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Sensory systems underlying sociality in the naked mole-rat

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Social interactions rely on the integration of information across multiple sensory modalities. In many species, individuals recognize conspecifics through combinations of auditory, olfactory, tactile, and visual cues, reflecting the capacity of neural systems to integrate diverse streams of sensory input. The naked mole-rat (*Heterocephalus glaber*) provides a powerful model system for understanding how social living shapes the evolution of such communication systems, particularly under conditions where visual information is largely absent. Naked mole-rats represent a rare example of mammalian eusociality, living in large multigenerational colonies organized around a strict reproductive hierarchy and cooperative care of offspring [1]. Here, we review evidence that naked mole-rats integrate multiple sensory modalities, focusing on audition, olfaction, and somatosensation to encode social identity.

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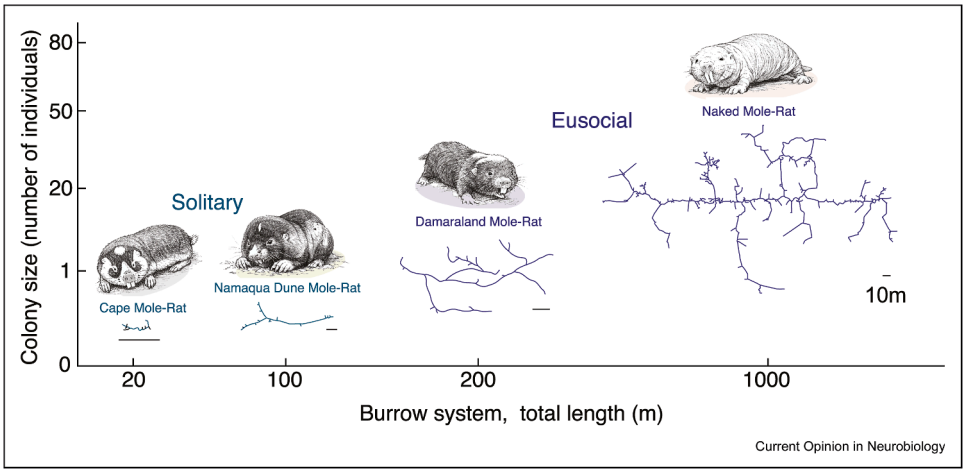
Introduction

One of the defining features of naked mole-rat colonies is their highly cooperative and hierarchical social structure. Naked mole-rats inhabit the semi-arid regions of Eastern Africa [2], where they live underground in extensive burrow systems that can exceed 3 km in length [3]. Life underground, combined with the challenges of an arid environment has imposed strong selective pressures shaping their behavioral and physiological adaptations [4–7]. These environmental constraints have important consequences for how sensory information is acquired and used during social interactions. At the same time, the large size (up to 295 members [3]) and dynamic composition of colonies, with new individuals continually added across generations, place substantial demands on mechanisms for social recognition and communication.

Naked mole-rats are considered to be the clearest example of a eusocial mammal [1,8,9]. Like the eusocial insects (i.e., bees and ants) [1,10] within each colony reproduction is usually restricted to a single breeding female (the queen), while individuals undergoing profound reproductive suppression share cooperative tasks, including colony defense, care of pups, and foraging [1]. The naked mole-rat is just one species belonging to the diverse African mole-rat family (Bathyergidae), yet interestingly current evidence suggests that they construct particularly extensive and complex subterranean tunnel networks in terms of both length and complexity compared to other species in the family (Figure 1) [3,11–13].

Naked mole-rats engage in numerous highly cooperative behaviors that require coordination and communication among colony members. One striking example is their foraging strategy. Naked mole-rats feed primarily on underground tubers that they encounter in the course of digging tunnels. Rather than consuming these resources immediately, they often harvest only part of the tuber, transporting it back to the colony and leaving the remainder intact. Remarkably, colonies have been

Figure 1



Comparative analysis of burrow architectures in four mole-rat species. Reconstructed burrow systems of four species for size comparison. The *Naked mole-rat* (*Heterocephalus glaber*) displays the most extensive and complex networks (reconstructed from Ref. [3]) when compared with other studied species in the African mole-rat family. The *Damaraland mole-rat* (*Fukomys damarensis*) (from Ref. [11]) constructs moderately complex systems, whereas the *Namaqua dune mole rat (Bathyergus janetta*) (from Ref. [12]) and *Cape mole-rat* (*Georychus capensis*) build much simpler and shorter tunnels (from Ref. [13]). Scale bar, 10 m.

observed to then return to partially consumed tubers once they have regrown [3], thus in effect sustainably managing their food resources. Such incredibly complex behaviors occur in complex three-dimensional environments in complete darkness and require coordinated navigation, collective exploitation of food resources (e.g., determination of who harvests, when, and how much is harvested), and distribution of food within the colony.

