

## Comparative Neurophysiological Studies of Hearing and Vocalizations in Songbirds

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*Summary.* 1. Acoustic neurons in the avian cochlear nucleus are tonotopically arranged according to the sites of innervation on the basilar membrane by the connecting primary auditory fibers.

2. The thresholds of single units vary distinctly with their characteristic frequencies. The distribution of unit thresholds matches extremely well with the behavioral audibility curve.

3. The numbers of units in the nucleus also vary with their CF's. The greatest number of units occurs within the frequency range in which auditory thresholds are lowest. Smaller numbers of units represent the frequency ranges higher or lower than the most sensitive region.

4. The upper range of single unit CF's shows distinct interspecific variation which is correlated with the differences in the range of vocal frequencies. The upper limit of CF may be correlated with the bird's size.

5. The lowest thresholds of single auditory neurons tend to fall uniformly between  $-60$  and  $-80$  DB (re. 1 dyne per  $\text{cm}^2$ ) among different species. The differences between the highest and lowest unit thresholds are also homogeneous ( $40-50$  DB) among different species.

6. Most songbirds do not seem to produce frequencies below 1 KHz but can hear them.

7. The popular belief that songbirds can hear frequencies inaudible to man is not supported by reliable evidence.

### Introduction

Calls and songs of birds have been extensively studied and their communicatory functions frequently discussed. Despite these trends relatively little is known about hearing in birds. The frequency range and absolute sensitivity of hearing, information essential for the discussion of auditory communication, are known in few species. This report presents a neurophysiological method for determining these characteristics of audition and discusses how they relate to the bird's vocalizations.

### Materials and Methods

Ten species were chosen for this report, although several more species were used for additional studies. Local wild birds were collected with mist nets. White-crowned

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sparrows were collected near Inverness, Marin County, California. Western meadow-larks had been originally obtained in California and were given to me by Dr. W. Lanyon. Dr. P. Marler supplied me with canaries bred in his laboratories.

Birds were anaesthetized with urethan; 0.005—0.01 ml (of solution containing 20 g of ethylcarbamate in 80 ml of water) per gram of body weight injected in the pectoral muscular mass. This drug allowed a relatively constant level of anaesthesia over a long period.

A special head-holder electrode-carrier assembly was designed; it consisted of a small vise for holding the bird's head by the bony bridge between its orbital cavities and a metal cylinder for restraining the body, all mounted on a home-made stereotaxic instrument. The cerebellum was removed by suction in order to expose the floor of the fourth ventricle where cochlear nuclei are visible.

Single units were isolated by tungsten microelectrodes made after the method of Hubel (1957). Nerve impulses were amplified by a Grass P612 amplifier, displayed on a Tektronix 502A oscilloscope and also monitored acoustically. Auditory units were first detected by their responses to broad-band noise bursts and then "tuned" with tone bursts by finding the sound frequencies to which the units were most sensitive or had the lowest thresholds of response, i. e., characteristic frequency (CF). Since most units fired "spontaneously", the determination of their thresholds had to be somewhat arbitrary: The stimulus intensity was reduced gradually until the stimulus-locked portion of the spikes disappeared or almost vanished. Nevertheless, insofar as consistent and reproducible values could be obtained by repeated measurements on the same units, the methods used here were reliable and sufficient for the purposes of this study.

The sound delivery system consisted of a General Radio 1310-A oscillator and 1450-TBR decade attenuator, a Grason-Stadler 455C noise generator and 829E electronic switch with rise and decay times set at 25 msec, a Mackintosh 40 power amplifier, and a Brüel & Kjaer 25 mm condenser microphone used as a closed earphone after the method described by Kiang (1966), or an open loudspeaker. Sound frequencies were measured with a Hewlett-Packard 52142 digital frequency counter.

Sound levels were measured near the ear opening either by a calibrated 6 mm B & K microphone in the case of the open loudspeaker or by a probe tube attached to a 12 mm B & K microphone in the case of the closed system, in combination with a General Radio 1900 wave analyser. The two methods sometimes gave different results; any leakage in the closed system grossly distorted sound calibration below 1 KHz, while at frequencies higher than 6 KHz calibration for the open loudspeaker was affected. This weakness could be partly overcome by placing the loudspeaker close to the bird's ear (12 cm).

Field sound recordings were made with a Nagra 111 tape recorder with an Altec-Lansing 681A dynamic microphone mounted on a 66 cm parabolic reflector equipped with a viewing device to facilitate focussing. Dr. W. Lanyon provided me with the recordings of meadowlark vocalizations. Sound-spectrograms were made with a Kay Electric Co. Sonagraph 7029A.

