

# Seeing and not seeing

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Recent studies revealed that although subterranean mammals inhabit a dark underground environment, they can still perceive light stimuli and use this to entrain their circadian activity rhythm. Regarding spatial orientation, olfactory and tactile cues are employed for short-distance; whereas for long-distance, subterranean mammals employ the earth's magnetic field and self-generated (vestibular and kinesthetic) cues. We suggest that seismic signals, utilized for long-distance communication, might also be used as an echolocation mechanism to determine digging depth and presence of obstacles ahead. Taken together, these mechanisms provide an equally efficient means of overall orientation and communication as those found in sighted mammals.

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### Abbreviations

SCN    suprachiasmatic nucleus  
SMs    subterranean mammals  
SO     spatial orientation

### Introduction

Eleven families of subterranean mammals (SMs) exist, belonging to three orders, concentrated mainly in Africa, Eurasia and North America [1]. Throughout evolution SMs have adapted to a dark, unventilated environment, with high carbon dioxide and low oxygen pressure [2]. Burrowing incurs high energetic costs [3] and risk of overheating [4]. Considerable convergence has occurred in SMs adaptations to digging and locomotion underground. Morphological adaptations include reduced external ears and tail, shortened limbs, degenerated eyes, long incisors (Rodentia species) or claws (Insectivora species) [1]. Physiological adaptations (blood, respiratory, and tissue myoglobin properties) have evolved to cope with the extreme hypoxic-hypercapnic atmosphere of the sealed burrows [2,5].

SMs dig complex underground tunnel systems that they rarely leave, comprising networks of shallow feeding tunnels and deeper ones connecting nest, food and sanitation chambers. Behavioral adaptations (e.g. adjusting burrow length and structure to food availability, soil moisture and body width) evolved to ensure minimal burrowing cost per energy intake [6,7,8]. Additional specialized behavioral skills have evolved to meet the challenge of survival and

reproductive success in the unique environment. Here, we briefly review the temporal and spatial orientation of SMs and the mechanisms involved in orientation, with emphasis on the blind mole rat as a representative species.

### Temporal orientation

The underground environment is characterized by predictable and stable humidity and temperature, food availability, no light or air currents, and low or absent predation. Because the light: dark cycle is the most widely used *Zeitgeber* (prompter) for circadian entrainment in most surface-dwelling organisms, the question arises whether SMs too show endogenous rhythmicity. Most SM species exhibit various degrees of structural and functional blindness, and thus might be predicted to have polyphasic activity rather than activity entrained to a specific time of day. This is indeed true for some subterranean species (*Amblysomus hottentotus* [9]; *Cryptomys hottentotus* [10]); whereas circadian activity occurs in others (*Spalax ehrenbergi* [11]; *Hetrocephalus glaber* [12]; *Georychus capensis* [13]). How do these species entrain their circadian rhythm in the constant dark environment? If light is the *Zeitgeber*, how do they receive and transmit the stimulus to the suprachiasmatic nucleus (SCN), where circadian rhythms are entrained in sighted mammals?

The blind mole rat demonstrated diurnal monophasic locomotor activity under controlled laboratory conditions [11]. Although its eyes are vestigial, its retina contains fully active photoreceptor rods that functionally resemble those in sighted animals [14]. In the laboratory, a single brief light pulse can entrain the circadian clock [15], and it is suggested that mole rats excavating soil to the surface in nature might be exposed to such pulses, which entrain their circadian clock [4]. Two projection tracing studies — using labelled monocular injection [16] and c-Fos immunohistochemistry technique [17] — revealed a neural link between the atrophied eyes and the SCN through the retino-hypothalamic tract (RHT), similar to that in sighted mammals. However, the typical mammalian connection between eyes (retina) and dorsal lateral geniculate nucleus (LGBd — part of the image processing system) existing in neonate mole rats, degenerates in adults (Figure 1) [16]. These two different developmental retinal projections explicate both the blind mole rat's sensitivity to light pulses and the absence of visual images [11]. In the *Zambian mole rat*, light stimulus induced neuronal activity in the retina, in brain regions responsible for light/dark discrimination and even in regions partly involved in image-forming, indicating the further role of light in this species [18]. Differentiation between light/dark in SMs can facilitate the organization of daily and annual cycles similar to those in surface mammals, despite the significant environmental differences.

