Creature column

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Bats

By Liora Las & Nachum Ulanovsky

Bats, the only flying mammals, comprise almost 25% of mammalian species. They are excellent navigators, highly social, and extremely long-lived. Their sense of echolocation has been studied for many years – but many species possess also excellent vision and olfaction. In recent years, bats have emerged as new models for neurobiology of navigation, social neuroscience, aging, and immunity.

Batman may not possess superpowers – but bats do. Their 'superpowers' include extreme longevity, highly efficient immune systems, powered flight, and echolocation – a sensory system that allows them to 'see' in the dark. Together, these characteristics have made bats a huge evolutionary success: bats comprise almost 25% of mammalian species, and they inhabit every possible ecological niche throughout the globe, except the polar regions. Bats are evolutionarily distinct from rodents and from primates: they form their own order, Chiroptera, which is closer to carnivores. They feed on diverse food sources, with different species foraging on insects, scorpions, frogs, fish, flowers, fruits or even blood. Bats are the masters of the night sky.

Longevity

Bats are the longest-living mammals in comparison to their body size. Brandt's bat is the mammalian record holder: this species weighs 6 grams and lives >40 years[1] (as compared to the 25-gram laboratory mouse that lives 2 years). Many other bat species are almost as long-lived. Bats also exhibit high resistance to cancer. Like other long-lived animals, bats reproduce and mature slowly: bats give birth to just one or two pups per year, they attain sexual maturity at ~1 year, and they reach adulthood at ~2 years. Extensive research focuses on the genetic, molecular and cellular mechanisms of bats' extreme longevity[1,2].

Immunity

Bats have an exceptional ability to host many viruses without developing clinical disease[3].

Fig. 1 | Egyptian fruit bat, *Rousettus aegyptiacus*. This species is an emerging model in behavioral neuroscience and social neuroscience.

Mounting research investigates the unique immune mechanisms that endow bats with this extreme tolerance; one key mechanism is active suppression of inflammatory responses[3,4].

Flight

Bats are outstanding fliers, capable of both fast flight and exquisite maneuvering. Some species are even able to hover in place or fly backwards, like hummingbirds. Research on bats' flight mechanisms has shown that bats dynamically modulate the tension of their wing membrane, changing the wing properties in midair. Bats also increase aerodynamic lift by 40% using vortices along the leading edges of their wings[5]. Ongoing research seeks to translate these findings to applications in aerial robotics.

Echolocation

Of the ~1,450 known bat species, ~1,250 species echolocate. Bat echolocation (biosonar) is a classic example of an active sensing system[6–8]. Echolocating bats emit brief sound pulses, usually at ultrasonic frequencies, and use the returning echoes to orient and forage. Bats estimate the distance to an object, with millimeter accuracy, by measuring the time delay between the emitted pulse and the returning echo. Some bats use the Doppler effect to measure target velocity and to detect insect wing movements. Bats use the structure of returning echoes to assess the shape and texture of objects. Together, echolocation provides bats with a rich 3D 'image' of the world.

While echolocation is bats' most-studied sensory system, many bat species also excel in vision and olfaction. Fruit bats have better visual acuity than rats or mice; remarkably, their visual acuity even exceeds human visual acuity at very low light levels (starlight). Fruit bats can also detect fruit odors at concentrations 1,000-fold lower than rats[8].

Bats in neuroscience research

Historically, neuroscience research on bats has focused on their echolocation and auditory perception. This research has revealed that the auditory system of some bat species contains neurons tuned to pulse–echo delay, equivalent to target distance, and neurons tuned to Doppler shift, equivalent to relative target velocity. Thus, the bat auditory system is well matched to process the information acquired by echolocation[7].

Over the last 15 years, we and others have introduced bats as models for studying the neural basis of broader mammalian behaviors – mostly spatial behaviors (navigation, spatial memory) and social behaviors. This line of work was done primarily in Egyptian fruit bats (Fig. 1), a species that is widespread throughout Africa and the Middle East. They breed well in captivity, making them a popular bat species in zoos worldwide. These bats are easy to work with in the lab and to train for various behavioral tasks. Importantly, they are a large bat species (~150–180 g for males; 60-cm wingspan), which can easily carry experimental equipment in flight. The body weight of an Egyptian fruit bats is about a third or half that of a laboratory rat, yet it has a similar brain size (~2 g). Their brain is a typical mammalian brain, with some anatomical features similar to those of rodents and others to those of primates[9]. Their distinct evolutionary lineage allows contrasting and comparing brain function in bats versus other mammals, in search of invariances versus unique adaptations in mammalian brains. For example, we showed that the largest brain oscillation in mammals, the hippocampal theta oscillation, is very different between bats and rodents, but is similar between bats and primates – which refuted several theories of hippocampal function that were all based on rodent studies[10].

We identified a list of behavioral characteristics and other features of these bats that

BOX 1

Why study bats in neuroscience?