## Results

### *1. Tonotopic Organization in the Cochlear Nucleus*

The avian cochlear nucleus consists of two major parts, nucleus magnocellularis and nucleus angularis. In a live bird the n. magnocellularis and a part of the n. angularis are clearly visible on the floor of

the fourth ventricle. The most caudolateral part of the n. magnocellularis overlaps the most posteromedial region of the n. angularis. More anterior and lateral regions of the angular nucleus are concealed by the cerebellar peduncle.

Boord and Rasmussen (1963), using degeneration methods, found orderly patterns of projection of primary acoustic fibers on the cochlear nuclei of the pigeon. If, as in mammals, acoustic fibers innervating different segments of the basilar membrane have different characteristic frequencies (CF's), there should be an orderly spatial distribution of CF's corresponding to the neuronal projection patterns. This prediction was verified in all the avian species used in this work. Here one example will suffice to illustrate the point.

Fig. 1 shows the distribution of CF's in the left cochlear nucleus of the house sparrow (*Passer domesticus*). Each column of numbers (frequency in hundreds of Hz) indicates the vertical sequence in which the units were encountered during the single unrepeatable penetration at the point occupied by the top most number. In the n. magnocellularis CF's increase towards the rostral tip and medial margin of the nucleus. Units with CF's higher than 3 KHz occur in the anterior third of the nucleus. While the 3 KHz zone extends caudally about one third (0.5 mm) of the lateral margin, it covers two-thirds of the medial margin. The majority of the units encountered in this area have CF's between 3 KHz and 4 KHz. Units with CF's between 4 KHz and 5 KHz are occasionally detected in the most anteromedial region where fibers from the most basal part of the basilar membrane terminate. CF's higher than 5 KHz are seldom encountered in the n. magnocellularis.

CF's between 1 KHz and 3 KHz occur in the area covering the middle third of the lateral border and the most caudal third of the medial margin. Units with their CF's lower than 1 KHz are present around the zone of overlap between the two nuclei. This area corresponds to the projection area of the most apical cochlear fibers in the pigeon.

There is a much clearer tonotopic organization in the angular nucleus than in the other nucleus. Units are arranged tonotopically in three directions; their CF's increase systematically in medial-to-lateral, rostral-to-caudal and ventral-to-dorsal directions. The presence of a distinct vertical tonotopic organization distinguishes this nucleus from the magnocellular nucleus. CF's above 2 KHz occur in the top layer, those between 2 KHz and 1 KHz in the intermediate zone and units with their CF's below 1 KHz in the bottom layer. Among the top-most units there is a clear tonotopic arrangement both in the mediolateral and in the rostro-caudal directions. Comparison of the columns in which there is a clear vertical tonotopic organization indicates the presence of a tonotopic arrangement in the intermediate layers along the same axes mentioned

above. In the zone of overlap between the two nuclei the *n. angularis* maintains its vertical tonotopic arrangement.

The highest CF encountered in this nucleus was almost always about 2 KHz higher than that recorded in the *n. magnocellularis*. For this reason, all units discussed below were obtained from the *n. angularis*.

### 2. Single Unit Frequency Ranges, Thresholds and Behavioral Audibility Curves

All species studied so far showed basically the same tonotopic organization. This makes it easy to determine the range and distribution of CF's in any given species. Since there is always some possibility of missing the highest and lowest CF's located in the peripheral areas of the nucleus, I probed the highest and lowest CF zones of the *n. angularis* in over fifty house sparrows to find narrow ranges of experimental

