

These observations show that opportunity for exchange of genetic material between all five groups of the region was present. An occurrence of this nature, based on observations from a single area, could be attributed to some unusual characteristic, such as high population density, were it not for evidence from other areas which indicates a pattern of widespread occurrence. In addition to the five groups considered in this report, I observed male shifts in a forest habitat 11 km away, with much lower population density. Neville (7) also reports the appearance of alien males during the mating season for groups in the Haldwani area, more than 150 km to the east. These observations, together with the persistence of this phenomenon on Cayo Santiago over several years, indicate that annual shifting of males between groups is basic to the species.

Composition of groups of rhesus monkeys is basically stable, and contacts with extragroup animals are antagonistic and unfriendly. Less than 4 percent of the total population in the study area changed groups, but this percentage is significant, for it constitutes fully one-third of the original adult males. It is doubtful if the transfer of adult females or immature individuals of either sex would be as costly in terms of social disruption. The theory that sexual attraction promotes group cohesiveness has been criticized on the basis that group composition is stable in those primate species which mate seasonally (8). In this species sexual attraction apparently extends across group boundaries, resulting in a limited redistribution of adult males.

An important consequence of intergroup transfer by adult males is the dissemination of genetic material among the groups of a region. The rhesus monkey has a vast geographical distribution, extending from eastern Afghanistan across much of the southern part of China (9). It is unlikely that populations from the extremes of this range would show only relatively minor phenotypic variation if groups were as impermeable to gene flow as is commonly believed. Furthermore, inbreeding is generally considered to reduce the evolutionary potential of a species through a reduction of genetic variation.

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10. Supported by NIH grant FR-00169 to the National Center for Primate Biology. I thank L. Schmidt for providing the opportunity to participate in the India Primate Ecology Project and P. Jay-Dolhinow for assistance in planning and conducting the field study. T. Srivastava (president of the Forest Research Institute, Dehra Dun, India) granted permission to study the monkey population on the institute grounds.

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Hearing, Single-Unit Analysis, and Vocalizations in Songbirds

Abstract. *Auditory neurons in the avian cochlear nucleus are systematically arranged according to their best frequencies. The thresholds of single auditory neurons at their best frequencies match the thresholds of hearing obtained by behavioral methods for the same frequencies. The upper range of single-unit best frequencies shows distinct interspecific variation which is correlated with the differences in the range of vocal frequencies. Most songbirds do not seem to produce frequencies below 1 kilohertz but can hear them.*

Bird vocalizations have become popular examples of auditory communication in animals. One of the most important prerequisites for communication is discrimination of signals. So far we have not been able to answer even the most basic questions, such as: "Can birds use the entire frequency range of their vocalizations in signaling?" and "What is the sensitivity of the bird's ear, and how is it related to the distance-transmission of its vocal signals?" This report shows how single-unit techniques can provide some of the information essential for answering these questions.

Birds were anesthetized with urethan. The cerebellum was removed by suction so as to expose the floor of the fourth ventricle where the cochlear

nuclei are visible. Tungsten microelectrodes were used to record single units in the cochlear nucleus. The electrode was placed on desired points in the nucleus under a Zeiss operating microscope with the aid of a head holder-electrode carrier assembly. Tone bursts 100 msec in duration were used as stimuli. The thresholds of auditory neurons were judged by the rate of discharge which was monitored both visually and acoustically (1). All experiments were conducted in a soundproof room.

Different auditory neurons, whether primary or secondary, respond to different ranges of frequencies. The frequency to which a fiber shows the lowest threshold is called the best frequency of that fiber. Systematic exploration of the cochlear nucleus shows orderly sequences of best frequencies, as expected from the pattern of termination of primary auditory fibers. High, intermediate, and low best frequencies correspond to fibers innervating, respectively, the basal, middle, and apical parts of the basilar membrane (2). This arrangement enables us to determine the range of best frequencies quickly and systematically. The range of best frequencies, especially at its highest limit, varies distinctly from species to species. The avian cochlear nucleus consists of two major subdivisions, nucleus magnocellularis and nucleus angularis. In all cases the highest best frequency encountered in the nucleus magnocellularis is about 2 kHz lower than that found in the nucleus angularis (3).

