ON THE HEARING OF BIRDS

BY JOHANN SCHWARTZKOPFF

COMMON sense suggests that birds can hear tones of the same range as those which they produce. However, precise investigations have revealed exceptions and limitations to this rule. All birds, for instance, can hear frequencies down to a minimum of about 50 cycles (table 1); but even the voice of the Great Horned Owl (*Bubo virginianus*) is considerably higher than this. The upper limit of hearing is usually reached at 20,000 cycles (reached after conditioning), but cochlear potentials have been detected at 25,000 to 30,000 cycles by using greater intensities of sound than those normally encountered by the ear. The notes of song birds, however, frequently contain still higher harmonics (Brand, 1938).

The highest sensitivity of hearing in a given species—which in song birds reaches the human threshold (Schwartzkopff, 1949) and in owls probably exceeds it—is mostly found at the modal center of the voice of that species. Among related species, the larger ones have lower voices, and hearing sensitivity shows a corresponding trend (compare *Corvus* and *Pica* with *Pyrrhula* and *Fringilla* in table 1). Such a shift is undoubtedly owing to differences in the dimensions of the vibrating parts (specific resonance). Exceptions to this size-voice relation are of ecological and physiological interest. For example, owls are very sensitive to tones above the midpoint of the voice of song birds (6000 cycles), but which correspond to the squeak of some mice. Baby chicks hear almost nothing but the low clucking of their mother (400 cycles) while the hen reacts with preference to the very high cheeping (above 3000 cycles) of her offspring (Collias and Joos, 1953).

Though one cannot always with certainty apply to physiology conclusions drawn from ethology, it seems that in the present case something having to do with the developmental stage of the middle ear of chicks impedes the reception of higher notes (table 2). There is probably a selective value in the chicks being able to hear only the mother and not their fellow chicks.

The mechanism of sound transmission by the middle ear has not yet been analyzed in detail. Its function might be even more important for birds than it is for man, for birds' ears are almost inaccessible to bone-conducted sound (Denker, 1907), being largely surrounded by air spaces. Removal of the middle ear reduces the sensitivity of hearing to 1/75 or 1/100 of the original value, even for high notes (Schwartzkopff, 1949, 1952). The influence of the middle ear on

the general and spectral sensitivity is known from human physiology (Pumphrey, 1948). If the outer ear opening and the drum are large, much sound energy can reach the middle ear. It depends then on the motility of the drum membrane whether this energy is uselessly reflected or is taken up by the middle ear and transferred to the inner ear. This mechanism, the so-called acoustical adaptation, is determined by several factors, such as the elastic properties of the ear drum, its damping by the air cushions of the middle ear cavity and communicating spaces, and by the resistance of the inner ear to sound vibrations.

TABLE 1

THE HEARING RANGE OF MAN AND SEVERAL BIRDS

Species	Lower limit cs./sec.	Highest sensitivity cs./sec.	Upper limit cs./sec.	Method	Author
Homo sapiens	16	1000–3000	20,000	—	—
Melopsittacus undulatus	40	—	14,000	D	Knecht, 1940
Sturnus vulgaris	<100	2000	15,000	D	Granit, 1941
Loxia curvirostra	—	—	20,000	D	Knecht, 1940
Passer domesticus	—	—	18,000	D	Granit, 1941
Erithacus rubecula	—	—	21,000	D	Granit, 1941
Chloris chloris	—	—	20,000	D	Granit, 1941
Pyrrhula pyrrhula	—	—	21,000	D	Granit, 1941
	<100	3200	—	D	Schwartzkopff, 1949
	<200	3200	20,000–25,000	C	Schwartzkopff, 1952
Fringilla coelebs	<200	3200	29,000	C	Schwartzkopff, 1955
Pica pica	<100	800–1600	21,000	C	Schwartzkopff, 1955
Corvus sp.	<300	1000–2000	< 8,000	D	Trainer, 1946
Falco sparverius	<300	2000	<10,000	D	Trainer, 1946
Anas platyrhynchos	<300	2000–3000	< 8,000	D	Trainer, 1946
Columba livia	<300	1000–2000	—	D	Trainer, 1946
	—	—	12,000	D	Wassiljew, 1933
	50	1800–2400	11,500	C	Wever and Bray, 1936
Asio otus	<100	6000	18,000	D	Schwartzkopff, 1955
Strix aluco	<100	3000–6000	21,000	C	Schwartzkopff, 1955
Bubo virginianus	60	1000	< 8,000	D	Trainer, 1946

D = conditioning.   C = cochlear potentials.