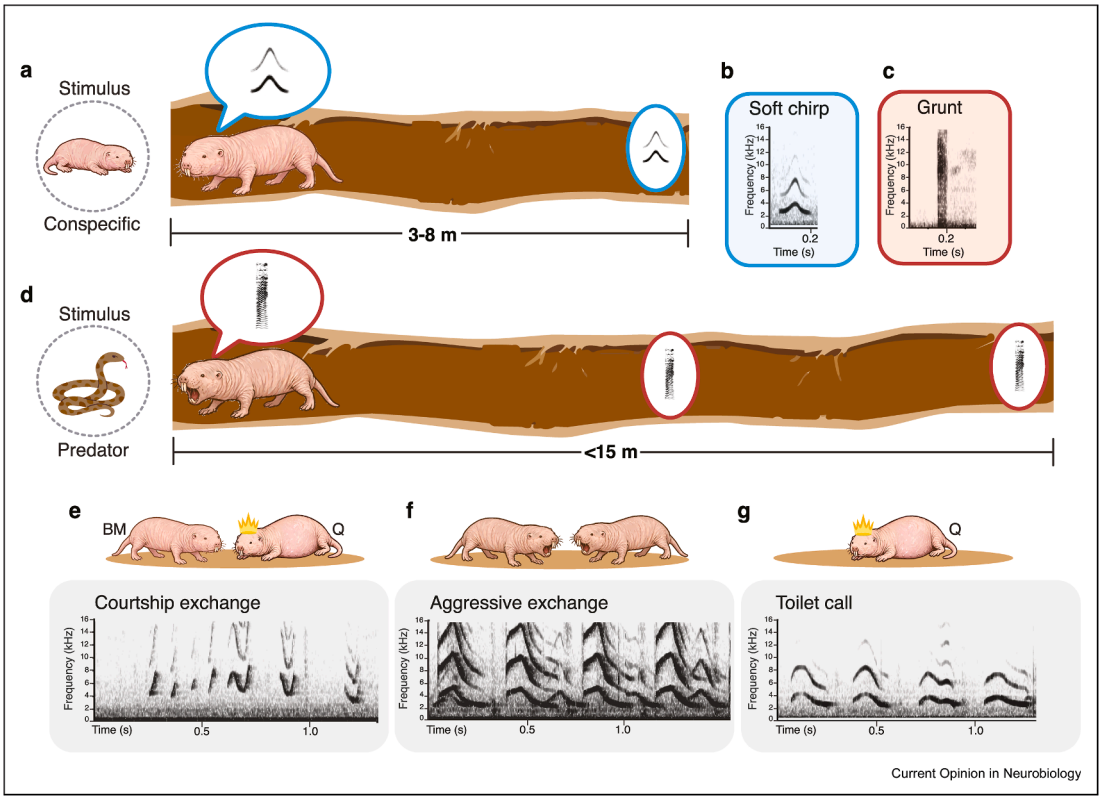
Within the burrow system, sensory information may be acquired and processed via multiple mechanisms. For example, an individual moving through a tunnel may initially detect and approach a conspecific using acoustic cues and subsequently confirm its identity through olfactory signals or direct tactile contact (e.g., snout-to-snout interactions [14]). In contrast, during direct encounters in confined tunnel spaces (e.g., climb-over events [14,15]) individuals may simultaneously engage multiple sensory modalities, touching, smelling, and listening to vocalizations or sounds produced by movement, requiring parallel processing of social information. Persistent olfactory cues may further provide stable identity signals influencing social interactions over extended timescales [16,17]. Naked mole-rats exhibit highly reduced visual systems [18] and thus must rely predominantly on other sensory systems, such as hearing, touch, and smell to achieve effective social communication and perform cooperative tasks [19,20]. Integration of multiple sensory cues likely serves to enhance the robustness of social communication by reducing recognition errors, as individuals can verify identity through independent modalities. Here, we highlight recent work demonstrating how distinct sensory modalities, auditory, olfactory, and somatosensory, are integrated to encode and transmit social information in naked mole-rats.

