Assuming that Kellermann's analysis really turns out to tell us about Ω (and not some subtle, indirect evolutionary change in the way active galactic nuclei operate), what Ω does it measure? It does not discriminate between different sorts of mass, whether ordinary or exotic, but it does depend on the distribution of that mass in space. Objects seen through low-density regions between galaxies would suffer the converse of gravitational lensing, and objects seen through mass concentrations will be lensed and will generally appear bigger and brighter. Indeed, astronomers have worried that selection in favour of the lensed, and thus apparently brighter, objects could seriously affect, for example, counts of radio sources. Detailed estimates⁶ indicate that such effects are weak in the case of source counts; analogous sums for Kellermann's analysis will no doubt keep a student somewhere out of mischief. \Box

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VISUAL SYSTEM -

Vision in blind mole rats

Jon H. Kaas

THE term 'blindsight' was invented to acknowledge the rather paradoxical observation that humans with extensive damage to the visual cortex and no awareness of their own visual capabilities can nevertheless perform a number of visually guided tasks¹. This is a dramatic indication that the visual 'system' is not a single processing stream with a single function, such as object identification, but a combination of subsystems, each depending on light that reaches the retina as a source of information, but then using the information in different ways and depending on different brain structures. Cooper et al., in a report on page 156 of this issue² on the structural organization of the visual system in behaviourally blind mole rats, demonstrate in an equally dramatic fashion the parcelling of the visual system into subsystems with quite different functions.

For most investigators, mole rats would hardly be thought of as suitable subjects for studies of the visual system. These mole-like rodents live in underground tunnels and would seem to have little use for vision. Indeed, they are distinguished from all other rodents by the absence of an opening in the skin for the eyes and by having the smallest eyes of any mammal. Cooper et al. report that the two major central targets of the eye, the lateral geniculate nucleus and the superior colliculus, are so greatly reduced in size in the mole rat that they are almost absent. This is what we would expect from other comparative and experimental studies. In true moles, for example, the eye is reduced in size and the central targets of the eye are also reduced³. Furthermore, because the development of different levels of the visual system are linked, any reduction or loss of the eve should be followed by reductions in central visual structures. Thus, rodents with mutations that lead to the reduction or absence of eyes⁴, and rodents blinded early in development⁵, have small superior colliculi and lateral geniculate nuclei.

In experiments of considerable technical difficulty, Cooper *et al.* managed to inject tracers into the rudimentary eyes of mole rats and demonstrate that most, but not all, of the central targets of the retina are greatly reduced. In contrast to the diminished pathways to the lateral geniculate nucleus, normally used for perception and object identification, and the diminished pathways to the superior colliculus, normally used for object localization, the projections to the hypothalamus are not only preserved, but are even enhanced relative to those of other rodents.

In mammals, the retinal inputs to the suprachiasmatic nuclei of the hypothalamus provide information about day lengths and thereby regulate biological rhythms or cycles that are important in reproduction and other daily and seasonal activity patterns⁶. Apparently, the tiny eyes beneath the skin of mole rats living in dark tunnels receive enough light to provide useful information about daily changes in ambient light levels, and nearly all of their remaining visual system is relegated to processing this information. Information on light levels and durations may be critical in timing the mating season for mole rats, and in regulating patterns of feeding and thermoregulatory behaviour^{2,6}.

The selective combination of reduction with preservation or enhancement of different components of the visual system of mole rats constitutes an instructive example of mosaic evolution the concept that different components or characters of complex systems can change independently⁷. How this was achieved in mole rats is unknown, but the heterogeneous pattern of alterations argues against the common supposition that the loss of the visual system in mole rats and other animals adapted to reduced visual environments is simply a consequence of relaxed selection pressure when vision is unused. Cooper *et al.* point out that there is a metabolic cost involved in maintaining a large visual system, and this cost can be especially significant in animals with a limited food supply. Thus, mole rats adaptively reduce behaviourally irrelevant components of the visual system while maintaining and enlarging components that remain important.

Mole rats also illustrate a solution to the general problem of scaling in biological systems. One of the basic interests of the eminent comparative physiologist Knut Schmidt-Nielsen has been how animals and parts of animals are structurally modified in order to preserve function when they become larger or smaller⁸. Reducing the size of the eye in mole rats or any other vertebrate would introduce several problems related to visual acuity and perception⁹. Most obviously, a very small eye would form a very small image on the retina, and without a corresponding but impossible reduction in the sizes of the photoreceptors, image quality would greatly suffer.

Furthermore, the ganglion cells and other neurons that process information from receptors and relay it to more central brain structures cannot be appreciably reduced in size. Thus, in very small eyes, photoreceptors and retinal ganglion cells are greatly reduced in number. Object identification and localization depend on information from large numbers of different classes of receptors and ganglion cells, although the numbers and classes of receptors and ganglion cells vary with the degree of precision needed for these tasks and the extent to which colour discrimination is included¹⁰. Mole rats sidestep most of these problems of scaling down the size of the eye by abandoning functions that are most impaired by size reduction, and devoting the meagre remnant of preserved receptors and ganglion cells to light detection and possibly to sex and well-being.

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