

Colony differences in auditory thresholds in the canary (*Serinus canarius*)

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Adult canaries (*Serinus canarius*) from a closebred colony of the Belgian "Waterslager" strain were trained with operant techniques to respond to pure tones. A psychophysical tracking procedure was used to measure absolute auditory thresholds in quiet and in noise. Absolute thresholds in the middle- to high-frequency region of the audiogram were between 30 and 40 dB higher (4–5 standard deviations) than those typically reported for other song birds including canaries of other strains and Waterslagers tested some years ago from another colony. Thus the Millbrook colony of domestic canary—an oscine songbird which learns its vocalizations by reference to auditory information—shows unusually high absolute thresholds for pure tones.

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INTRODUCTION

The existing data on hearing in songbirds from both physiological and behavioral studies show a maximum sensitivity approaching human thresholds in a narrow frequency region between 2.0 and 5.0 kHz with dramatically decreasing sensitivity above and below this frequency region (Dooling, 1980, 1982; Konishi, 1970). Previous behavioral and physiological studies of hearing in the canary have shown that it is similar to these other songbirds (Konishi, 1969; Marler *et al.*, 1973; Dooling *et al.*, 1971).

The domestic canary, a cardueline finch, has been bred for hundreds of years for the quality of its plumage and its song (Guttinger, in press; Stresemann, 1923). More recently, canaries from a closebred colony of the Belgian Waterslager strain in Millbrook, NY, have been the focus of both behavioral and neuroanatomical studies of vocal learning (Waser and Marler, 1977; Nottebohm, 1980a). As is characteristic of other oscine songbirds, canaries from this closebred colony learn their song by reference to auditory information (Marler and Waser, 1977; Waser and Marler, 1977). Now we report that canaries from this particular closebred colony of Belgian Waterslagers have elevated thresholds for pure tones that stand in marked contrast to previous data on hearing in the canary (Dooling *et al.*, 1971; Konishi, 1969).

I. EXPERIMENT 1

A. Materials and methods

1. Subjects

Nine adult canaries (*Serinus canarius*) were selected at random from a large mixed colony and trained with operant conditioning techniques to respond to pure tones. Five of these canaries were of the Belgian Waterslager strain obtained from a closebred colony at the Rockefeller University Field Research Center, Millbrook, NY (four males, one female); one was an American Singer canary (a male) obtained

from Cornell University, and three were of the German "Roller" strain obtained from a local pet supplier (one male, two females). During this study, all birds were housed at the University of Maryland and kept on the same normal light cycle. All testing was done between the months of July and March.

2. Apparatus

The apparatus and training procedures have been described previously (Park *et al.*, 1985). The birds were tested in a small wire cage (25 × 25 × 25 cm) which was mounted in an anechoic chamber (2.5 × 5.0 × 2.5 m). Pure-tone stimuli were presented from a loudspeaker mounted 42 cm directly above the bird's head. A standard pigeon grain hopper was used for food delivery, and response keys were constructed from microswitches and LEDs. The bird reported detection of a pure tone by pecking the microswitches. All aspects of stimulus presentation during both training and testing were controlled by a Zenith H-89 microcomputer operating a Coulbourn Instruments Dynaport serial interface. The audiometric circuits consisted of logic and analog modules from Coulbourn Instruments. Sound field calibration was accomplished by placing the microphone of a General Radio 1982 sound level meter in the position normally occupied by the bird's head during testing.

3. Training and threshold testing procedure

The bird was trained by standard operant techniques to peck one key (observation key) repeatedly when it did not hear a tone and to peck a second key (report key) when it did. A correct response or hit (a peck on the report key during tone presentation) was reinforced with food. A false alarm (a peck on the report key when no tone was presented) was punished with a 4-s timeout period during which the lights were extinguished in the test chamber. Food-deprived birds

