

Central Visual System of the Naked Mole-Rat (*Heterocephalus glaber*)

SAMUEL D. CRISH, CHRISTINE M. DENGLER-CRISH, AND
KENNETH C. CATANIA*

Department of Biological Sciences and Neuroscience Program, Vanderbilt University,
Nashville, Tennessee

ABSTRACT

Naked mole-rats are fossorial rodents native to eastern Africa that spend their lives in extensive subterranean burrows where visual cues are poor. Not surprisingly, they have a degenerated eye and optic nerve, suggesting they have poor visual abilities. However, little is known about their central visual system. To investigate the organization of their central visual system, we injected a neuronal tracer into the eyes of naked mole-rats and mice to compare the neural structures mediating vision. We found that the superior colliculus and lateral geniculate nucleus were severely atrophied in the naked mole-rat. The olivary pretectal nucleus was reduced but still retained its characteristic morphology, possibly indicating a role in light detection. In addition, the suprachiasmatic nucleus is well innervated and resembles the same structure in other rodents. The naked mole-rat appears to have selectively lost structures that mediate form vision while retaining structures needed for minimal entrainment of circadian rhythms. Similar results have been reported for other mole-rat species. Taken together, these data suggest that light detection may still play an important role in the lives of these “blind” animals: most likely for circadian entrainment or setting seasonal rhythms. © 2006 Wiley-Liss, Inc.

Key words: brain; evolution; vision; superior colliculus; eye; blind

A well-developed visual system is metabolically costly, so one would expect a reduction in the visual systems of subterranean rodents where light levels are minimal. However, animals with occasional access to the surface can make use of brief light exposure for setting circadian and seasonal rhythms. Studies of both Ansell's mole-rat (*Cryptomys anselli*) and the blind mole-rat (*Spalax ehrenbergi*) have revealed severe atrophy of many of the structures involved in form vision, yet some of the structures involved in other types of light detection appear unchanged. This has led to the suggestion that light cues are still used to mediate aspects of behavior in at least some fossorial species (Cooper et al., 1993; Nemec et al., 2004).

Naked mole-rats (Fig. 1) are fossorial rodents from eastern Africa in the same family (Bathergidae) as Ansell's mole-rat. Naked mole-rats live underground in large eusocial colonies with division of labor and separate castes that have different social, morphological, and behavioral characteristics. Only a few colony members are reproductively active, which results in a high level of genetic similarity in the colony due to inbreeding (Jarvis, 1981).

In addition to social and physiological adaptations to life underground, mole-rats exhibit several sensory modifica-

tions. Sound attenuates rapidly underground, and presumably because of this environmental constraint, mole-rats have degraded hearing with poor sound localization abilities (Heffner and Heffner, 1993; Brittan-Powell et al., 2001). However, naked mole-rats are somatosensory specialists with a novel array of somatic vibrissae for guiding orienting behavior (Crish et al., 2003a; Park et al., 2003) and large front incisors used for digging tunnels and manipulating objects. They have a correspondingly hypertrophied somatosensory cortex for processing tactile information that includes a greatly expanded representation of the dentition (Catania and Rempel, 2002).

*Correspondence to: Kenneth C. Catania, Department of Biological Sciences and Neuroscience Program, Vanderbilt University, VU Station B Box 35-1634, Nashville, TN 37235.
E-mail: kenneth.catania@vanderbilt.edu

Received 25 August 2005; Accepted 18 October 2005

DOI 10.1002/ar.a.20288

Published online 17 January 2006 in Wiley InterScience (www.interscience.wiley.com).



Fig. 1. Side view of the naked mole-rat. Note the lack of fur, small eye, small external ear, and large, protruding incisors.

As in many other fossorial animals, naked mole-rats have small eyes (≤ 1 mm in diameter), a degenerated retina, and an atrophied optic nerve (Nikitina et al., 2004; Hetling et al., 2005), implying that they are blind. Many other physical malformations of the peripheral visual system in these rodents have been identified recently by Nikitina et al. (2004). However, naked mole-rats do exhibit some visual abilities, such as muscular control over the iris, potentially allowing them to regulate light entering the eye (Nikitina et al., 2004). This suggests that the eye may still be capable of detecting light/dark differences. In support of this possibility, some naked mole-rats demonstrate an ability to modulate their circadian rhythms based on different light-dark cycles (Riccio and Goldman, 2000a, 2000b), but this capacity varies from mole-rat to mole-rat. The degenerated eye, combined with an ability to photoentrain, may indicate that during the course of evolution, the naked mole-rat (like Ansell's mole-rat or Spalax) lost structures mediating form vision but selectively retained other aspects of light detection (Cooper et al., 1993; Nemec et al., 2004).

