NEUROSCIENCE

Neural representations of space in the hippocampus of a food-caching bird

H. L. Payne[1], G. F. Lynch[2], D. Aronov[1]*

Spatial memory in vertebrates requires brain regions homologous to the mammalian hippocampus. Between vertebrate clades, however, these regions are anatomically distinct and appear to produce different spatial patterns of neural activity. We asked whether hippocampal activity is fundamentally different even between distant vertebrates that share a strong dependence on spatial memory. We studied tufted titmice, food-caching birds capable of remembering many concealed food locations. We found mammalian-like neural activity in the titmouse hippocampus, including sharp-wave ripples and anatomically organized place cells. In a non–food-caching bird species, spatial firing was less informative and was exhibited by fewer neurons. These findings suggest that hippocampal circuit mechanisms are similar between birds and mammals, but that the resulting patterns of activity may vary quantitatively with species-specific ethological needs.

Vertebrates differ greatly in their forebrain anatomy but are capable of markedly similar cognitive functions. The extent to which these functions share neural mechanisms across species is unclear. One example is spatial memory, which depends on hippocampal regions in fish, reptiles, birds, and mammals (*1*–*4*). Despite shared embryological origin (*5*, *6*), these regions differ in anatomy and cytoarchitecture (*7*–*9*). Non-mammals also appear to lack hippocampal activity patterns that are central to models of spatial memory: place cells, the firing of which represents location during movement through space (*10*, *11*), and sharp-wave ripples (SWRs), which replay activity during immobility and sleep (*12*, *13*). Unlike place cells observed in mammals, hippocampal activity reported in non-mammals is neither confined in space nor stable over time (*14*–*18*). In addition, non-mammalian SWRs have only been found outside of the hippocampus (*19*–*22*).

The prevailing explanation for these findings is that non-mammalian spatial memory operates through mechanisms that are fundamentally distinct from those in mammals and do not require place cells or SWRs (*14*, *22*). However, another possibility is that these firing patterns exist across vertebrates but are quantitatively different or less prevalent in non-mammals and thus difficult to detect. We also considered the possibility that differences in hippocampal activity are related to species-specific ethological demands. In fact, mammals with well-documented hippocampal activity (rodents, primates, and bats) are all renowned for their spatial abilities (*10*, *23*, *24*). Therefore, it may be informative to determine whether classic hippocampal activity patterns exist in a non-mammal that also has exceptional spatial memory.

We chose to record in a food-caching bird, the tufted titmouse. Food-caching birds are memory specialists capable of remembering many scattered, concealed food locations (*25*). Accurate cache retrieval requires the hippocampus, which is enlarged in food-caching birds (*2*, *3*, *26*). We designed miniature microdrives that allowed these small birds to move freely in a two-dimensional arena. We recorded in the hippocampus (fig. S1) while titmice foraged for randomly dispensed sunflower seed fragments (Fig. 1, A to C, fig. S2, and movie S1). These experiments mimicked classic rodent studies that probed neural representations of space without explicitly requiring memory use (*27*).

Two clusters of recorded units were revealed by analysis of electrophysiological properties (n = 538 and 217 cells). Cells in the first cluster had lower firing rates, wider spikes, a larger first peak of the spike waveform (Fig. 1, D and E), and were more bursty (CV2 1.1 ± 0.2 and 0.9 ± 0.1, respectively, $P = 10^{-88}$, t test) than cells in the second cluster. These properties match those of excitatory and inhibitory neurons in the mammalian hippocampus, respectively (*28*, *29*). Spike time cross-correlograms for pairs of simultaneously recorded neurons confirmed this categorization (fig. S3). Thus, similar criteria can distinguish putative excitatory and inhibitory neurons in birds and mammals.

We observed spatially localized neural activity in the titmouse hippocampus (Fig. 1F). We used conventional criteria (see the supplementary materials and methods) to quantify spatial tuning ("spatial information") and the stability of this tuning within a session ("spatial stability"). Neurons for which both measures were larger than would be expected by chance ($P < 0.01$) were considered significantly spatial (321/538 excitatory and 144/217 inhibitory cells). The firing fields of such excitatory neurons fully tiled the environment (fig. S4), reminiscent of rodent place cells. We will therefore refer to significantly spatial excitatory neurons as "place cells."

