

Are There Place Cells in the Avian Hippocampus?

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Abstract

Birds possess a hippocampus that serves many of the same spatial and mnemonic functions as the mammalian hippocampus but achieves these outcomes with a dramatically different neuroanatomical organization. The properties of spatially responsive neurons in birds and mammals are also different. Much of the contemporary interest in the role of the mammalian hippocampus in spatial representation dates to the discovery of place cells in the rat hippocampus. Since that time, cells that respond to head direction and cells that encode a grid-like representation of space have been described in the rat brain. Research with homing pigeons has discovered hippocampal cells, including location cells, path cells, and pattern cells, that share some but not all properties of spatially responsive neurons in the rodent brain. We have recently used patterns of immediate-early gene expression, visualized by the catFISH method, to investigate how neurons in the hippocampus of brood-parasitic brown-headed cowbirds respond to spatial context. We have found cells that discriminate between different spatial environ-

ments and are re-activated when the same spatial environment is re-experienced. Given the differences in habitat and behaviour between birds and rodents, it is not surprising that spatially responsive cells in their hippocampus and other brain regions differ. The enormous diversity of avian habitats and behaviour offers the potential for understanding the general principles of neuronal representation of space.

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Introduction

Place cells in the hippocampus of the rat were first described by O'Keefe and Dostrovsky [1971]. They are defined electrophysiologically by the spatially localized firing of the cell when the animal is in a specific location. A place cell may have more than one disjoint place field, and the shape of a place field can change as the shape of the environment and the objects it contains change [Muller and Kubie, 1987; O'Keefe and Burgess, 1996]. An individual place cell may have different place fields in different environments, and collectively the firing patterns of place cells are thought to create an allocentric representation of space. Hippocampal place cells, along with grid cells in the medial entorhinal cortex, and head direction

cells found in a variety of cortical and subcortical areas including the presubiculum, entorhinal cortex, thalamus, and striatum are part of a brain network representing space, routes, and events that make it possible for rats to orient and navigate [Moser et al., 2008].

Place cells in the rat hippocampus provide information on the two-dimensional (2D) surface that rats traverse in most laboratory experiments. But for some animals, orientation and navigation have a vertical component, too, and birds may provide valuable information on how this third dimension is represented. Simple translational flight by birds in two dimensions over the earth's surface may not tax a 2D representation of space, but vertical movement during ascending or descending flight or evading a predator requires a representation of space in three dimensions, as does moving within a tree or up and down a cliff searching for food or returning to a nest.

Three-dimensional (3D) representation of space by cells in the hippocampus has been examined in flying bats [Yartsev and Ulanovsky, 2013; Sarel et al., 2017]. The place fields of place cells in the hippocampus of free-flying Egyptian fruit bats (*Rousettus aegyptiacus*) are spherical volumes [Yartsev and Ulanovsky, 2013]. Other cells in CA1 of the bat hippocampus are tuned to the direction and distance toward a goal. As the bat flies, and the vector between the moving bat and its goal changes, different goal direction cells become active or fall silent [Sarel et al., 2017]. Rat spatial neurons, in contrast, appear to reduce the problem of navigating in 3D space to navigation in a 2D plane, even when that plane is inclined, vertical, or inverted [Jeffrey et al., 2015]. Rat spatial neurons treat the plane of locomotion as the space in which orientation occurs, sometimes with loss of resolution if the plane of locomotion departs from the horizontal.

A basic question, then, is are there place cells in the avian hippocampus? Research with homing pigeons by Bingman and his colleagues has directly addressed this question, and the answer appears to be, no, neurons in the homing pigeon hippocampus do not have the characteristics of classic rat place cells [Siegel et al., 2002; Hough and Bingman, 2004; Siegel et al., 2005; Hough and Bingman, 2008; Kahn et al., 2008]. But current understanding of rat hippocampal place cells has become more nuanced than their classic description as more has been discovered about the space-specific response properties of neurons in the rat hippocampus, and the homing pigeon hippocampus clearly does contain cells with firing rates that vary predictably in space. There are cells that fire when a pigeon reaches a spatial goal in a maze and others that fire when it traverses a path in a maze. There are cells that

cease firing when a pigeon enters a maze, and cells that fire in a patterned arrangement when a pigeon moves through an open field. In research with brown-headed cowbirds (*Molothrus ater*), we have used a different approach to look for spatially responsive cells in the avian hippocampus. Using immediate-early gene expression to visualize neuronal activity, we have found cells that respond repeatedly to the same spatial environment but distinguish between different spatial environments [Grel-la et al., 2016].

In this paper, we review what is known about spatially responsive neurons in the avian hippocampus and address the broader question of whether the organization and neuronal populations of the rat hippocampus provide an appropriate model for understanding the representation of space in the hippocampus of birds.

