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Short communication

Rotation of visual landmark cues influences the spatial response profile of hippocampal neurons in freely-moving homing pigeons

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Abstract

Pigeon hippocampal neurons display two spatial response profiles: location fields frequently at goals, and path fields connecting goals. We recorded from 15 location and six path cells, with color cues positioned near four goal locations. Following color cue rotation, most location cells (12/15) shifted their response fields; path cells (5/6) lost their fields. Therefore, local visual cues can independently define a reference frame for location cells, but path cells may be more broadly tuned to context or alternative reference frames.

Keywords: Hippocampus; Place cells; Pigeon; Navigation

In freely-moving homing pigeons, hippocampal formation (HF) neurons display two seemingly complementary spatial response profiles [7,16], which by their nature would support HF-dependent spatial cognition [1,2]. *Location cells* (about 25% of those recorded) display statistically-reliable, local regions (patches) of higher activity that predominantly occur at or near goal (food bowl) locations. Location cells are found in both sides of the HF. *Path cells* (about 25% or more of the cells found in the left HF) display increases in activity when pigeons are moving along maze corridors connecting goal locations. Path cells are directionally modulated in a way suggesting sensitivity to where a pigeon is going to or coming from [7,16], and are found only in the left HF. However, for both profiles, position in space generally explains less of the overall firing rate variance (as demonstrated by lower position reliability), compared to rat hippocampal place cells [12,14].

The discovery of location and path cells, and the reliable firing rate increases they display at important locations, naturally raises the question of what environmental features enable the discrimination of different locations. A pigeon engaging in HF-dependent navigation prevailingly relies on visual landmarks [2,4,17]. This leads to the hypothesis that the spatial response profiles are controlled, at least in part, by the visual properties of an environment. The current experiment was designed to examine the role of local visual cues in establishing and maintaining spatial response profiles.

Five adult homing pigeons (*Columba livia*), between 350 and 450 g in weight and of undetermined sex, were used. During training and recording, the birds were maintained at 85% of their free-feeding body weight to encourage exploration for food using hunger as an incentive.

The recording environment was an analogue eight-arm radial arena identical to that used in a previous study [6]. The arms were painted white, so that a colored light would illuminate the entire arm. Four arms contained different colored light cues and a sand-filled bowl that was supplied with food pellets via tubes originating from outside the arena (the other four arms contained sand-filled food bowls only). The bowls were re-baited (out of sight of the animal) continuously, so that each baited arm had a similar motivational significance. The light colors were randomly set to one of two spatial configurations (clockwise from the northwest bowl: (1) Blue/Red/Green/Yellow or (2) Red/Green/Yellow/Blue). In addition to the colors, it was possible that birds could have used non-arena cues such as

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the overhead fluorescent lighting, camera, wires, and subtle shape/color differences in the curtains, as well as extra-maze sounds (experimenter, pellets rolling in tubes, and audio from the unit amplifier) as spatial cues. A bird was trained three times per week until it moved rapidly between bowls for at least 10 continual minutes. At the end of training, the pigeons typically directed their movements only to the baited arms, periodically altering their sampling direction (clockwise or counter-clockwise). No bird maintained the same sampling direction throughout an entire session. While pellets made sounds through the tubes, no bird was observed to alter its behavior following pellet sounds.

The headstage [6] consisted of three implanted tetrodes bundles driven down 960 μm (initially), with a reference electrode implanted into the nidopallium. We implanted headstages into either the left (three birds) or right (two birds) HF, each placed at a 30° angle medially to target ventral HF and avoid puncturing the central cerebral sinus. The recording software (DataWave, DataWave Technologies, Berthoud, CO) enabled simultaneous recording from two "stereotrodes" (each using two wires from different tetrode bundles). Neural activity was linked with bird position using a headstage-mounted infrared LED.

Pigeons were given several days to recover from surgery, then retrained to move through the arena with a recording cable (attached to the headstage) clipped to a harness. Recording sessions started when a bird readily moved between all bowls within the arena with no evidence of headstage discomfort or fear of the tethered recording cable.