It has been known for a long time that the air chambers of the skull are exceedingly well developed in birds which hear well. The two middle ear cavities of all birds communicate by way of these chambers. However, the communication between these cavities has no influence upon hearing proper, for only slow changes of air pressure can spread from one ear to the other (Wada, 1923; Schwartzkopff, 1952). It is conceivable that this mechanism, working like a differential pressure gage, provides the flying bird a means of perceiving air streams.

The transfer of the acoustical vibration from the ear drum to the inner ear is provided by means of a force transformation: vibrations of large amplitude are converted into vibrations of small amplitude

TABLE 2

AREA RELATIONS OF THE DRUM MEMBRANE, THE COLUMELLA FOOTPLATE, AND BODY
IN SEVERAL BIRDS

Species	Body area (weight ⅔) "cm²"	Relative drum size (drum area) / (body area)	Area transformation of middle ear (drum area) / (footplate area)
Phylloscopus trochilus*	4.5	0.021	28
Parus caeruleus	5.1	0.016	26
Hippolais icterina*	5.7	0.015	29
Sylvia atricapilla*	6.6	0.019	29
Hirundo rustica	7.4	0.010	19
Fringilla coelebs*	7.9	0.015	28
Pyrrhula pyrrhula	9.0	0.013	24
Passer domesticus	9.6	0.0094	22
Turdus merula	20.9	0.0077	22
Pica pica	35.5	0.0075	23
Corvus corone	65.5	0.0053	23
Asio otus	44.9	0.0107	40
Strix aluco	66.4	0.0089	30
Columba livia (domestic)	47.8	0.0043	14
Buteo buteo	86.1	0.0039	18
Podiceps cristatus	86.0	0.0016	16
Phasianus colchicus	113.0	0.0033	28
Gallus gallus (domestic)			
adult	153.0	0.0019	22
40 days old	27.6	0.0052	17
1 day old	10.5	0.0066	11

* Outstanding songsters, producing very high notes.

but great force at the oval window. The elasticity of the drum membrane and the adjacent processus of the ear ossicle, the extra-columella, gives the apparatus low sonic resistance. Because the area of the drum is large and that of the columella footplate in the oval window is small, the force is amplified. A study of the dimensions of these two areas and their relation to body size shows that small birds generally have relatively large drum membranes. If this were not true, their auditory sensitivity would be poor. The owls again do not fit into this series (table 2). Their unusually large drum indicates the exceptional acuity of their ear. The relative sizes of the drum and the columella footplate are correlated with the manner of life. Efficient songsters in whom one may expect an auditory apparatus working with as little distortion as possible are distinguished by a high transformation quotient, yet even they are surpassed by the owls.

Owing to their nocturnal mode of life, owls depend on the ear to an exceptional degree, and they show still further specializations. The round window is about five times greater than the oval one. The motility of the auditory ossicle is further improved. Moreover

by this arrangement, the columella not only describes piston-like motions, as it does in species which hear less well (Pohlman, 1921), but it also acts as a lever. Since the movements of this lever produce considerable turning moments at the remarkable velocity of the sonic vibrations, the pressure upon the hinge, namely the elastic connection with the footplate in the oval window (annulus fibrosus), must be reduced. This is done through "mass equilibration": the inner surface of the footplate is prolonged into a tip which projects
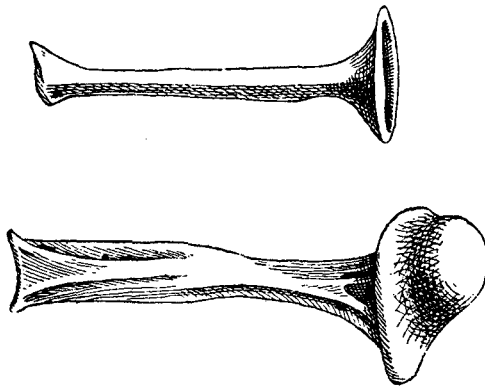