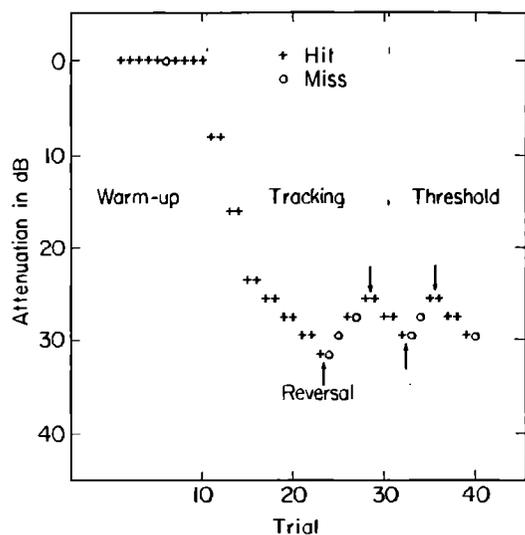


FIG. 1. The results of a typical test session consisting of 40 trials. After the first ten trials, stimulus intensity is reduced following two correct responses and increased following a miss. Initial step size is set at 8 dB. Within 10 dB of the bird's suspected threshold, step size is automatically reduced to 2 dB. Threshold for a given session is defined as the mean of the reversal points occurring over the last ten trials.

were trained and tested in daily sessions consisting of 40 trials. The birds were trained with a 1.0-kHz pure tone presented at 83 dB SPL until they attained a level of 90% correct combined with a false alarm rate of less than 10% over a session of 40 trials. Threshold testing commenced at this point.

During threshold testing, the probability of tone onset following an observation response was 0.10. For the first ten trials, the tone intensity was fixed at a level 10 to 50 dB above the bird's suspected threshold. For the next 30 trials, the same procedure was continued but stimulus levels were contingent on the bird's responses. Two successive correct responses (hits) lowered stimulus intensity for the next trial by one step, while one incorrect response (miss) raised the stimulus intensity for the next trial by one step. At the start of a session, step size was first set to 8 dB and then to 2 dB at an intensity within 10 dB of the bird's suspected threshold. This procedure is somewhat similar to the adaptive tracking procedure described by Levitt (1970) but, in the present case, the task is a YES/NO task rather than a two-interval forced-choice task. Testing was continued at a given test frequency until the difference between the tracking reversal points over the last ten trials of a session was less than 4 dB. The threshold for this session was then defined as the mean of the high and low reversals over the last ten trials. Typically, two to four reversals were observed during the last ten trials of a session. The final threshold value at a test frequency was a median threshold from three test sessions. The order of frequencies tested was randomized and a different random order was used for each bird.

A schematic diagram of the events in a typical test session is shown in Fig. 1. The bird is first tested on ten trials at a fixed intensity followed by a tracking procedure with a step size of 8 dB. Within 10 dB of the bird's suspected threshold, step size is reduced to 2 dB. The threshold from the record in

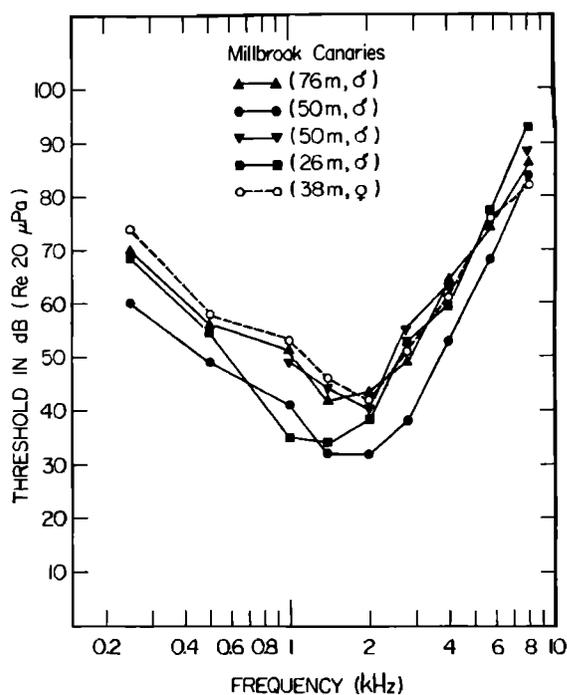


FIG. 2. The audibility curves for each of the canaries from the Millbrook colony. The age (in months) and the sex of each bird are given next to each symbol. There were no differences between old and young birds or between the four male birds and the female bird.

Fig. 1 was determined by subtracting the final attenuator value (in this case - 28 dB) from the sound-pressure level of the tone at the start of the session.

B. Results

The results for the five Millbrook canaries are shown in Fig. 2. These five canaries were very consistent in their threshold performance showing a narrow range of maximum sensitivity between 1.0 and 2.0 kHz and steeply decreasing sensitivity above and below this region. Threshold sensitivity decreased approximately 10 dB/oct for frequencies below 1.0 kHz and about 20 dB/oct for frequencies above 2.0 kHz. At high frequencies (i.e., above 4.0 kHz), the birds showed very high thresholds for detection of pure tones.