For recording sessions, a pigeon was first enclosed in an unbaited "holding space" arm, where the experimenter searched for isolated unit activity. If isolated activity was not found, the electrodes were driven deeper by 40 μm. We then waited 5–10 min to allow the electrodes to stabilize at the new depth, and then resumed searching electrodes for activity. If satisfactory activity was not found after 320 μm, the bird was removed from the arena, returned to the home cage, and re-tested on a subsequent day.

When isolated units were detected online, a baseline recording of 5 min was made. Then, the barrier into the arena was lifted and the bird was allowed to move freely during the *pre-rotation session phase*. For this phase, we randomly selected one of the two possible light configurations. As a pigeon ate food pellets from each bowl, pellets were added after the pigeon left the visited arm. A pigeons was allowed to explore for at least 10 min, when it was returned to the visually-isolated holding space. The lights were switched to the alternate configuration (90° clockwise or counter-clockwise rotation). The bird was re-released into the arena for a second 10-min *post-rotation session phase*.

A candidate unit had to meet several criteria to be included in our dataset: (1) >3:1 signal-noise ratio between spike amplitude and overall background activity; (2) the bird visited all of the color-associated arms >20 times during both recording phases; (3) inter-spike interval >5 m s to indicate neuronal isolation; (4) at least one clearly-defined "patch" with >9 contiguous pixels of at least 2× the extra-patch firing rate, (5) each patch pixel was visited >3 separate times during both sessions, (6) unit amplitude and waveform characteristics did not change across sessions. Of 51 recorded neurons, 21 met these criteria.

All isolated unit activity was analyzed offline using DataWave Discovery (for unit waveform and time stamp extraction) and custom-written software [6] in MatLab (MathWorks, Inc., Natick, MA). We analyzed the firing rate profile (change in spike rate across a recording session), spatial response profile (rate maps), within-phase reliability (Pearson's correlation of rate maps across sequential 5-min epochs, where 1 indicates perfect correlation, and 0 indicates no relation), and spatial coherence (measure of local orderliness of spatial firing [11]).

For each unit, the rate maps of the two phases were compared for changes in patch locations and overall firing rate. Location cells had roughly circular patch patterns, while path cells had linear patch patterns along corridor(s) connecting bowls [6]. Also, the two rotation phases were partitioned into separate 5-min rate maps to determine changes in spatial response profile within a phase. Within-phase partition map reliability scores were calculated for each neuron.

Rate maps were inspected to determine if the spatial response profile of a neuron: (a) remained unchanged following light rotation, (b) exhibited patches that rotated with the rotation of the lights, or (c) exhibited a change in field(s) of higher firing rate inconsistent with the rotating lights. First, we verified that the patches during the pre-rotation phase rotated in the correct direction with the lights such that post-rotation patches were approximately 90° clockwise or counter-clockwise relative to the pre-rotation phase. Second, mean overall firing rate within pre-rotation patches of each location cell were compared to the same pixel locations during the post-rotation phase. If patches rotated, firing rates of pixels in pre-rotation patch locations should be greater than in the post-rotation recording. Similarly, firing rates of pixels composing post-rotation patches should be greater than in the pre-rotation recording. Finally, we determined if mean patch firing rates, even though at different locations, differed from pre- to post-rotation recording. If a cell had several patches, all patches had to rotate in the appropriate light-related direction to be scored as a successful rotation.

All values are reported as mean ± S.E.M. Based on the original classification scheme of location and path cells [6], we found 15 location cells (example in Fig. 1) and six path cells (example in Fig. 2). The distribution in firing rates (mean 6.4 ± 1.6 spikes/s, range 0.03–30.6) and coherence (mean: 0.55 ± 0.03, range 0.03–0.77) were consistent with previously reported values [6].