Spatially Responsive Cells in the Homing Pigeon Hippocampus

Spatially responsive cells of four kinds have been identified in the hippocampus of homing pigeons. These cells have been detected while pigeons walked in open fields or in the alleys of plus mazes or radial-arm mazes.

Location Cells

Location cells show peaks in activity that are often near goals in plus mazes and radial-arm mazes, specifically near food cups at the end of maze arms [Hough and Bingman, 2004; Siegel et al., 2005]. These single units, however, are not merely sensitive to the presence of food reward. A location cell may show increased activity at the goal end of some but not all arms in a four-arm plus maze, or show increased activity at the goal of one maze arm and at the half-way point along a different maze arm. Location cells have a mean of 2.3 different locations in which they are active in the same environment [Siegel et al., 2005]. Location cells are probably the most place cell-like single units discovered in the homing pigeon hippocampus. Place cells in the rat hippocampus are also found disproportionately in the vicinity of behaviourally important locations [Hollup et al., 2001] and show remapping that conforms to the walls and boundaries of a spatial environment. In general, however, pigeon hippocampal location cells have less temporal stability than rat place cells, and less temporal stability than pigeon hippocampal path cells described below.

Two measures are used to quantify the spatial specificity of rat place cells and pigeon location cells, coherency

and reliability. Both measures use spatial rate maps, which are the spatial distribution of the firing rate of the cell over the maze or arena in which the animal is moving. Coherency measures the correlation in the rate map between firing rate in a given spatial unit, e.g. a pixel in a video record of the pigeon's track, and firing rate in the eight neighbouring units that surround that spatial unit, for all spatial units in the maze or the arena. Pigeon location cells have a spatial coherence of 0.34 compared to a spatial coherence in rat place cells of 0.81 [Siegel et al., 2005]. Reliability measures the similarity in rate maps between the first part and the last part of an observation session. Although location cells have higher reliability than expected by chance, they tend to have lower reliability than place cells, that is, their rate maps tend to change over time [Siegel et al., 2005].

Like rat place cells, the regions in space in which a pigeon location cell fires are determined by surrounding features and landmarks. Hough and Bingman [2008] trained pigeons to navigate a radial-arm maze in which the goal arms were individually illuminated by lights of different colors. When the configuration of lights was rotated 90° the fields of maximum activity of location cells also rotated by 90° [Hough and Bingman, 2008]. Evidence that location cells of the pigeon hippocampus do not behave like place cells of the rodent hippocampus, however, comes from an experiment in which pigeons explored an open arena instead of maze arms in a plus or radial configuration [Kahn et al., 2008]. In such an environment, location cells essentially do not occur.

Path Cells

Path cells fire when a pigeon moves between goal locations along an alley in a plus maze or radial-arm maze [Hough and Bingman, 2004; Siegel et al., 2006]. Path cells may fire in more than one alley of a maze. Trajectory-dependent cells of this kind occur much more often in the left hippocampus than the right [Siegel et al., 2005].

Arena-Off Cells

Some single units in the pigeon hippocampus show the unusual property of high activity in a holding chamber next to the maze, which ceases when the bird enters the maze and resumes when the bird exits the maze and is returned to the holding area [Hough and Bingman, 2004; Siegel et al., 2005].

Pattern Cells

Pattern cells exhibit patches of firing regularly distributed over multiple locations in an open arena [Kahn et al.,

2003]. These patches of activity have distinct boundaries with abrupt decreases in firing rate between the patch and the immediate surrounding area in which the pattern cell is not active. Pattern cells are not observed when pigeons move through a maze; location and path cells are not observed when pigeons move through an open arena in which pattern cells are active [Kahn et al., 2008]. Pattern cells also have a low firing rate compared to location and path cells. The individual patches of activity of pattern cells, although distinct and dispersed throughout an open arena in grid-like fashion, do not appear to form a hexagonal pattern like that formed by grid cells in the rat entorhinal cortex, although further analysis of the firing properties of pattern cells might well reveal additional regularities in their distribution [Kahn et al., 2008].

Unlike place, head direction, and grid cells in the rat, which are localized in identified regions of the hippocampus and neighbouring brain areas, spatially responsive cells in the homing pigeon do not appear to be localized to any of the anatomical subdivisions of the avian hippocampus and are found throughout its rostral caudal axis [from A3.5 to A8.0; Karten and Hodos, 1967]. The distribution of both path and pattern cells, however, is lateralized [Siegel et al., 2006; Kahn et al., 2008].

Context-Dependent Cells in the Cowbird Hippocampus

We used a different approach to examine how neurons in the hippocampus of brown-headed cowbirds respond to spatial context. As in some of the previous work with homing pigeons, we observed birds as they walked on the floor of a large open arena searching for food.

