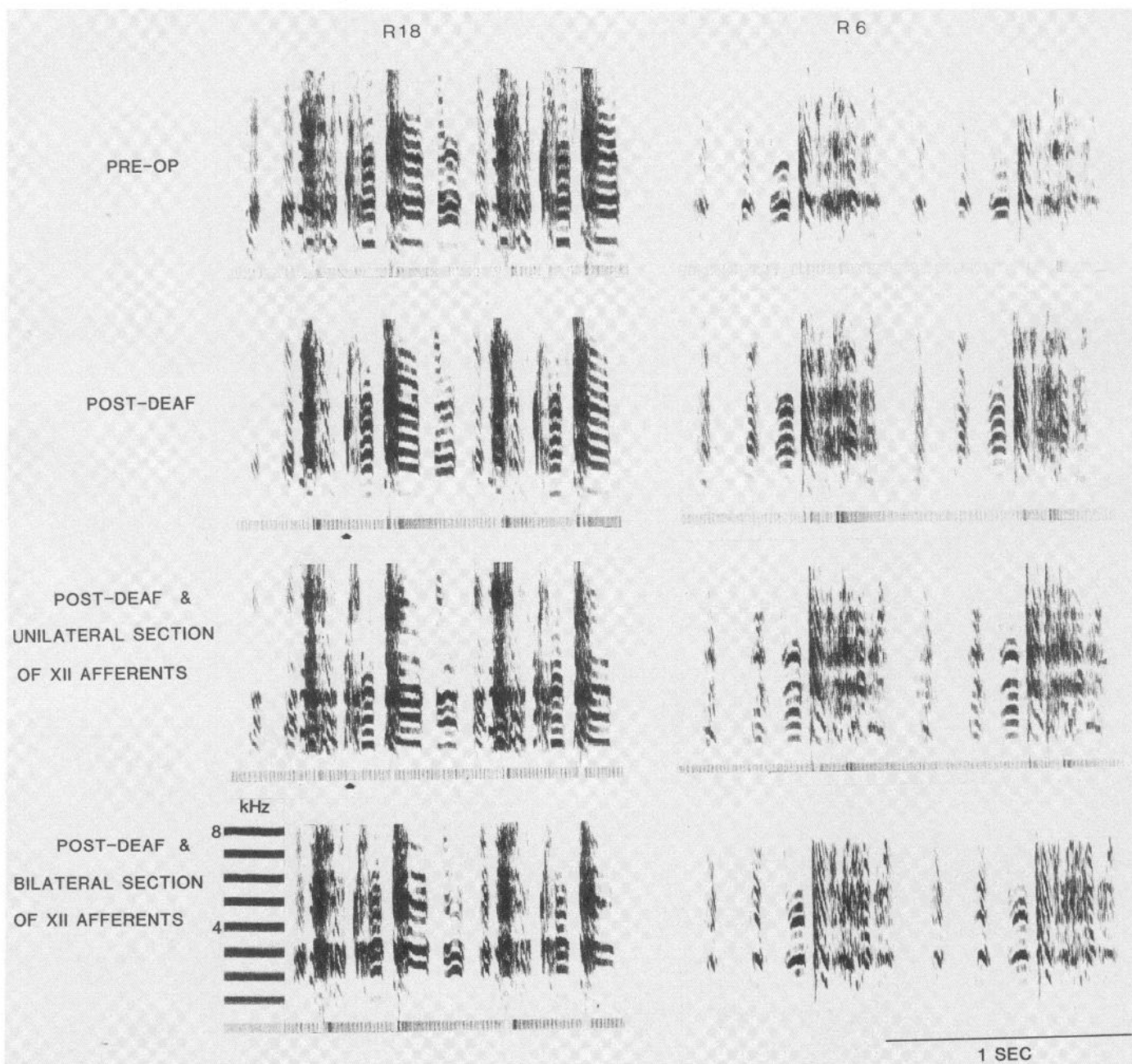


Figure 5. Sonograms for birds before they were operated, after deafening, again following unilateral section of hypoglossal afferent fibers, and finally after bilateral section of hypoglossal afferents.