Although a few recent studies have investigated the naked mole-rat's ocular anatomy (Nikitina et al., 2004; Hetling et al., 2005), their central visual system remains unexplored. In the current study, we used intraocular injections of an anterograde neuroanatomical tracer to investigate the organization and size of visual projections from the mole-rat eye to the central nervous system. For comparison to sighted species, we performed the same experiments on mice (C57 black). We chose this species because it is a rodent with a similarly sized brain and a more typical visual system that has been well characterized (for example, see Godement et al., 1984).

MATERIALS AND METHODS

Animals

Four adult naked mole-rats were used (three females and one male). Animals came from a colony kept at Vanderbilt University. Naked mole-rats were maintained in a temperature and humidity-controlled room and were housed in chambers interconnected with plastic tubing (for complete housing details, see Artwohl et al., 2002). Animals selected for the study were not reproductively active and represented different sizes and weights.

Four adult mice (two females and two males) of the C57 black strain were used for anatomical comparison of na-

ked mole-rats to sighted rodents. These animals were housed at the Department of Biological Sciences at Vanderbilt University under a 12-hr/12-hr light-dark cycle.

Surgical Procedure

Naked mole-rats were anesthetized with 100 mg/kg ketamine HCL and 2 mg/kg xylazine (i.p.). The temperature of each animal was maintained with a warm water bottle. For each subject, one eye was swabbed with betadine and a small incision (1 mm) was made in to access the recessed eye. Control mice were injected in the same manner as described, with the exception that no incision was needed.

After the eye was exposed and stabilized, a Hamilton syringe with a glass pipette tip was used to pressure-inject a 1 μ l volume of 4% wheat germ agglutinin-conjugated horseradish peroxidase (WGA-HRP) or cholera toxin subunit B-conjugated HRP (CTB-HRP) solution (Sigma Aldrich) into the eye. After each injection, the eye was covered with a 5% lidocaine ointment (Fougera, Melville, NY) and the animal received 0.5 mg/kg Buprenex (s.c.) for postsurgical pain relief. All animals recovered uneventfully from the procedure. Forty-eight hours later, animals were given an overdose of nembutal (100 mg/kg) and transcardially perfused with 0.01 M phosphate-buffered saline (PBS) followed by 2% paraformaldehyde in PBS. Brains were removed and postfixed in 2% paraformaldehyde for 2–4 hr. Brains were then cryoprotected overnight in 30% sucrose/PBS.

Histological Processing

A freezing microtome was used to cut 50 μ m sections of each brain. Alternate sections were processed for visualization of transported label using a modified tetramethylbenzidine (TMB) procedure of Gibson et al. (1984). The remaining sections were used for neuroanatomical identification and were processed for cytochrome oxidase (CO) using the methods of Wong-Riley and Carroll (1984), or for myelin using the gold chloride technique of Schmued (1990).

Terminal fields were reconstructed with camera lucida. Photomicrographs were taken of selected sections using a Spot 2 camera (Diagnostic Imaging, Sterling Heights, MI) on a Nikon E800 microscope. To calculate volumes, the area of the structure of interest was measured in each section and multiplied by the distance between the sec-

tions. All animal procedures followed NIH guidelines and were performed according to standards set by the Animal Welfare Act and Vanderbilt University IACUC.

RESULTS

Naked mole-rats exhibited a profound atrophy of their central visual system. Retinal projections terminated primarily in contralateral structures with very sparse or nonexistent ipsilateral projections. Details of each nucleus are summarized below as compared to mice.

Most structures in the mole-rat midbrain were similar in size to corresponding structures in the mouse midbrain; however, the mole-rat superior colliculus (SC) was severely reduced when compared to the mouse SC (Fig. 2). In the superior colliculus, the retinal projection was mostly contralateral, with a sparse ipsilateral projection in some animals. This projection was limited to a thin layer 30–100 μm thick in cross-section. The mouse projection was typically about 300 μm thick (Fig. 3). The entire mole-rat SC averaged 42% of the volume of the mouse SC (mole-rat, 1.41 mm^3 ; mouse, 3.34 mm^3). The retinal projection to the SC in the naked mole-rat averaged only 15% of that of the mouse SC (mole-rat, 0.08 mm^3 ; mouse, 0.53 mm^3).

Notably, the mole-rat SC did not appear to be uniformly degenerated, but it appeared to have fairly normal layering in the intermediate and deep layers. We are basing our nomenclature on Wiener (1986). Although the first layer in the intermediate SC (layer IVa) is difficult to distinguish from layer III using myeloarchitecture or sections stained for CO, layer IVb is readily apparent and consists of large and distinctive rostrocaudally oriented fiber tracts that do not extend to the lateral edge of the SC. These were clearly visible in the CO-stained naked mole-rat SC (Fig. 2) and in sections stained for myelin (Fig. 4), providing an unambiguous, homologous landmark in both species. Ventral to IVb, a CO-rich lamina appeared to be layer IVc in both the mole-rat and mouse. Layers V–VII consist of mediolaterally oriented fiber bundles. In mole-rats, these were apparent in both CO-stained sections (Fig. 2) and sections stained for myelin (Fig. 4). Layer V and VI were distinguished from layer VII by the characteristic restriction of fibers near the midline (Figs. 2 and 4) (Wiener, 1986). Layers V and VI are usually distinguished from each other by the presence of cell bodies in layer VI; however, this was difficult to distinguish in the mole-rat colliculus.