Now let us investigate whether single-unit best frequencies are related to audible frequencies. In the cat the range of single-unit best frequencies and that of audible frequencies determined by behavioral methods are in excellent agreement. Interestingly, the lowest thresholds of single primary units at their best frequencies coincide with the audibility thresholds for the same frequencies (4).

The above correlation seems to hold also for songbirds, even when the thresholds of second-order neurons are used. Figure 1 presents a comparison of an audibility curve averaged for four birds (5) and the distribution of single-unit thresholds from one canary (*Serinus canarius*). The behavioral and the single-unit data are in good agreement except for the highest- and lowest-frequency regions. These differences can be easily explained by the fact that

the behavioral study used higher stimulus intensities for those regions. The units having the highest and lowest best frequencies can respond, respectively, to still higher and lower frequencies when the stimulus intensity is raised. Similar results were obtained for the starling (*Sturnus vulgaris*), for which both behavioral and neurophysiological data are available (6).

The above comparison suggests that the frequency-dependent sensitivity of hearing may be determined in the cochlear nucleus or even more peripherally in the ear. In few cases is a behavioral perceptual performance so directly correlated with neuronal responses. The brain seems to use fully the information the ear supplies in terms of the frequency-dependent sensitivity of hearing.

The frequency-dependent sensitivity is only one aspect of hearing. Birds may have to extract more information from their sound signals. This might require parallel "channels" in the auditory system. In fact, if we sample units at regular intervals for the entire area of the nucleus angularis and plot the numbers of units according to their best frequencies, the greatest number of units occurs within the frequency range where unit thresholds are lowest. Small numbers of fibers represent both the lowest and highest ranges of best frequencies.

I have demonstrated above that the distribution of single-unit thresholds can approximate the audibility curve. The next question is whether the hearing threshold curve of a species is correlated with its vocalizations. If there is any correlation, this should be most easily detected by comparing species which differ clearly in the frequency range of their vocalizations (7). In this study two species, the house sparrow (*Passer domesticus*) and the slate-colored junco (*Junco hyemalis*), were chosen for comparison.

Most of the vocalizations of the house sparrow (Fig. 2A) are confined to a frequency range between 2 and 5 kHz. The highest best frequency obtained so far is 6.5 kHz. The lowest threshold of single units is located around 2 to 3 kHz.

The calls and song of the junco (Fig. 2B) predominantly occupy frequency ranges near and above 5 kHz. Some of the calls exceed 10 kHz. The peak of single-unit sensitivity lies between 3 and 6 kHz. The highest best frequency obtained so far in the junco is 8.6 kHz.

In one experiment, a unit which had a threshold of -41 db (referred to 1 dyne/cm²) at its best frequency (8455 Hz) responded to a tone of 11,678 Hz with a corresponding rise in its threshold to -10 db (referred to 1 dyne/cm²).

The above comparison indicates a

correlation between the upper range of single-unit best frequencies and the range of vocal frequencies, although the highest vocal frequency tends to exceed the highest best frequency in most cases. Similar results were obtained for several other songbirds. No correlation, however, exists in the lower range of