## Individual spatial orientation

Spatial orientation (SO) is among the most fundamental cognitive processes required for survival; it is essential for finding food, locating potential mates, defending territory, escaping predators and avoiding obstacles.

SMs inhabiting complex underground tunnel systems require a highly-developed directional sense in order to avoid unnecessary costly digging. Few studies of SO have been done on SMs, due to the inherent difficulties of observation in both laboratory and the field. Of these studies, all indicate that SMs exploit highly-developed SO for homing activity [19], orientation within their tunnel systems [20], and accurate reconnection of damaged burrows with new tunnels [20–23]. Recently, in a field study we showed that blind mole rats, whose tunnels were experimentally blocked, burrowed a bypass to rejoin the disconnected section. Moreover, they were able to estimate the blocking obstacle's dimensions, type (wood, stone or open ditch) and relative position, and accordingly selected the best-fit bypass strategy to ensure minimum digging [24]. Simulating mole rat tunnel systems in the laboratory revealed their high spatial-learning ability and long-term memory retention of complex routes [25•]. Such efficient SO in SMs suggested the existence of underlying mechanisms suited to their unique sensory environment.

## Sensory perception

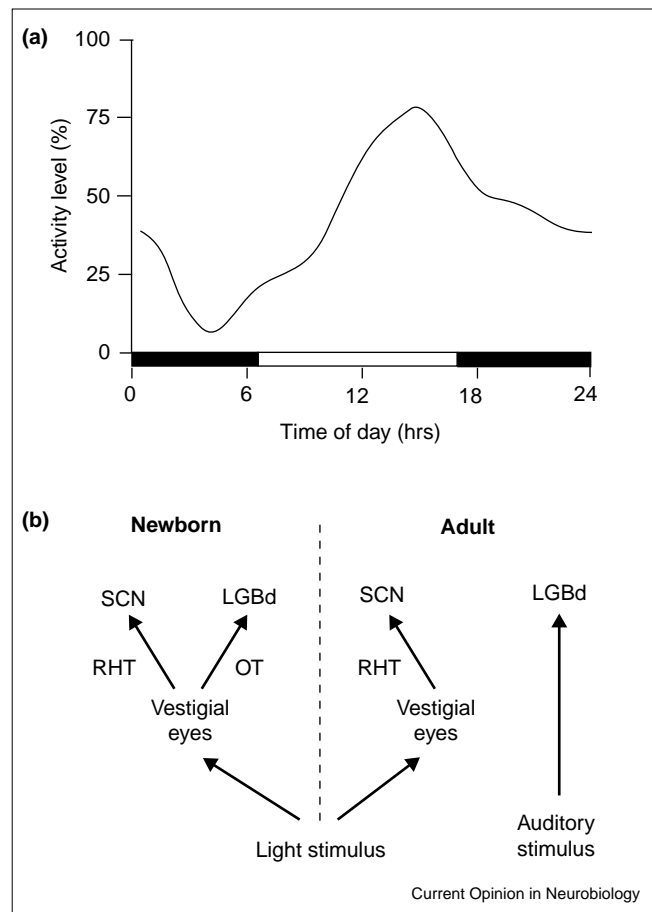
Unlike surface-dwelling mammals' access to many external cues for orientation, sensory perception in SMs is highly restricted. Vision is excluded. Olfactory cues are ineffective for long-distance navigation to a new area due to lack of airflow, but could assist short-distance food search [26]. Localization of airborne sounds is very poor or absent [27,28], with SMs hearing range limited to low frequency sounds, strongly attenuated by the soil and effective only over short distances [29].