In rats, place cell firing is most strongly tuned to position 100 to 200 ms in the future (*27*). Despite different methods of locomotion in titmice and rats (discrete hops versus continuous walking), titmouse place cells were also tuned to future position (median delay 225 and 250 ms for spatial information and stability, respectively, n = 321 place cells; both greater than zero, $P < 10^{-14}$, Wilcoxon signed-rank test; Fig. 1G and fig. S5). Some neurons also displayed head direction and speed tuning (254/522 and 224/538 excitatory cells, respectively; fig. S6). Note that many place cells (107/318) were not modulated by head direction, implying that their spatial tuning could not be explained entirely by visual inputs (*30*). Place cells were also found in separate experiments on a linear track (77/105 excitatory cells) and displayed directional tuning [54/77 place cells; fig. S7, as in (*18*)]. The titmouse hippocampus therefore displays multiple features of spatial activity observed in mammals, suggesting that mechanisms of hippocampal coding in birds are not fundamentally distinct from those in mammals.

We investigated whether place cells were anatomically organized within the hippocampus by systematically varying recording locations. We constructed a three-dimensional model of the titmouse hippocampus (fig. S1) and registered recording locations to this template. Spatial information and stability were correlated to location along the anterior-posterior axis ($P < 10^{-4}$ for both; see the supplementary materials and methods; Fig. 2) but not along the other stereotaxic axes ($P > 0.27$; fig. S8) or between published subdivisions of the avian hippocampus (*31*) ($P > 0.18$). Place cells were concentrated in the anterior two-thirds of the hippocampus, with incidence increasing from <10% to >70% of excitatory cells from the posterior to the anterior pole. In rodents, place cells followed a similar gradient along the dorsoventral ("long") axis (*32*), which is in fact hypothesized to be homologous to the avian anterior-posterior axis (*6*, *33*).

Why did previous recordings in birds not reveal similar spatial representations (*15*, *18*)? If spatial coding is related to ethological demands or experiences, then place cells may be less common, less spatially informative, or more anatomically restricted in other species. To explore these possibilities while ruling out the effects of experimental technique, we repeated our experiments in the zebra finch, a species that, like those previously studied, does not cache food.

Zebra finches exhibited similar behavior to titmice in the random foraging task (fig. S2).

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As in titmice, zebra finch hippocampal neurons had electrophysiological characteristics matching those of putative excitatory and inhibitory cells (fig. S9A). A fraction of these neurons had spatially modulated firing (48/179 excitatory cells and 13/59 inhibitory cells were significantly spatial). As in titmice, place cells were predictive of future location (fig. S9B), were found mainly in the anterior hippocampus (fig. S9, C to E), and exhibited firing that tiled the environment (fig. S4). However, despite these similarities, there appeared to be differences in spatial coding between species. To quantify these differences, we sought to account for the larger size of the titmouse hippocampus and for uneven sampling of the long axis. We therefore compared activity across species in two ways, using landmarks defined functionally or anatomically.

First, we defined functionally an anterior segment of the hippocampus in each species as the region with a high density of place cells (see the supplementary materials and methods). This segment was proportionately larger in titmice than in zebra finches (60% versus 49% of the anterior-posterior extent of the hippocampus). Further, even within this anterior segment, place cells were more prevalent in titmice (64% versus 47% of cells at the anterior pole; Fig. 3A). To illustrate this difference, we sorted cells in the anterior segment