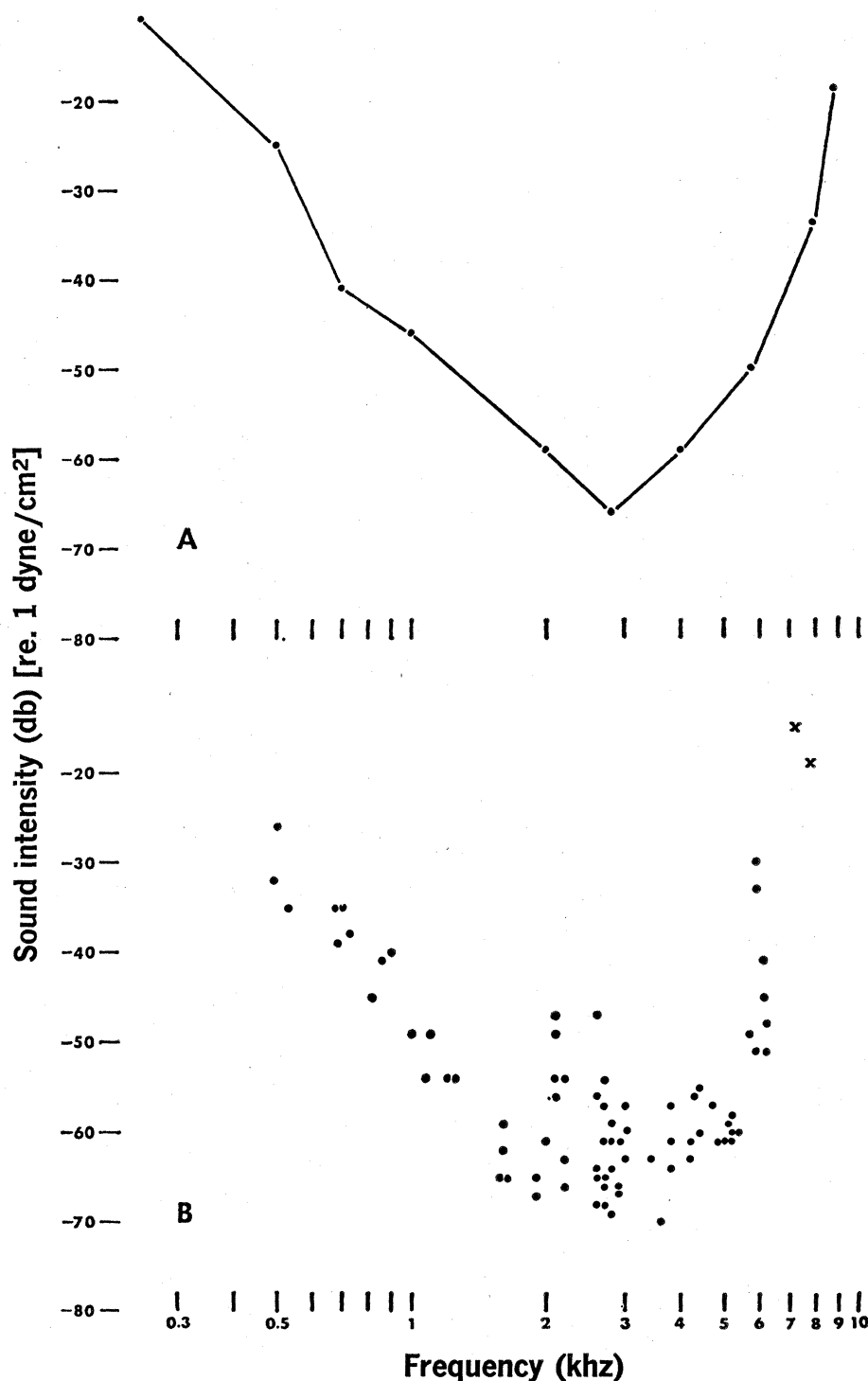


Fig. 1. Hearing and single-unit thresholds in the canary. (A) Behavioral audiometric curve, average of four birds [from Dooling *et al.* (5)]. (B) Thresholds of single units at their best frequencies in one individual; X indicates that units with the highest best frequency (6.2 kHz) respond to still higher frequencies (7.2 to 7.7 kHz) with a corresponding rise in their thresholds.