Acoustic communication

More than 70 years ago, early field and laboratory studies reported descriptions of naked mole-rats vocalizing in multiple behavioral contexts [21–23]. In 1991, Pepper et al. pioneered the first systematic investigation of naked mole-rat vocal behavior, identifying 17 distinct call types [15]. Work from our group expanded this repertoire to identify at least 25 distinct vocalizations [20]. Not only do naked mole-rats exhibit a large vocal repertoire, but their calls map to specific social contexts and behaviors, showing vocal specialization across colony subgroups (Figure 2) [15]. For example, certain calls are restricted to juveniles, while others are used primarily by breeding individuals (e.g., the queen), such as the toilet call (Figure 2e–g) [15,20].

Among the 25 currently identified vocalization types, the soft chirp occurs most frequently (Figure 2a,b) [15]. It is typically produced during close physical contact between colony members and is often described as a greeting or contact call. Temporal analyses show that soft chirps can be produced in antiphonal sequences, suggesting a coordinated call-and-response structure similar to contact calls observed in other social mammals and birds [24–26].

Figure 2



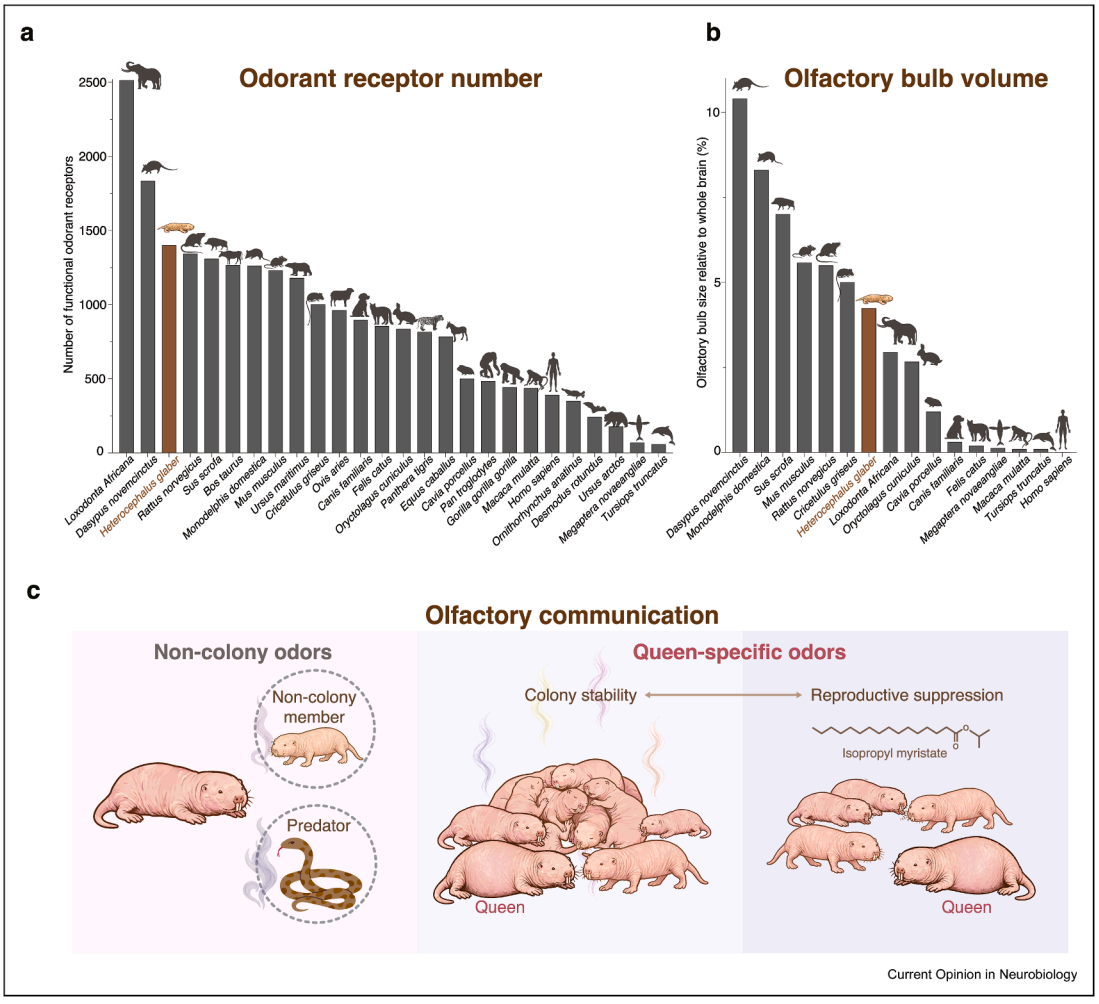
Naked mole-rats use vocalizations during multiple behavioral contexts. (a) In response to conspecifics, naked mole-rats produce soft chirp vocalizations which are estimated to propagate between 3 and 8 m through tunnel systems (as described in Ref. [30]). (**b**) Example of a soft chirp vocalization (modified with permission from Ref. [20]). (**c**) Example of a grunt vocalization. (**d**) Grunts are used as alarm calls in response to predators and other colony disturbances (described in Ref. [41]) and are estimated to propagate up to 15 m in tunnel systems (as described in Ref. [30]). (**e**–**g**) Naked mole-rats use vocalizations in courtship exchanges (**e**), aggressive exchanges (**f**) and selectively by specific individuals (e.g., the breeder-specific use of the toilet call) (**g**). Toilet call in (**g**) reproduced with permission from Ref. [20]. Q denotes queen and BM denotes breeding male.