Interestingly, in sighted animals, the superficial layer covers the majority of the intermediate and deep SC except in the most caudal and lateral aspects, whereas in the naked mole-rat, there are very large portions of the SC that appeared to lack any superficial layer (as identified by retinal innervation). The extent of this characteristic varied from mole-rat to mole-rat.

The mole-rat lateral geniculate nucleus (LGN) was much reduced when compared to the LGN in similarly sized mice. This can be best appreciated by examining the distribution of label in the LGN of mice and mole-rats at the same scale (Fig. 5). Recall that the overall size of the midbrain is similar in these two species, yet the mouse LGN dwarfs the mole-rat LGN. In sections processed for CO and myelin, the mole-rat lateral geniculate nucleus appeared to be compressed into either a single layer or several poorly differentiated layers 80–250 μm thick at its largest extent. This can be contrasted with the much

larger mouse LGN, which is typically 350–450 μm in thickness. Though degenerated, the LGN did retain a separation into dorsal (d) and ventral (v) components as the intergeniculate leaflet is still present (Fig. 5). Volume of the mole-rat LGN averaged about 10% of the mouse LGN (mole-rat, 0.05 mm^3 ; mouse, 0.46 mm^3). The dorsal LGN (dLGN) is much more reduced than the ventral LGN (vLGN) when each of these structures is compared to the same structure in the mouse. Mole-rat dLGN is 5% of the size of the mouse dLGN, whereas the mole-rat vLGN is 18% of the size of the mouse vLGN.

As in other mole-rats (Nemec et al., 2004), the olivary pretectal nucleus (OPN) was the most prominent pretectal nucleus in the naked mole-rat. This structure is rostral to the SC and has a distinctive oval shape. The mole-rat OPN was substantially smaller than the OPN of mice (Fig. 6), having a volume of 15–25% of the mouse OPN (mole-rat, < 0.01 mm^3 ; mouse, 0.03 mm^3), yet the mole-rat OPN retained its characteristic olive-shaped morphology. Other pretectal nuclei received retinal projections but were difficult to distinguish.

As seen in both Spalax and Ansell's mole-rat, the naked mole-rat's suprachiasmatic nucleus (SCN) was still present and received a retinal input (Fig. 7). This structure was 0.025 mm^2 in cross-section. This is consistent with the sizes reported for other rodents, including other mole-rats, hamsters, and mice (Youngstrom and Nunez, 1986; Cooper et al., 1993; Nemec et al., 2004), although it is slightly larger (approximately 15%) in cross-section when compared to the mouse. This projection was not as dense as the projections reported in either Ansell's mole-rat or Spalax. Finally, in contrast to Ansell's mole-rat or Spalax, we found no indication that the eye projects to the contralateral SCN.

We found no evidence of any direct retinal projection to the bed nucleus of the stria terminalis (BNST) or any other limbic structures, as has been reported in other animals such as Spalax (Cooper et al., 1993). Also, as in Ansell's mole-rat (Nemec et al., 2004), the accessory optic system appeared greatly reduced and difficult to distinguish.

DISCUSSION

In naked mole-rats, the main subcortical nucleus involved in image formation, the LGN, was considerably atrophied with an apparent loss of its characteristic-stratified organization (for details of LGN organization in other animals, see Kaas and Huerta, 1988). These findings support the conclusion suggested from investigation of peripheral structures (Nikitina et al., 2004; Hetling et al., 2005) and cortical mapping (Catania and Remple, 2002) that naked mole-rats lack the ability to form visual images. Although form vision may be lost in these mammals, a well-organized LGN is not required for light detection, pupil constriction, and contrast cues (Kaas and Huerta, 1988) and evidence suggests that these visual abilities may be conserved in naked mole-rats (Nikitina et al., 2004). The capacity to distinguish light/dark cues is thought to be useful for these subterranean mammals because the presence of light can be an indicator that an animal has left the safety of its tunnels or the burrow system has been opened (Nikitina et al., 2004).