These inherent limitations in sensory perception have forced SMs to evolve alternative compensatory mechanisms of orientation, relying on other sensory cues including the earth's magnetic field, self-generated (internal) cues, and seismic waves (Figure 2).

## Geomagnetic field

Using the earth's magnetic field for orientation has been experimentally demonstrated in the *Zambian mole rat* and blind mole rat. Following artificial shift of the geomagnetic north, animals of both species shifted location of their sleeping nest accordingly [30,31••]. The blind mole rat also used the geomagnetic field to reach a goal in a complex labyrinth [31••]. The magnetic sensory pathway in both species is light-independent [30,31••], suggesting the involvement of magnetite-based magnetoreceptors [32] rather than the photoreceptor-based mechanism suggested for amphibians and birds [33]. Recently, Nemeč *et al.* [34•] showed the superior colliculus region of the *Zambian mole rat* to contain neurons that

Figure 1



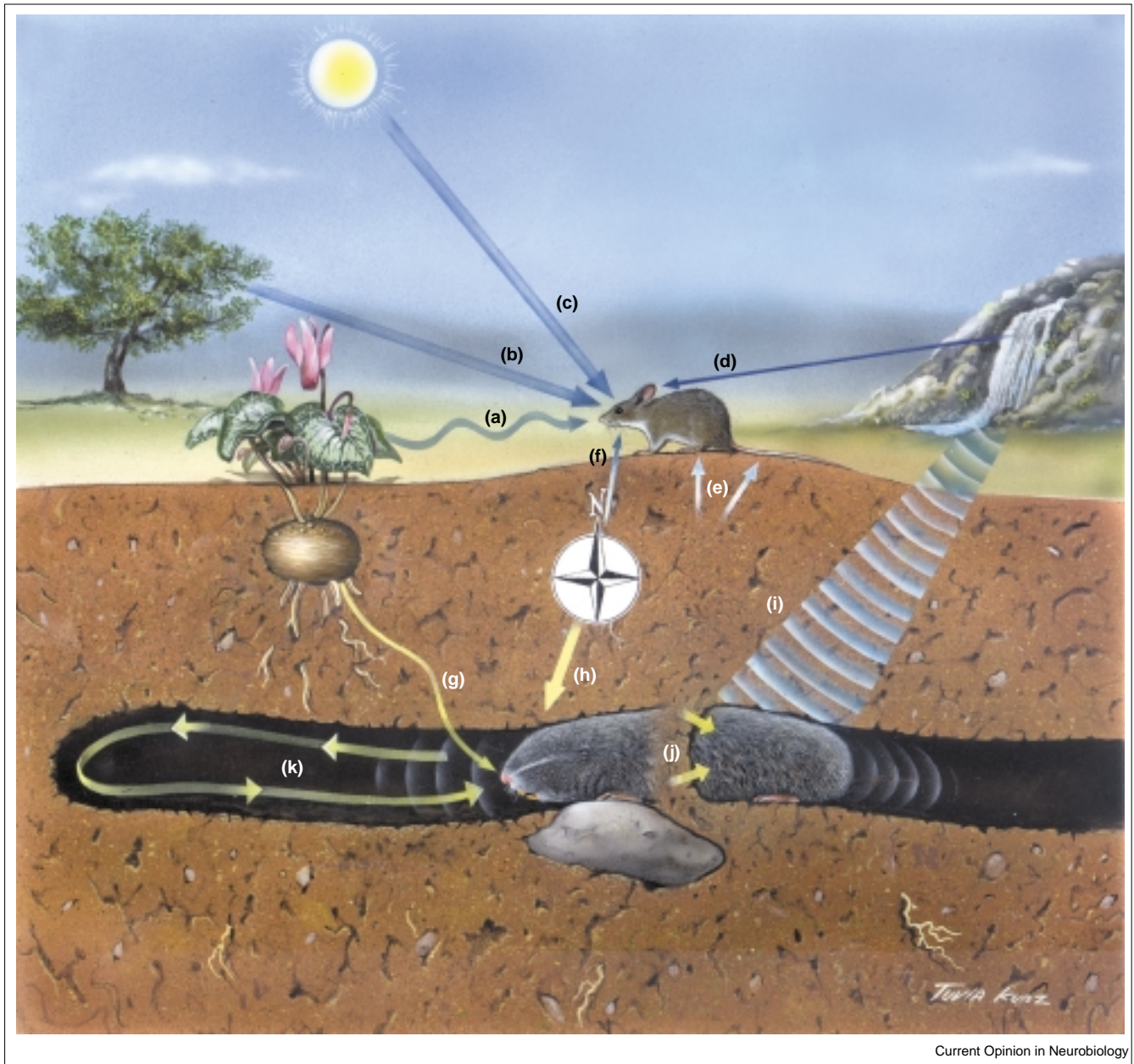
Circadian activity rhythm of the blind mole rat. (a) Diurnal monophasic locomotor activity in the blind mole rat under controlled laboratory conditions [11]. Black bars on the horizontal axis represent hours of darkness. Percentage of activity is calculated by summarizing the activity of the animals for each hour during five days of recording [4,11]. (b) A schematic diagram of the circadian (SCN, suprachiasmatic nucleus) region and part of the visual (LGBd, dorsal lateral geniculate nucleus) system in newborn and adult mole rats. In the adult mole rat, the connection between the vestigial eyes to the LGBd degenerates, and instead, this region receives auditory stimuli [16]. RHT, retinohypothalamic tract; OT, optic tract.