During pre-rotation recording, location cells exhibited 2.5 ± 0.4 patches, 20.0 ± 3.6 pixels per patch, and a mean patch-firing rate of 10.6 ± 3.4 spikes/s. During the post-rotation recording, the same cells had 2.5 ± 0.5 patches, 18.0 ± 2.0 pixels per patch, and a mean patch-firing rate of 7.5 ± 2.6 spikes/s. These characteristics were not significantly different (*two-tailed pairwise t-tests*, d.f. = 14, $P > 0.20$ for all three). With one exception, all location cells had fields of higher firing rates (patches) at or near food bowls. Mean within-patch firing rates were 5.2 ± 1.8 times higher than the non-patch mean arena-firing rate during the pre-rotation session, and 2.4 ± 0.4 times higher during the post-rotation session.

Of the 15 location cells, 12 shifted their patches in parallel with the rotated lights (e.g., Fig. 1). The other three

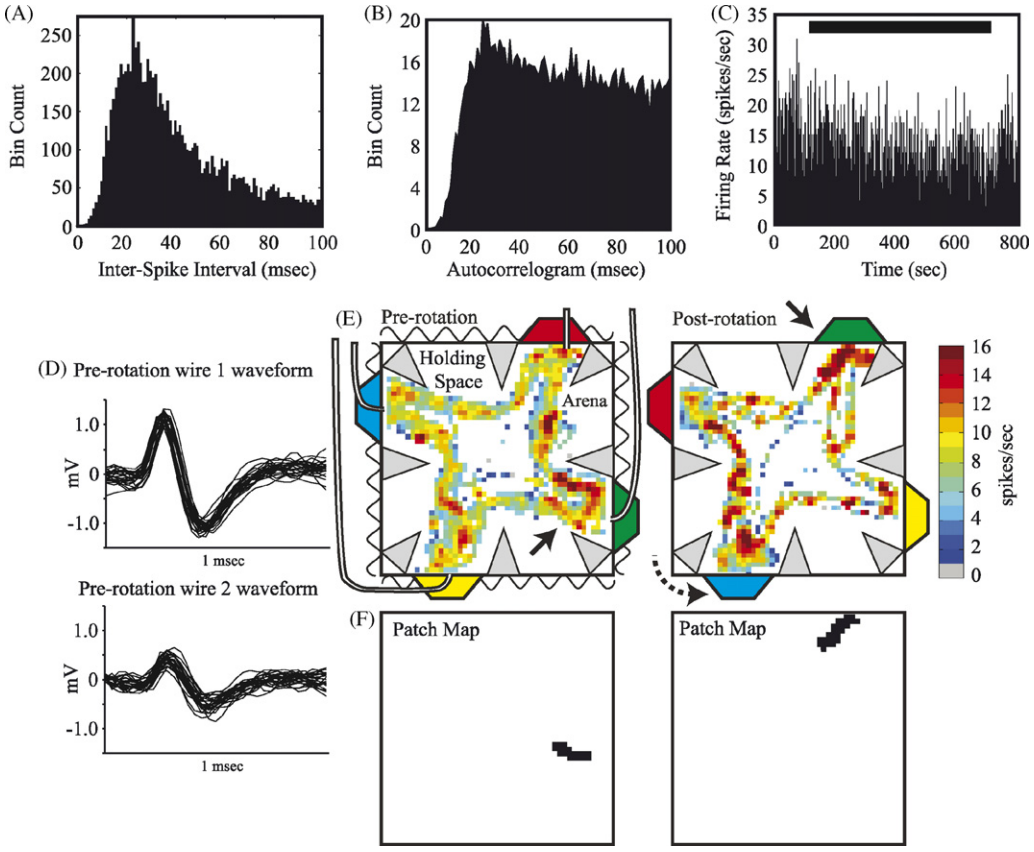

Fig. 1. Neural parameters and rate maps of a representative location cell, with one patch (>9 contiguous pixels) of higher activity, demonstrating a 90° counter-clockwise patch rotation in a right HF-implanted bird. (A) Inter-spike interval (ISI) plot with a 24-m s peak ISI interval. (B) Autocorrelogram with no evidence of rhythmicity or bursting. (C) Firing rate of unit across a recording session, with a slight decline in firing rate through the recording session. Black bar: bird running in the arena. (D) Representative waveforms using the first 25 neural impulses across two electrodes. Unit exhibited good isolation and was closer to wire 1. (E) Rate maps pre- and post-rotation. This location cell maintained its increased firing rate at the bowl associated with the green-light arm (solid arrows). There was little difference between pre- and post-rotation patches with respect to mean patch size (15.0 and 19.0 pixels, respectively), mean within-patch firing rates (both 24.1 spikes/s), or overall non-patch firing rate (12.0 spikes/s for both). (F) Patch map for unit showing areas defined by 9+ contiguous pixels of >2× mean arena firing rate. Figure conventions: high firing rates (scale to right): red pixels; low firing rates: blue pixels; visited pixels with 0.0 firing rate: grey pixels; wavy lines: light-blocking curtains; triangles: wedges separating arms; tubes: food delivery tubes to baited arms; trapezoids: color of arm illumination; dotted arrow: light rotation direction. Arena size: 1.75 m (L) × 1.75 m (W) × 1 m (H).

