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# AN ENVIRONMENTAL LIMIT ON ABSOLUTE AUDITORY SENSITIVITY IN NON-AQUATIC VERTEBRATES

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There is little consensus as to which factor or factors limit auditory sensitivity in any vertebrate. It is proposed here that ambient noise of environmental origin ultimately limits, at a common level, the lowest auditory thresholds found in both the non-aquatic mammals (including man) and in the most sensitive birds, the owls (Strigiformes). Greater sensitivity than that found in these vertebrates is unlikely to have evolved since it would be of little or no adaptive value.

## *The Problem*

Determining the factors which may limit any specific sensory capacity is problematic. There is no single well defined methodology for such an exercise but a comparative approach would seem to be of some utility. Also, it seems clear that in the case of auditory sensitivity, account must be taken not only of the ultimate limit upon sensitivity set by the physical properties of matter and radiation, but also of the environment in which the auditory system evolved.

## *The Comparative Data*

Both birds and non-aquatic mammals are included in the analysis. These two groups are considered together since they differ in the structure of both their middle and inner ears, and in the elaborations of their outer ear structures, but it seems likely that all of these structures evolved in parallel within the same acoustic environment.

Table 1 presents data on lowest auditory thresholds (the intensity co-ordinate of the lowest point on the audiogram) in 20 avian and 2 mammalian species. Masterton et al. (1969) concluded that at higher phyletic levels of the Mammalia lowest threshold varied little across species and man and cat are considered as representative of this group of mammals.

Interspecific comparisons of absolute auditory sensitivity should take cognizance of the degree of intersubject and interlaboratory variability typically found in this particular parameter of auditory capacity. This variability is exemplified in the published audiograms of the pigeon (C. livia) and man (Figure 1).

When account is taken of this variability, analysis of Table 1 leads to the conclusion that in the owls (Strigiformes) lowest thresholds do not differ significantly from those of the higher mammals. Individual cat, owl and human subjects would appear to be drawn from populations with similar distributions of lowest threshold and that this sensitivity is the highest of any vertebrate tested to date. A further comparison does suggest that owls are more sensitive than the other avian species considered here.

TABLE 1

| Order | Family | Species | No. of subjects | Lowest Threshold (dB SPL re 20μNm$^{-2}$) | Reference |
|---|---|---|---|---|---|
| CLASS AVES | | | | | |
| Columbiformes | Columbidae | Columba livia | 6 | 1 | Harrison and Furumoto (1971) |
| " | " | " " | 2 | 13 | Heinz, Sinnot and Sachs (1977) |
| " | " | " " | 6 | 14 | Heise (1953) |
| " | " | " " | ( 1 | 13 | Stebbins (1970) |
| | | | ( 1 | 20 | |
| Passeriformes | Corvidae | Cyanocitta cristata | 2 | 11.5 | Cohen, Stebbins and Moody (1978) |
| " | Icteridae | Molothus ater | 6 | 16 | Heinz et al. (1977) |
| " | " | Agelaius phoeniceus | 10 | 16 | Heinz et al. (1977) |
| " | Fringillidae | Serinus canarius | 4 | 8 | Dooling, Mulligan and Miller (1971) |
| " | " | Carpodacus mexicanus | 2 | 8.2 | Dooling, Zoloth and Baylis (1978) |
| " | " | Spizella pusilla | 2 | 6.8 | Dooling, Peters and Searcy (1979) |
| Psittaciformes | Psittacidae | Melopsittacus undulatus | 4 | 0 | Dooling and Saunders (1975) |
| Galliformes | Meleagrididae | Meleagris gallopavo | 2 | 16 | Maiorana and Schleidt (1972) |
| Strigiformes | Tytonidae | Tyto alba | 1 | -16 | Konishi (1973) |
| " | Strigidae | Strix aluco | 6 | -17 | Dijk (1973) |
| " | " | Asio otus | 6 | -22 | " |
| " | " | Nyctea scandiaca | 1 | -19 | " |
| " | " | Ketupa zeylonesis | 1 | -9 | " |
| " | " | Bubo bubo | 1 | -20 | " |
| " | " | Bubo nipalensis | 1 | -5 | " |
| " | " | Otus leucotis | 1 | -6 | " |
| " | " | Otus scops | 1 | -6 | " |
| " | " | Strix virgata | 1 | -7 | " |
| " | " | Strix seloputo | 1 | -12 | " |
| CLASS MAMMALIA | | | | | |
| Primates | Hominidae | Homo sapiens | 5(Group B) | -12 | Sivian and White (1933) |
| Carnivora | Felidae | Felis silvestris | | -17 | Miller et al. (1963) |

*Sources of constraint upon absolute auditory sensitivity*

Both environmental and physiological noise sources have been proposed as candidates for limiting the absolute sensitivity of the mammalian auditory system. Thermo-acoustic agitation of the tympanic membrane (Sivian and White, 1933), self-noise (Wever and Lawrence, 1954; Diercks and Jeffress, 1962) and thermal agitation within the cochlea (Harris, 1967) have all been discussed as possible sources of constraint upon the lowest threshold.