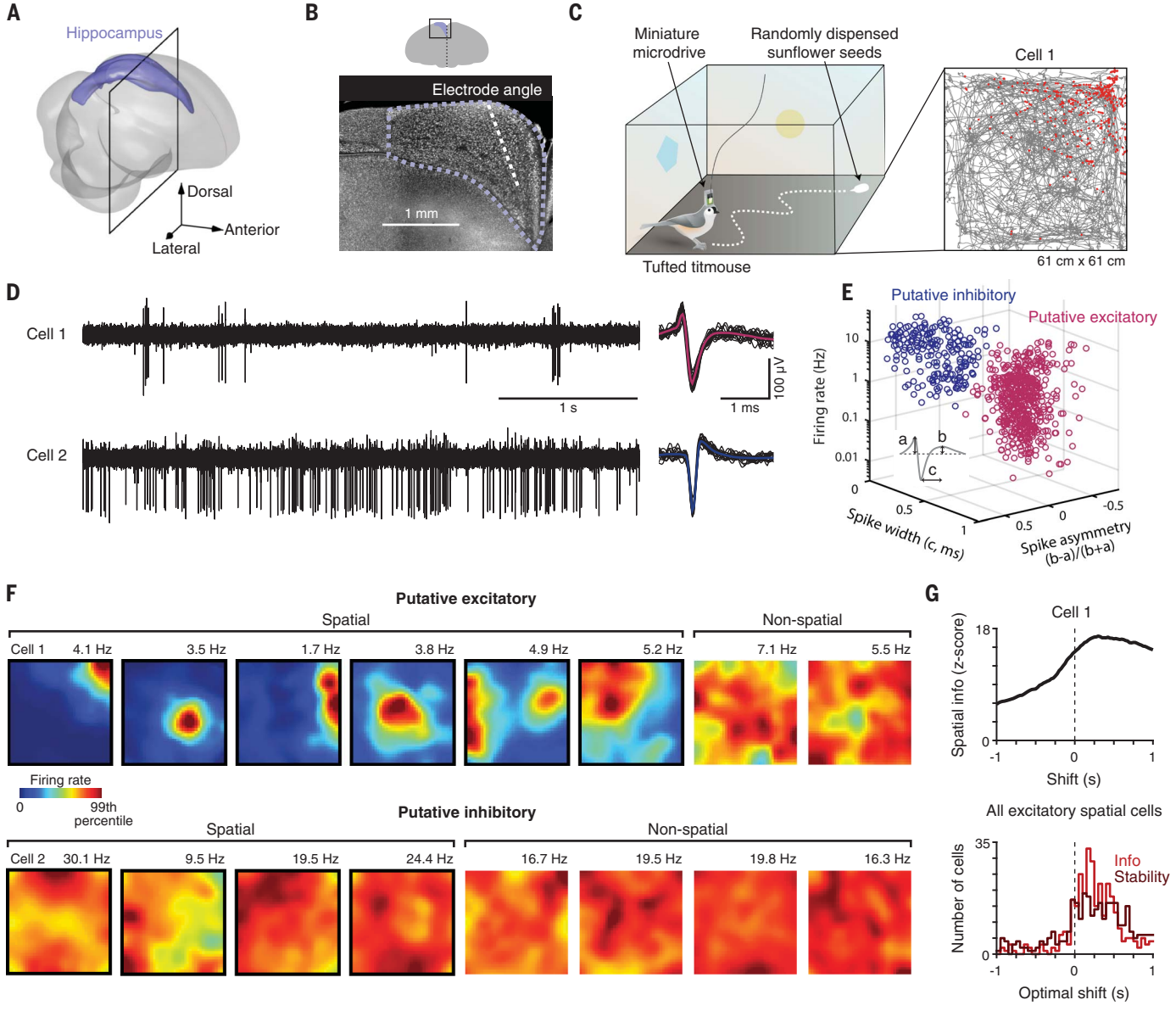

Fig. 1. Place cells in the hippocampus of tufted titmice. (**A**) Reconstruction of the titmouse hippocampus. (**B**) Fluorescent Nissl-stained coronal section at the location indicated by the black box in (A). Dashed purple line is the hippocampal boundary. Dashed white line is the electrode approach angle. (**C**) Left, schematic of the random foraging arena. Right, bird's trajectory (gray lines) and locations of spikes (red dots) for an example hippocampal cell. Cell 1 refers to the same neuron in all panels. (**D**) Voltage traces and 20 spike waveforms for two example cells (black: example waveforms; pink or blue: mean). (**E**) Electrophysiological characteristics for all cells recorded during the random foraging task, classified as excitatory cells (n = 538) and inhibitory cells (n = 217). (**F**) Example spatial rate maps for excitatory and inhibitory neurons. Numbers above plots indicate maximum of color scale. (**G**) Top, spatial information as the time shift between spikes and behavior was varied for an example cell. The peak at a positive shift ("optimal shift") means that spikes were most informative about the bird's future position. Bottom, histogram of optimal shifts for spatial information and spatial stability.

by spatial information and compared neurons with corresponding rank. For all ranks, spatial information was higher in titmice than in zebra finches (Fig. 3B).