The results for the American Singer and the Roller canaries are shown in Fig. 3. Data for these canaries are plotted in relation to the average threshold from the five Millbrook canaries and earlier data from another colony of Belgian Waterslager canaries tested by a different behavioral procedure several years ago (Dooling *et al.*, 1971). Results for both the American Singer and the Roller canaries tested in the present study agree well with data on the auditory sensitivity of canaries of the Belgian Waterslager strain from this earlier study. By contrast, the mean absolute thresholds for Waterslager canaries from the Millbrook colony are higher than those of all other canaries. At frequencies above 1 kHz, the differences between groups of canaries are quite pronounced with Millbrook canaries showing absolute thresholds 35 to 50 dB above those of other canaries.

It is unlikely that these differences are due to motivational differences between groups of canaries in the testing

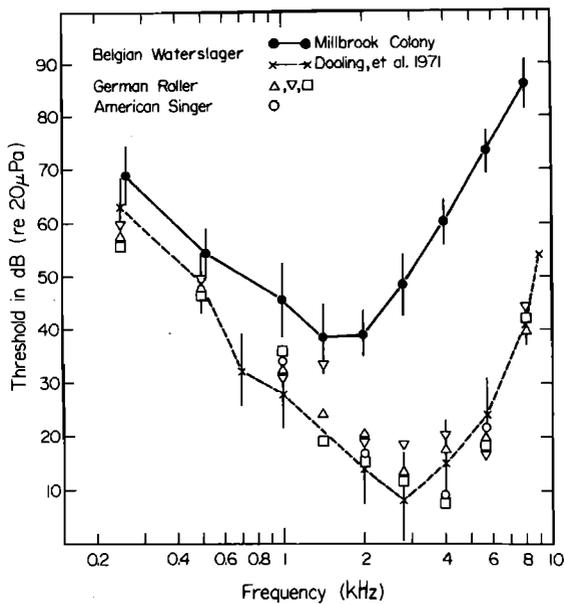


FIG. 3. The mean auditory curve (solid circles, solid line) of five Millbrook canaries is shown in comparison with data from other canaries. Auditory sensitivity of the American Singer canary (open circles) and three German Roller canaries (open symbols) tested in the present study corresponds well with published data for canaries of the Belgian Waterslager strain but from another colony (dashed line).

situation. There were no differences at threshold between the two groups of canaries either in false alarm rate or in response latency. Average false alarm rate and response latency at threshold were 7.8% and 1.07 S for Millbrook canaries and 9.9% and 0.96 S for the other canaries. Differences were not significant by a two-way ANOVA (group by test frequency) either in false alarm rate ($df = 1, 55$, $F = 2.35$, $p > 0.10$) or response latency ($df = 1, 55$, $F = 2.57$, $p > 0.10$).

As a check on the possibility that absolute auditory sensitivity changed with the season, as is clearly the case with vocal behavior in these birds (Nottebohm, 1981), one bird was tested at 1.0 and 4.0 kHz several times throughout the year. There were no differences in absolute auditory thresholds obtained in July, November, and March.

II. EXPERIMENT 2

The results of experiment 1 indicate that Waterslager canaries from the colony in Millbrook show elevated absolute thresholds. Experiment 2 was undertaken to determine whether these canaries are unusual with respect to another basic psychoacoustic measure—the critical masking ratio. The threshold for pure tones masked by broadband noise provides one measure of the frequency resolving capabilities of the auditory system (Scharf, 1970), and these data are already available for another avian species, the budgerigar (*Melopsittacus undulatus*).

A. Materials and methods

1. Subjects

The subjects in this experiment were four Waterslager canaries from the Millbrook colony and three Roller canaries from experiment 1. In addition, three other species of

small birds were tested to provide comparative data: a budgerigar (*Melopsittacus undulatus*), a song sparrow (*Zonotrichia melodia*), and a swamp sparrow (*Zonotrichia georgiana*).

2. Apparatus

The apparatus was the same as that employed in experiment 1. A background of broadband noise was produced by a Coulbourn Instruments noise generator and this noise was presented continuously in the test chamber. Noise spectrum levels of -8, 2, 12, 22, and 32 dB SPL were used to mask a 2.0-kHz test tone.