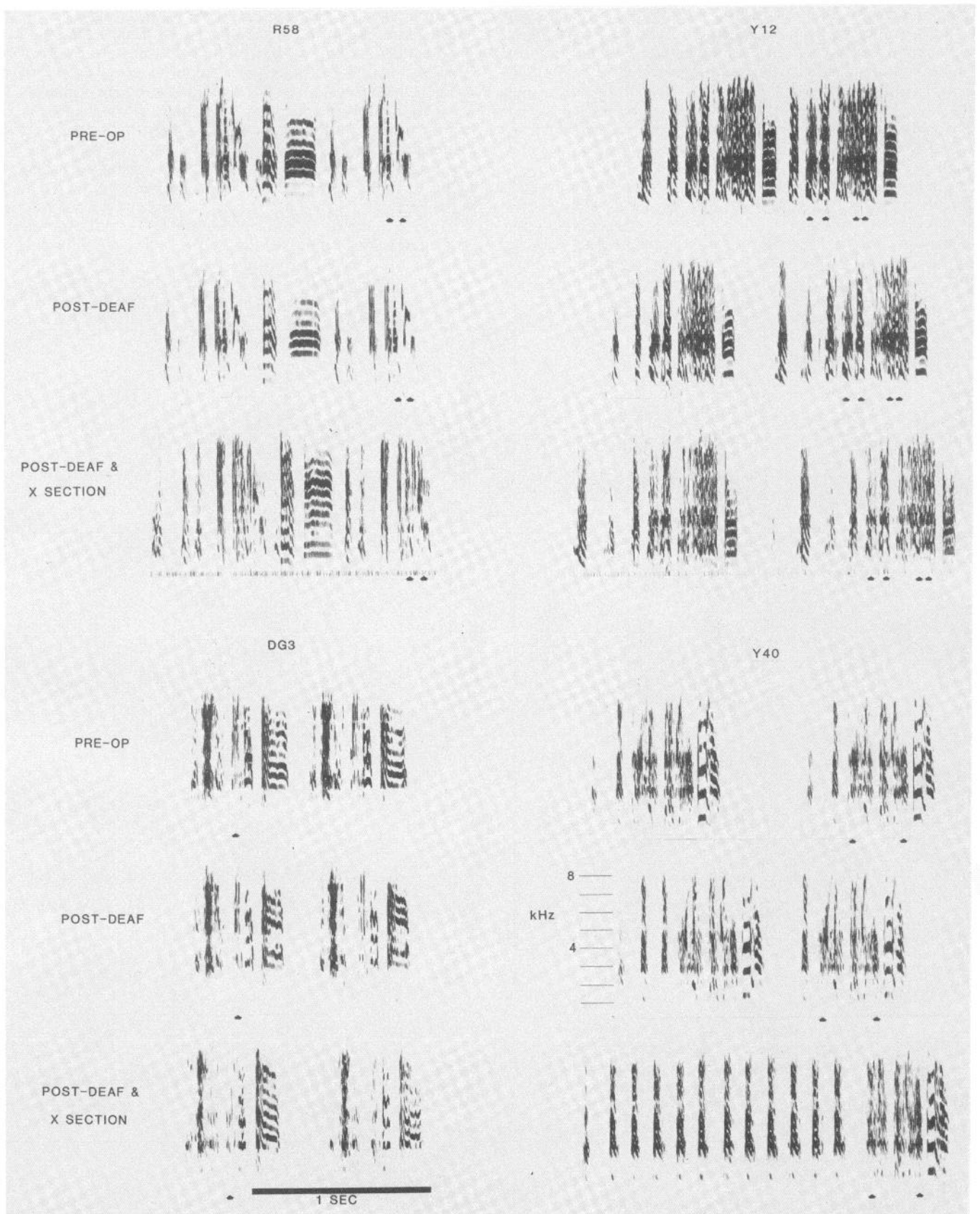


Figure 6. Sonograms for birds before they were operated, after deafening, and again following bilateral section of hypoglossal afferents. See the text for further details.



modulated note and the one immediately preceding it seen toward the end of this complex suffered the greatest change after the hypoglossal afferents had been cut.

There were no changes in the song pattern of Y 12 as a result of deafening, but some changes in song were observed following the nerve section operation. The note complex marked by *double arrows* in Figure 6 seemed to contain mostly noise in the upper frequencies, and the stereotyped fundamental frequency modulation seen at the end of this note complex was gone. The fundamental frequencies of the two notes preceding this complex were also changed (see Fig. 6, *single arrows*), and the regularly spaced harmonic frequencies seen preoperatively in these notes were replaced to a large extent by noise.

The song pattern of DG 3 changed somewhat as a result of deafening; there was slightly more noise in some song elements, and the syllable marked by *arrows* in Figure 6 was not a good copy of its predeafening version. Following section of the hypoglossal afferents the song of this bird showed very minor modifications compared to the postdeafening song; for example, the higher frequencies in the first note of the song were absent.

The song pattern of Y 40 did not change as a function of deafening. Following section of hypoglossal afferents the fundamental frequencies of the song bout did not change, but high frequency noise was present in two notes (marked by *arrows* in Fig. 6) where there had been silence before. Although the form of Y 40's song notes changed very little as a result of either operation, one marked change in the singing behavior of this bird following section of the hypoglossal afferents was the extensive repetition of the introductory song note. Instead of repeating the entire song pattern several times, as was the case preoperatively, this bird now produced one song pattern preceded by 4 to 12 or more introductory notes during each bout of singing. When the entire song unit was produced by this bird, as in the other three birds, the overall pattern and tempo of the song did not change.