Interestingly, the vLGN appeared less degenerated than the dLGN. There is evidence that the vLGN plays a role other than form vision. This structure has been dem-

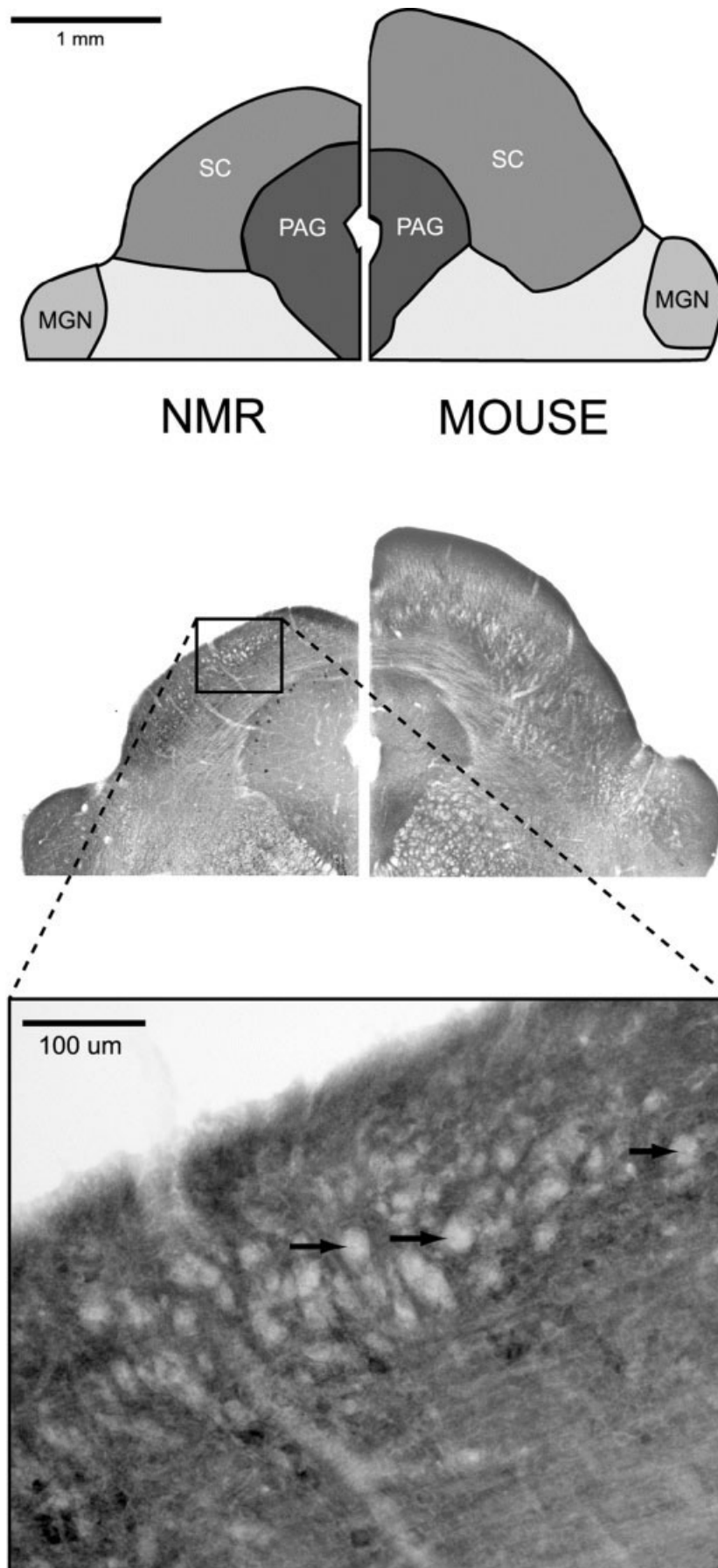


Fig. 2. Cytochrome oxidase-reacted sections of mole-rat and mouse midbrain. The mole-rat SC is considerably reduced when compared to the mouse SC. Other midbrain structures are comparable in size between the two species. In the bottom panel, arrows indicate some of the

large rostrocaudally oriented fiber tracts that compose layer 4b. SC, superior colliculus; MGN, medial geniculate nucleus; PAG, periaqueductal gray.

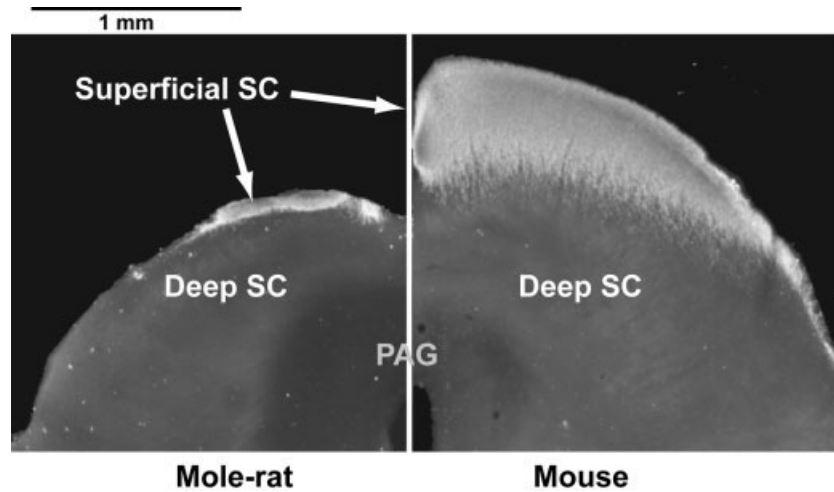


Fig. 3. WGA-HRP reactivity in the mole-rat and mouse superior colliculus (SC). The small retinal projection in the naked mole-rat is constrained to the superficial layers and does not extend across the deeper layers of the SC.