Second, we identified a reliable anatomical landmark that divided the hippocampus roughly in half volumetrically (see the supplementary materials and methods). We compared spatial information and stability between species on the anterior and posterior sides of this landmark. Both measures were larger in titmice than in zebra finches in the anterior hippocampus (n = 136 and 44 excitatory cells with peak rates >3 Hz, respectively, $P < 0.001$; Fig. 3C) but not in the posterior hippocampus (n = 14 and 19 cells, $P > 0.5$; species difference was larger in anterior versus posterior hippocampus, $P < 0.01$; Fig. 3D). These analyses revealed a difference between species: Place cells were more abundant and activity was more spatially informative and stable in titmice than in zebra finches.

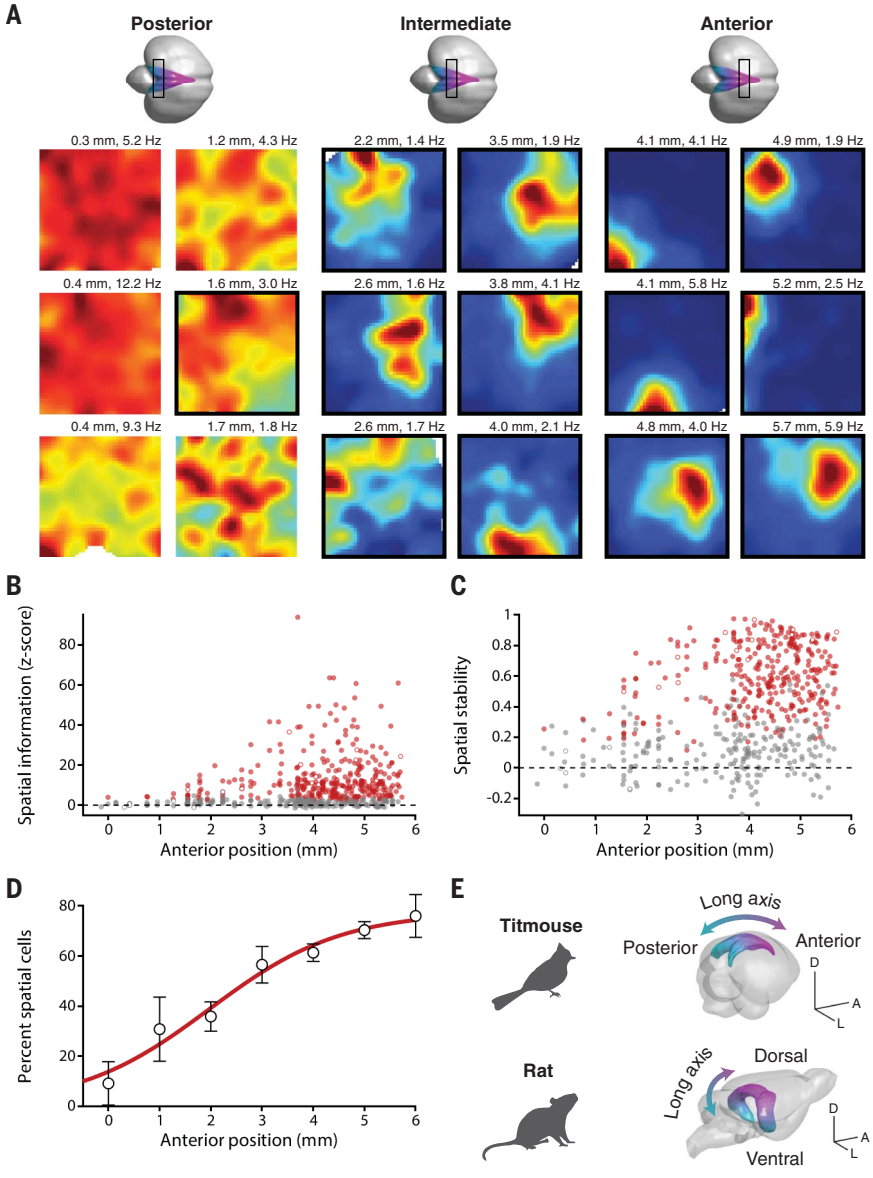

Fig. 2. Spatial representations are organized along the long axis of the hippocampus. (**A**) Example spatial rate maps for excitatory neurons from posterior, intermediate, or anterior hippocampus, plotted as in Fig. 1. Place cells are outlined in black. The location on the anterior-posterior axis (distance from lambda) is indicated above each map. (**B**) Spatial information, normalized by taking the z-score of the actual value relative to a shuffled dataset, plotted for all 538 excitatory cells. Red indicates place cells, gray indicates non–place cells, and open markers are the example cells in (A). (**C**) Spatial stability plotted as in (B). (**D**) Fraction of excitatory cells that passed place cell criteria binned across anterior position. Error bars indicate mean ± SEM; red line is the logistic sigmoid function fit. (**E**) Schematic of the spatial gradient along the hippocampal long axis in tufted titmice and in rats [three-dimensional model generated using published data (*48*)]. Scale bars, 5 mm.

In addition to the similarities in "online" activity during locomotion, are there also similarities in "offline" activity? In the mammalian hippocampus, periods of quiescence contain SWRs defined by (i) a fast "ripple" oscillation in the local field potential (LFP), (ii) a slower "sharp-wave" deflection, (iii) synchronization of spikes to the ripple, and (iv) propagation across the hippocampus (*12*, *34*). We