Efficient underground navigators: The Ansell's mole-rats from Zambia (Fukomys anselli) (photo by S. Malewski)

Navigation Underground

Dr Pascal Malkemper, currently a Postdoc in the Keays Lab at the IMP in Vienna, takes us on a subterrestrial journey.

Imagine you're on your way to work. As usual you pick up a chai latte at your local Starbucks and board the underground at Putney Bridge. You shuffle onto the train before it lurches forward, crowded with passengers. All of a sudden, there is a power cut – no power and no lights – only pitch-black darkness. Without a map, compass or even a torch would you be able to walk the rest of your way through the maze of tunnels to King's Cross station? Probably not. Navigation through this labyrinth without Ariadne's thread would be an impossibility for most, but for some mammals, it is an everyday reality.

Navigation in total darkness

More than 300 mammalian species are adapted to life underground. Strictly subterranean species rarely, if ever, surface but spend their whole life in the dark: they sleep, forage, reproduce and die underground. While the subterranean habitat provides considerable benefits, such as climatic stability and safety from predators, it presents specific challenges when it comes to navigation. It is highly monotonous and lacks many cues used by above ground navigators. The total darkness and the restricted movement of air severely limit the use of visual landmarks, auditory and olfactory cues.

Underground navigation has been particularly well studied in two groups of strictly subterranean mammals: African mole-rats *(family Bathyergidae)* and blind mole rats *(family Spalacidae)*. Although they are not closely related they share many fascinating sensory adaptations and navigation skills related to their underground habitat. While mole-rats do not migrate, they do need to orient within three-dimensional tunnel systems that are dynamically changing and often extend over several kilometres. The branching of mole-rat burrows is even more complicated than the star-shaped pattern common to city subways (Figure 1). Efficient navigation within the maze of tunnels between foraging grounds, food storage chambers, latrine chambers and nest chambers is important for everyday survival. Moreover, digging is costly. To avoid lengthy detours, the animals need to be able to dig tunnels straight and systematically into new terrain when searching for fresh food patches or linking neighbouring tunnels.

How do mole-rats accomplish such demanding navigational tasks? For most animal navigators, including humans, visual input is crucial. Beacons and landmarks, the sun and other celestial bodies are important orientation cues. Although all mole-rats, including the blind mole rats, have eyes, they are rudimentary, only discriminating between light and dark. If challenged by your local optometrist they would not be able to see the big letters at the top of the chart, because they would not be able to make out the chart to begin with. So, when it comes to navigation, mole-rats are essentially blind.

Deprived of vision, many animals navigate with a mechanism called path integration or dead reckoning. They continuously add the vector direction and length of the outward movement so that they can calculate the homeward-vector at every point of their journey. The calculation relies on efferent motor copies and feedback from proprioceptors (which are sensory receptors that receive stimuli from within the body) and the vestibular system (which is a sensory system that is essential to balance and equilibrium). While these systems are good, they are not perfect and cumulate small errors at every step of the calculation. Evidently, with longer distances, more errors accumulate. The resulting angular drift is why humans are unable to keep a straight course in a featureless environment and walk in circles. Animals must repeatedly reset the path integrator using stable external references to correct the errors if they wish to perform accurate integration over a longer distance. By taking snapshots, so-called 'fixes' of the visual surroundings, rats and mice reset their path integrator when exploring unfamiliar terrain. Living in total darkness, what could mole-rats use as a stable reference?

The Earth's magnetic field – a reliable reference underground

More than 30 years ago, Hynek Burda, back then a postdoc at Frankfurt University who had just established the first African mole-rat colony in Germany, was puzzled by the very same question. "It was fascinating how these animals could dig perfectly straight tunnels over long distances", Burda recollects, "I couldn't help but think that these animals must possess an inbuilt compass." To test his bold idea, he convinced Roswitha and Wolfgang Wiltschko, Frankfurt zoologists famous for discovering the magnetic compass of migratory birds, to help him perform the critical experiments. "We wanted to use an assay as simple and controlled as possible", Burda remembers. Having noticed a peculiar preference of the mole-rats to run in clockwise circles in their home cages, the scientists decided to test the mole-rats in a featureless circular arena to find out whether this directionality is related to the magnetic field. The mole-rats, however, had other plans. Confronted with the experimental setup they behaved completely differently than back in their cages. Instead of running in circles, the animals began to collect paper strips from the embedding and piled them up to what appeared to be a nest. "When I realised this, I started recording the nest positions and – Ta-Da! – they were clustered in the southeast", says Burda, "The mole-rats had come up with an assay - now we had to perform the crucial test by changing the magnetic field." Using a pair of Helmholtz-coils from the Wiltschko lab, Burda rotated magnetic North in the arena by 120 degrees counterclockwise. Astonishingly, the animals followed and built their nests in the artificial southeast. "While we still have no explanation for the nest direction preference, we had discovered an elegant and robust way to demonstrate magnetoreception in a mammal", Burda resumes. Indeed, the nest building assay became the most widely used test for a magnetic sense in rodents.