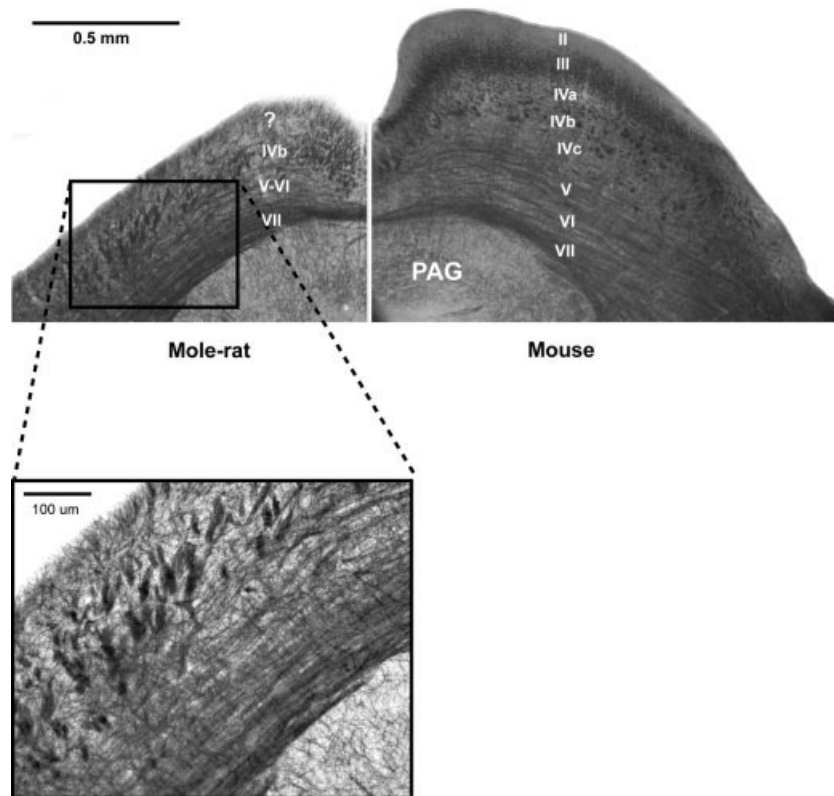


Fig. 4. Sections of mole-rat and mouse superior colliculus stained for myelin. Layering designation based on the nomenclature of Wiener (1986). Note that the naked mole-rat has a relatively normal intermediate and deep SC. The apparent degeneration of the mole-rat SC appears to be due to a specific reduction of the superficial layers (layers 1–3).

onstrated to project to the SCN, carrying information concerning both photic and nonphotic cues (Abe and Rusak, 1992) that influence the circadian clock. If so, this structure may retain many of its characteristics, much as the SCN is postulated to retain its function.

The relatively pronounced OPN is not surprising, considering recent research on the naked mole-rat eye. In addition to the ability for general light detection, naked mole-rats retain some of the eye musculature and organization that is not present in other species of mole-rat,