Brown-headed cowbirds are generalist brood parasites. Female brown-headed cowbirds lay their eggs in the nests of over 200 different species of hosts, and hosts that accept these eggs then incubate them and raise the young cowbird along with their own offspring. Female cowbirds search for and remember the locations of potential host nests and revisit potential host nests to monitor the stage of host egg laying [White et al., 2009]. Relative to the size of the telencephalon, female brown-headed cowbirds have a larger hippocampus than males [Sherry et al., 1993], as does another generalist brood parasite in the same genus, the shiny cowbird (*Molothrus bonariensis*) [Reboreda et al., 1996]. More recent results, however, indicate that this sex difference also occurs in non-parasitic members of the Icterid family to which cowbirds belong [Guigueno et al., 2016]. Female cowbirds show greater

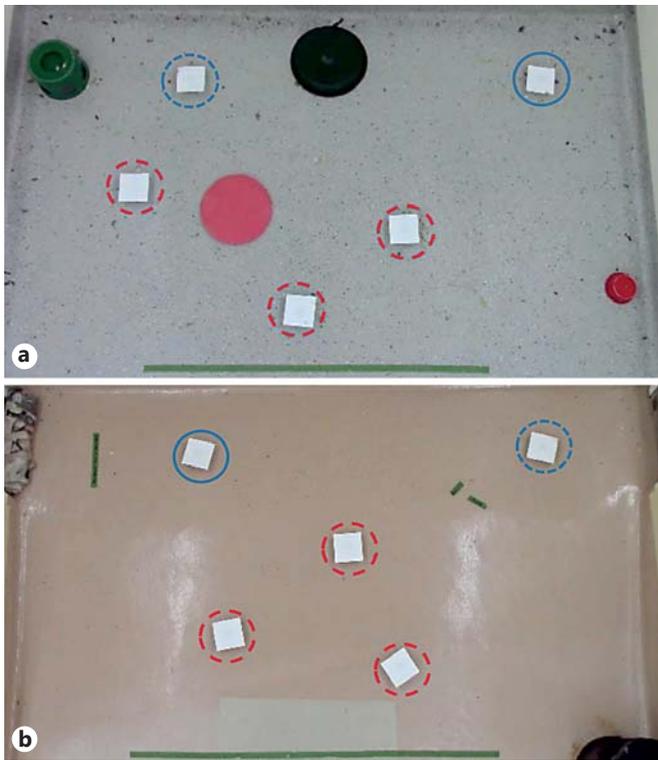


Fig. 1. Overhead camera views of testing rooms A (a) and B (b). Rooms were the same size but discriminable by colour of the floor and door, features of the walls, and objects on the floor. An inverted green pail, two round rubber mats, and an inverted red food cup are visible in room A. In room B, a rolled rubber mat (upper left) and an inverted black pail (lower right) are visible. Food cups (circled) were covered by a card that the bird displaced to obtain food. Solid blue circle: always baited. Dashed blue circle: never baited. Dashed red circles: randomly baited. Reprinted from Grella et al. [2016].

adult hippocampal neurogenesis than males, and this elevated level of neurogenesis occurs following breeding [Guigueno et al., 2016].

Cowbirds feed on the ground, taking seeds and insects, often in association with cattle – hence the name cowbird – and prior to European contact in association with bison in the central plains of North America. Cowbirds perform well on spatial tasks. In an open field search task in which birds were required to find and remember for 24 h which one of 25 food cups was baited with food, females performed significantly better than males [Guigueno et al., 2014]. In a touch screen task, however, which required birds to recall which spatial location on a screen was associated with food reward, males performed better than females [Guigueno et al., 2015].

We investigated the 2D spatial responsiveness of cells in the cowbird hippocampus by visualizing expression of the immediate-early gene *Egr1* [also known as ZENK, Zif268, NGFI-A and Krox-24; Grella et al., 2016]. *Egr1* has been shown to reliably report place cell activity in rats [Marrone et al., 2011]. We used patterns of *Egr1* expression to visualize the activity history of individual neurons and determine whether cowbird hippocampal cells discriminated between two familiar environments in which the bird searched for food.

Birds searched for food in cups placed on the floor of two rooms, both 2.4×3.6 m. Five cups were placed on the floor in a different arrangement in each room (Fig. 1). One cup, in a different location in each room, was always baited, three cups were randomly baited (to encourage search), and one cup was never baited. The rooms were readily discriminable. Room A had a grey-flecked concrete floor, a light green door, colour pictures on the walls, and on the floor an inverted green pail, two round rubber mats, and an inverted red food cup. Room B had a tan non-flecked floor, a grey door, two 45×45 cm steel panels at floor level, and a depression in the floor 1.9 m wide that increased in depth from 5 to 15 cm as it ran from one wall to the other (this channel carried running water when the room housed shorebirds in other research). An inverted black pail and a rolled fabric mat were placed on the floor of this room. All birds were trained in both rooms until they could reliably distinguish between them. The test of whether or not the birds learned to discriminate between the rooms was whether they went first to the baited cup in each room, which they did with 96% accuracy on test days (Fig. 2).