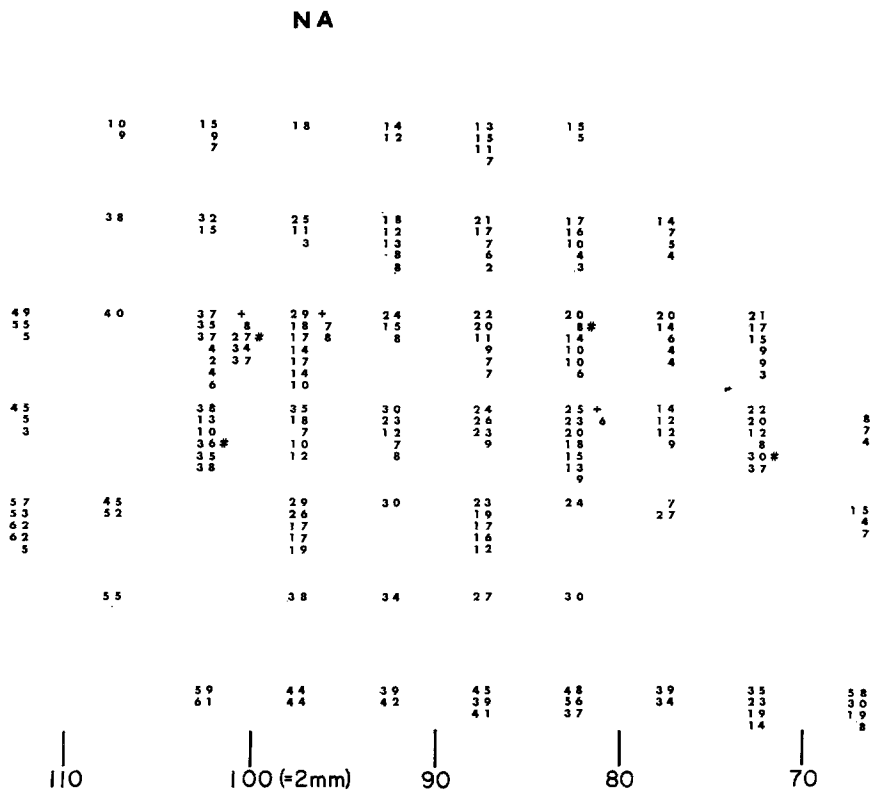
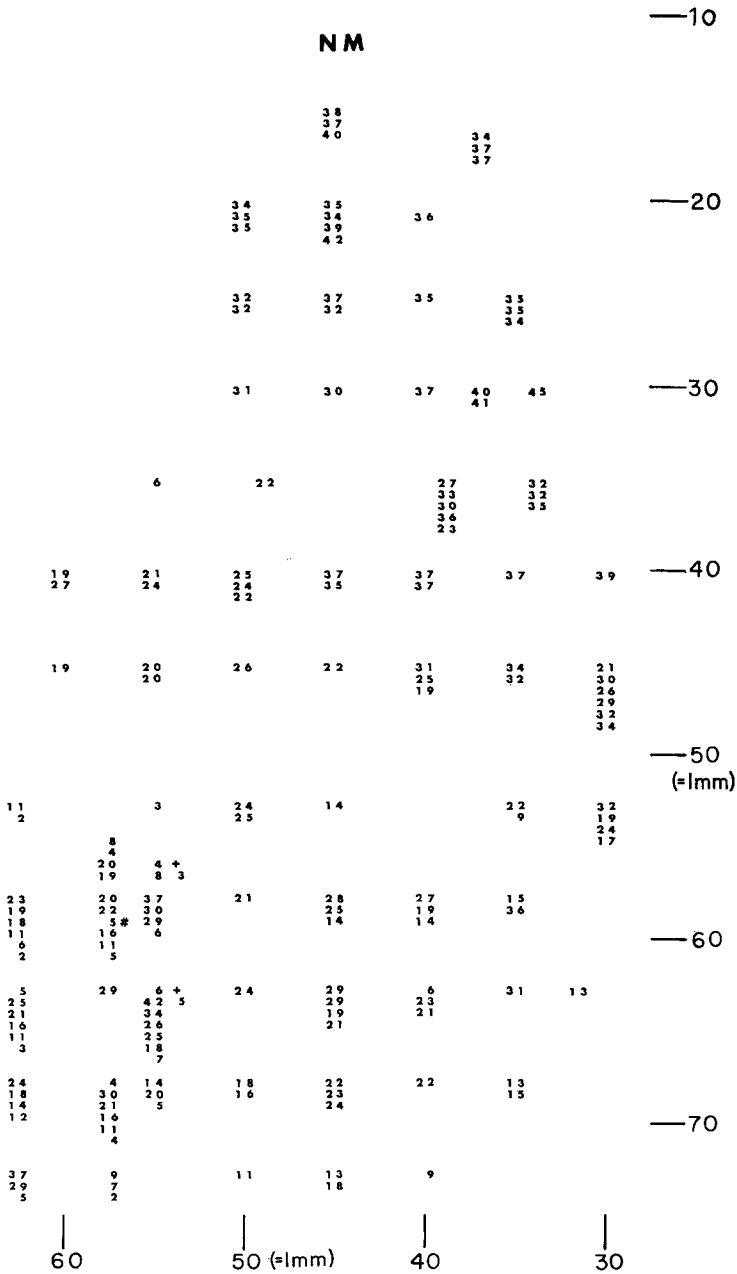


Fig. 1. Tonotopic organization in the cochlear nucleus of the house sparrow. Numbers indicate characteristic frequencies in hundreds of Hertz. Each column of numbers indicates the vertical sequence in which the units were encountered during one unrepeated penetration at the coordinate point occupied by the top most number. CF's increase towards the medial margin and the anterior tip in the nucleus



magnocellularis (*NM*). In the nucleus angularis (*NA*) CF's increase caudad, laterad and dorsad. + denotes the continuation of the columns from left to right for the lack of space # points out irregularities in tonotopic arrangement. Abscissa; distance from the midline of the medulla. Ordinate; distance from the ventral lip of the aqueduct of Sylvius. Unit of scale 1/50 mm

variation, 6.0—6.5 KHz and 135—200 Hz, in the upper and lower limits of CF's respectively. With similar margins of error, I determined the lowest and highest CF's for different species (Table).