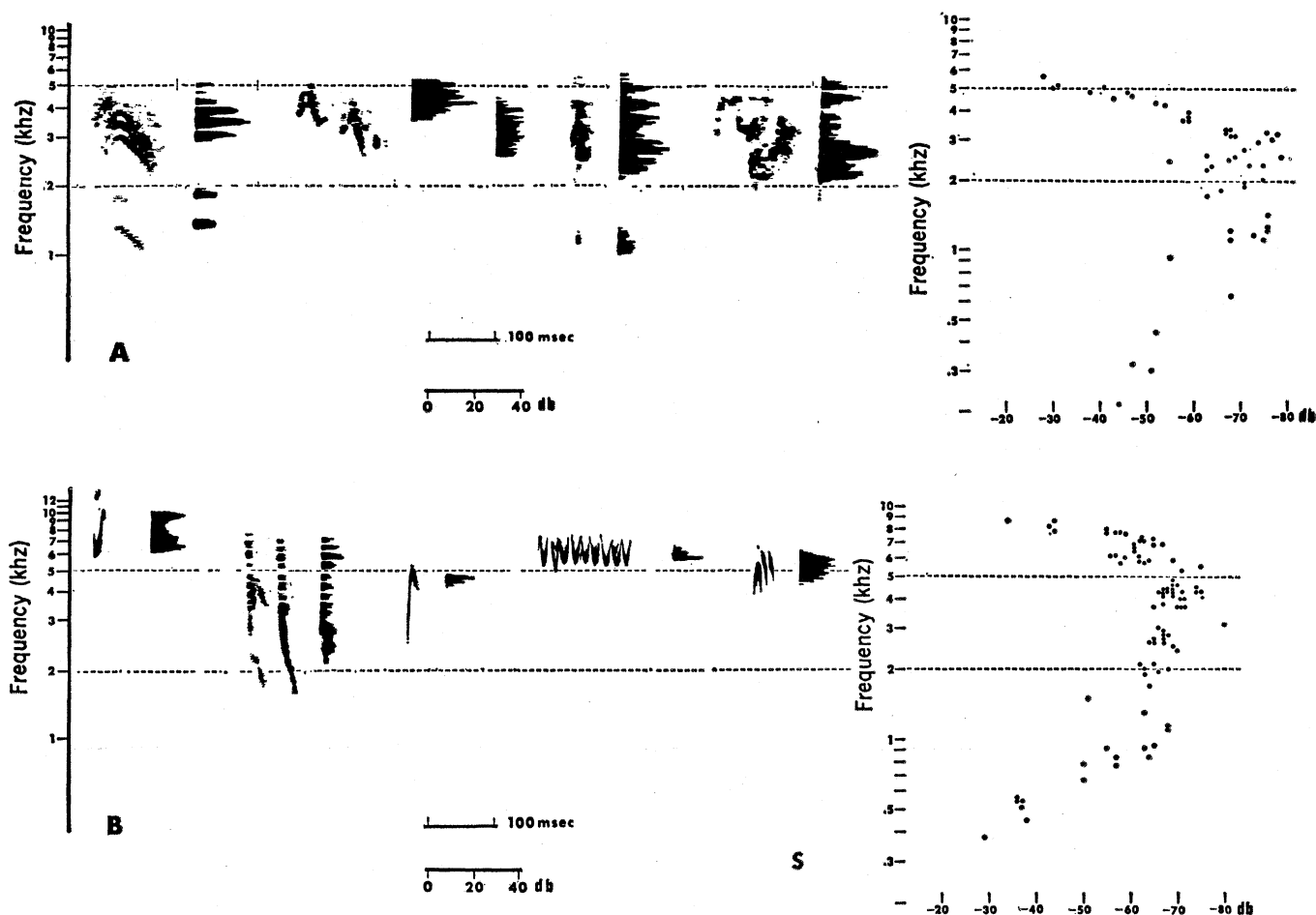


Fig. 2. Single-unit thresholds and vocalizations for (A) house sparrow and (B) slate-colored junco. Narrow-band time-frequency sound-spectrograms of vocalizations and their frequency-amplitude profiles are compared with single-unit thresholds obtained from one individual of each species; *S* denotes the typical sound component in the species song. Sound frequencies are shown in logarithmic scales. All decibel values with a negative sign refer to 1 dyne/cm². The time scale is for time-frequency spectrograms, and the bar scale in decibels is for frequency-amplitude profiles (7).

frequencies. Few songbirds produce frequencies below 1 kHz, yet all songbirds studied so far are rather sensitive to low frequencies. This may be to their advantage in detecting broadband noises created by stalking predators.