examined activity during sleep (see the supplementary materials and methods) in the avian hippocampus and found events with these characteristics (for titmice, see Fig. 4, A and B; for zebra finches, see fig. S9; 100–200 Hz ripple frequency band). SWRs were frequent (0.3 to 1.1 events/s, n = 5 titmice). Both excitatory and inhibitory cells increased firing during SWRs but preferred different phases of the ripple oscillation (fig. S10). In contrast to ripple-frequency oscillations, we did not observe oscillations at lower frequencies, including in the theta band [similar to bats (*35*); fig. S11].

To analyze SWR propagation, we implanted electrode arrays spanning >5 mm of the hippocampal long axis. About half of the events occurred on more than one electrode, and some spanned most of the recorded extent of the hippocampus (length constant 0.90 mm; Fig. 4, C to E). Propagation speed was 0.12 ± 0.07 m/s (median ± median absolute deviation, n = 15,790 SWRs), with a bias for propagation in the posterior-to-anterior direction (70% of SWRs). Avian SWRs are therefore global, propagating events in the hippocampus.

During mammalian SWRs, current sinks and sources (net electrical current flowing into or out of cells, respectively) occur within specific layers of the hippocampus (*36*). Does a similar laminar organization exist in birds? We examined SWRs across the hippocampal transverse plane in titmice either by incrementally advancing microelectrodes or by recording synchronously across depths with silicon probes. We found that the sharp-wave component often inverted from positive to negative polarity between dorsal and ventral locations (Fig. 4F). To relate these changes in waveform to electrical currents, we calculated the current source density (CSD) either across the entire transverse plane or collapsed along the radial axis (Fig. 4, G and H). The CSD was organized along the radial axis, with a current source dorsal to a sink. Thus, SWRs display laminar organization in the titmouse hippocampus (Fig. 4I).

There have been relatively few studies of neural activity in the non-mammalian hippocampus, and these studies have not reported neurons resembling classic place cells. Rather, they found other types of spatial neurons,

