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Brain Research Bulletin 75 (2008) 356–364

BRAIN RESEARCH BULLETIN

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Review

The visual system in subterranean African mole-rats (Rodentia, Bathyergidae): Retina, subcortical visual nuclei and primary visual cortex

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Received 14 August 2007; accepted 17 October 2007
Available online 26 November 2007

Abstract

We have studied the visual system of subterranean mole-rats of the rodent family Bathyergidae, for which light and vision seem of little importance. The eye diameter varies between 3.5 mm in *Bathyergus suillus* and 1.3 mm in *Heterocephalus glaber*. The small superficial eyes have features typical of sighted animals (clear optics, well-developed pupil and well-organized retina) and appear suited for proper image formation. The retinae are rod-dominated but possess rather high cone proportions of about 10%. The total number of retinal ganglion cells and optic nerve fibres ranges between 6000 in *Bathyergus suillus* and 2100 in *Heliophobius argenteocinereus*. Visual acuity (estimated from counts of peak ganglion cell density and axial length of the eye) is low, ranging between 0.3 and 0.5 cycles/degree. The retina projects to all the visual structures described in surface-dwelling sighted rodents. The suprachiasmatic nucleus is large and receives bilateral retinal input. All other visual nuclei are reduced in size and receive almost exclusively contralateral retinal projections of varying magnitude. The primary visual cortex is small and, in comparison to other rodents, displaced laterally. In conclusion, the African mole-rats possess relatively well-developed functional visual subsystems involved in photoperiodicity, form and brightness discrimination. In contrast, visual subsystems involved in coordination of visuomotor reflexes are severely reduced. This pattern suggests the retention of basic visual capabilities. Residual vision may enable subterranean mammals to localize breaches in the burrows that let in light thus providing a cue to enable mole-rats to reseal such entry points and to prevent entry of predators.

Keywords: Microphthalmia; Ocular regression; Subterranean mammals; *Cryptomys*; *Fukomys*; *Georychus*

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doi:10.1016/j.brainresbull.2007.10.055

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1. Introduction

Until recently, our understanding of the visual system of subterranean mammals was mainly based on seminal studies in the blind mole-rat *Spalax ehrenbergi* which has regressed and rudimentary visual structures [2,4,22 and citations therein]. Over the last years, studies covering a larger range of subterranean mammalian species have 'unearthed' an unexpected diversity of ocular and retinal features [reviewed in 21,28]. Similarly, it was shown that not all visual brain nuclei are equally degenerate across species [reviewed in 21]. Taken together, these findings suggest different visual capabilities and adaptations in different subterranean rodents. They challenge the widely held view that vision is an expendable sense underground. Here we describe the visual system of the African mole-rats (Bathyergidae), a group of rodents unrelated to *Spalax*, which have independently adopted a strictly subterranean mode of life, and discuss the potential role of vision for these "blind" creatures.

2. Eye morphology

Eye sizes vary substantially across bathyergid species (Fig. 1). The axial length of the eye ranges between 3.5 mm in *Bathyergus suillus* and 1.3 mm in *Heterocephalus glaber*. In contrast to the blind mole-rat, African mole-rat eyes feature normal properties: eyelids, clear optics, an iris with a pupillary aperture, and a well-developed retina lining the back of the eye (Fig. 1). This indicates the capability of image-forming vision.

Small eye size limits the image size on the retina, resulting in poor image quality and visual acuity. An additional corollary of small eye size is a small pupil limiting the photon flux to the retina. Furthermore, the lens in many species (except the naked mole-rat *Heterocephalus glaber*) is small in relation to the eye size (Fig. 1; [23]). This is surprising because nocturnal surface-dwelling mammals, like rat and mouse, have relatively large lenses to collect light effectively. Relatively small lenses are a characteristic of diurnal mammals and not expected in animals adapted to subterranean darkness. A similar paradox is found in the photoreceptor arrangements (see below).

3. Retina

The general morphology and layering of the retina is preserved, but the thickness of the layers varies greatly across species, indicating different processing capacities (Fig. 2).

3.1. Photoreceptors

Retinal thickness is determined to a large extent by the thickness of the outer nuclear layer (ONL), which contains the photoreceptor somata (Fig. 2A–F). Higher packing densities of photoreceptors (mostly rods) result in more tiers of somata in the ONL. The retinae of the bathyergid species have a thinner ONL than e.g. rat, indicating lower packing densities of photoreceptors (Fig. 2A–F). This is even more obvious in en-face views at the level of the photoreceptor inner segments, directly showing the photoreceptor mosaic (Fig. 2G, H). The photoreceptors of Ansell's mole-rat *Fukomys anselli* (denoted as *Cryptomys anselli* in previous papers) have substantially larger inner and outer segment diameters than those of the rat and hence a lower packing density. Photoreceptor densities amount to 100,000–150,000/mm^2 in *F. anselli* and *F. mechowii* [29]. In comparison, photoreceptor densities average 400,000/mm^2 in the laboratory hooded rat [9] and 450,000/mm^2 in the house mouse [13]. This difference is puzzling, since both subterranean and nocturnal rodents are thought to be adapted to low-light vision.

Bathyergids have rod-dominated retinae but possess significant cone populations. In three bathyergid species, we have identified the spectral cone types and analyzed their distribution [29]. In *F. anselli* nearly all cones express a short-wave-sensitive (S) opsin (commonly blue- or ultraviolet-sensitive) in their outer segments. Many of these S cones co-express small amounts of a middle-to-long-wave-sensitive (L) opsin (commonly green- or yellow-sensitive), but there are only few pure L cones expressing exclusively L opsin. The exact spectral tuning of the cone opsins is not known. Cone densities in *F. anselli* are 8000–15,000/mm^2, and similar cone densities are found in *F. mechowii* and *Heterocephalus glaber*, i.e. in these species about 10% of the photoreceptors are cones. The laboratory rat has a markedly sparser cone population (about 1% of the photoreceptors) than the above species, with a majority of L cones and a minority of S cones.

Thus, the African mole-rats appear more similar to diurnal surface-dwellers (having 8–95% cones) than to nocturnal ones (having <1–3% cones) [28]. The high cone proportions and low rod densities suggest that the photoreceptor arrangements are more adapted to higher light levels than to the lightless underground ecotope. With two spectral cone opsins, the African mole-rats have the potential for dichromatic colour vision, provided that the appropriate retinal and cortical circuits for colour processing are also preserved.