had un-shifted patches ($n = 2$), or shifted to the opposite arm (180°, $n = 1$). In the 12 shifted cells, the spatial response field rotation was typically detectable within the first 5 min (two neurons rotated later in the post-rotation session). The mean post-rotation reliability (0.29 ± 0.06), calculated between the first and second 5-min recording epochs, did not differ from similarly-examined pre-rotation scores (0.32 ± 0.06; *two-tailed pairwise t-test*, $t = -0.770$, d.f. = 14, $P = 0.45$). Patch rotation was verified by comparing mean firing rates of patches between the original location and the rotated location, across the pre- and post-rotation firing rate maps. There was a significant decrease in the mean firing rate at the original patch location(s) (80.5% decrease ±0.04, *one-tailed pairwise t-test*, $t = -4.43$, d.f. = 11, $P = 0.03$), and a significant increase in the mean firing rate at the post-rotation patch location(s) (42.9% increase ± 0.1, *one-tailed pairwise t-test*, $t = -3.86$, d.f. = 11, $P = 0.04$). Finally, the mean firing rate of pre-rotation patches (10.4 ± 3.9) was not significantly different from the post-rotation patches (8.0 ± 2.7; *two-tailed pairwise t-test*, $t = 1.35$, d.f. = 11, $P = 0.21$). Therefore, the arm colors prevailingly guided the spatial tuning of the sampled avian HF location cells.

By contrast, none of six path cells shifted their paths in parallel with the light rotation. One cell displayed a pre-rotation spatial response profile with two paths (corridors). In the post-rotation session, the path components were abolished, but a location patch was seen where the paths intersected (blue arm; Fig. 2). One cell shifted its path response field inconsistent with the light rotation (180°). The remaining four path cells had their patch(es) of higher activity completely disrupted, similar to the path fields in Fig. 2. The overall disruption of selectivity was supported by patch loss; cells displayed 2.4 ± 0.8 patches during pre-rotation recordings, but only 0.4 ± 0.2 patches during post-rotation recordings (*two-tailed pairwise t-test*, $t = 2.60$, d.f. = 5, $P = 0.048$). This was not due to a decrease in reliability: the mean within pre-rotation (0.39 ± 0.11) and post-rotation (0.40 ± 0.14) reliability between the first two 5-min recording epochs was not significantly different (*two-tailed pairwise t-test*, $t = 0.05$, d.f. = 5, $P = 0.96$).