3. Training and testing procedure

The training and testing procedure was similar to that used in experiment 1. The birds were first trained and tested in the quiet. Once final thresholds were determined in quiet, testing in noise began. The birds were tested as in experiment 1 but in the presence of a background noise with a spectrum level of 32 dB. As in experiment 1, threshold testing was continued for a number of sessions until a session occurred in which the difference in tracking reversal points over the last ten trials was less than 4 dB. For the next session, noise level was reduced 10 dB and the procedure was repeated. In all, masked thresholds were obtained at five different noise levels as well as in quiet.

B. Results

The results are shown in Fig. 4. A linear relation exists between the masked threshold of a pure tone and the level of background noise for all birds except Waterslager canaries from the Millbrook colony. At high masking noise levels, all birds show the expected pattern of pure-tone thresholds

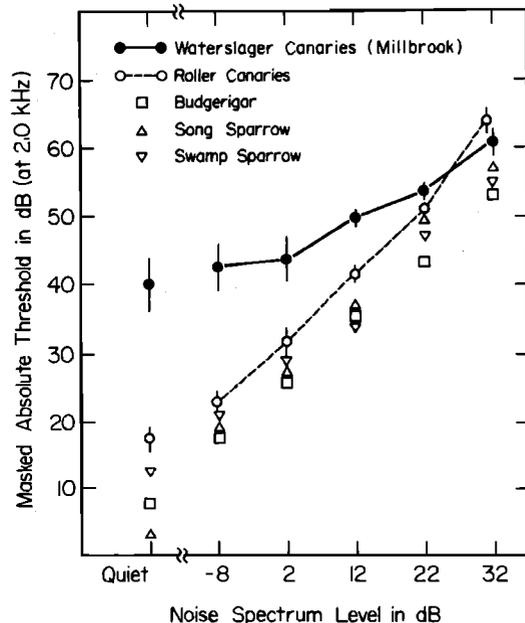


FIG. 4. Average masked absolute threshold for a 2.0-kHz pure tone as a function of background noise level for Millbrook canaries (solid line, solid circles), three German Rollers (open circles, dashed line), and three other species of small birds tested in the same apparatus with the same procedure.

which are dependent on noise level. At low noise levels, the average masked threshold for Millbrook canaries is independent of noise level, demonstrating that these masking noises are subthreshold. These results further support the conclusion that differences in absolute sensitivity between Millbrook canaries and other small birds are due to sensory deficits rather than motivational differences between birds in the testing situation. Inspection of the data from individual Millbrook birds at high masking noise levels indicates there may also be a slight difference in slopes of the masking functions between Millbrook canaries and other birds. With each 10-dB increase in masking noise level, threshold increases about 8.5 dB for Millbrook canaries and about 10.5 dB for all other birds. False alarm rates and response latencies for all birds in this experiment were similar to those of experiment 1.

III. EXPERIMENT 3

To the extent that critical ratios reflect the spectral resolving capability of the ear (Scharf, 1970; Dooling and Saunders, 1975), experiment 2 indicates that, for above threshold acoustic signals, the Millbrook canaries show spectral frequency resolving power comparable to the other canaries tested and somewhat worse than that of the budgerigar and two sparrows. A final experiment was conducted to determine how well these Millbrook canaries could detect intensity differences in acoustic signals.

A. Materials and methods

1. Subjects

Three of the Millbrook canaries used in experiments 1 and 2 were also used in experiment 3.

2. Apparatus

The apparatus was the same as that employed in experiments 1 and 2 with the following exception. The output of the noise generator was split. One output was fed to a mixer/amplifier. The other output was fed to an electronic switch, a programmable attenuator, and then to the same mixer/amplifier. Changing the level of attenuation resulted in an increment in the intensity of an otherwise continuous broadband noise signal. The electronic switch was driven with a 10-Hz pulse and set for rise/fall times of 20 ms. During a trial, this resulted in an increment in the intensity level of noise for a total duration of 70 ms (20-ms rise/fall and 30-ms plateau).

3. Training and threshold testing procedure

Three Millbrook canaries were trained to respond to 70-ms increments in the intensity of a continuous broadband noise. During a trial, these intensity increments occurred at the rate of five per second. The birds were trained initially with the broadband noise set at an overall level of 80 dB SPL with an increment in intensity of 6 dB SPL.