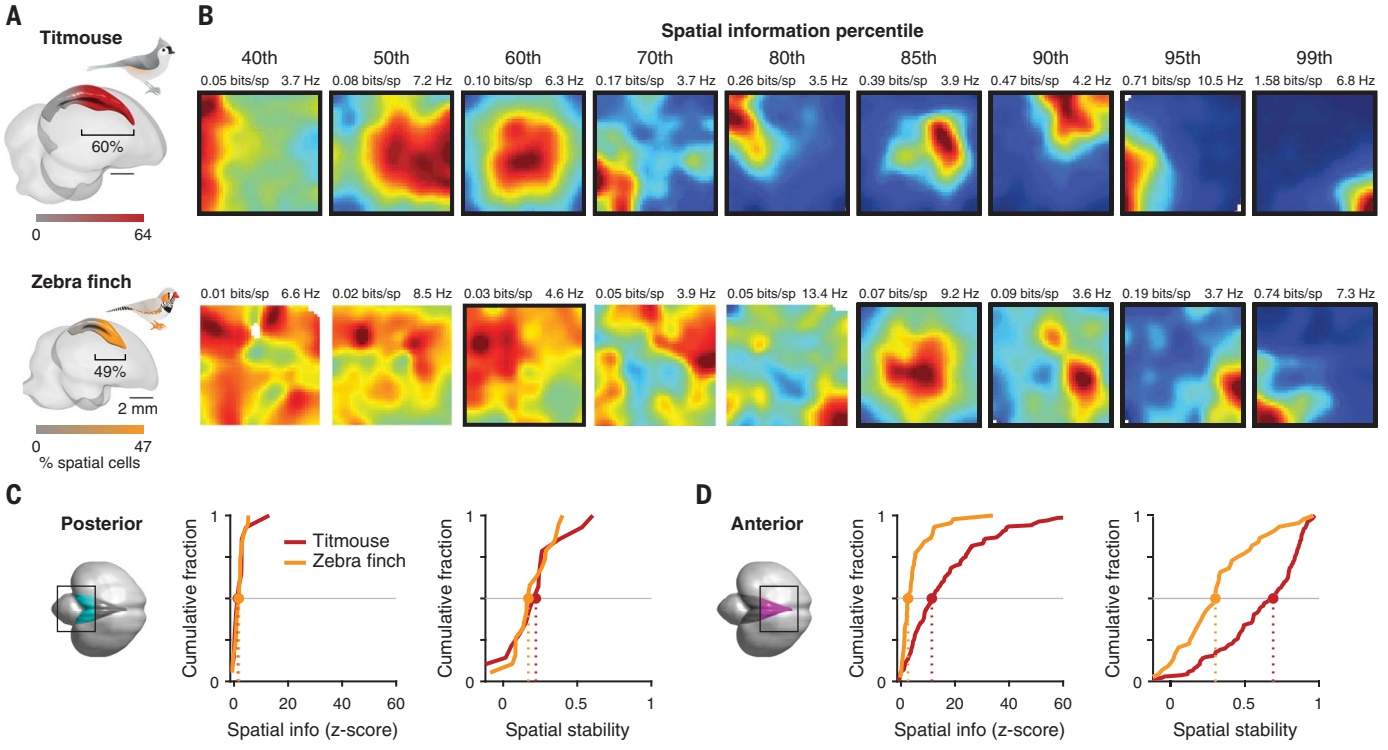

Fig. 3. Spatial representations differ across avian species. (**A**) Titmouse (top) and zebra finch (bottom) hippocampus colored according to a logistic sigmoid fit to the percentage of place cells at each anterior position. The bracket indicates the percent of hippocampal length anterior to the inflection point of this fit. (**B**) Example spatial rate maps. All excitatory cells within the bracketed region in (A) with peak rates >3 Hz were ranked by spatial information, and rate maps for the cells corresponding to the given percentiles are shown. Place cells are outlined in black. Raw spatial information (left) and maximum of color scale (right) are given above each plot. (**C**) Cumulative distributions of normalized spatial information and spatial stability for excitatory cells with peak rates >3 Hz from the posterior hippocampus, defined anatomically dotted lines indicate median values. (**D**) Same as (C) but for the anterior hippocampus.

including head direction cells, border cells, and broadly tuned cells (*14*–*18*). By contrast, we found place cells that fired in restricted regions of space and, as a population, tiled the environment. As in mammals, these cells were anatomically organized along the long axis of the hippocampus. Our findings provide evidence for shared neural mechanisms underlying spatial representation across hippocampal circuits separated by 320 million years of evolution (*5*).

Mechanisms that produce place cells are debated but are hypothesized to depend on specialized internal connections within the hippocampus (*37*). Furthermore, patterns of external inputs are thought to explain differences in spatial coding along the long axis (*38*). Our results suggest that similar features of hippocampal circuitry may give rise to the observed place cells in birds.