More recent work from our group demonstrated that acoustic features of the soft chirp display colony-specific vocal dialects that can encode both colony membership and individual identity [27]. Audio playback experiments further confirmed that animals preferentially respond to calls with their own colony dialect. Cross-fostering experiments revealed that pups raised in foreign colonies can adopt the vocal dialect of their foster colony, demonstrating social learning and the cultural transmission of these vocal signatures. Interestingly, the queen plays a stabilizing role in this system: when a queen is removed from the colony, the cohesiveness of the colony dialect decreases until it re-emerges with a new queen [27]. These findings indicate that naked mole-rat vocal dialects function as a socially maintained group identity signal, linking acoustic communication to the maintenance of the naked mole-rat's complex social organization.

The acoustic properties of naked mole-rat vocalizations are strongly shaped by the subterranean environment. Mole-rat burrows function as acoustic waveguides with enhanced propagation of low-frequency sounds [28]. Although no measurements to date exist from wild naked mole-rat colonies, studies in burrows of similarly sized African mole-rats show that lower frequencies especially between ~200 and 800 Hz, propagate particularly well underground [29]. Consistent with these limitations, naked mole-rat vocalizations are predominantly low-frequency signals, with soft chirps reported in the frequency range of 2.5–6.1 kHz [20,26,27,30]. Experimental sound propagation studies show that soft chirps are estimated to travel approximately 3–8 m through tunnel-like structures in the lab whereas broadband frequency alarm calls (so called grunts) are estimated to propagate even further up to 15 m (Figure 2c,d) [30].

Receiver physiology also reflects the same environmental pressures, and the hearing range of naked mole-rats is similarly influenced by the underground environment. Behavioral audiograms as well as auditory

Figure 3



Olfactory capacity and function in naked mole-rats. (**a**) Number of functional odorant receptor genes across mammalian species. The naked mole-rat (highlighted in brown) possesses a relatively large repertoire compared to many mammals (adapted with permission from Ref. [19]). (**b**) Olfactory bulb volume as a percentage of total brain size across mammals. The naked mole-rat (highlighted in brown) shows a comparatively enlarged olfactory bulb (adapted from Refs. [35,69–79]). (**c**) Olfactory cues mediate several key aspects of social organization in naked mole-rat colonies. Left: Non-colony-specific odors can be used to distinguish nestmates from unfamiliar conspecifics and generate defensive responses toward predators (described in Refs. [37,40,41]). Right: Queen-derived odors contribute to social cohesion within the colony. A queen-associated chemical signal, isopropyl myristate, contributes to reproductive suppression by inhibiting reproductive activation in subordinate individuals (as described in Ref. [45]).