A descending method of limits procedure was used for measuring thresholds. The descending series began with a noise increment of 6 dB by selecting 0 dB of attenuation on the programmable attenuator. Following each correct response, the attenuator setting was increased by an additional

2 dB. Threshold was defined as the intensity increment halfway between the last correct and incorrect responses. In all, an intensity difference limen for noise was measured at five levels having overall sound-pressure levels of 60, 70, 80, 85, and 90 dB SPL.

B. Results

The results are shown in Fig. 5. At broadband noise levels greater than 70 dB SPL, canaries from the Millbrook colony showed an average intensity difference limen of about 1.2 dB. This value corresponds well with data from the budgerigar obtained with a behavioral procedure under very similar stimulus conditions (Dooling and Searcy, 1981) and is also consistent with intensity difference limens for other small birds (Dooling, 1980, 1982). False alarm rates and response latencies of the birds in experiment 3 were similar to those observed in the two previous experiments. A human subject (KO) tested with the same sound delivery system showed an intensity difference limen of 1.1 dB at an overall background noise level of 80 dB SPL.

IV. DISCUSSION

The present study shows that Waterslager canaries from the Millbrook colony have elevated absolute thresholds compared to other small birds including canaries from other colonies. While the reasons for these unusually high thresholds are not clear, an otoscopic examination of the external ear and tympanic membrane ruled out obvious conductive

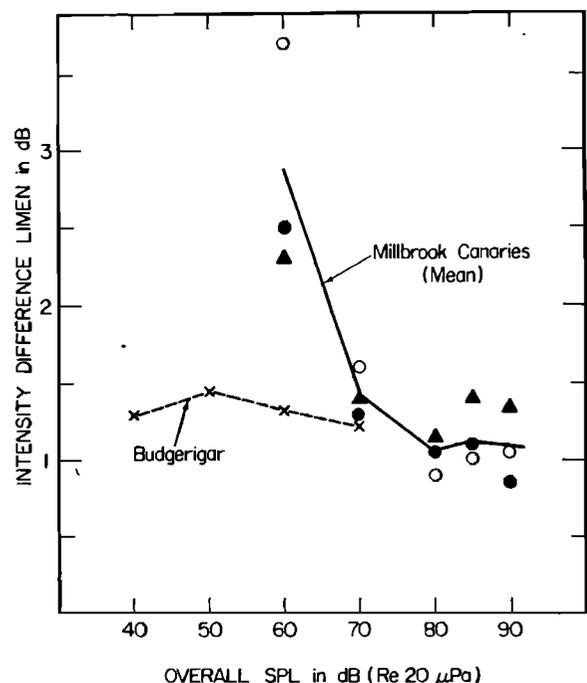


FIG. 5. The intensity difference limen in dB [ΔI in dB or $10 \log(\Delta I / I + 1)$] (Grantham and Yost, 1982) for broadband noise is plotted for three Millbrook canaries and the budgerigar. Data for the budgerigar are from Dooling and Searcy (1981). Below 70 dB, the intensity difference limen for Millbrook canaries rises dramatically since stimuli at this level are near the bird's absolute threshold. Symbols for Millbrook canaries are the same as those in Fig. 1.

problems such as mites, scar tissue, or a perforated tympanic membrane. Our cursory otoscopic examination would not have detected conductive problems due to middle ear dysfunction.

Other potential causes for the threshold differences reported here are less easily evaluated but the data do address several of the more obvious possibilities. Since male and female canaries show profound differences in vocal behavior, the possibility exists that there are differences between males and females in auditory sensitivity. The individual data presented in Fig. 2 show no differences between the female and the four male canaries from the Millbrook colony. There were also no differences in absolute thresholds between males and females for the normally hearing birds. Thus sex differences are an unlikely explanation for the present findings.

There were age differences among our samples but these differences also do not provide a reasonable explanation for the present results. At the time of testing, the Millbrook canaries ranged in age from 26 to 76 months. The Millbrook canary with the lowest thresholds was 50 months old while the 26-month-old Millbrook canary had even higher thresholds (see Fig. 2). The German Rollers were all 22 months old and the American Singer was 40 months old. The Belgian Waterslagers with normal thresholds from the earlier study (Dooling *et al.*, 1971) were between 9 and 26 months old. On the average, the Millbrook canaries are older than the other canaries tested but the age range of both samples is large and the overlap sufficient so that changes in hearing with age cannot easily account for the threshold differences reported here. Unfortunately, the youngest Millbrook canary tested was 26 months old. Therefore it remains an open question whether or not Millbrook canaries are born with normal auditory sensitivity.