We also report SWRs in the avian hippocampus. It is unknown whether these events originate in the hippocampus itself. In fact, SWRs have been reported in other brain regions of birds and reptiles (*19*–*21*). Regardless of their origin, it is unclear why hippocampal SWRs are experimentally detectable in birds. In mammals, hippocampal SWRs are thought to be detectable because of crystalline cytoarchitecture: a dense pyramidal cell layer and parallel dendrites that allow summation of small currents into large LFP fluctuations (*12*). In the avian hippocampus [unlike in nonavian reptiles and mammals (*9*)], cell clustering is modest and limited to a medial V-shaped region, and dendrites are not strictly aligned (*7*, *31*, *39*) (Fig. 1B). It is possible that detectable SWRs result from a more subtle arrangement of cells in birds. It is also possible that they result from other patterns of hippocampal organization along the radial axis, such as differences in synaptic input (*36*, *40*), morphology (*41*), or intrinsic cell properties (*7*). Note that the organization of current flow in birds is inverted along this axis compared with mammals (source is superficial to sink; Fig. 4I). This is reminiscent of the inverted cerebral cortex in mammals compared with other amniotes (*5*). Regardless of the mechanisms, our results suggest that as-yet-unidentified patterns of radial axis organization may exist in the avian hippocampus.

Despite these similarities across clades, there were also significant differences between bird species. We found weaker spatial coding in zebra finches than in titmice. Previous studies reported even weaker place coding in other non–food-caching birds (pigeons and quails): a near absence of place cells (*18*) and low reliability of spatial patterns across time (*15*). Apparent differences between zebra finches and these species could potentially be due to the relatively sparse sampling of the anterior hippocampus in previous recordings. However, because we densely sampled the entire anterior-posterior extent of the hippocampus, stronger place coding in titmice likely reflects a true species difference.

There are many innate and experience-related differences between titmice and other recorded birds, but it is tempting to speculate that enhanced spatial coding in titmice is related to the demands of food caching. Place cell activity is sparse (*42*); that is, firing occurs in a small fraction of the environment. Although sparse coding requires more neurons, it may allow new memories to form quickly without interfering with old memories (*42*, *43*). Increased sparsity may thus confer an adaptive advantage to food-caching birds. Our results demonstrate functional and anatomical similarity in a higher brain region of distant vertebrates. At the same time, these findings contribute to the growing evidence