Table. *Highest and lowest characteristic frequencies and weights in different birds*

Species	No. of birds used	Average weight (g)	Lowest CF (Hz)	Highest CF (Hz)
Western meadowlark ( <i>Sturnella neglecta</i> )	2	100	250	6,200
American robin ( <i>Turdus migratorius</i> )	5	74	282	7,676
Starling ( <i>Sturnus vulgaris</i> )	5	70	251	6,251
White-crowned sparrow ( <i>Zonotrichia leucophrys</i> )	10	28	655 <sup>a</sup>	8,851
White-throated sparrow ( <i>Zonotrichia albicollis</i> )	10	28	150	9,016
House sparrow ( <i>Passer domesticus</i> )	55	25	135	6,566
Canary ( <i>Serinus canarius</i> )	6	20	403	6,497
Slated-colored junco ( <i>Junco hyemalis</i> )	10	20	350	8,682
Song sparrow ( <i>Melospiza melodia</i> )	10	20	447	9,382
Chipping sparrow ( <i>Spizella passerina</i> )	6	10	501	8,514

<sup>a</sup> uncertain.

Does the interspecific variation in the CF ranges reflect the different frequency ranges of hearing? In order to answer this question, we must first investigate whether single unit CF's can be related to the frequency characteristics of hearing.

Auditory neurons with different CF's have distinctly different thresholds. Units with CF's near the highest or lowest limit have higher thresholds than those with intermediate CF's. This variation in unit thresholds coincides with the frequency-dependent variation of audibility thresholds. Fig. 2A shows an average audibility curve of four canaries obtained by Dooling (1969). A similar composite audibility curve of the starling determined by Trainer (1946) is shown in Fig. 3A. In both cases the thresholds of hearing were determined by avoidance conditioning

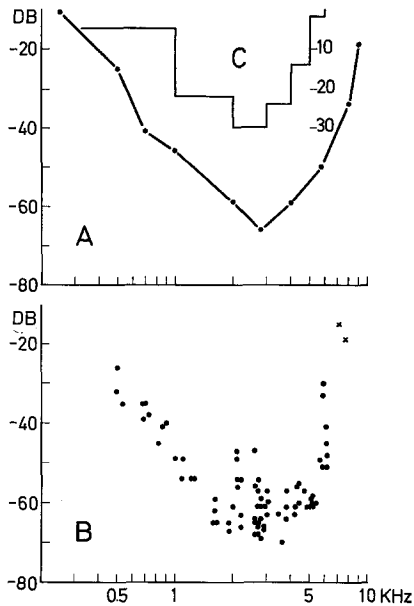


Fig. 2 A—C. Behavioral audibility curve, single unit thresholds and numbers in the canary. A Behavioral audiometric curve, average of four birds (from Dooling, 1969). B Thresholds of single units at their CF's in one individual.  $\times$  indicates that units with the CF of 6.2 KHz (near the highest limit) respond to still higher frequencies 7.2—7.7 KHz with a corresponding rise in their thresholds. C Numbers of units classified according to their CF's from another bird

methods. Figs. 2B and 3B show the distributions of thresholds of single units at their CF's obtained from one individual of the corresponding species.

Except for the low end of the starling curve, the frequency ranges of the audibility curves extend beyond the lowest and highest single unit CF's, since the behavioral studies used higher stimulus intensities near the upper and lower frequency limits of hearing. The single units with the highest or lowest CF respond respectively to still higher or lower frequencies with corresponding increases in their thresholds. This is illustrated by  $\times \times$  in Fig. 2B where two units with the CF of 6.2 KHz responded to tones of 7.2 and 7.7 KHz with accompanying rises in their thresholds by 30—35 DB.

From the above comparison, it is safe to assume that the distribution of single unit thresholds covering the entire range of CF's in one individual can approximate the audibility curve of its species. There is certainly individual variation in the distribution of single unit thresholds, but different individuals show similar general trends (Fig. 3B, C and D).