respond to magnetic stimuli, possibly involved in the magnetic compass orientation mechanism.

## Internal information

Another vital orientation mechanism for SMs is reliance on internal (vestibular, somatosensory and proprioceptive) information acquired from their own movement. Recently, using a multi-route maze, we showed that blind mole rats use internal cues to determine the departure-goal vector, enabling them to select the most direct routes when returning to the goal [35]. This mechanism allows SMs to select paths in their burrow system, to substitute or dig new tunnels, to detour obstacles, and to return directly to a desired tunnel section, with minimum digging. The ability to use shortcuts through self-generated cues (termed 'path integration') involves the vestibular system [36,37] and the hippocampal region [38–40].

Figure 2



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The major external sensory stimuli available for spatial orientation in surface-dwelling mammals (e.g. house mice) compared with those in subterranean mammals (e.g. blind mole rat). Line width indicates level of importance of the sensory cues for these species (thicker line = greater importance). Surface-dwelling mammals can use: (a) local olfactory cues or odor trail; (b) visual local (landmark) cues (e.g. locations of trees or objects); (c) compass (celestial) visual cues (e.g. sun or stars); (d) airborne

auditory cues (e.g. from waterfall); (e) somatosensory (tactile) cues perceived mainly from the lower part of the body (e.g. limbs, tail); and (f) natural geomagnetic field cues. Subterranean mammals can use: (g) olfactory local cues; (h) natural geomagnetic field; (i) seismic cues (e.g. from waterfall); (j) somatosensory cues perceived from almost all body parts; and (k) propelled air (when the animal is in motion) rebounding from the tunnel walls or from a blocking object, and at close distance.

In SMs, both vestibular system [41] and hippocampus [42] are better developed than in rats, further suggesting the crucial role of internal information for spatial orientation.

### Seismic signals

Use of seismic signals for directional orientation in SMs to locate prey was suggested by Mason and Narins [43\*\*] for

the Namib Desert golden mole (*Eremitalpa granti*). *Eremitalpa* orients in a non-random manner towards grassy hummocks that contain prey items (mainly termites) and generates intense seismic signals, probably from wind blowing the grass [44]. The highly enlarged auditory ossicles of *Eremitalpa* may have evolved for detection of such seismic vibrations [43\*\*, 45].