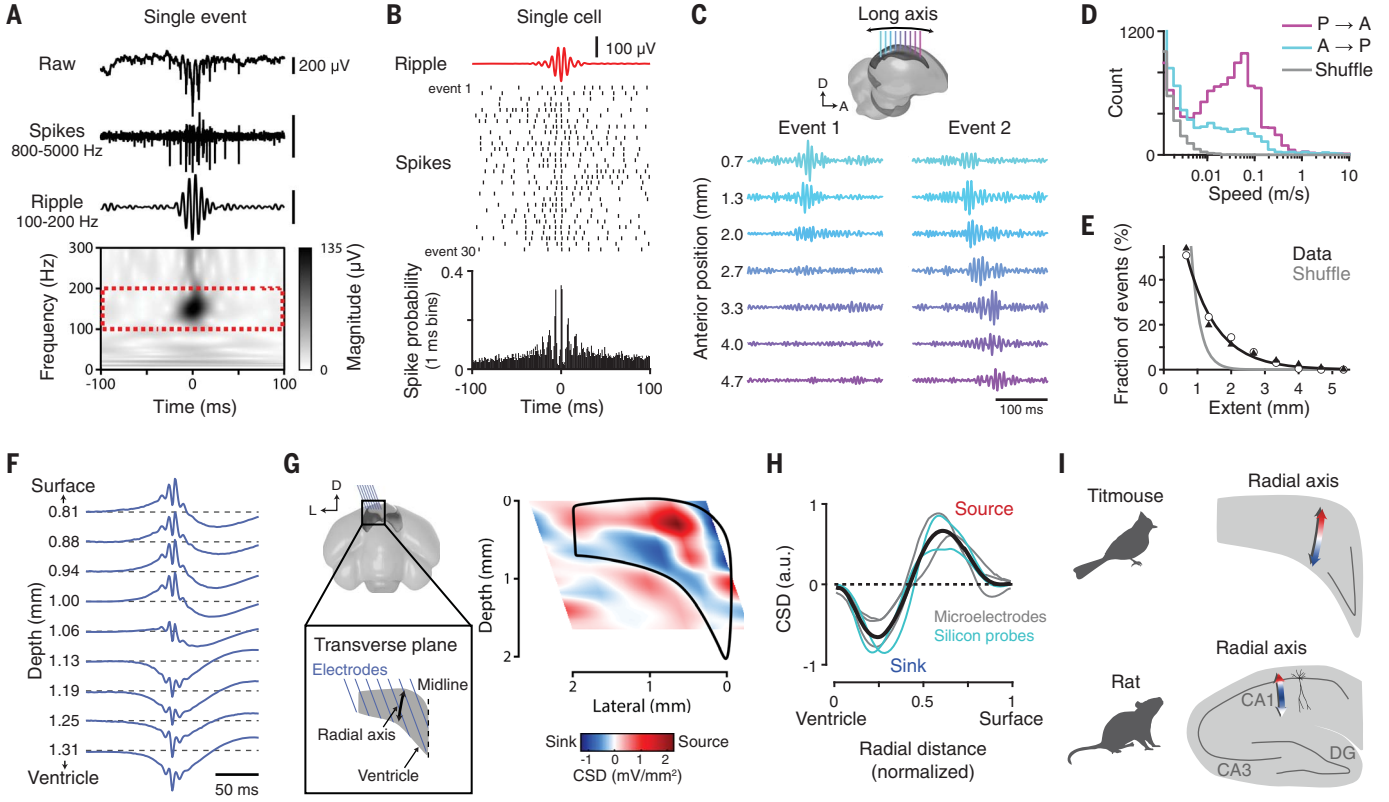

Fig. 4. SWRs in the avian hippocampus. (**A**) Single SWR in the titmouse hippocampus across frequency bands. (**B**) Spike raster (top, 30 consecutive SWRs) and spike histogram (bottom, all SWRs) aligned to SWR times (defined in the supplementary materials and methods) for a single cell. (**C**) Top: electrode placement along the hippocampal long axis. Bottom: example SWRs detected on multiple electrodes. Event 1 is more locally restricted, whereas Event 2 propagates through the entire recorded length of the hippocampus. (**D**) Speed of SWRs propagating in the posterior-to-anterior (P→A) and anterior-to-posterior (A→P) directions compared with shuffled data. (**E**) Distribution of SWR extent along the long axis. Markers indicate individual titmice; black line is the exponential fit to all points; gray line is the exponential fit to shuffled data. (**F**) LFP averaged across SWRs recorded sequentially at different depths in the hippocampus. (**G**) Left: electrode placement within the transverse plane of the hippocampus. Right: Two-dimensional CSD map within the transverse plane of one bird. Hippocampus outlined in black. (**H**) One-dimensional CSD across the radial axis. Gray and cyan lines represent data from individual birds; black line is the average. (**I**) Layered CSD organization during SWRs across species. In rat, the primary current sources (red) and sinks (blue) correspond to the pyramidal cell layer and the stratum radiatum, respectively (*36*).

that hippocampal coding may vary according to the ethological demands of different species (*23*, *24*, *44*–*47*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S11
Movie S1
References (*50*–*65*)

View/request a protocol for this paper from Bio-protocol.

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Conserved spatial memory mechanisms

Food-caching birds are memory specialists that can remember thousands of hidden food items. Using electrophysiological recordings from freely behaving birds, Payne *et al.* analyzed neuronal activity in the likely hippocampus homolog of two bird species, the tufted titmouse and the zebra finch. They chose these two species to compare, respectively, birds that do and do not display food-caching behavior. Place cells and typical hippocampal firing patterns that resembled rodent neuronal activity could be detected in the extreme memory specialists. Compared with titmice, however, spatial activity was noticeably weaker and less abundant in zebra finches. These findings provide evidence that the neural processes underlying spatial memory are remarkably conserved across widely divergent hippocampal circuits separated by millions of years of evolution.

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