It is proposed here that none of these provide an adequate explanation of the comparative data and it is suggested that a further source of constraint - naturally occuring minimum ambient noise levels - should be considered. This minimum noise level typically occurs at night. Figure 2 presents a measure of the minimum ambient noise. It is hypothesised that the masking level produced by these minimum sounds in man and birds indicates that auditory sensitivity beyond that of the owls and the mammals would be of no adaptive value since thresholds would always be masked by this minimum ambient sound. Thus it is suggested that the ultimate limit on auditory sensitivity is determined by the minimum ambient sound of the aerial environment.

It is further argued that auditory sensitivity in the diurnal birds, such as the pigeon, is limited at a higher level than in the owls because of the higher levels of ambient sound typically experienced during the day.

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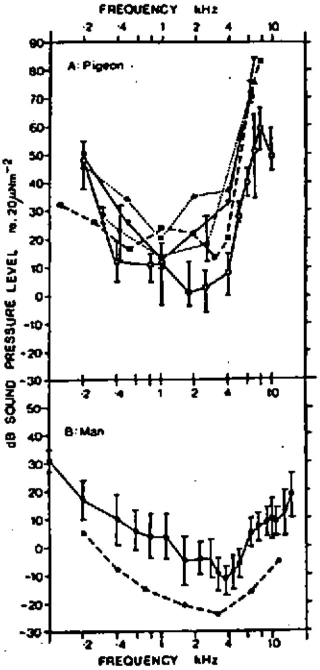

Figure 1. A. Audiograms of the pigeon (Columba livia) determined by behavioural training techniques in four different laboratories. The audiograms of Harrison and Furumoto (1971) (○——○) and Heise (1953) (●·····●) are the mean audiograms of 6 subjects and the standard deviations about the mean are indicated by vertical lines. The audiograms of Heinz et al. (1977) (■---■) is the mean of two birds while those of Stebbins (1970) (▲····▲, ▼——▼) show the audiograms of two individual birds.

B. Audiograms of man (●——●) from Sivian and White (1933, Figs. 4 and 5, table II). This is the average Binaural Minimum Audible Field (M.A.F.) of Group B (n=5); subjects facing the sound source; vertical lines indicate mean deviation from average. ●---● , M.A.F. of Sivian and White's subject R.L.V.,; subject facing sound source.

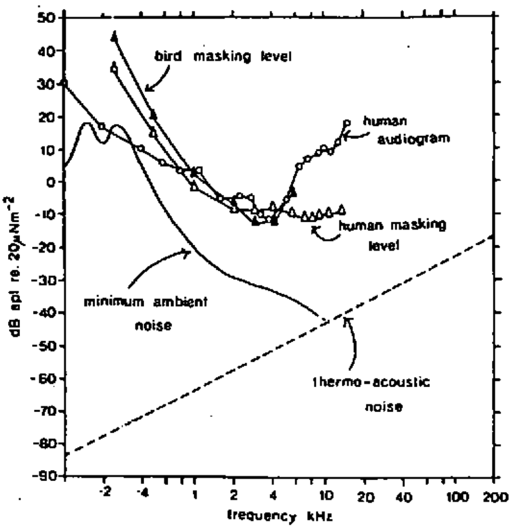

Figure 2. The continuous solid line is the minimum ambient sound spectrum level (1Hz bandwidth) recorded on a windless night in a study of the ambient sound levels produced under different atmospheric conditions. Recordings were made at the Arne Peninsula, Dorset, England in mid-June, and are courtesy of the Ministry of Defence, Procurement Executive, and were communicated to me by K. Dixey. A moving coil microphone (STC type 4021) was calibrated against a standard condenser microphone in an anechoic room. Microphone output was amplified by a purpose built low-noise battery operated amplifier and the output recorded in the field by a Leevers-Rich battery operated tape recorder. The overall system was calibrated by injecting known voltages in to the microphone circuit so that, from the measured sensitivity of the microphone, output voltages could be related to s.p.l.'s at the microphone. With the microphone replaced by a 20.5 ohm resistor the wideband output level for the microphone resistance noise and equipment noise combined, was found to be equivalent to an s.p.l. of +10dB (re 20μNm$^{-2}$). The wideband (.1-8.0 kHz) minimum ambient sound level recorded was equivalent to +38dB s.p.l. The signals were analysed using a Muirhead-Pamatrada wave analyser with a 5Hz bandwidth. The average level per cycle bandwidth was calculated from the analyser readings.

The continuous dotted line is the RMS spectrum level of thermo-acoustic noise in air at 293°K (Hunt 1957). Solid lines with data points are the auditory masking levels produced by the minimum ambient and thermo-acoustic noise spectrums for a bird (Melopsittacus undulatus) (▲) and man (△). The human audiogram (○) is the average binaural minimum audible field from Sivian and White's (1933) group B and is included here as representative of mammalian sensitivity below about 5kHz. This particular audiogram was recorded under conditions comparable to those used in recording the other audiograms of Table 1. Masking levels were calculated using critical ratio (CR) data from the following sources: human, Hawkins and Stevens (1950), all frequencies except 10.5 and 13.0kHz, which were calculated using the critical bandwidth data of Scharf (Scharf 1970) and the assumption that C.R.'s are 4dB less than critical bandwidths. Masking levels were calculated as equal to the spectrum level of the ambient sound plus the CR for each species at each frequency. C.R.'s for the bird were taken from Dooling and Saunders (1975).