Patterns of nuclear and cytoplasmic *Egr1* expression showed whether hippocampal cells discriminated between the two test environments. On test days, birds either searched the same room twice in succession (A:A, B:B) for 5 min each or searched different rooms (A:B, B:A) for 5 min each, with a 25-min interval in their home cage in both cases before the first and second search epoch. A group of control birds remained in their home cage for an equivalent 35-min period. On test days, following search of the second room in the sequence, all birds were sacrificed within 3 min of the end of the trial for visualization of *Egr1* mRNA by the catFISH (cellular compartmental analysis of temporal fluorescence in situ hybridization) technique [Guzowski et al., 1999]. The logic of this experimental design is that hippocampal cells that were active only in the second room in the sequence would express *Egr1* only in the cell nucleus because of the initiation of transcription no more than 8 min previously.

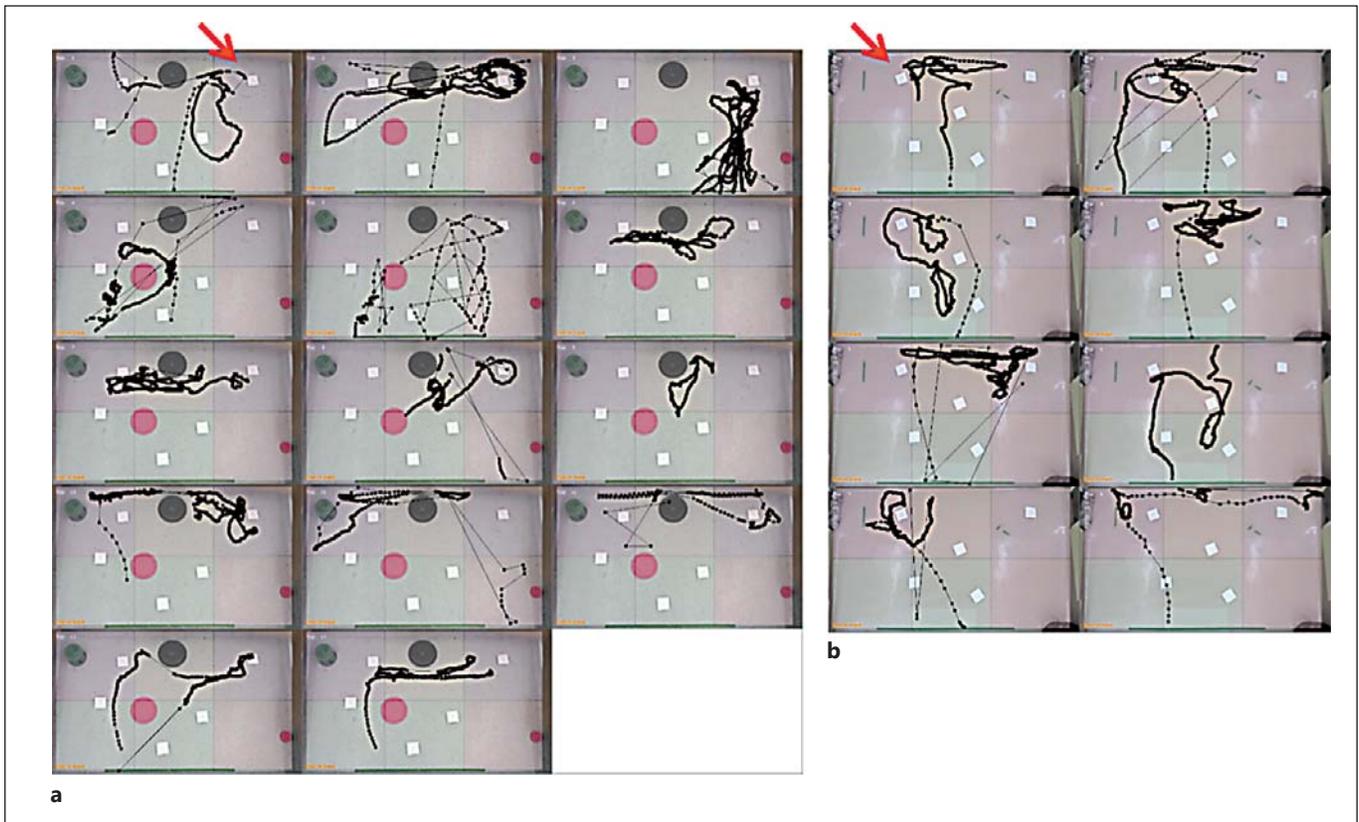


Fig. 2. Tracks of birds on test trials. **a** Room A. **b** Room B. Tracks of the birds (in black) visualized with Noldus EthoVision. Birds generally walked on the floor but occasionally made hops or short flights, indicated by increased spacing between fixation points.