Figure 3



Use of seismic vibrations produced by head drumming for long distance intraspecific communication and possibly also for spatial orientation in the blind mole rat. In seismic communication between two mole rats (upper left section), the sender transmits the seismic message by drumming the top of its head against the tunnel roof, while the recipient receives the signals through the lower jaw, by pressing the side of its head against the tunnel wall (frontal view). The head

drumming occurs in sequences of about 4 taps/sec, whose intense energy is concentrated in low frequency sound (see lower left inset) [62]. The mole rat can also use the rebound vibrations produced by head drumming to determine location and material type of blocking obstacles (lower right section), as well as to determine its digging depth and thus maintain its tunnel parallel to the surface (upper right section).

Evidence for use of seismic cues for orientation has also been found in the blind mole rat. A preliminary field study showed that it frequently produces seismic vibrations — by striking its head against the tunnel roof — when burrowing bypass tunnels (T Kimchi, J Terkel, unpublished data). This head-drumming might be used for echolocation, in which vibrations reverberating from different types of obstacles could be perceived.

Spectral analysis revealed single seismic signals at a frequency range of 150–250 Hz and low velocity (85 m/s), to which mole rats have been shown to respond (see section on Intraspecific spatial orientation). Calculations regarding the use of such seismic waves for echolocation below ground revealed their ability to locate small, shallow

buried objects or air space with a vertical resolution of 10–30 cm (T Kimchi, M Reshef, J Terkel, unpublished data). Such a mechanism of orientation could explain the mole rat's ability to maintain its tunnel at constant depth (10–20 cm deep) parallel to the surface [4] as well as to determine the size, matter and relative location of an obstacle it must detour (Figure 3) [24].

#### Tactile cues

For short distance orientation, SMs use mainly their highly developed tactile sense. All SMs, even the naked mole rat, possess sensory vibrissal hairs connected to sensitive mechanoreceptors dispersed over different body parts [46,47], contributing to efficient orientation in their narrow burrows [48]. Indeed, in the blind mole rat it has been

shown that animals learning a maze with paths twice the width of their body diameter performed worse in the early stages than those tested in a maze allowing tight contact with the walls [49]. In a recent laboratory study, we found that, when in motion, the blind mole rats are also able to detect blocked tunnels over one metre ahead, probably by sensing the propelled air rebounding from the obstacle (T Kimchi, J Terkel, unpublished data) (Figure 2). In nature, the blind mole rats always dig their tunnels to exactly the diameter of their own body width, resulting in them obtaining maximum tactual information. It is reasonable to assume that the high level of tactual information acts in two ways: for short-distance orientation the mole rat will perform better in detecting obstacles in its tunnels by sensing the rebounding air (as noted above); whereas for long-distance orientation a narrow tunnel enables the efficient gathering and integration of self-generated position information (somatosensory and kinaesthetic) for use by the mole rat in its navigation mechanism that relies on such internal information (as noted earlier).

Several species of moles possess a snout with unique pressure-sensitive structures (Eimer's organs); snout-surface contact provides the animal with information on its surroundings [47,50]. The star-nosed mole (*Condylura cristata*) possesses a highly specialized nasal tactile structure, comprising 22 fleshy flexible appendages distributed around the nostrils, covered with tens of thousands of Eimer's organs [51]. This unique nose, actively used to explore the environment, continually makes contact with objects of interest, mainly to detect prey (earthworms) [51]. Catania and Kass [52] traced this nasal architecture's representation as star-like rays in the somatosensory cortex, indicating its primary importance for sensation. In the Eastern mole, organization of the somatosensory cortex represents the vibrissae, rhinarium and the forelimb [53\*]. The blind mole rat too reveals a highly-developed somatosensory cortex, extending into the occipital cortex, which serves vision in sighted mammals [54,55].