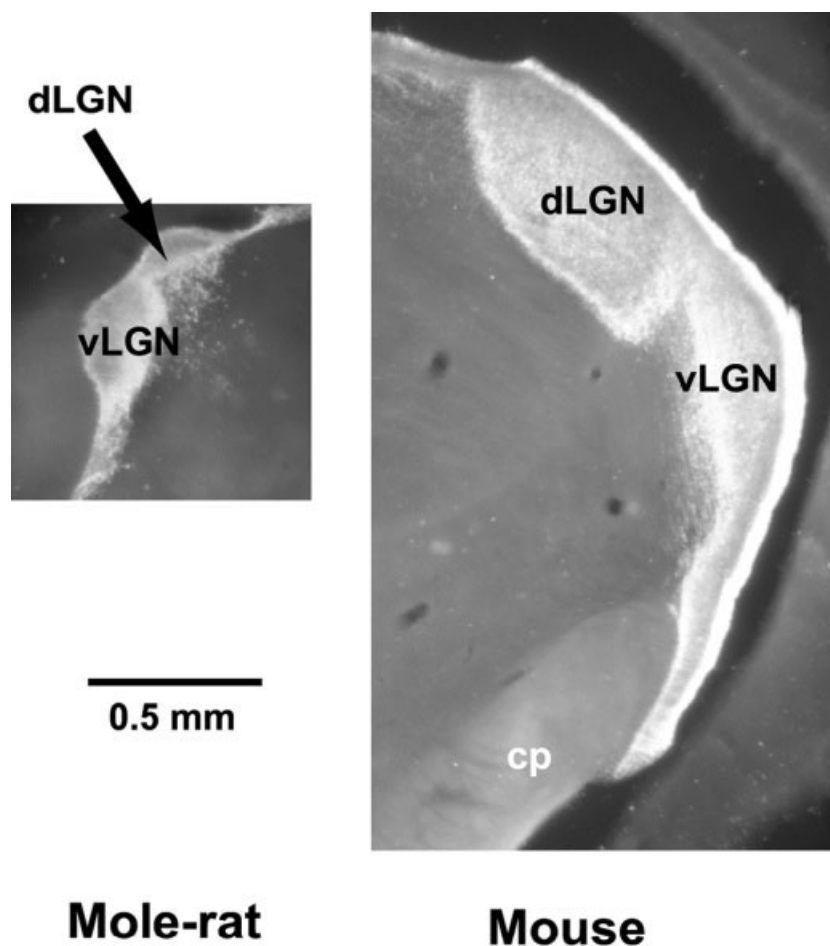


Fig. 5. WGA-HRP reactivity in the mole-rat and mouse lateral geniculate nucleus (LGN). The naked mole-rat LGN is considerably reduced when compared to the mouse LGN. It has lost its characteristic layering, yet retained a division into dorsal and ventral components separated by the intergeniculate leaflet. dLGN, dorsal lateral geniculate nucleus; vLGN, ventral lateral geniculate nucleus; cp, cerebellar peduncle.

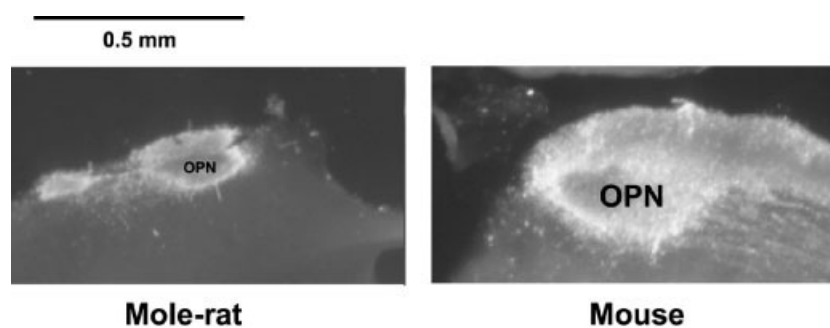


Fig. 6. WGA-HRP reactivity in the mole-rat and mouse pretectum. The naked mole rat's pretectum is substantially reduced when compared to the mouse pretectum. However, it does retain aspects of its morphology. Shown here is the olivary pretectal nucleus (OPN), an important structure for pupillary constriction in response to light, a visual behavior the mole-rat retains (Nikitina et al., 2004).

possibly indicating that they retain the ability to constrict their pupils in response to various light levels (Nikitina et al., 2004). Brightness discrimination and the pupillary light reflex have been linked to the OPN (Clarke and

Ikeda, 1985). Although control of the pupil may seem useless for a species that presumably has little or no visual abilities other than light detection, there may still be an adaptive significance to mediating light levels. Con-

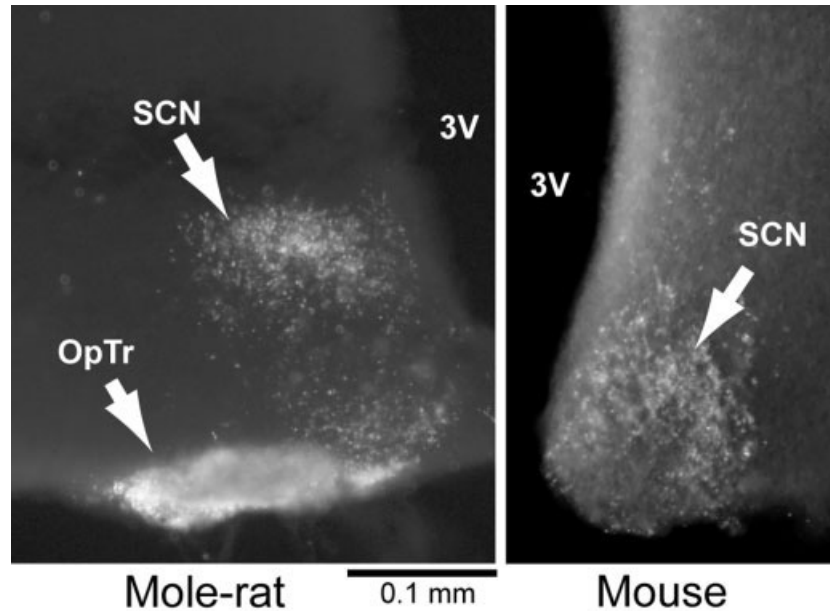


Fig. 7. Retinal projection to the suprachiasmatic nucleus (SCN) in the mole-rat and mouse. OpTr, optic tract; 3V, third ventricle. The naked mole-rat has a sizable, moderately innervated SCN, suggesting that it has selectively retained the ability to detect light for photoentrainment.

sider, for example, that mole-rats are potentially exposed to drastic extremes in light levels when going from the total darkness of the burrow system to the full intensity of daylight. Although this is presumably uncommon in day-to-day activities, it seems possible that the occasional exposure to such extremes could form the basis for retaining some control over the iris.