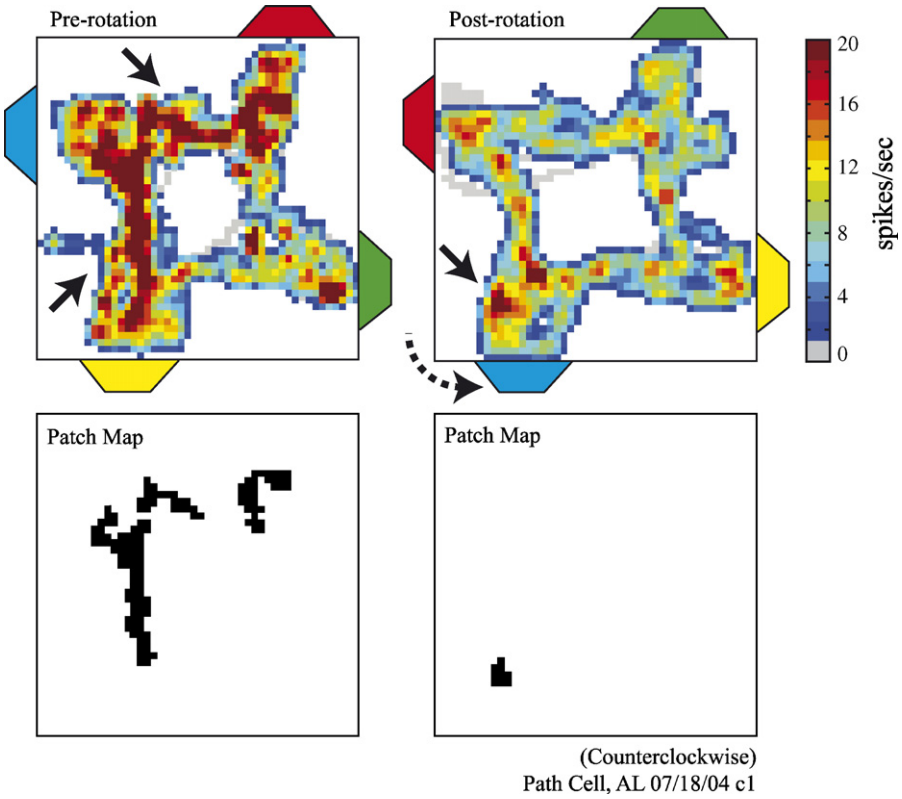

Fig. 2. Pre-rotation (left) and post-rotation (right) rate maps of a representative path cell demonstrating disruption of a path response in a left hippocampus-implanted bird. The path responses (top left) and patches (bottom left) in the N and W corridors (solid arrows) were abolished following light rotation, and one location patch (9 pixels), not evident in pre-rotation, was present in the SW (blue light) arm in the post-rotation session, the color at the intersection of the two pre-rotation paths. Figure conventions as in Fig. 1, panel E.

All recorded neurons were histologically verified to be within the boundaries of HF [9] by labeling electrode depth using marker lesions, and finding them in 50-μm frozen sections of the preserved brain. Isolated neurons were recorded from throughout the various anatomical subdivisions of the homing pigeon HF, but were prevailingly taken from the dorsomedial, ventromedial, and ventrolateral areas [as described in 7]. There were no apparent differences in spatial response profile or rotation tendency across these subdivisions.

The results of the current study reveal that local visual cues distributed in an environment can serve as a reference to shape the spatial response fields of homing pigeon HF neurons. Rotating an array of visual cues during a recording session routinely led to either rotations (location cells) or disruptions (path cells). The data are consistent with the notion that the avian HF is prevailingly recruited to support visually-guided spatial cognition [1,2,15], as it is in monkeys [13], but perhaps less so in rats [3,10].

The discovery of visual control of the spatial response properties of HF neurons is the first experimental demonstration of an external feature controlling homing pigeon HF neuronal activity. In addition to this principal finding, the data offer opportunities for speculation regarding the neuronal implementation of HF-dependent spatial cognition. First, location cells often had their fields of higher activity shift in parallel with rotation of the visual cues. By contrast, there was a clear tendency for path cells to have their field(s) of higher activity disrupted following rotation of the visual cues. For location cells, the visual cues associated with a goal location seems to serve as a local reference determining increased activity, independent of the spatial relationship between that location and the rest of the testing environment (non-rotating cues such as computer location, overhead light orientation, or other subtle room-dependent cues). By contrast, path cells may be more sensitive to the spatial relationship between the local light cues and the overall spatial properties of the environment such as the light cue/bowl positions relative to global arena (non-rotated) visual cues. When that relationship is disrupted following rotation of the light cues, the path sensitivity disappeared, suggesting that path cells may be more tuned to the context [5,8] of the relationship between the local light cues and the other properties of the environment.