- Bats are mammals
- They have excellent navigation and spatial memory[7]
- They move volumetrically in 3D space, enabling study of 3D neural coding[12–14]
- They move long distances, enabling study of neural coding of large spaces[11]
- They move fast, allowing investigation of rapid neural dynamics[18]
- They have two distal sensory systems, vision and echolocation, enabling comparison of neural coding of space using two senses[19]
- Echolocation serves as a model for active sensing[6–8,17]
- Echolocation calls are measurable at millisecond precision, quantifying sensory dynamics during free behavior
- Increased echolocation rate is an index of attention during free behavior[18]
- Bats exhibit vocal learning[20,21]
- They are highly social mammals[15,16]
- They enable study of the aging brain in a long-lived species[1,2]
- They are wild mammals that adapt well to the lab

Resources

- Genome: reference-quality genomes have been generated for multiple bat species, including Egyptian fruit bats[4]
- Viral tools: these allow calcium imaging of neural activity[22]
- Stereotaxic brain atlases: these exist for several bat species, including Egyptian fruit bats[9]

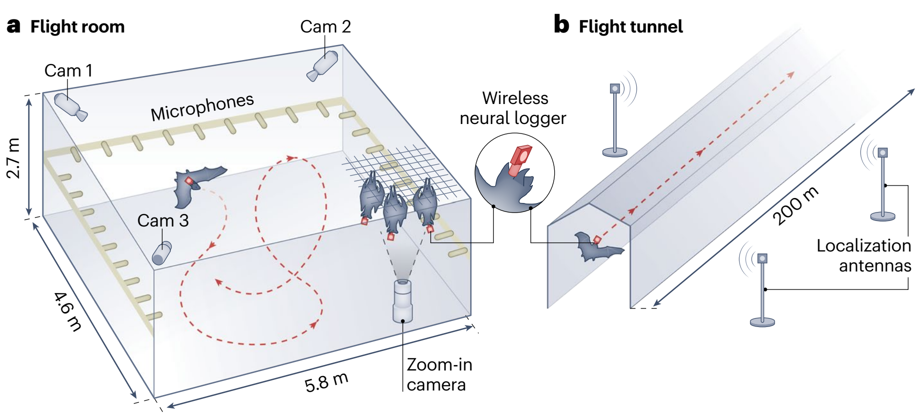

Fig. 2 | Experimental setups used for studying the neural bases of behavior in bats. a, Flight room, used in studies of 3D coding and social coding in the brain[12–14,17]. **b**, Schematic of our 200-meter-long flight tunnel (now extended to 700 meters). Adapted with permission from ref. 11, AAAS.

provide experimental advantages (Box 1). They allow us to explore general questions in behavioral neuroscience, which are often easier to investigate in these bats than in rodents – the standard mammalian models in neuroscience. To record neural activity, we developed a series of wireless neural loggers: tiny devices that store neural and behavioral data on board the animal as it flies[11]. These miniature neural loggers allow recording ~100 neurons simultaneously (and growing), while also recording the animal's vocalizations and its movements using on-board behavioral sensors: ultrasonic microphone, accelerometer, gyroscope, magnetometer, GPS and altimeter. We use these devices in bats to investigate central questions in behavioral systems neuroscience.

Neural representation of 3D space. By studying bats flying in a flight room (Fig. 2a), we learned how various spatial neurons – place cells, head direction cells and grid cells – that for decades were investigated on 2D surfaces are activated in 3D space. We found that 3D place cells exhibit spherical receptive fields[12]; 3D head direction cells represent 3D directions in toroidal coordinates[13]; and 3D grid cells exhibit fixed local distances between their activity fields, but not a global lattice – arguing against theories of grid cells that predicted such a lattice[14].

Neural representation of kilometer-scale spaces. Bats, like many other animals, navigate long distances[7,8]. This allowed us to ask how the brain represents large spaces. To address this, we constructed a 200-meter-long tunnel (Fig. 2b). We found that the neuronal representation of large spaces is completely different from that of small spaces. While place cells in small laboratory environments exhibit single receptive fields in both rodents and bats, we discovered that in the 200-meter large environment, place cells exhibit multiple receptive fields, and field sizes of the same neuron differ up to 20-fold[11].

Social neuroscience. Most bat species live in large colonies and are therefore extremely social animals. This allowed us to ask how other animals are represented in the brain in a social setting. We investigated this in pairs of bats performing a mimicry task and found that there are social place cells – hippocampal neurons that represent the position of another individual[15]. We also established a 'Big Brother' recording room, where we record from groups of socially interacting bats (Fig. 2a). This setup allows us to investigate numerous social signals in the brain, including the positions of multiple other bats and their identities, sexes, hierarchy and social affiliation.

Future neuroscience research on bats will continue using bats' unique abilities and natural behaviors (Box 1). In the social domain, studies will investigate the neural bases of bats' extreme sociality – whereby bats exhibit observational learning, reciprocal food sharing, cooperation and altruism[15,16]. In the domain of spatial navigation, neural recording experiments will expand toward more complex, large and naturalistic spatial environments, including the outdoors. Thus, studies in bats will keep pushing the envelope in the neuroscience of natural behaviors.

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Competing interests

The authors declare no competing interests.