### Intraspecific spatial orientation

Most SMs are solitary and territorial. Established territories remain largely fixed for life, rarely overlapping [56,57], and defended against intruding neighbours. Solitary SMs are sensitive to the presence of neighbours, and vacated territories (through death or emigration of the resident individual) are immediately occupied by a new individual, leaving no vacuum [57–59]. Most SMs are aggressive and, out of the reproductive season, avoid potentially fatal encounters. A radio-telemetric study of mole rats revealed that an individual approaching another's territory too closely will reverse its direction [59]. Temporal avoidance (two individuals using the same tunnel part at different times) is described in moles [60]. However, for successful reproduction, locating and reaching distant potential mates is essential. All SMs thus require a means of long-distance communication.

Seismic vibrations, unlike airborne sounds, efficiently travel long distances in the underground niche. Many SMs

are shown to be sensitive to seismic waves; some have been observed producing such vibrations [61\*]. Two solitary and highly aggressive SMs, the Cape mole rat and the blind mole rat, evolved seismic signalling for long-distance intraspecific communication [62,63]. This enables avoidance of unwanted encounters, and facilitates reproductive encounters.

The two species produce their seismic signals differently. While the Cape mole rat produces the signals by drumming its hind legs on the burrow floor, the blind mole rat produces them by rapidly striking the flattened anterodorsal surface of its head against the tunnel roof [62,64]. The head drumming of the blind mole rat produces low frequency vibrations (150–250 Hz) [62], compatible with both the animal's hearing capacity [27] and optimal subterranean transmission properties, based on geophysical measurements [65]. The recipient mole rat receives the signals by pressing its lower jaw against the tunnel wall; the vibrations are transmitted via the jaw articulation to the auditory ossicles (Figure 3) [66]. An electrophysiological study revealed high intensity responses in the auditory brain stem to such vibrations when the animal's lower jaw was pressed firmly against the tunnel wall, suggesting that these signals are conducted by bone and mainly processed in the auditory system [67]. An alternative suggestion is that these vibrations are transmitted through the body's mechanoreceptors and processed in the somatosensory system [68]. Digging vibrations too may be detected by neighbours and serve as territorial advertisement to other subterranean species [63].

### Conclusions and future prospects

Efficient organization in time and space is crucial for successful survival in the animal kingdom. The stable biotic and abiotic conditions, total darkness and restricted external cues of the underground environment raise intriguing questions regarding SMs temporal organization, SO and communication.

Most SMs demonstrate efficient temporal organization and possess clear circadian activity. All are spatially well organized, and possess well-developed SO and communication means, enabling constant awareness of their own and their neighbours' positions in the complex tunnels.

Over millions of years of selective adaptation to underground life, SMs evolved convergent specialized behaviors, sensors and neural systems to facilitate the necessary skills for efficient survival and reproduction — as successfully as sighted, surface-dwelling mammals. Despite the objective difficulties in studying SMs, our understanding of their behavior has advanced considerably in recent years. Questions remaining open include, for example, what and where are the magnetoreceptors; and what region in the brain is responsible for magnetic signal processing? Anatomical and neurophysiological studies in rainbow trout, which identified magnetite crystals as possible

magnetoreceptors and a neural path response to magnetic fields [69,70<sup>\*</sup>], might also be pertinent to SMs. Still ahead lies investigation of the blind mole rat's (and possibly other SMs sensitive to seismic waves) use of seismic signals for echolocation to detect and avoid obstacles, and perhaps also to determine burrowing depth. Experimental manipulation techniques, altering the characteristics of seismic feedback from the surroundings and observing the subsequent orientation in space, offer just one of the promising approaches to determining whether such signals indeed constitute part of a unique mechanism of orientation in SMs. These, and other questions, pose fascinating areas of research for the future.

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