A clear view on the mole-rat magnetic sense

Perhaps it is not a big surprise that mole-rats have a magnetic compass. The Earth's magnetic field is omnipresent and a stable reference used by many migratory animals. Burda's initial discovery inspired experiments which revealed that mole-rats indeed use their magnetic sense for navigation. But many open questions remain. While the magnetic sense

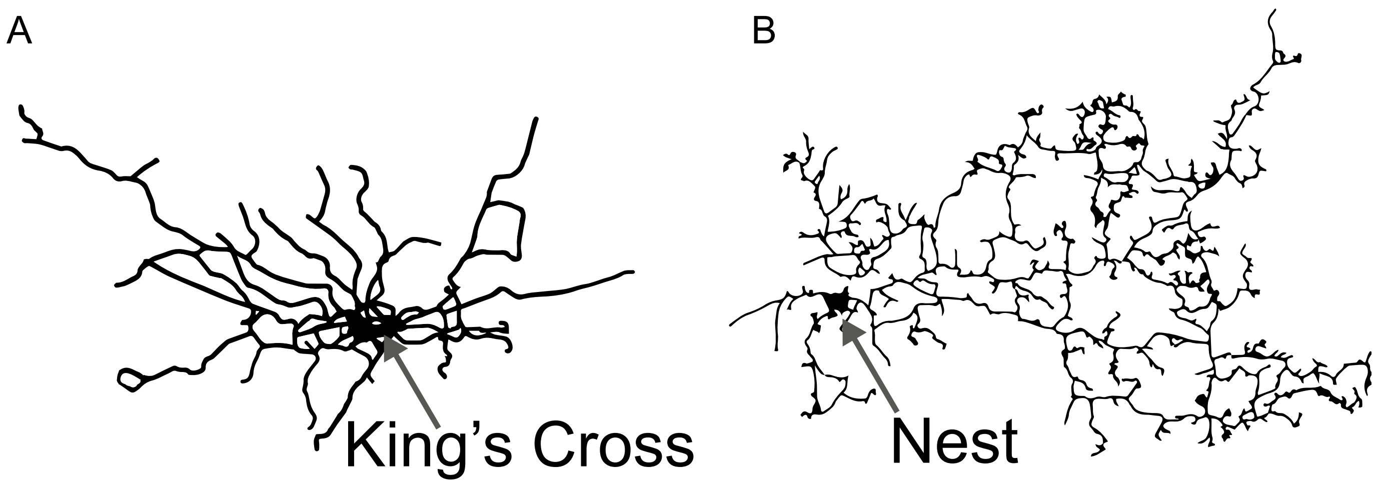
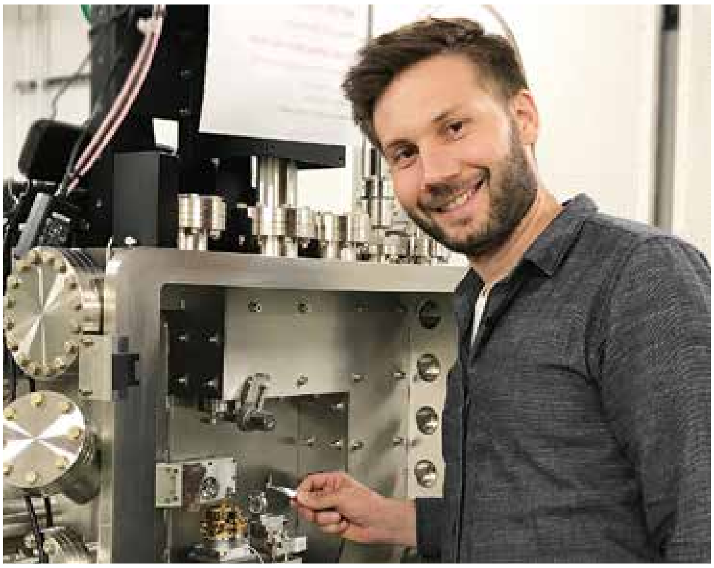


Figure 1: Complex underground tunnel systems. Geographic maps of (A) London Underground and (B) a mole-rat burrow.

of mole-rats is behaviourally well characterised, we know next to nothing about the neurological correlates. Which brain areas process magnetic cues? Where are the mole-rat magnetoreceptors? And how do they work? These are the questions I am interested in. Several lines of evidence suggest that mole-rats possess a subpopulation of cells with tiny compass needles. Finding such nanometre-sized magnetite crystals in an animal the size of a hamster is harder than finding a needle in a haystack. Hence, animal cells with magnets still await their discovery. My work focusses on a new approach to streamline the search.