Birds uncovered first the baited food bowl in each room (red arrows) on 96% of trials, but also explored each room on test trials, as shown by tracks.

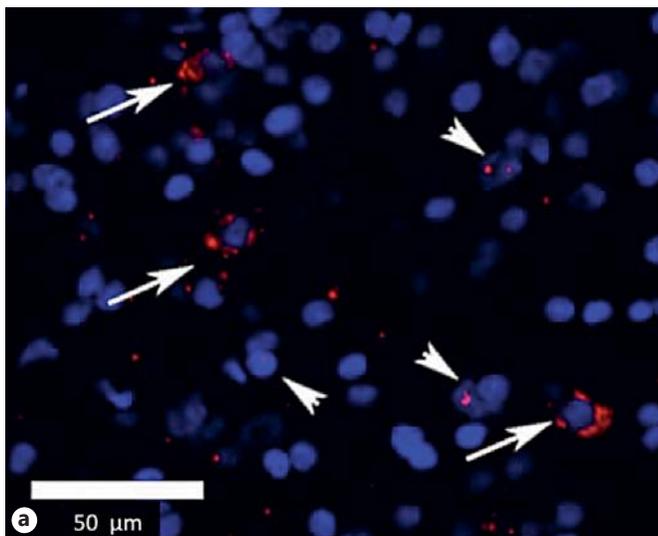
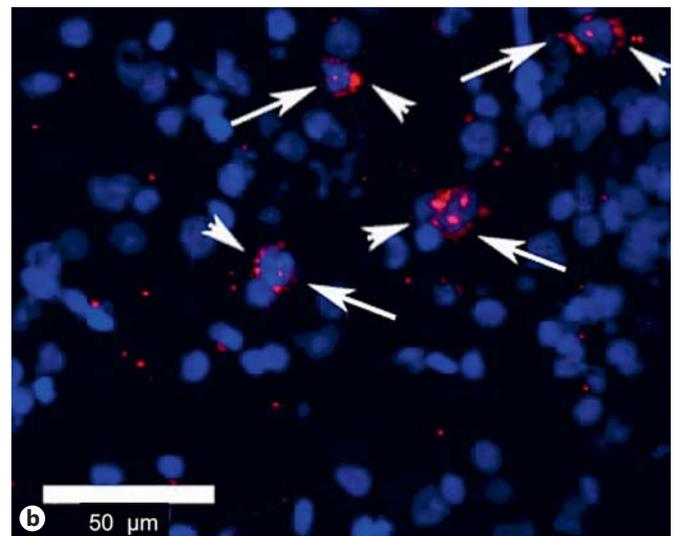


Fig. 3. *Egr1* mRNA expression in cowbird hippocampal neurons. Neurons (blue DAPI) were identified morphologically. **a** Neurons with *Egr1* mRNA (red) in either the nucleus (arrowheads) or the cytoplasm (arrows) in birds exposed to two different spatial con-



texts, indicating cells that were active in one spatial context but not the other. Reprinted from Grella et al. [2016]. **b** Neurons with *Egr1* mRNA (red) in both nucleus and cytoplasm in birds exposed to the same spatial context twice.

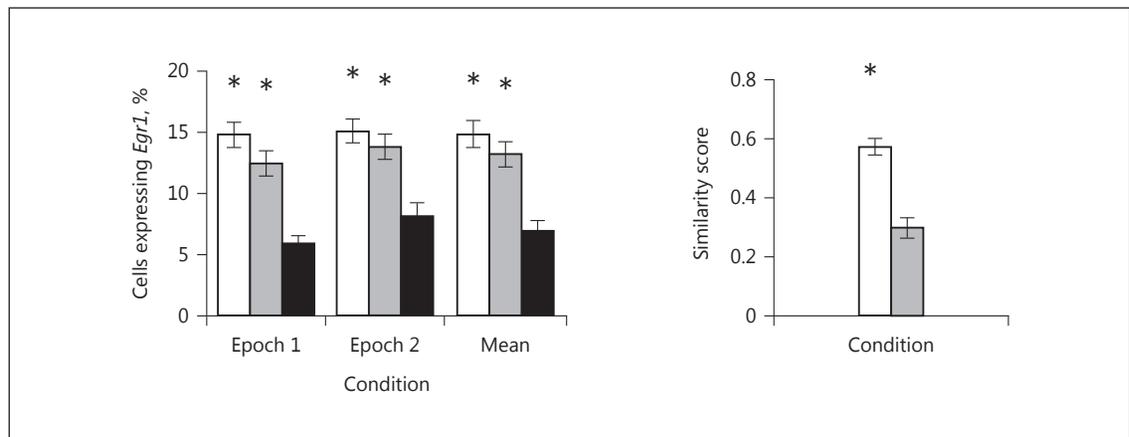


Fig. 4. Percent of cowbird hippocampal cells expressing *Egr1* (a) and similarity score (b) for birds that searched either different rooms or the same room twice. **a** Cowbirds that searched for food in an open room had significantly more cells expressing *Egr1* than birds that remained in their home cage (black bars) whether they searched the same room twice (white bars) or searched two different rooms (grey bars; * $p < 0.05$ vs. home cage). Epochs 1 and 2 refer to the first and the second room, respectively. **b** Similarity scores show that cells expressing *Egr1* in both the first and second room occurred significantly more often when birds searched the same room twice (white bar) compared to birds that searched two different rooms in succession (grey bar; * $p < 0.05$). Reprinted from Grella et al. [2016]. Similarity score: $(D - p(E1E2)) / (L - p(E1E2))$, in