It is popularly believed that the songs and calls of birds contain sound frequencies inaudible to man and that songbirds can hear those sounds. With some exceptions, professional views have also supported the popular belief. Responses to frequencies as high as 20 to 29 kHz have been reported for songbirds in some early studies in which either cochlear microphonics or behavioral conditioning methods were used (8). Even though curves of sensitivity as a function of frequency obtained by cochlear microphonics and behavioral methods are in agreement in the indication of the most sensitive frequency range, cochlear microphonics may be registered well beyond the

actual high- and low-frequency limits of hearing (9). This cannot be taken to mean an extension of auditory sensitivity, since there is no theoretical or practical criterion for the correlation of 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 1 μ v of cochlear microphonics. Conventional methods cannot register cochlear microphonics less than about 0.1 μ v.

In the early reports of high-frequency sensitivity in birds, the sound source used was the Galton whistle, for which the complete elimination of undesirable frequencies is difficult (10). When we exclude work of uncertain methodology, there is no evidence that the songbird is able 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 fre-

quencies in their vocalizations. Many birds produce brief calls with abrupt onset and cutoff. These sounds inevitably contain wide ranges of frequencies due to the physics of sound production.

The old belief in the songbird's superior hearing is partly due to the fact that man cannot recognize rapid frequency and amplitude modulations common in bird vocalizations. There is some evidence that the songbird's ear can register such sounds (11).

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References and Notes

1. Sound was delivered either by an open loudspeaker or by a 25-mm B & K condenser microphone used as an earphone in a closed system. Sound levels were measured near the ear opening by means of a wave analyzer used in combination with either a calibrated 6-mm B & K microphone in the case of the open loudspeaker or a probe tube attached to a 12-mm B & K microphone in the case of the closed system. The two methods sometimes

- gave different results; any leakage in the closed system grossly distorted sound calibration below 1 khz, whereas at frequencies higher than 6 khz calibration for the open loudspeaker was affected. This difficulty could be avoided by placing the loudspeaker close to the bird's ear (12 cm).
2. R. L. Boord and G. L. Rasmussen, *J. Comp. Neurol.* **120**, 463 (1963).
 3. For this reason, all data on single-unit thresholds and frequency range in this paper were obtained from the nucleus angularis.
 4. N. Y.-S. Kiang, *Discharge Patterns of Single Fibers in the Cat's Auditory Nerve* (M.I.T. Press, Cambridge, Mass., 1966). In birds, variation in thresholds among units having similar best frequencies is partly due to experimental conditions. Brain pulsation due to respiration and circulation often made the threshold measurement unreliable. Preparations devoid of this and other conditions, such as bleeding, showed narrower ranges of variation in the thresholds of single units with similar best frequencies. The distribution of best frequencies from such preparations was rather consistent from individual to individual, thus allowing the use of data from a single bird to represent its species.
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 7. I have tried to record as many calls as possible for each species, but I cannot claim to have collected all the vocalizations. The logarithmic intervals on the spectrogram do not match with those on semilogarithmic paper for the entire frequency range. When calls and song consist of repetitions of the same or similar sounds, only one element is shown in the figure. No song was recognized in the sparrow.
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Fissure Basalts and Ocean-Floor Spreading on the East Pacific Rise

Bonatti has suggested (1) that a continuous single band of basaltic lava, 40 to 60 km wide, crops out along the crest of the East Pacific Rise (EPR) for a distance greater than 800 km between 6° and 14°S. The evidence for such a band is largely deduced from the character of echo-sounding records along four transverse profiles in the region, corroborated by dredging and bottom photographs which established exposed rock at some localities on the sea floor. My purpose is to introduce evidence from heat flow and other measurements which makes it (i) unlikely that the hypothesized outcrop is as broad or as continuous as Bonatti implies and (ii) probable that other modes of magmatic emplacement may be equally important.