I am convinced that a deeper understanding of the mole-rat brain will expedite the search for the primary receptor cells. Several regions of the mole-rat brain have been shown to fire in response to Earth-strength magnetic fields, but the extent and function of the neuronal networks involved in magnetic orientation are virtually unknown. To explore these networks, we are analysing snapshots of the brain activity during magnetic orientation. To obtain these snapshots, we analyse the brains of mole-rats after performing a magnetic orientation task such as the nest building assay. We label all active neurons with a fluorescent dye and make the brains transparent *(Figure 2 below).* A computer maps the position of all active neurons and, by comparison to control animals, reveals all brain areas involved in magnetic orientation. As we know the connectivity between many brain areas and the periphery, this approach allows us to trace the flow of information back from the brain to the receptors and reduces the amount of tissue that we need to screen for magnets. To maximize our chance of finding the cells we then employ state of the art detection methods such as high-resolution (15 Tesla) MRI scans or the very powerful X-rays at synchrotrons to find the tiny compass needles.



The author on the hunt for magnetic compass cells using high intensity X-rays at the Diamond Light Source near Oxford, UK

Hopefully, in the next few years, these approaches will shed light on the incredible navigational abilities of mole-rats in total darkness.

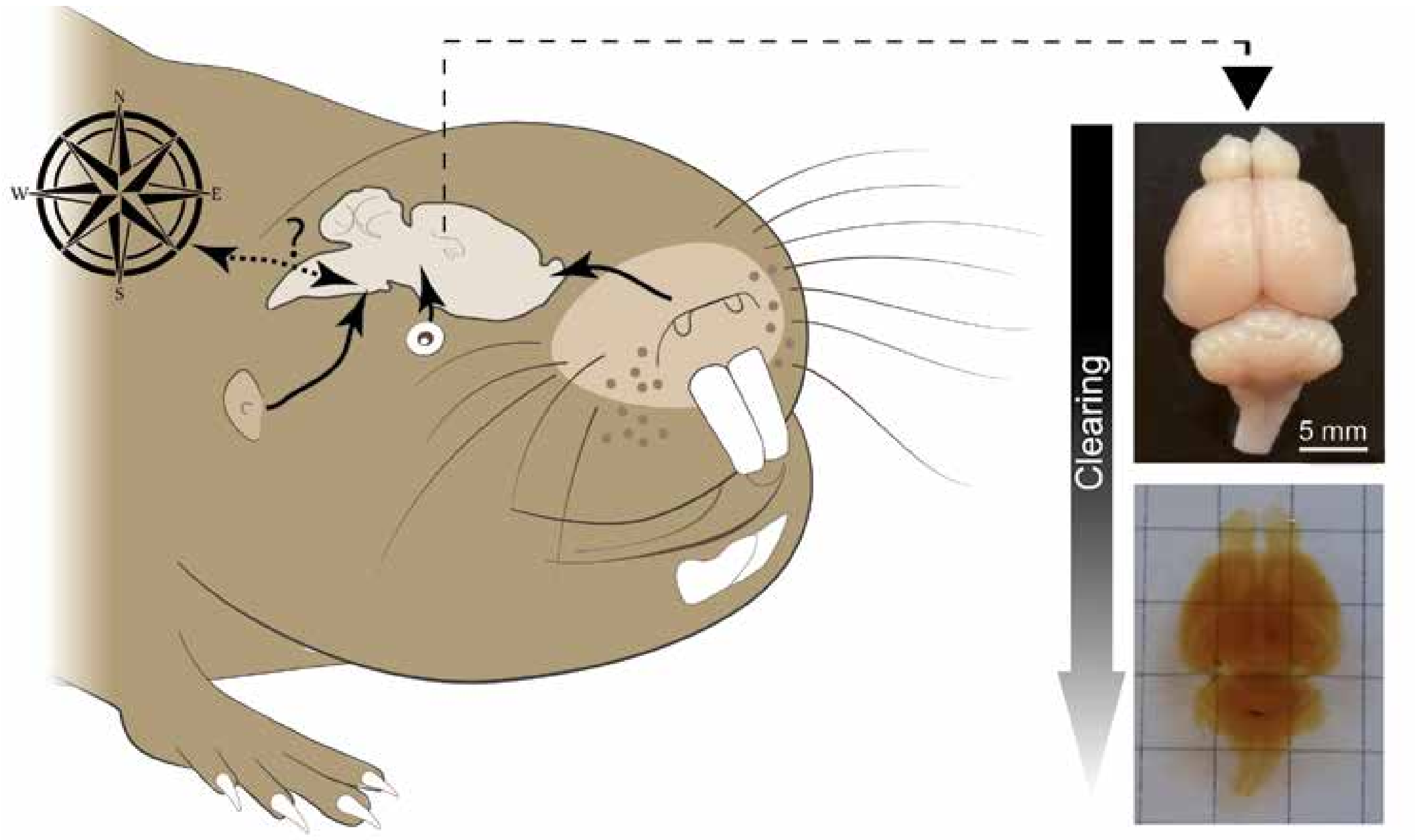


Figure 2: A neurobiological approach to finding the magnetoreceptors in mole-rats. Information from all senses (e.g. smell, vision, hearing) is processed in the brain. The same is true for the magnetic sense. We make mole-rat brains transparent to reveal the areas that processes magnetic stimuli. Knowledge of these brain areas will facilitate the search for the magnetoreceptors.