which E1 is the proportion of the total cell population active in epoch 1, which includes cells containing *Egr1* in both cellular compartments and cells containing *Egr1* solely in the cytoplasm. E2 is the proportion of the total cell population that is active in epoch 2, which includes cells containing *Egr1* in both cellular compartments and cells containing *Egr1* solely in the nucleus. D is the proportion of the total cell population containing *Egr1* in both cellular compartments, $p(E1E2)$ is the joint probability $E1 \times E2$, and L is the smaller of E1 and E2. The score ranges from 0.0, indicating similarity due to chance, to 1.0, indicating that all cells expressing *Egr1* in epoch 1 also express *Egr1* in epoch 2 [Vazdarjanova and Guzowski, 2004].

In contrast, cells that were active in the first room in the sequence would show *Egr1* expression in the cytoplasm and not in the nucleus. This is because after 25 min the distribution dynamics of immediate-early gene transcription would cause the mRNA transcripts to mobilize out of the nucleus and into the cytoplasm. Cells that were active in both rooms would be expected to exhibit both nuclear and cytoplasmic *Egr1* mRNA expression (Fig. 3).

We found that approximately 15% of hippocampal cells were active in each room and expressed *Egr1* following foraging, significantly more than in cowbirds that remained in their home cage (Fig. 4). We calculated a similarity score [Vazdarjanova and Guzowski, 2004] (see Fig. 4 for the similarity score formula) to determine the probability that a cell expressed *Egr1* in both rooms and found that, as predicted, significantly more cells expressed *Egr1* in both the nucleus and the cytoplasm when the birds visited the same room twice than when they visited different rooms [Grella et al., 2016]. This indicates that cells in the cowbird hippocampus differentiate between the two spatial contexts, tending to fire either in room A or room B, but firing repeatedly when the spatial context is repeated. Individual neurons in the cowbird

hippocampus thus differentiate between the two rooms, achieving pattern separation between spatial contexts that are broadly similar but differ in visual features and in where food is located. When the same spatial context is repeated, cells that fired in that context the first time fire again.

Are these cells in the cowbird hippocampus indeed behaving like mammalian place cells? While place cell activity in the rat hippocampus is coupled to immediate-early gene expression [Marrone et al., 2011], this technique does not tell us specifically where in either room the cowbird hippocampal cells were firing. The cells we found in the cowbird hippocampus appear spatially tuned, however, and thus are candidates for location cells and path cells of the kind described in the hippocampus of homing pigeons. Pattern cells in the pigeon hippocampus are more likely to be detected in the absence of stable goal locations [Kahn et al., 2008]. This is different from the test situation we used for cowbirds – in which familiar food locations were one of the features by which the two rooms were distinguished – making it somewhat less likely that the cells we observed were pattern cells, but this is of course purely speculative. We do not know if the cells we

detected are, for example, tied to specific goal locations, like location cells in the pigeon hippocampus. Because the food search task was the same in both rooms, with a single baited food cup, three unbaited cups, and one randomly baited cup, and the rooms were the same size and equally familiar, the contextual differentiation that was observed in cell firing was due not to the nature of the task but to the spatial context of the environment, but how that context is coded by cowbird hippocampal cells and what spatial properties these cells respond to is not shown by this experiment.

Final Comments

Birds should be a potentially rich source of data on the representation of space by the hippocampus. They fly in three dimensions, hop from branch to branch in trees, and walk on the ground, meeting Finkelstein et al.'s [2016] criteria for volumetric navigation, multilayered navigation, and planar navigation. There is also spectacular diversity in how birds move through, exploit, and remember space: hummingbirds navigate between flowers and hover in front of blossoms – stationary even in crosswinds – to extract nectar; food-storing birds remember the spatial locations of caches; brood parasites search for and remember the locations of potential host nests; homing pigeons and long-distance migrants navigate over distances ranging from a few kilometers to thousands of kilometers; penguins navigate over long distances on and under the water, and puffins spend a good deal of their time underground in burrows.