FIGURE 1. The auditory ossicles of *Uria aalge* (top) and *Strix aluco*; the latter species possesses outstanding hearing abilities. Notice the prolongation of the internal surface of the footplate in the owl. From Krause (1901).

into the perilymph of the inner ear; and the tip has a special shape which prevents the formation of eddies (figure 1). Finally, the inner ear of owls is much longer than one would expect from body size (Schwartzkopff, 1955). This suggests that owls may possess an unusual ability to analyze sound, though this has not yet been investigated physiologically.

Likewise, the assumption remains unproved that the great asymmetry of the ears of many owls causes differences in the spectral properties of the received sound and this facilitates locating its origin (Freye, 1953; Pumphrey, 1948). Undoubtedly the owls are able—as has been studied more exactly in song birds (Schwartzkopff, 1952)—to make use of the differences in intensity between the ears. In this, the opercular flaps are of great importance. But also the time difference between the arrival of the sound signal at the two ears assists these birds in locating their prey. Owls reach at least the human difference threshold (3×10^{-5} sec.). The heads of song birds are too small to permit drawing advantage from such a time difference (Schwartzkopff, 1952).

It seems that information on pitch discrimination is available only from song birds, parrots, and pigeons. While the first two groups reach human abilities, the performance of pigeons remains below even that of some fishes (table 3). Ecological considerations render the comparative values for these birds reliable, for the voices of song birds and parrots have much wider ranges of pitch than those of pigeons. The finding that birds, experimentally rendered deaf, sing rather well, even years after the operation, cannot be considered as a decisive argument against the correlation between song development and hearing. How birds achieve pitch discrimination is still a mystery.

TABLE 3

SOUND DISCRIMINATION IN MAN, BIRDS, AND FISH

Species	Optimal range in cycles per second	Discrimination threshold in per cent	Author
Home sapiens	1000–3000	0.3	Ranke, 1953
Melopsittacus undulatus	1000–3000	0.3–0.7	Knecht, 1940
Loxia curvirostra	1000–3000	0.3–0.7	Knecht, 1940
Columba livia	1000–2000	6	Wassiljew, 1933
Phoxinus laevis	400–1000	3	Dijkgraaf, 1952
Sargus annularis	150–450	<9–15	Dijkgraaf, 1952