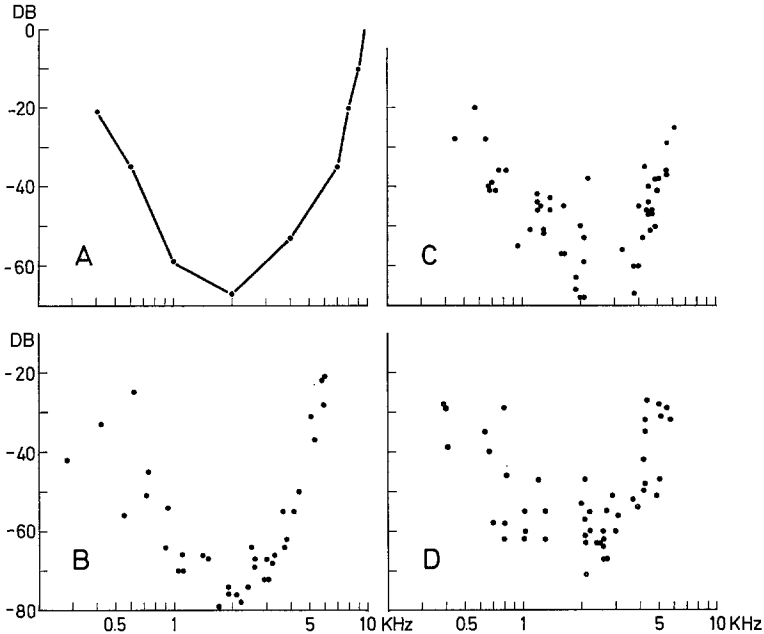


Fig. 3 A—D. Behavioral audibility curve and single unit thresholds in the starling. A Audibility curve (from Trainer 1946). B, C, and D Distributions of single unit thresholds from three different birds. Note that different individuals show the same general trends

Some of the individual differences are perhaps due to the experimental conditions. For instance, brain pulsation due to respiration and circulation affects single unit thresholds.

Another single unit parameter that correlates with the audibility curve is the numbers of units (Fig. 2C). If we sample units at regular intervals for the entire area of the nucleus angularis and plot their numbers according to their CF's, the greatest number of units is found in the frequency range where the unit and hearing thresholds are lowest. Smaller numbers of units occur in the ranges higher or lower than the most sensitive one. In the *n. magnocellularis* the distribution of units is more skewed toward the most sensitive range.

### 3. Hearing and Vocalizations

Knowing that the distribution of unit thresholds can approximate the audibility curve, we now compare hearing and vocalizations in six different species (Fig. 4A—F). The figures are self-explanatory, but a few general remarks may be added.



a) The upper range of unit best frequencies seems to be correlated with the range of vocal frequencies except for the starling.

b) The position of the lowest threshold is to some extent correlated with that of the highest CF: The higher the upper limit of CF, the higher the frequency range of the lowest unit threshold.

c) Although their relative amplitudes are small, the highest vocal frequencies tend to exceed the highest CF's in most species.

d) Vocal frequencies seldom reach below 1 KHz, but all species extend their hearing sensitivity well below 1 KHz.

e) The lowest unit thresholds are similar among different species; i. e. they fall between  $-60$  and  $-80$  DB (re.  $1 \text{ dyne/cm}^2$ ).

f) The differences between the lowest and highest unit thresholds also tend to be similar among different species; i. e. about  $40-50$  DB except for the robin and the chipping sparrow in which the data are somewhat incomplete.

## Discussion

### *1. The Significance of Tonotopic Organization*

The histological results of Boord and Rasmussen (1963) and the neurophysiological counterparts presented here clearly indicate that the CF's of secondary auditory fibers are systematically correlated with the segments of the basilar membrane that their connecting primary fibers innervate. High, intermediate and low CF's correspond respectively to the basal, middle and apical segments of the membrane.

In the chicken the maximum amplitude of vibration moves from the apical to the basal regions of the basilar membrane as the sound frequency increases. This is correlated with increasing stiffness of the membrane from the apical to the basal segments (Békésy, 1944). Everything that has been said above also applies to the mammalian cochlea (Lewy, 1936; Rose, Galambos and Hughes, 1960; Schuknecht, 1960). These facts suggest that the avian basilar membrane may function as a mechanical wave analyzer and that the place principle proposed for the mammalian cochlea may be applicable to birds.