Are neuronal populations of the rat hippocampus a suitable model for understanding the avian hippocampus? Place cells and head direction cells identical to those of rats have not been found in the avian hippocampus. Pattern cells in the pigeon hippocampus may serve some of the functions of rodent grid cells but differ in some ways from grid cells. But place, head direction, and grid cells may be only a partial taxonomy of spatially responsive cells in the rat brain. Border cells are found in the entorhinal cortex and subiculum [Savelli et al., 2008; Solstad et al., 2008, Lever et al., 2009], and route-sensitive cells occur in the posterior parietal cortex [Nitz, 2006; Harvey et al., 2012; Wilber et al., 2014]. Other spatially responsive cells in the rat hippocampus more similar to those found in homing pigeons may remain to be discovered. Given the relatively small number of studies of spatially sensitive neurons in the avian hippocampus compared to the thousands of studies with rodents, it is also

possible that unit activity more comparable to that found in mammals exists in birds and remains to be discovered.

Are the spatially responsive cells in the rat hippocampus a good model of what to expect or what to search for in the avian hippocampus? There are two broad alternative answers to this question. The first is, no, there is no reason to expect the representation of space in the avian hippocampus to resemble the representation of space in the rodent brain. Although evolutionarily homologous, the hippocampus of birds and the hippocampus of mammals are anatomically very different, the result of 320 million years of evolutionary divergence. The avian hippocampus may have evolved different neural algorithms that are more suitable for moving rapidly through space in flight. The extraction of spatial information from visual input, including skylight polarization, and other modalities, such as geomagnetic sensory input, may have produced an avian hippocampus with very different units and rules of operation than its rodent homologue. Much of the discussion of rodent place, head direction, and grid cells has emphasized the role of these cells in path integration by a nocturnal rodent that navigates by olfaction and kinaesthesia through burrows underground and along familiar paths on the surface. Birds are diurnal and highly visual. There is evidence that the firing patterns of spatially responsive cells in the hippocampus of the similarly diurnal and visual rhesus macaque (*Macaca mulatta*) are quite different from those found in rodents [Feigenbaum and Rolls, 1991; Rolls and O'Mara, 1995]. In addition, birds are able to navigate over both very long distances in flight and short distances on foot. It should not be a surprise that the spatially responsive neural units in the hippocampus of rats and pigeons are not the same. The other broad answer, however, is that for any animal to determine where it is in space there must be cells in the brain that are responsive to the combination of sensory input that indicates this place here, not that place there, in other words situates the animal in an allocentric frame of reference. How these cells participate and interact in the spatial representation network may differ between birds and rodents, but finding these cells and determining their function would still seem to be a valuable goal. The avian hippocampus is likely a site of integration of sensory information underlying magnetic and celestial compass information, visual landmarks, spatial geometry, olfactory navigation and magnetic map information [Mouritsen et al., 2016]. As Mouritsen et al. [2016] point out, there are obvious similarities at the conceptual level between the maps and compasses that are the basis of most theorizing about bird navigation and the place cells, grid cells, and

head direction cells dedicated to processing map-like representations of space and bearing in rodents. In bats, the occurrence of hippocampal cells that resemble the place cells of rodents but with additional properties adapted to flight in 3D space and the discovery of other spatially responsive cells in the bat hippocampus [Sarel et al., 2017] encourage this latter view that there probably are common neural principles for representing space in the hippocampus of birds and mammals.