### Discussion

The results presented here are largely consistent with the hypothesis that vocal production in adult zebra finches is controlled by central pathways which develop during the time of song learning and which are not heavily dependent on peripheral sources of feedback thereafter. It has been known for some time that deafening adult birds has no major disruptive effect on song behavior (e.g., Konishi, 1965). Our initial experiments in hearing birds further showed that eliminating afferents from the vocal organ also did not produce major disruptions in song structure. However, it might have been the case that reliance on either auditory or syringeal feedback could suffice for normal adult song production. Our later experiments indicate that this is not so. Birds which were deafened and then underwent section of hypoglossal afferents failed to show substantial disruption of preoperative song. This result indicates that vocal learning does not entail transfer of control from auditory feedback to sensory feedback from the syrinx. If such were the case, then we would expect section of hypoglossal afferents to produce the same extensive disruption that deafening exerts on the song of young birds. In contrast, the postoperative changes that we observed were for the most part extremely minor.

Because we do not know what type of receptor is associated with afferent fibers from the syrinx, we cannot speculate on what sort of information these fibers may be carrying. However, even though the nature of this information is unknown, the important fact remains that excluding sensory information from the syrinx produces no immediate substantial disruption of song behavior.

Of course, we have examined only the contribution of audi-

tory feedback and of feedback from the vocal organ and, therefore, cannot rule out the possibility that feedback from other parts of the periphery is important. However, if peripheral feedback in general were important for vocal production, we would strongly suspect input based on hearing and/or on the exercise of the vocal organ to be of paramount importance. The fact that elimination of these two sources of input in adult birds has no drastic effect on vocal production suggests to us that singing behavior is controlled (at least partially) by a central control program which is formed during the course of song learning.

Control experiments in which birds were deafened and then had either the left or right descending vagus sectioned yielded no effect on song behavior. However, it is quite possible that pulmonary fibers in the descending branch of X contribute to song production, but that bilateral lesion of respiratory fibers is necessary to detect such a contribution. The absence of any change in song behavior following section of the descending vagus also serves as a control for the effects observed due to section of hypoglossal afferents in another way. It is possible that merely exposing the anastomosis and isolating the nerves in preparation for sectioning has some adverse effect on song, perhaps via stretching or movement of hypoglossal efferents. The lack of any effect on song behavior in the control birds argues against this possibility. Of course, we cannot be completely sure that unintentional irritation or partial damage to the efferent XII nerves did not occur in *any* experimental bird. Since many experimental birds did not change their song patterns at all following section of hypoglossal afferents, it is conceivable that the small number of birds subjected to control surgery was not sufficient to detect potential effects of unintentional damage to the efferent XII roots. Thus, there is some possibility that the changes which occurred following syringeal deafferentation resulted from disturbance of motor innervation. However, we feel it likely that the minor effects observed are attributable to section of hypoglossal afferent fibers and are not a byproduct of damage to syringeal efferents.

We did not assess the long-term consequences for song behavior of combined deafening and section of hypoglossal afferent nerves. Deafened birds which underwent unilateral section of hypoglossal afferents were recorded to at least 2 weeks following the nerve section operation. All three birds in this group which exhibited changes in their song patterns showed partial or complete recovery over a period of 8 to 19 days. Such recovery may have been due to nerve regrowth; unfortunately, we were unable to determine by visual inspection whether regrowth had occurred at this time due to the large amount of connective tissue that had accumulated around the section. An alternative possibility is that the intact, contralateral side was somehow able to compensate for the lesioned fibers. At any rate, the possibility that feedback along hypoglossal afferent fibers is necessary for long-term maintenance of song behavior has not been ruled out by the present experiments. It seems plausible to us that a central network controlling vocal production could be dependent on peripheral feedback for its continued maintenance.

Both deafening and section of hypoglossal afferent fibers exerted some small effects on song in individual cases. Of a total of 20 birds deafened in this study, 4 exhibited some minor changes from their preoperative song patterns. These findings are comparable to those of Price (1979), who reported that the song of one of four zebra finches deafened at approximately 320 days had degenerated 6 months following the operation. The effect of lesioning hypoglossal afferents in deafened birds was most clearly demonstrated by simultaneous bilateral section of these fibers (see Fig. 6); the song patterns of all four birds which were subjected to this procedure changed following the nerve section operation, although these changes were also

quite minor. A total of 22 birds underwent unilateral section of XII afferents (including the four control birds which were reoperated to section X rostral to the anastomosis); of these, the song patterns of six birds changed following the operation. If, in fact, these minor but noticeable changes in song are attributable to section of hypoglossal afferents, the question arises as to why a subset of birds should be (mildly) susceptible to syringeal deafferentation (or, for that matter, deafening). If we assume that a central control program for song does develop and requires peripheral feedback for its long-term maintenance, then there might exist a continuum along which birds are distributed, depending upon how well "established" their central control program is. This idea may be supported by the finding that the only bird in our study whose song was greatly disrupted following unilateral section of hypoglossal afferents (DG 310) also exhibited substantial change in song behavior as a result of deafening.

Our results have encouraged us to think that learned song performance in adult zebra finches is not immediately dependent on peripheral feedback. However, since song learning in juvenile birds requires auditory feedback, it will be important to determine whether syringeal afferents also contribute to song development. If so, feedback derived from the vocal organ would be similar to auditory feedback in that both are necessary during an early period of life for song to develop normally.

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