Schwartzkopff (1955) and Schwartzkopff and Winter (1960) argued that the shortness, large breadth/length ratio, lack of conspicuous tapering and contact with the tegumentum vasculosum would remove the conditions for the avian basilar membrane to perform mechanical wave analysis. Schwartzkopff (1958) further proposed a theory of neurophysiological resonance: when an auditory fiber fires several times in response to a single click, the intervals between the impulses are constant and correspond to the reciprocal of the unit's CF. This phenomenon is not unique to birds (Kiang, 1966) and need not be explained in terms of

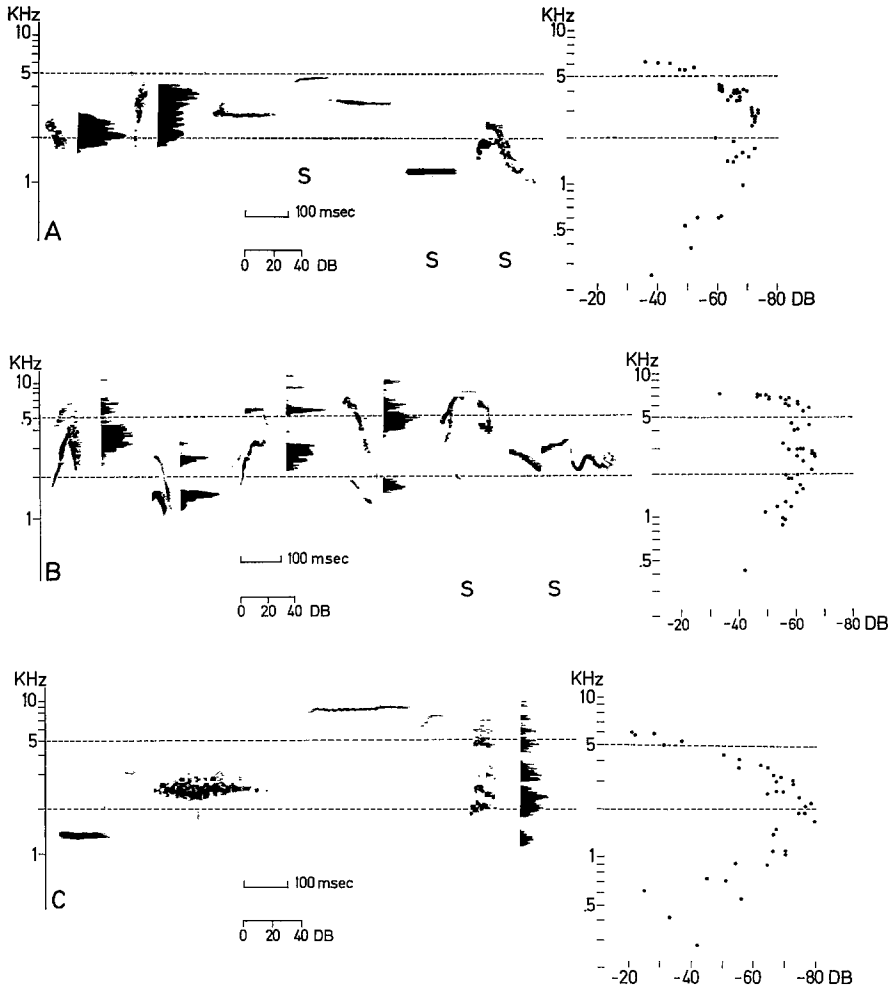
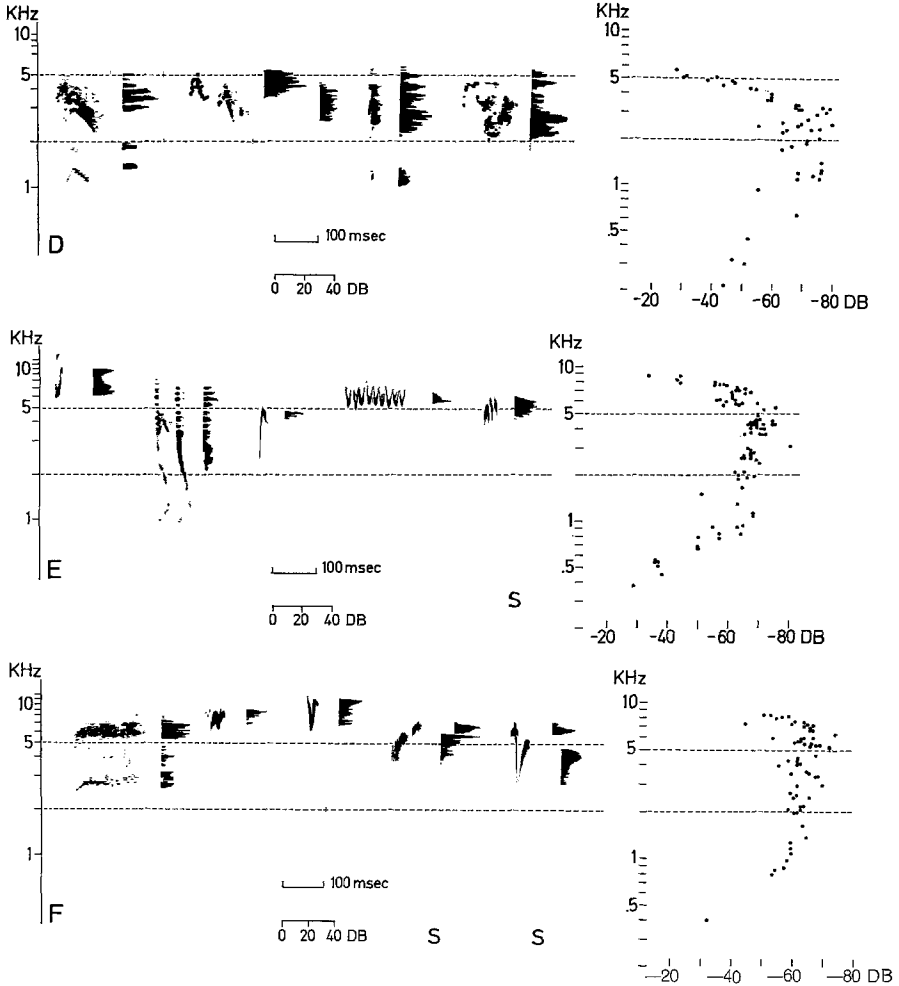