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References

- Feigenbaum JD, Rolls ET (1991): Allocentric and egocentric spatial information processing in the hippocampal formation of the behaving primate. *Psychobiology* 19:21–40.
- Finkelstein A, Las L, Ulanovsky N (2016): 3-D maps and compasses in the brain. *Annu Rev Neurosci* 39:171–196.
- Grella SL, Guigueno MF, White DJ, Sherry DF, Marrone DF (2016): Context-dependent *Egr1* expression in the avian hippocampus. *PLoS One* 11:e0164333.
- Guigueno MF, MacDougall-Shackleton SA, Sherry DF (2015): Sex differences in spatial memory in brown-headed cowbirds: males outperform females on a touchscreen task. *PLoS One* 10:e0128302.
- Guigueno MF, MacDougall-Shackleton SA, Sherry DF (2016): Sex and seasonal differences in hippocampal volume and neurogenesis in brood-parasitic brown-headed cowbirds (*Molothrus ater*). *Dev Neurobiol* 76:1275–1290.
- Guigueno MF, Snow DA, MacDougall-Shackleton SA, Sherry DF (2014): Female cowbirds have more accurate spatial memory than males. *Biol Lett* 10:20140026
- Guzowski JF, McNaughton BL, Barnes CA, Worley PF (1999): Environment-specific expression of the immediate-early gene *Arc* in hippocampal neuronal ensembles. *Nat Neurosci* 2:1120–1124.
- Harvey CD, Coen P, Tank DW (2012): Choice-specific sequences in parietal cortex during a virtual-navigation decision task. *Nature* 484:62–68.
- Hollup SA, Molden S, Donnett JG, Moser MB, Moser EI (2001): Accumulation of hippocampal place fields at the goal location in an annular watermaze task. *J Neurosci* 21:1635–1644.
- Hough GE, Bingman VP (2004): Spatial response properties of homing pigeon hippocampal neurons: correlations with goal locations, movement between goals, and environmental context in a radial-arm maze. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 190:1047–1062.
- Hough GE, Bingman VP (2008): Rotation of visual landmark cues influences the spatial response profile of hippocampal neurons in freely-moving homing pigeons. *Behav Brain Res* 187:473–477.
- Jeffrey KJ, Wilson JJ, Casali G, Hayman RM (2015): Neural encoding of large-scale three-dimensional space – properties and constraints. *Front Psychol* 6:297.
- Kahn MC, Hough GE, ten Eyck GR, Bingman VP (2003): Internal connectivity of the homing pigeon (*Columba livia*) hippocampal formation: an anterograde and retrograde tracer study. *J Comp Neurol* 459:127–141.
- Kahn MC, Siegel JJ, Jechura TJ, Bingman VP (2008): Response properties of avian hippocampal formation cells in an environment with unstable goal locations. *Behav Brain Res* 191:153–163.
- Karten HJ, Hodos W (1967): A Stereotaxic Atlas of the Brain of the Pigeon. Baltimore, Hopkins.
- Lever C, Burton S, Jeewajee A, O’Keefe J, Burgess N (2009): Boundary vector cells in the subiculum of the hippocampal formation. *J Neurosci* 29:9771–9777.
- Marrone DF, Adams AA, Satvat E (2011): Increased pattern separation in the aged fascia dentata. *Neurobiol Aging* 32:e23–e32.
- Moser EI, Kropff E, Moser M-B (2008): Place cells, grid cells, and the brain’s spatial representation system. *Annu Rev Neurosci* 31:69–89.
- Mouritsen H, Heyers D, Güntürkün O (2016): The neural basis of long-distance navigation in birds. *Annu Rev Physiol* 78:133–154.
- Muller RU, Kubie JL (1987): The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *J Neurosci* 7:1951–1968.
- Nitz D (2006): Tracking route progression in the posterior parietal cortex. *Neuron* 49:747–756.
- O’Keefe J, Burgess N (1996): Geometric determinants of the place fields of hippocampal neurons. *Nature* 381:425–428.
- O’Keefe J, Dostrovsky J (1971): The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res* 34:171–175.
- Reboreda JC, Clayton NS, Kacelnik A (1996): Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *Neuroreport* 7:505–508.
- Rolls ET, O’Mara SM (1995): View-responsive neurons in the primate hippocampal complex. *Hippocampus* 5:409–424.
- Sarel A, Finkelstein A, Las L, Ulanovsky N (2017): Vectorial representation of spatial goals in the hippocampus of bats. *Science* 355:176–180.
- Savelli F, Yoganarasimha D, Knierim JJ (2008): Influence of boundary removal on the spatial representations of the medial entorhinal cortex. *Hippocampus* 18:1270–1282.
- Sherry DF, Forbes MRL, Khurgel M, Ivy GO (1993): Females have a larger hippocampus than males in the brood-parasitic brown-headed cowbird. *Proc Natl Acad Sci USA* 90:7839–7843.
- Siegel JJ, Nitz D, Bingman VP (2002): Electrophysiological profile of avian hippocampal unit activity: a basis for regional subdivisions. *J Comp Neurol* 445:256–268.
- Siegel JJ, Nitz D, Bingman VP (2005): Spatial-specificity of single-units in the hippocampal formation of freely moving homing pigeons. *Hippocampus* 15:26–40.
- Siegel JJ, Nitz D, Bingman VP (2006): Lateralized functional components of spatial cognition in the avian hippocampal formation: evidence from single-unit recordings in freely moving homing pigeons. *Hippocampus* 16:125–140.
- Solstad T, Boccarda CN, Kropff E, Moser M-B, Moser EI (2008): Representation of geometric borders in the entorhinal cortex. *Science* 322:1865–1868.
- Vazdarjanova A, Guzowski JF (2004): Differences in hippocampal neuronal population responses to modifications of an environmental context: evidence for distinct, yet complementary, functions of CA3 and CA1 ensembles. *J Neurosci* 24:6489–6496.
- White DJ, Ho L, Freed-Brown G (2009): Counting chicks before they hatch: female cowbirds can time readiness of a host nest for parasitism. *Psychol Sci* 20:1140–1145.
- Wilber AA, Clark BJ, Forster TC, Tatsuno M, McNaughton BL (2014): Interaction of egocentric and word-centered reference frames in the rat posterior cortex. *J Neurosci* 34:5431–5446.
- Yartsev MM, Ulanovsky N (2013): Representation of three-dimensional space in the hippocampus of flying bats. *Science* 340:367–372.