The mole-rat SC, unlike the mole-rat LGN, did retain many aspects of its stratified organization. The reduction in overall collicular volume appears to come from a specific reduction or elimination of superficial layers. Even with this reduction, the retinal projection, although small, was constrained to the most superficial layer of the SC. The lack of apparent superficial layers in the SC toward the caudal pole raises some interesting questions. One possibility is that some of the layers are still present but have lost retinal innervation. Another possibility is that, as the animal ages, there is a gradual retraction of the retinal innervation due to the lack of visually driven activity.

The lack of well-developed superficial layers may have consequences beyond visual processing. The superficial layers of the SC (which are exclusively visual in most mammals) have been suggested to be essential for proper development of the nonvisual sensory maps. In other animals, experimental manipulations of vision result in distorted collicular (or tectal) maps of the nonvisual modalities (Drager and Hubel, 1976; Rauschecker and Harris, 1983; Sparks and Nelson, 1987; Knudsen and Brainard, 1991).

The organization and development of the naked mole-rat's somatosensory representation in the SC remains to be investigated. Behavioral evidence suggests that there is a well-ordered somatosensory map in the mole-rat SC (Crish et al., 2003a, 2003b), but this needs to be confirmed with electrophysiological methods. Another blind fossorial mammal, the star-nosed mole, has a superior colliculus

completely dominated by somatosensation in the form of a well-ordered map of body surface (Crish et al., 2003c). In addition, the SC in Ansell's mole-rat has been linked to magnetoreception (Nemec et al., 2001). Although no evidence of this sense has been reported in naked mole-rats, it has not yet been systematically examined.

The relative conservation of the naked mole-rat SCN is consistent with anatomical investigations in other species of mole-rat (Cooper, et al., 1993; Nemec et al., 2004) and with recent behavioral studies indicating some naked mole-rats have the ability to photoentrain (Riccio and Goldman, 2000a, 2000b). Overall size and apparent density of the retinal projection to the SCN seemed comparable between naked mole-rats and other rodent species (Youngstrom and Nunez, 1986; Cooper, et al., 1993; Nemec et al., 2004).

The lack of any limbic projection in the naked mole-rat BNST is not surprising. Evidence of these projections is rare and, when found, is usually sparse in other animals. Even so, in *Spalax*, this projection is postulated to allow the solitary animals to synchronize their hormonal states with each other for the purposes of mating (Nemec et al., 2004). Since they exhibit eusociality, most naked mole-rats are nonreproductive. As we only used nonreproductives, the neural circuitry involved in hormonal regulation and production could have been immature and this projection may be expected in reproductively active animals. However, it is possible this projection is not seen because the animals live in colonies. They have constant access to each other and can synchronize any hormonal rhythms by conspecific communication, rather than relying on external cues.

In summary, the naked mole-rat appeared to have a severely degenerated visual system. Structures responsible for form vision such as the lateral geniculate nucleus of the thalamus, the superior colliculus, and visual cortex

(Catania and Remple, 2002) were severely atrophied. Considering the mole-rat lives in an environment where visual cues are almost nonexistent, a well-developed, metabolically costly visual system would be of little or no use. However, the animal does have occasional access to the surface, making light cues potentially useful for determining when the animal is out of the tunnel system and for setting circadian or seasonal rhythms. The main brain structure implicated in circadian photoentrainment, the suprachiasmatic nucleus, appeared comparable to sighted animals in size and retinal input (see also Cooper et al., 1993).

ACKNOWLEDGMENTS

Supported by National Science Foundation grants 0518819 and 0454761 and a Career Award (to K.C.C.).