Fig. 4 A—F. Hearing and vocalizations. A Western meadowlark, B American robin, C Starling, D House Sparrow, E Slate-colored junco, and F Chipping sparrow. Narrow-band time frequency sound spectrograms of vocalizations and their frequency amplitude profiles are compared with the distribution of single unit thresholds obtained from one individual of each species. *S* denotes the typical sound compo-

neuronal resonance. It is perhaps due to the damped oscillation of that segment of the basilar membrane that the unit innervates.

The well known argument that a continuous elastic membrane cannot perform the sharp "tuning" exhibited by single auditory neurons seems to be widely accepted. This argument, however, always refers to the measurement of basilar membrane vibration by Békésy (1949). Johnstone



nent in the species' song. Sound frequencies in logarithmic scales. Note that the log intervals on the sound spectrograms and those on the semi-log paper do not match for the entire range of frequencies. All minus DB values refer to 1 dyne per  $\text{cm}^2$ . The time scale is for time-frequency spectrograms profiles and the DB scale is for frequency-amplitude profiles

and Boyle (1967), using the Mössbauer technique measured the absolute amplitude of vibration in the Guinea-Pig basilar membrane and found much sharper tuning than that known so far from Békésy's relative measurement. It is, of course, conceivable that finer frequency discrimination is performed by neuronal mechanisms such as lateral inhibition (Békésy, 1967).

The functional significance of the tonotopic organization in terms of auditory communication may be briefly discussed below. Many avian sound signals have complex wave forms. One of the methods to characterize such wave forms is spectral analysis. The spectral energy distribution in any appropriate temporal segment of complex sound can be coded in terms of "places" on the basilar membrane. The projection of the basilar membrane via the place-labelled lines can preserve the spectral characteristics for further analysis by more central stations.

### *2. Single Unit Thresholds and Audibility Curves*

The good agreement between the thresholds of single units at their CF's and hearing thresholds for the same frequencies poses important questions. There are several places where the frequency-dependent differences in unit thresholds may arise; the middle ear mechanical characteristics, the basilar membrane, hair cells, primary auditory fibers and secondary units in the cochlear nucleus. The cat's primary auditory fibers show similar threshold differences. The middle ear frequency response characteristics are responsible for these differences (Kiang, Marr and Demont, 1967). This means that all the cat's primary auditory fibers have the same range of thresholds regardless of their CF's.

It is not always easy to correlate single unit studies with perceptual performances evaluated by behavioral methods. When these two methods are combined, they become a powerful tool for the study of perception and its physiological mechanisms. The results reported above offer a case in point. In birds the central auditory stations above the cochlear nucleus play no role in determining either the frequency-characteristics or the absolute thresholds of hearing, although the involvement of centrifugal control was not excluded in the present study.

The frequency-dependent sensitivity is only one aspect of hearing. Birds may have to perform more analyses on sound signals such as finer frequency and amplitude discrimination. This might require parallel "channels" in the auditory system. The skewed distribution of units in different frequency ranges may be reflecting this sort of functional requirement.

