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OUTLOOK

Place-cell coding in flying birds

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Summary

A research article recently published in PNAS by Agarwal and colleagues (*Proceedings of the National Academy of Sciences, 120*(5), Article e2212418120, 2023) identified place cells in the brain of flying birds, specifically in the anterior hippocampus and in a neighbouring region, the posterior hyperpallium apicale, with fewer detected in a more distant visual area. In contrast to mammalian place cells, these avian place cells changed based on the direction of flight.

Since O'Keefe's pioneering work on place cells in the 1970s, leading to the Nobel Prize in Physiology and Medicine in 2014, a multitude of papers have examined how the brain spatially experiences its environment. However, both pioneering and recent work has focused almost exclusively on rodents. Given the diverse movement strategies that exist in the natural world, approaches that facilitate the inclusion of nonterrestrial movement strategies, such as flying or swimming, are critical in understanding how ecology and evolution have shaped the brain's *cognitive map* (Tolman, 1948, p. 193) and technologies that enable the inclusion of these alternate movement strategies are essential to this effort. Recent work on spatially responsive cells in flying barn owls (*Tyto alba*) by Agarwal et al. (2023) is a solid start at filling this gap.

Using a wireless electrophysiology system consisting of custom-made microdrives with tetrodes, Agarwal et al. (2023) recorded action potentials of single neurons. Probes were placed in three pallial areas of the brain—the hippocampus, the posterior hyperpallium apicale, which neighbours the hippocampus, and the central hyperpallium (visual Wulst), which is more distant from the hippocampus. Out of the seven barn owls used in the study, the recording locations in the brain were verified with standard histology in two individuals and with micro-CT scans in another two. The subjects, all free flying, underwent two flying tasks: (1) flying back and forth between two perches placed approximately 2 meters apart, and (2) flying between four perches 1–2 meters apart, with a feeding box randomly assigned to one of the perches. For the first task, the owls were trained to fly back and forth continuously, whereas for the second task, owls freely explored the room and were given the opportunity to feed from the box for 20 seconds when they landed on the rewarded perch, which randomly changed locations throughout the study. The authors described three types of spatially responsive cells: (1) place cells, (2) flight direction cells, and (3) and cells that fired based on the owl's perching position between flights. These cell types were detected in all brain areas examined, but to a lower extent in the visual Wulst. Unlike mammals, owl place cells varied based on the direction of movement.

Various types of spatially responsive neurons have been extensively described in mammals. A place cell is a neuron that fires when the organism is located in a specific location in space. Its firing rate is at its maximum in the middle of this space and decreases as the animals move away, creating a place field. Rats have two-dimensional place fields, whereas flying bats have three-dimensional place fields (Yartsev & Ulanovsky, 2013). Usually, a place cell will fire independently of the animal's position and direction. Head direction cells integrate the animal's position, whereas boundary (or border) cells respond to an environmental boundary. Finally, grid cells are activated at regular intervals as an animal moves through an open space, acting as an internal coordinate system. Within the brain, place and boundary cells are located in the hippocampus whereas grid cells and head direction cells are located in the entorhinal cortex and multiple brain regions, respectively. Together, these cells make up a comprehensive positioning system in the mammalian brain, sometimes referred to as the inner Global Positioning System (GPS).

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How is Agarwal et al.'s (2023) work novel? This may not be readily obvious. Spatially responsive cells have been described primarily from rodent studies, although complimentary research on primates and humans have yielded similar results, with robust place and grid cells identified across these taxa. Payne et al. (2021) identified place cells in birds for the first time, restricted in the anterior part of the hippocampus, with place cells being more numerous in the food-storing tufted titmouse (*Baeolophus bicolor*) than the non-food-storing zebra finch (*Taeniopygia guttata*). However, as Agarwal et al. (2023) pointed out, birds in Payne et al. (2021) were not flying, only walking/hoping. Given that flying is the primary mode of locomotion for most birds, examining place cells and other spatially responsive cells within this locomotory context is essential. Having said this, Yartsev and Ulanovsky (2013) already described place cells in flying bats. As such, the novelty of Agarwal et al.'s (2023) work is quite specific—flying birds.

It would have been helpful to elaborate on the ecological relevance of the study, as this research could inspire novel neuroecology research. Neuroecology is defined as the study of "adaptive variation in cognition and the brain" (Sherry, 2006, p. 168). Payne et al. (2021) showed that food-storing species had more numerous place cells than non-food-storing zebra finches. Using a similar approach in flying birds could be quite insightful. Barn owls are an interesting choice for a neuroscience study, as they are phylogenetically and behaviourally distant from typical model species such as zebra finches, pigeons, and quail. They differ also from species used in typical neuroecology studies on spatial cognition such as food-storing and migratory birds. A more expanded justification for using barn owls, alongside a discussion of potential ecologically relevant comparative species, would have complemented nicely the more technically heavy parts of the manuscript. Are there closely related owl species that rely less on navigation? Which ecological parameters vary between owl species (e.g., foraging behaviour, migration) that could affect spatial cognition? For example, comparing nocturnal to diurnal owls or central-place foragers to those that do not return to a home base could be interesting. Barn owl home ranges consist of hundreds of hectares; how do measurements covering a few meters scale up to an entire home range—and, indeed, for those owls that migrate across continents? Nevertheless, Agarwal et al.'s (2023) study presents a stepping stone to several exciting venues for future neuroecology research using wireless electrophysiology systems.

Agarwal et al. (2023) took a thorough approach of implanting tetrodes in three areas of the dorsal pallium (anterior hippocampus, posterior hyperpallium apicale, and the visual Wulst). However, except for hippocampus, it was unclear why these areas were selected. This is particularly surprising as barn owls are often held up as the ultimate auditory predatory, with ears offset from one another to facilitate triangulation by sound, and so we might expect the visual Wulst to be less important in locating prey. Predictions were not stated in the introduction, just preliminary results, suggesting that a more exploratory approach was taken. Although it is true that both the hippocampus and hyperpallium play central roles in spatial cognition, the evidence is strongest for the hippocampus. It is not clear why comparing results to a well-characterized primary visual area was important for this particular study. It would have been more meaningful to select an area not associated with spatial cognition at all, as a control (e.g., nucleus rotundus). Were the authors expecting visual Wulst to have any place cells? If not, perhaps this was their "control" region. Also, the potential issue that place cells were not found in the posterior region of the hyperpallium apicale, but were actually instead recorded in a more lateral area of the hippocampus, cannot be understated. Having said this, the authors were clear about this possibility throughout the manuscript. Moving forward, having a representative sample of study species brains with clearly labeled boundaries would be helpful in more accurately setting the probes. One possibility would be to use a whole-brain tissue clearing approach with a parvalbumin stain to clearly denote the hippocampus–hyperpallium apicale boundary.

Avian spatial abilities have perplexed humans for millennia. Migrants fly tens of thousands of kilometers across continents, nutcrackers remember tens of thousands of cache sites, and foraging seabirds return to the same meter of sea after commuting a thousand kilometers. Agarwal et al. (2023) have brought us one substantial step toward understanding the cognitive map of these diverse and remarkable strategies, leading to a better respect for our natural world.

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