LITERATURE CITED

- Abe H, Rusak B. 1992. Stimulation of the hamster ventral lateral geniculate nucleus induces Fos-like immunoreactivity in suprachiasmatic nucleus cells. *Neurosci Lett* 148:185–189.
- Artwohl J, Hill T, Comer C, Park T. 2002. Naked mole-rats: unique opportunities and husbandry challenges. *Lab Anim* 31:32–36.
- Brittan-Powell EF, Okanoya K, Dooling RJ, Comer C, Park T. 2001. The auditory brainstem response of the fossorial naked mole-rat. *Soc Neurosci Abst* 724:12.
- Catania KC, Remple MS. 2002. Somatosensory cortex dominated by the representation of teeth in the naked mole-rat brain. *Proc Natl Acad Sci USA* 99:5692–5697.
- Clarke RJ, Ikeda H. 1985. Luminance and darkness detectors in the olivary and posterior pretectal nuclei and their relationship to the pupillary light reflex in the rat: I, studies with steady luminance levels. *Exp Brain Res* 57:224–232.
- Cooper HM, Herbin M, Nevo E. 1993. Ocular regression conceals adaptive progression of the visual system in a blind subterranean mammal. *Nature* 361:156–159.
- Crish SD, Rice FL, Park TJ, Comer CM. 2003a. Somatosensory organization and behavior in naked mole-rats: I, vibrissa-like body hairs comprise a sensory array that mediates orientation to tactile stimuli. *Brain Behav Evol* 62:141–151.
- Crish SD, Dengler-Crish CM, Comer CM. 2003b. The superior colliculus and tactile orienting behavior in the naked mole-rat. *Soc Neurosci Abst* 187:14.
- Crish SD, Comer CM, Marasco PD, Catania KC. 2003c. Somatosensation in the superior colliculus of the star-nosed mole. *J Comp Neurol* 464:415–425.
- Drager UC, Hubel DH. 1976. Topography of visual somatosensory projections to mouse superior colliculus. *J Neurophysiol* 39:91–101.
- Gibson AR, Hansma DI, Houk JC, Robinson FR. 1984. A sensitive low artifact TMB procedure for the demonstration of WGA-HRP in the CNS. *Brain Res* 298:235–241.
- Godement P, Salaun J, Imbert M. 1984. Prenatal and postnatal development of retinogeniculate and retinocollicular projections in the mouse. *J Comp Neurol* 230:552–575.
- Heffner RS, Heffner HE. 1993. Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*), with an overview of central auditory structures. *J Comp Neurol* 331:418–433.
- Hetling JR, Baig-Silva MS, Comer CM, Pardue MT, Samaan DY, Qtaishat NM, Pepperberg DR, Park TJ. 2005. Features of visual function in the naked mole-rat *Heterocephalus glaber*. *J Comp Physiol A* 191:317–330.
- Jarvis JUM. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* 212:571–573.
- Kaas JH, Huerta MF. 1988. The subcortical visual system of primates. *Comp Prim Biol* 4:327–391.
- Knudsen EI, Brainard MS. 1991. Visual instruction of the neural map of auditory space in the developing optic tectum. *Science* 253:85–87.
- Nemec P, Altmann J, Marhold S, Burda H, Oelschlagel HH. 2001. Neuroanatomy of magnetoreception: the superior colliculus involved in magnetic orientation in a mammal. *Science* 294:366–368.
- Nemec P, Burda H, Peichl L. 2004. Subcortical visual system of the African mole-rat *Cryptomys anselli*: to see or not to see? *Eur J Neurosci* 20:757–768.
- Nikitina NV, Maughan-Brown B, O'Riain MJ, Kidson SH. 2004. Postnatal development of the eye in the naked mole-rat. (*Heterocephalus glaber*). *Anat Rec* 277:317–337.
- Park TJ, Comer C, Carol A, Lu Y, Hong HS, Rice FL. 2003. Somatosensory organization and behavior in naked mole-rats: II, peripheral structures, innervation, and selective lack of neuropeptides associated with thermoregulation and pain. *J Comp Neurol* 465:104–120.
- Rauschecker JP, Harris LR. 1983. Auditory compensation of the effects of visual deprivation in the cat's superior colliculus. *Exp Brain Res* 50:69–83.
- Riccio AP, Goldman BD. 2000a. Circadian rhythms of locomotor activity in naked mole-rats (*Heterocephalus glaber*). *Physiol Behav* 71:1–13.
- Riccio AP, Goldman BD. 2000b. Circadian rhythms of body temperature and metabolic rate in naked mole-rats. *Physiol Behav* 71:15–22.
- Schmued LC. 1990. A rapid, sensitive histochemical stain for myelin in frozen brain sections. *J Histochem Cytochem* 38:717–720.
- Sparks DL, Nelson JS. 1987. Sensory and motor maps in the mammalian superior colliculus. *Trends Neurosci* 10:312–317.
- Wiener SI. 1986. Laminar distribution and patchiness of cytochrome oxidase in mouse superior colliculus. *J Comp Neurol* 244:137–148.
- Wong-Riley M, Carroll EW. 1984. Effect of impulse blockage on cytochrome oxidase activity in monkey visual system. *Nature* 307:262–264.
- Youngstrom TG, Nunez AA. 1986. Comparative anatomy of the retino-hypothalamic tract in photoperiodic and non-photoperiodic rodents. *Brain Res Bull* 17:485–492.