Between 12½° and 15°S, near the southern part of the region under discussion, there are three published profiles of relatively detailed heat-flow measurements across the EPR crest (2). The average spacing between these measurements is about 40 to 45 km. At the stations along these profiles, there was little difficulty in obtaining at least 2 m of sediment penetration by a temperature gradient probe. Similar profiles of heat-flow measurements on the Rise crest have been obtained at 8°S (3) and also at 17°S (4). On a few stations of the latter profile, the corer struck hard rock after penetrating a few meters of sediment, but these stations were geographically scattered

along the profile which otherwise provided a continuous sequence of successful measurements across the EPR crest.

A result of the heat-flow measurements is that the highest values are not always found at the Rise crest, but rather along two or more bands, similar in width to the outcrop suggested by Bonatti. These bands may be relatively continuous and approximately parallel to the trend of the Rise. The uniform sediment cover and lack of other surface evidence for these heat-flow bands led Von Herzen and Uyeda (2) to postulate cooling from subsurface dikes at relatively shallow depths beneath the sea floor. It may be that Bonatti's investigations have revealed several places where one or more of these dikes crop out at the sea floor, although the lack of position coordinates on his profiles precludes a direct comparison. However, my subsequent personal communication with Bonatti suggests that the rock outcrop region on his profile *AA'* closely coincides with a high heat-flow band east of the Rise crest, and those on profiles *CC'* and *DD'* with a similar band to the west. The rock outcrop along profile *BB'* may be closer to the Rise crest, although there are no heat-flow profiles in the vicinity.

The topographic relief along profiles between 12½° and 15°S, and at 8°S, is similar to that shown by Fig. 2 of Bonatti (1). On profiles at 8°S, 12½°S, and 18°S, there is one region near the

Rise crest, ranging from about 20 to 30 km in width, which generally shows a strong and reverberant echo from the 12-khz depth sounder and is less than 3000 m in depth. Presumably, this is the type of reflection from outcropping rock noticed by Bonatti, although he did not define the characteristics of the reflections. On the other profiles near 14½°S no such regions were detected, other than an occasional hill several hundred fathoms in height above the surrounding level of the sea floor.

Therefore, the basalt band is apparently of smaller width and not as continuous as implied by Bonatti, as deduced from the relatively close spacing of heat-flow measurements and the nature of the echo-sounding records cited above. Bonatti did not discuss whether all of his dredge hauls and bottom photographs from the hypothesized outcrop band indicated rock, and conversely, whether any samplings outside of this band indicated only sediments. I agree that 12-khz echo-sounding records are useful to distinguish hard rocks from smooth sediments at the sea floor, but, as the records are susceptible to electronic nuances and subjective interpretation, they cannot be considered infallible.

It is curious that the band characterized by strong and reverberant echoes frequently appears smoother than sedimented regions near the Rise crest. The echo-sounding records for the sedimented regions generally show numerous overlapping echoes from hills 10 to 40 m in height and 0.2 to 2 km in width. If the band of strong echoes represents newly formed rock near the Rise axis, its relative smoothness appears inconsistent with constant sea-floor spreading, because sedimentation on the spreading sea floor should only produce further smoothing. It may be that the extrusion of rock on the sea bottom produces a relatively smooth surface on this scale, and that this process is relatively unusual on this part of the EPR. Perhaps intrusion of relatively thin and viscous dikes to produce the myriad of small hills on the EPR is a more common process.

If Bonatti's assumed sedimentation rate of 1 cm per 10³ years has been reasonably constant and uniform over the Rise crest, most rock outcrops on the relatively smooth topography of the crest should be fairly well covered with sediment within 10⁵ years or so. At a spreading rate of 4 cm/year for this