If Millbrook canaries are born with normal auditory sensitivity, which they subsequently lose, there could be any number of environmental factors responsible, as well as other possibilities including hereditary or degenerative disorders. Exposure to loud noise is one very common cause of elevated auditory thresholds (Davis and Silverman, 1978) and this possibility deserves careful attention. Previous studies of the effects of noise on hearing in the canary as measured by single unit thresholds in cochlear nucleus show that a 200-day exposure to broadband noise at 95 to 100 dB SPL can cause permanent threshold shifts (Marler *et al.*, 1973). In a more detailed study, budgerigars exposed for 72 h to a 1/3-oct band of noise at 107 dB SPL also showed a permanent threshold shift. Interestingly, maximum threshold shift occurred at the frequency of exposure with only a slight spread of threshold shift to lower and higher frequencies (Dooling, 1980; Saunders and Dooling, 1974). Thus budgerigars and canaries can suffer permanent hearing damage from exposure to loud noise. Perhaps loud song from many birds in the large breeding colony at Millbrook is sufficient to cause a threshold shift in some birds. This could be the case even though the Millbrook canaries in this study were maintained at the University of Maryland for periods of 6 months to 3 years prior to testing, ruling out the possibility of any temporary threshold shift.

There are, however, several pieces of evidence that argue against this simple hypothesis. First, adult budgerigars and sparrows housed with canaries for long periods of time in the same large colony room at Millbrook show normal auditory thresholds. Second, the 26-month-old Millbrook canary with elevated thresholds was born in a relatively quiet residential environment (the home of Professor Peter Marler), then reared in a sound isolation box for 8 months before being transferred to the large canary colony at Millbrook. This argues against the possibility of an early sensitive period for acoustic trauma (Bock and Saunders, 1977). Third, the peak energy in Waterslager canary song occurs in the region of 2 to 4 kHz (Dooling *et al.*, 1971; Guttinger, in press); yet a considerable amount of threshold shift is observed in Millbrook canaries at frequencies above 4 kHz. Fourth, it is likely that commercially available birds such as budgerigars and the Roller canaries used as controls in the present study spent some time in a large aviary where the din from many birds singing could approach that of the large canary colony at Millbrook. If exposure to loud song is the cause of threshold shifts in Millbrook canaries, then, compared to other birds, Millbrook canaries are more susceptible to hearing loss caused by exposure to loud song of other canaries.

From the present data, it is also impossible to completely rule out an environmental toxin of some sort (i.e., antibiotics in the feed) as responsible for the colony differences reported here. The arguments against this hypothesis, however, are similar to those above. In addition, two of the control birds (the budgerigar and the swamp sparrow shown in Fig. 3) were maintained for several years in the same environment and fed a similar diet. These birds show absolute auditory thresholds typical of other small birds including other canaries.

The reason for elevated thresholds in Millbrook canaries remains unclear, but the pattern of elevated thresholds is suggestive. For humans and other mammals, this pattern of hearing loss—that of near normal low-frequency thresholds but elevated middle- and high-frequency thresholds—usually indicates a sensorineural loss rather than a conductive loss (Davis and Silverman, 1978). The fact that this colony of canaries has been closebred for over a decade also raises the possibility that the hearing loss may be genetically transmitted. Inherited hearing deficits involving peripheral auditory system structures are a common finding in highly inbred strains of mice and are often associated with pigmentation abnormalities (Steel *et al.*, 1983).

In considering possible causes for the threshold differences reported here, it is tempting to speculate that the breeding of canaries over the years for beautiful plumage or pigmentation or clear, distinguishable song characteristics may have involved selection for elevated auditory thresholds. The differences in song between various strains of canary are well known among aviculturists. Roller canaries, in particular, are known to sing a much softer song than Belgian Waterslagers (Mundinger, 1985). Perhaps the louder song characteristic of Waterslagers as a breed involves elevated auditory thresholds in some birds. While this is an interesting and viable hypothesis, it is difficult to reconcile

with results of an earlier study (Dooling *et al.*, 1971) showing auditory thresholds in Belgian Waterslager canaries typical of those found in other birds (Fig. 3).