### *3. Hearing and Vocalizations*

A glance at the Table and Fig. 4 shows distinct differences in the frequency ranges of hearing and vocalizations among different species. It seems only partly true that the sizes of birds and their vocal frequencies are correlated. Greenewalt (1968) finds no correlation between the size and the highest vocal frequency among birds. Vocal frequencies in birds are dependent not only on the size of the sound generating

membrane but are also regulated by its tension which is controlled by the air sac pressure and the syringeal muscles. However, it is quite possible that the lowest vocal frequencies are correlated with the size of the membrane because larger membranes are physically needed for the production of low frequency sound. Note that passerine vocal signals tend to lack frequencies below 1 or even 2 KHz (Fig. 4).

By the same token, the size of the ear drum may be correlated with the frequency range of hearing. The size of the ear drum was not measured. The weights and the highest CF's are compared (Table). The three small birds, the song sparrow, the junco and the chipping sparrow have definitely higher CF's than the three large species, the western meadowlark, the American robin and the starling. However, when we compare the canary and the house sparrow on the one hand and the white-crowned and white-throated sparrows on the other, we find clear differences in the highest CF's among birds in similar weight ranges. This may be reflecting the taxonomic differences between these two groups. It will be interesting to compare the lengths of the basilar membranes with the highest CF's among different species.

It is popularly believed that songbirds can hear sound frequencies inaudible to man. With some exceptions professional views have also supported the popular view. Responses to frequencies as high as 20—29 KHz have been reported for songbirds in some old studies in which either cochlear microrphonics or behavioral conditioning methods were used (Schwartzkopff, 1955). While frequency sensitivity curves obtained by cochlear microphonics and behavioral methods agree in indicating the most sensitive frequency range, cochlear microphonics may be registered well beyond the actual high and low frequency limits of hearing (Wever, 1959). This cannot be taken to mean an extension of auditory sensitivity, since there is no theoretical or practical criterion to correlate the magnitude of cochlear microphonics with the threshold of hearing. In birds and mammals both single unit and behavioral thresholds are about 30 DB below the stimulus intensity level that yields one microvolt of cochlear microphonics. Conventional methods cannot register cochlear microphonics smaller than about 0.1 microvolt.

The behavioral tests in the old studies which report high-frequency sensitivity in birds used the Galton whistle in which the complete elimination of undesirable frequencies is difficult (Granit, 1941; Knecht, 1940; Wassiljew, 1933). When we exclude work of uncertain methodology, there is no evidence for the song bird's ability to hear frequencies inaudible to man. Also, it is not at all necessary to assume that birds should be able to hear the entire range of frequencies in their vocalizations. Many birds produce brief calls with abrupt onset and cut-off. These

sounds inevitably contain wide ranges of frequencies due to the physics of sound production.

Finally, we will discuss the parameters of sound that may be used in vocal communication in relation to the results reported above. The songs of many sympatric birds broadly overlap with one another in their frequency ranges. Unless different species clearly differ in the frequency ranges of their hearing, the frequency ranges alone would be inadequate to code species diversity and other messages. The house sparrow cannot hear the junco vocalizations well, while the junco can hear the sounds of the sparrow well. Even such a unidirectional bias would be advantageous in avoiding confusion in vocal communication. However, if we take the slate-colored junco and the chipping sparrow which are sympatric in large areas of North America, their audibility curves as well as vocal frequency ranges overlap almost completely.

Recent studies with field play-back methods indicate the importance of the frequency and temporal parameters of song for species recognition (Falls, 1963; Brémond, 1967). The spectral characteristics of vocal signals vary distinctly from species to species, yet their significance in avian communication has not been demonstrated. In the bullfrog (*Rana catesbeiana*) the spectral characteristics of the so-called mating call codes species specificity (Capranica, 1965). Furthermore, when the numbers of primary auditory fibers are plotted according to their CF's, the resulting histogram matches with the distribution of spectral energy in the mating call (Frishkopf and Goldstein, 1963). Thus, the frog's ear is "tuned" to its mating call.

From Fig. 4, it is obvious that the bird's ear is not so narrowly tuned to the species song. Furthermore, in all species the most dominant vocal frequencies do not seem to coincide with the most sensitive range of hearing but are located above that range. This is also true of the canary in which more complete sound samples were collected and statistically analyzed (Mulligan and Olsen, 1969). The average dominant frequency of eleven different vocalizations is 3.8 KHz versus 2.8 KHz, the lowest threshold point in the audibility curve (Fig. 2A). Higher frequencies are more advantageous for directional hearing, but why should not the most sensitive range be more exclusively used for intraspecific communication? Birds may be choosing the frequency range in which they can obtain the best signal/noise ratio.

All birds studied so far can hear sound frequencies well below 1 KHz. This ability may be advantageous in detecting broad-band noises made by stalking predators. Since the attenuation of sound is approximately proportional to the square of its frequency, the low frequency components of the enemy noises are more useful in detecting distant predators.

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