A last speculation is related to the effect rotating the lights had on path cells. There was a hint that regions of higher activity that characterize some path cells may be partially dissociable. Although path cell "corridor" regions of higher firing rate were disrupted with light rotation, regions of higher activity at goal locations could persist and rotate with cues [16]. This change in activity following local cue rotation is strikingly similar to the changes seen in rat place cells when a rat is navigating versus simply foraging [5]. As such, corridor response profiles may reflect higher-order processing of information from location cells. For example, path cells may integrate multiple location cell fields associated with local, goal-dependent visual cues with goal-independent frames of reference (in our study,

aspects of the environment that do not rotate). When the goal cues are rotated independently of the other candidate frames of reference, this misalignment between goal-dependent and goal-independent information results in path cells reverting to lower order goal-dependent spatial response profiles.

Whether these speculations will stand up to more thorough testing remains to be seen. However, the demonstration that the spatial response properties of HF neurons are controlled by local visual features represents an important advance in our understanding of HF control of spatial cognition.

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References

[1] Bingman VP, Siegel JJ, Gagliardo A, Erichsen JT. Representing the richness of avian spatial cognition: properties of a lateralized homing pigeon hippocampus. Rev Neurosci 2006;17:17–28.
[2] Colombo M, Broadbent N. Is the avian hippocampus a functional homologue of the mammalian hippocampus? Neurosci Biobehav Rev 2000;24:465–84.
[3] de Araujo IET, Rolls ET, Stringer SM. A view model which accounts for the spatial fields of hippocampal primate spatial view cells and rat place cells. Hippocampus 2001;11:699–706.
[4] Gagliardo A, Ioalé P, Bingman VP. Homing in pigeons: the role of the hippocampal formation in the representation of landmarks used for navigation. J Neurosci 1999;19:311–5.
[5] Hok V, Lenck-Santini P-P, Roux S, Save E, Muller RU, Poucet B. Goal-related activity in hippocampal place cells. J Neurosci 2007;27: 472–82.
[6] Hough GE, Bingman VP. Spatial response properties of homing pigeon hippocampal neurons: correlations with goal locations, movement between goals, and environmental context in a radial-arm arena. J Comp Phys A 2004;190:1047–62.
[7] Hough GE, Pang KCH, Bingman VP. Intrahippocampal connections in the pigeon (*Columba livia*) as revealed by stimulation evoked field potentials. J Comp Neurol 2002;452:297–309.
[8] Jeffery KJ, Anderson MI. Dissociation of the geometric and contextual influences on place cells. Hippocampus 2003;13:868–72.
[9] Karten HJ, Hodos W. A stereotaxic atlas of the brain of the pigeon (*Columba livia*). Baltimore, MD: Johns Hopkins; 1967. p. 195.
[10] Knierim JJ, Kudrimoti HS, McNaughton BL. Interactions between ideothetic cues and external landmarks in the control of place cells and head direction cells. J Neurophysiol 1998;80:425–46.
[11] Muller RU, Kubie JL. The firing of hippocampal place cells predicts the future position of freely moving rats. J Neurosci 1989;9:4101–10.
[12] O'Keefe J, Dostrovsky J. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. Brain Res 1971;34:171–5.
[13] Rolls ET. Spatial view cells and the representation of place in the primate hippocampus. Hippocampus 1999;9:467–80.
[14] Sharp PE. The neural basis of navigation: evidence from single cell recordings. Boston, MA: Kluwer; 2002. p. 280.
[15] Sherry DF, Vaccarino AL. Hippocampus and memory for food caches in black-capped chickadees. Behav Neurosci 1989;103:308–13.
[16] Siegel JJ, Nitz D, Bingman VP. Lateralized functional components of spatial cognition in the avian hippocampal formation: evidence from single-unit recordings in freely moving homing pigeons. Hippocampus 2006;16:125–40.
[17] White AR, Strasser R, Bingman VP. Hippocampus lesions impair landmark array spatial learning in homing pigeons: a laboratory study. Neurobiol Learn Mem 2002;78:65–78.