The actual seat of hearing, the cochlea, shows rather uniform features throughout the whole class of birds (figure 2). As mentioned above for the drum membrane, the cochlea increases relatively but not absolutely with decreasing body size (Schwartzkopff, 1955). Thus, the organs of the small-sized, good songsters (and "hearers") remain smaller than those of large-sized representatives of the same or of other systematic groups. This finding is not easily compatible with the assumption of a peripheral sound analysis by means of spatial separation of sensory elements excited by different tones (resonance theory). The same difficulty arises when one considers that the basilar membrane of a parrot (*Amazona amazonica*) is 2.6 mm. in length (Denker, 1907), whereas that of man with about the same pitch discrimination is 31 mm. Other arguments against peripheral sound analysis are adduced from the compact design of the sensory cells. Thirty to fifty of these lie close to each other in one cross-section of the basilar membrane and remain joined with the tectorial membrane for life (differing in this respect from those of mammals). There are no arcs of Corti by which the hair cells of mammals, arranged in a few separate rows, are each supported and isolated. The steadily increasing width of the basilar membrane—a fundamental support of any resonance theory—is not found in the cochlea
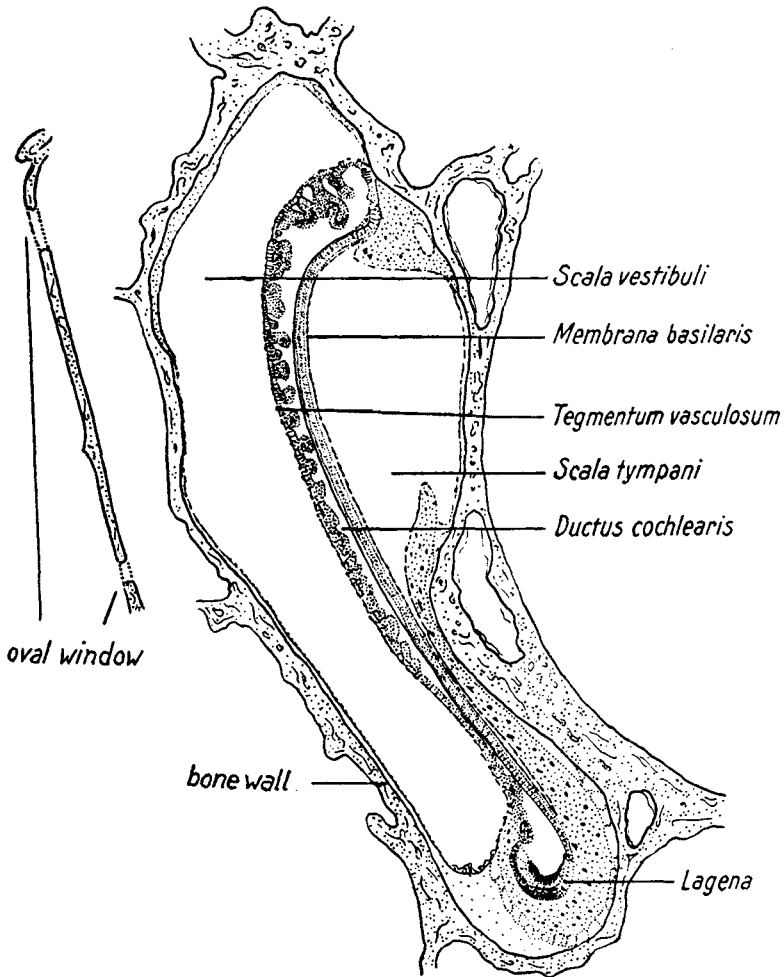
FIGURE 2.   The inner ear of the dove; longitudinal section.   The oval window has been projected from another plane of section into this one.   Notice size and situation of the window in respect to the basilar membrane; these are most commonly reprinted falsely from an erroneous scheme of Satoh.

of birds.   Finally, the roof of the canal containing the sensory cells (ductus cochlearis) has become in birds the heavy tegmentum vasculosum, rich in unicellular glands and small blood vessels.   Such a structure will damp any resonating vibrations of the inner ear liquor.   The corresponding structure in mammals is the peculiarly delicate membrane of Reissner.

Except for the tegmentum vasculosum, which is peculiar to birds,

the inner ear as a whole is more similar to the primitive stage of fishes than to the highly developed organ of mammals. Only the fact that the sensory macula of the labyrinth which serves for hearing (Schwartzkopff, 1949) is distinctly stretched in birds supports the idea of sound analysis by means of spatial distribution of the excitation (length/width relation: parrot 13/1, fish ca. 2/1, man 100/1). According to the subdivision of the ductus cochlearis by the villi of the tegmentum vasculosum it might be possible that 20 to 30 different notes could be projected upon the organ of Corti. But in this way, at best only one per cent of the tonal sensitivity of species which hear well can be explained. In view of the fact that even some fishes are able to distinguish tones quite well (table 3)—that is, they show well developed central sound analysis without any peripheral analyser—sound analysis in the brain must, I am convinced, also be postulated for birds.

The objection readily made against such a hypothesis—that it is a flight into the inscrutable and therefore "illegitimate"—is not substantiated by today's level of electrophysiological technique; even less since important difficulties have been raised against the resonance theory, which is more readily subject to experiments (Ranke, 1953; Wever, 1949).

The idea outlined here has been particularly influenced by the study of Wever's dualistic theory of hearing (Wever, 1949). This author, by careful calculation of the events in the inner ear of mammals, comes to the conclusion that even in that group only a part of sound analysis takes place in the periphery and that the lower and some of the middle tones are transferred directly to the brain (volley principle) and identified there.

It seems to me that only by prosecuting such ideas further can a theory of hearing be developed which is applicable in comparative physiology. We will then have a general picture of the hearing of vertebrates in which mammals stand at the end of an evolutionary trend but do not differ fundamentally from birds or from lower groups, either by the anatomy of their hearing organ or by its physiology.

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