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ABSTRACT

Behavioral tests of absolute sensitivity and sound localization in African naked mole rats show that, despite their communal social structure and large vocal repertoire, their hearing has degenerated much like that of other subterranean species. First, their ability to detect sound is limited, with their maximum sensitivity being only 35 dB (occurring at 4 kHz). Second, their high-frequency hearing is severely limited, with their hearing range (at 60 dB sound pressure level [SPL]) extending from 65 Hz to only 12.8 kHz. Third, determination of

Frequency (in kHz)

Fig. 1. Spectrum of noise band used for sound locali zation and for noise-detection thresholds.

(7.62-cm

p

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20 A
B ----- A

100 400 600 1000
Duration of Noise Burst (in msec)

Fig. 3. DeMolaj�0428�0 Tc 9.1 0 0 9.91g�03 64583.j8 0mvalueas

<i:
LL

0.1 s duration

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I

.00
18 dB 28 dB

.00
19dB 30 dB

<ll

U 1.00 1.00 c Mole Rat C Mole Rat D CIl
E

0 .80 .80 ~ .~ 1.------.0 s duration

a.. 1.05 duration
.60 .60

.40 - - - - -:;:-:u-chance .40 - - - - -~~chance
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O~~

o~ 0.1 s duration 0.1 5 duration .20 .20

.00 -'---,-----,---- .00 -'---,----.---
19dB 25 dB 23 dB 30 dB

Hearing Level

Fig. 5. Sound-localization performance for four mole rats at a fixed angle of 1800 separation as a function of the intensity of the noise burst above t hreshold. Intensity above threshold (i.e., hearing level) varies beca use of individual differences in sensitivity to the short and long signa ls. Note that the animals could not localize the O.l-second noise burst above chance regardless of intensity, whereas performance for the longer l.O-second noise burst is well above chance for both intensities. Thus, the inability to locali ze brief noise bursts cannot easily be attributed to reduced sensitivity to brief signals. Dashed line inclicates the .01 level of chance, which varies between indi viduals owing to differences in false alarm rates.

the original 100-millisecond noise burst. For example, for mole rat A, the original 1,000-millisecond stimulus was 28 dB HL, whereas the 100-millisecond stimulus was 18 dB HL. Therefore testing was repeated with the 1,000-millisecond stimulus attenuated to 18 dB HL and the

100-millisecond stimulus amplified to 28 dB HL. Testing
with the two durations at the 28 sec

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Fig. 7. A: PhotomicrogTaph of a transverse section through the brain of a naked mole rat at the level of the PVCN and DCN. B: Higher magnification view of DCN showing the fusiform cell layer (arrow). C: PVCN showing unclassified large cells and dorsal gTanu le cell cap

Briefly, all the major auditory nuclei appear to be present and in their normal configuration; none are hypertrophied and none are absent. Yet, as illustrated in the following figures, the nuclei are all relatively small and the structures normally involved in binaural processing for sound localiza-tion are exceedingly so.
The brainstem of a mole rat is illustrated at the level of the cochlear nucleus in Figure 7. Figure 7A is a low-magnification view of the brainstem through the posterior portion of the posterior ventral cochlear nucleus (PVCN) at the level of the greatest extent of the dorsal cochlear nucleus (DCN). At higher magnification a distinct fusiform cell layer can be seen in the DCN, but the granule cells, one of the more variable features of cochlear nuclei in different species (e.g., Merzenich et al., '73; Moore, '80), are scattered throughout the DCN. Large multipolar cells are concen-trated dorsomedially in the DCN (Fig. 7B). The PVCN contains scattered, primarily large, cells (Fig. 7C) that cannot unequivocally be assigned to specific cell types in the absence of Golgi material. There is a concentration of granule cells in a thin band between the DCN and PVCN that continues anteriorly as a granule cell cap over the ventral cochlear nucleus. Rostrally (0.5 mm) the PVCN contains a greater concentration of cells and its gTanule cell cap continues anterior to the DCN (Fig. 7Dl.
Figure 8A illustrates the auditory brainstem of the naked mole rat at the level of the anterior ventral cochlear nucleus (AVCN) and the posterior portion of the superior olivar0

brainstem ofa naked mole rat 0.9 mm rostral to Figure 7A, showing the AVCN with the granule cell layer (arrowhead) continuou s with the cerebellar granule cell layer, the LSO, MSO, and MTB. B: Higher magnification view of th e AVCN, revealing only a few spherical cells, two of which are indicated by arrows. C: Higher magnification view of the MSO, MTB, and VTB. D: Four neurons in the MTB contacted by

exit of the seventh nerve; however, it contains few neurons. Finally, the sparseness of fibers in the trapezoid body (Fig. 8F) suggests that binaural interactions may be minimal in this species compared with most mammals.
Further rostrally in the auditory system, the lateral lemniscus with its embedded nuclei are illustrated in

Figure 9A. Figure 9B illustrates the configuration of the posterior inferior colliculus (lC

1.0 mm
-~ Fig. 9. A: Photomicrograph of a transverse thionine-stained section
through the left lateral lemniscus O.S mm anterior to Figure SA. There
are three groups of cells within the lateral lemniscus that may
correspond to the dorsal (DLL), intermediate (ILL), and ventral (VLL)
nuclei of the lateral lemniscus (although the latter may instead be a
rostral periolivary nucleus). B: Adjacent protargol-stained section
through the posterior IC illustrating its three major regions as de-scribed by Helfert et a1. ('9U, the central nucleus (CIC), dorsal cortex
(DC), and lateral nucleus (LN). C: Transverse thionine-stained section
through the rig·ht caudal thalamus, 1.9 mm anterior to A, illustrating
the configuration of the medial geniculate body (MG). Note that cells fill
the nucleus all the way to its lateral edge.

10 !J.m

Naked Mole Rat

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. 13.5-16

. 16-18.5

. 18.5-21

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1 mm

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Fig. 10. A-D: Photomicrographs of thionine-stained g'anglion cells at the locations marked by corresponding letters in E. N, nasal; S, superior; T, temporal; scale bar for A-D = 10).Lm. E: Ganglion cell density distribution in the retina of a naked mole rat. The filled circles
of different sizes inc'.icate the density of ganglion cells at 100-).Lm
intervals in thousands of gang'lion cells per mm2 (gaps in the 100-).Lm
grid are areas where cells could not be counted because of shrinkage or
vitreal debris). The x indicates the location of the very small optic disk,
and the dashed line indicates the approximate horizon of the retina.

dense ganglion cells is The983230 0 .0 130.78 4.55 3961 390m�(The98367360 .0 130.78 4i01 26i1 411m�(The9835517 .0 130.78 4h.55 3961)Tj7�(The98373.31 0

and upper hearing range.
The fact that some of the energy in mole rat vocalizations extends beyond their hearing range is a result of the production of harmonics. Indeed, vocalizations often con-tain abrupt onsets and offsets, generating high frequencies that are " nonfunctional" in the sense that the animals do not use them to identify the sounds and that, in fact, may be beyond their hearing range. Examples of such vocalizations are bird calls that extend beyond 10 kHz (Konishi, '69) and rodent vocalizations that extend beyond 100 kHz (Sales and Pye, '74). However, in spite of their large vocal repertoire, frequent vocalizations, and the high-frequency content of some of their vocalizations, naked mole rats are relatively insensitive to sound and are unable to hear high frequen-cies. Indeed, their hearing ability closely resembles that of solitary subterranean