Another interesting hypothesis suggests that some natural selection might have taken place over the last decade in the canary breeding room in Millbrook (Nottebohm, 1985). The idea here is that excessive auditory input may normally interfere with breeding. Good breeders may be characterized by high hearing thresholds in females that enable them to hear only their mate singing nearby. Young males may inherit a raised hearing threshold from their mothers and counter it by imitating only nearby males and singing a louder song, allowing the process of song learning to progress without obvious disruption. One test of this hypothesis would be to compare the hearing thresholds of good and poor breeders.

Although Millbrook canaries that we tested show a considerable threshold elevation for pure tones, the results from the masking and intensity difference limen experiments provide additional information important for interpretation of these findings. Masked thresholds, or critical ratios, can be taken as one measure of the frequency resolving power of the auditory system (Scharf, 1970; Dooling and Saunders, 1975). By this measure, Millbrook canaries have frequency resolving capabilities similar to those of other canaries for acoustic signals above about 50 to 60 dB SPL. A complete test of this hypothesis, as well as that of slope differences in masking functions between Millbrook canaries and other canaries, will require testing of more birds at more noise levels. The same holds true for the results on intensity difference limens. Our preliminary findings indicate that Millbrook canaries have normal intensity resolving power at audible sound levels.

That Millbrook canaries have normal hearing for above threshold acoustic signals is a rather crucial point. Adult male canaries typically produce song at peak sound-pressure levels approaching 85 to 95 dB SPL measured 1 m from the source. Therefore, in spite of dramatically elevated auditory thresholds, there is no question that one bird could hear another singing in close proximity. Experiments aimed at studying song learning and song perception in Millbrook canaries have always involved song stimuli presented at these same high levels (Kroodsma, 1976; Waser and Marler, 1977; Marler and Waser, 1977). Both auditory feedback and an external acoustic model are normal ingredients in the acquisition of song in Millbrook canaries. Results from several earlier studies on this point are quite robust: Canaries surgically deafened when young (Marler and Waser, 1977; Guttinger, 1981) or reared in high levels of noise (Marler and Waser, 1977; Marler *et al.*, 1973) develop extremely abnormal vocalizations. When deafening occurs in adulthood, song deteriorates over a period of months (Nottebohm *et al.*, 1976).

The data are not sufficient to decide among the various hypotheses why some Millbrook canaries show elevated thresholds for pure tones. Nevertheless, these data are interesting and relevant for a number of reasons. From the standpoint of audiology and the study of abnormal hearing processes, the canaries from the Millbrook colony can be

characterized as having a moderate hearing loss (i.e., a 40- to 55-dB loss in sensitivity). Though far from conclusive, the evidence so far points toward an inherited, rather than acquired, loss and one that is sensorineural, rather than conductive, in origin. One obvious next step in the investigation of this phenomenon would be to test very young birds. If the hearing loss in Millbrook canaries is congenital, then there are likely to be even broader consequences since it is known that an early hearing loss can have profound effects on both the organization and function of the developing central nervous system (Willott and Lu, 1982; Webster and Webster, 1977).

Regardless of the cause of elevated thresholds in Millbrook canaries, further investigation of this phenomenon should prove to be quite interesting. From a behavioral and biological perspective, the elevated thresholds reported here may have relevance for the evolution of song in canaries, natural and artificial selection in the breeding of these birds, and the mechanisms of song learning.

From a somewhat different perspective of the study of hearing disorders, the canary may also provide useful information. Canaries must learn their vocalizations by reference to auditory information. Therefore, unlike all other animal models of hearing disorders, the canary offers the possibility of studying the effect of hearing loss on the learning and development of complex vocal behavior. A vast amount is already known about the neuroanatomy of vocal behavior in oscine songbirds such as the canary from the elegant work of Nottebohm and his colleagues (DeVoogd and Nottebohm, 1981; Goldman and Nottebohm, 1983; Nottebohm, 1980b, 1981; Nottebohm and Arnold, 1976; Nottebohm *et al.*, 1976; Paton and Nottebohm, 1984). Thus an oscine songbird such as the canary may provide unique and valuable contributions toward our understanding of the effects of hearing loss on complex vocal behavior and its neuroanatomical foundations.

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