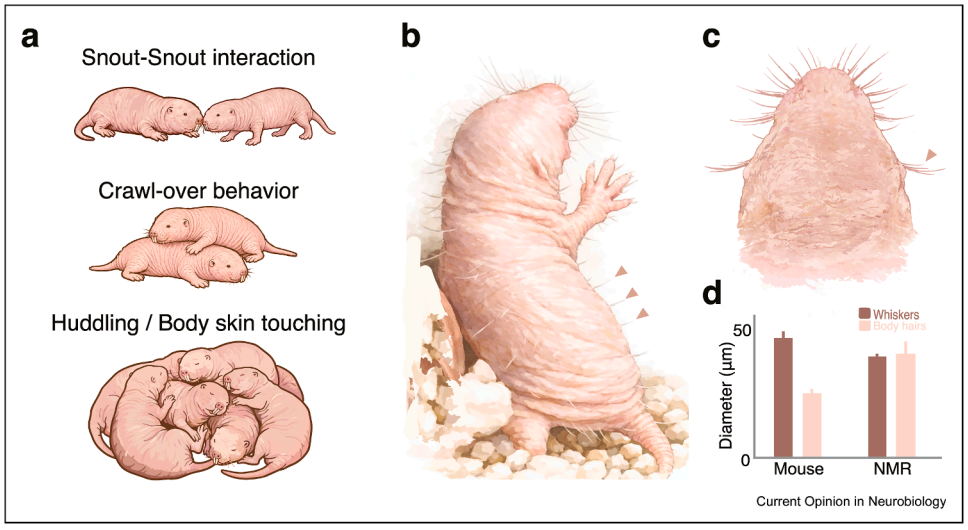
brainstem response (ABR) measurements reveal that naked mole-rats hear frequency signals spanning roughly 65 Hz to ∼12.8 kHz, with overall poor sound-localization abilities [28,30]. This is consistent with the constraints of the underground environment, where sound localization is bi-directional within the tunnel systems and low-frequency sounds propagate most effectively. At the anatomical level, comparative studies show modifications of the cochlea and hair-bundle structures that reduce cochlear amplification [31,32], suggesting that these changes in hearing sensitivity represent an adaptation to subterranean life rather than being a degenerative trait.

While vocalizations allow colony members to communicate across several meters of tunnel, many social interactions occur at closer range, where animals can directly contact and smell one another. Despite its long range of transmission (up to 8 m) [30], the soft chirp is frequently observed when individuals are in physical contact and climbing over one another [14,15,30]. In this context, olfactory and tactile cues likely complement acoustic signals for social identification.

Olfactory communication

Rodents, like many mammals, rely on both the main and accessory olfactory systems, including the main olfactory

Figure 4



The tactile hair system and touch-based behaviors in naked mole-rats. (**a**) Examples of common touch-based social behaviors in naked mole-rats, including snout-to-snout interactions, crawl-over dominance behavior, and huddling/body contact within the colony. (**b**) Distribution of tactile body hairs in the naked mole-rat. Body hairs are arranged in a stereotyped pattern along the trunk, and their positions are highly conserved across individuals (modified with permission from Ref. [56]). (**c**) Close-up view of the head showing specialized facial hairs. In addition to mystacial whiskers, naked mole-rats possess specialized tactile hairs near the ears (border hairs) and under the chin (not shown in this illustration). (**d**) Comparison of hair shaft diameter between mice and naked mole-rats (modified with permission from Ref. [56]).

epithelium and the vomeronasal organ, for mediating social communication [33,34]. Naked mole-rats exhibit a well-developed olfactory system compared to many other mammals (Figure 3a,b), with approximately 1400 functional odorant receptor genes and an olfactory bulb comprising ∼4.5% of total brain volume [19,35]. Interestingly, naked mole-rats have been reported to possess a relatively small vomeronasal organ [36], yet its functional significance remains poorly understood.

Olfactory signals have been shown to contribute to social organization in naked mole-rat colonies by influencing task allocation and division of labor, for example, through queen-associated odors that modulate worker behavior [37]. These signals are distributed via behaviors such as sniffing, anogenital nuzzling, urination, and scent marking [38,39]. Beyond social functions, olfaction is also critical for environmental assessment, including food localization and evaluation, predator detection (e.g., snakes), and monitoring disturbances [40,41] (Figure 3c).

A key implication of these olfactory functions is the ability to mediate conspecific discrimination, colony odor preference, and possibly even individual recognition [42–44] (Figure 3c). In recent work from our group, we ablated the olfactory epithelium using methimazole, a well-established method to eliminate olfactory receptor neurons [46]. In naked mole-rats, this treatment caused near-complete loss of olfactory sensory neurons, abolished attraction to food odors, and markedly reduced the initiation of aggression between high-ranking individuals from different colonies. Importantly, treated animals could still respond defensively when challenged, indicating that olfaction is required for detecting and evaluating social cues but not for executing aggression itself [45]. Together, these results provide direct causal evidence that key social behaviors depend on intact olfactory input.

Additionally, we measured volatile compounds that were collected from individuals across multiple colonies using polydimethylsiloxane-based sampling and thermal desorption gas chromatography–mass spectrometry (TD–GC–MS), a method widely used to capture complex odor blends [47]. While hundreds of compounds were detected, multivariate analyses showed that odor profiles clustered by colony, indicating distinct and stable chemical signatures rather than a uniform species-wide scent. This colony-specific variation may contribute to colony recognition, which in turn could modulate aggression toward outsiders and support social cohesion within the colony. The lack of strong sex differences among nonbreeders suggests these profiles may encode colony identity rather than individual traits.

Furthermore, our chemical profiling across hundreds of individuals identified isopropyl myristate (IPM) as a queen-enriched compound that was nearly absent in non-breeders. Its levels peak during ovulation and are

enriched in vaginal and anal secretions. Notably, it was not detected in urine, which may explain why earlier studies failed to identify a urinary primer pheromone in naked mole-rats [48]. As a long-chain, low-volatility ester (MW ≈ 270 g/mol) IPM is well suited as a persistent signal in subterranean environments, with behavioral assays showing detectability at distances of up to 148 cm. Whole-brain analyses further revealed activation of olfactory and limbic circuits following IPM exposure, linking detection to neural processing [45].

Remarkably, IPM can modulate reproductive physiology: chronic exposure elevates prolactin and suppresses progesterone in non-breeding females preventing ovarian activation [45]. This mirrors hyperprolactinemia-induced infertility via inhibition of GnRH release [49], suggesting co-option of a conserved endocrine pathway [50,51]. Moreover, high-ranking individuals showed marked avoidance of isopropyl myristate, aligning with recent evidence that reproductive activation varies across subordinates, with only those already physiologically prepared successfully reproducing [52]. Additionally, IPM suppresses aggression and can block queen succession for extended periods (up to 12 weeks) [45] (Figure 3c). Thus, olfaction in naked mole-rats not only contributes to social recognition but also to direct endocrine regulation, linking sensory input to colony-wide control of fertility.

While these chemical signals can provide persistent information about colony membership and reproductive hierarchy, naked mole-rats also rely on physical contact in addition to acoustic and olfactory communication during daily interactions. In their confined tunnel environment, frequent close encounters allow tactile cues to rapidly confirm identity and support cooperative behaviors.

Tactile communication

Social touch is widespread across the animal kingdom [53]. In humans, it includes behaviors such as handshakes and hugs, whereas rodents display tactile interactions such as body sniffing and allogrooming. Experimental studies in mice have shown that tactile deprivation leads to pronounced impairments in social behaviors [54]. In addition to direct tactile interactions, subterranean rodents can detect substrate-borne vibrations that propagate through tunnel systems [32]. In some subterranean species, rhythmic head-drumming generated seismic signals that may be used for long-distance communication, contributing to territorial spacing, alarm signaling, and possibly courtship [55]. Naked mole-rats in particular possess an unusual tactile system that is markedly different from other rodents.

Naked mole-rats frequently engage in behaviors such as body rubbing, huddling, and head-to-head contact (Figure 4a). Within colonies, naked mole-rats perform frequent snout−to-snout contacts, occurring at roughly twice the frequency observed in mice. Through such contacts, individuals were shown to rapidly identify conspecifics, whereas removal of these facial hairs significantly delayed social recognition [14].

In addition to the specialized whisker pad that is also present in mice, naked mole-rats exhibit numerous other specialized hair groups, for example, beneath the chin and behind the ear (Figure 4b,c). Their snout vibrissae show a unique spatial organization, located more anteriorly and centrally on the snout compared to mouse mystacial whiskers. On the body, naked mole-rats possess a stereotypical grid-like pattern of approximately 80 long body hairs (about 40 per side) arranged in stereotypical rows [56]. Compared to typical mouse guard hairs, naked mole-rat body hairs are thicker in diameter and structurally resemble vibrissae (Figure 4d), containing a denser sensory innervation than typical pelage hairs of rodents [57,58]. Together, these hairs form an array that covers the entire head and body. Initial work from our group showed that mechanoreceptors that innervate naked mole-rat body hairs have two unique properties not found in mouse mechanoreceptors. First, sensory neurons innervating these hairs have a remarkably highly tuned direction sensitivity. Mechanoreceptors are only activated when the hair is moved in a restricted direction [58]. Ongoing work in the lab is aimed at defining the angular sensitivity of these receptors [59]. The second unique feature of naked mole-rat body mechanoreceptors is that they fire continuously to a constant static displacement of the hair [58,59]. Both these features are interesting, as constant bending of the hair produced by locomotion of the animal along a narrow tunnel could give a directionally tuned neural signal containing information about distance traveled as well as direction. The unique physiology of body hair mechanoreceptors has so far only been studied superficially, and it is not yet clear how the central connectivity of these specialized mechanoreceptors is organized.

Consistent with the unique nature of peripheral mechanoreceptors, it has already been described that the cortical representation of somatosensation appears to be larger in the neocortex of naked mole-rats, compared with mice [60,61]. Conversely, the visual cortex is substantially smaller in the naked mole-rat compared with mice [61]. Areas in the brainstem and cerebellum responsible for processing somatosensation are similarly expanded [62−64], while brain regions that normally process visual inputs, like the superior colliculus, have been shown to process tactile information in naked mole-rats [65], suggesting that the unique sensory hairs of the naked mole-rat may provide information about position in space as a replacement for vision. Consistent with this idea, we found that naked mole-

rats can be trained to execute a navigation task but lose this ability after body hairs are trimmed (Luo and Lewin, unpublished data). We propose that somatosensory systems in the naked mole-rat may support navigation in the subterranean environment, enabling detection of nearby obstacles, and may also facilitate tactile-based social interactions [14].

Discussion

Cooperative living is relatively rare within the animal kingdom and there are few examples of laboratory-based animal models for social living [66]. Understanding how behaviors are socially regulated and transmitted within naked mole-rat colonies may offer valuable insights into the mechanisms linking eusociality, cooperative living and the neural encoding of social identity in mammals. The naked mole-rat has been viewed as almost unique in the animal kingdom and its social organization has long been thought to be driven by adaptation to a challenging, resource limited environmental niche [7]. Recent work sampling mole-rat tissues collected from a wide range of field sites across East Africa has now identified three deeply divergent lineages with the *Heterocephalus* genus, including one new species, not yet studied in any laboratory environment [67]. Interestingly, this species now designated *H. phillipsi* appears to inhabit even harsher environments than naked mole-rats originally collected in northern Kenya by Jarvis et al. [9,67]. Genomic analyses indicate that *H. phillipsi* diverged from the *H. glaber* around 4 million years ago. It will be interesting to see which physiological features, especially those associated with sociality, have undergone selection in this newly identified species.

Yet ongoing laboratory work in naked mole-rats (*H. glaber)* has allowed for new insights into the importance of hearing, smell, and touch in guiding social interactions. Much like humans can recognize loved ones by touch, smell, sound of voice, or sight, naked mole-rats too are capable of encoding identity across multiple sensory streams (auditory, olfactory, and tactile). Recent work reviewed here shows that all three of these systems contribute to social identity signaling in naked mole-rats. However, it is a significantly larger challenge to evaluate the unique features of the central processing of these three sensory streams. It is, however, increasingly feasible to apply the tools of modern neuroscience to address circuit mechanisms [68]. Large-scale single-neuron calcium imaging, silicon probe recordings (e.g., Neuropixels) and non-invasive brain imaging like functional ultrasound imaging are all methods being applied to understand how the naked mole-rat brain is wired. Future work will also be needed to understand how these three sensory modalities integrate in the brain to drive social decision-making.

Declaration of competing interests

The authors declare no conflicts of interest.

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Data availability

No data was used for the research described in the article.

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* of special interest
** of outstanding interest

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