Supplementary Online Materials

Detailed Materials and Methods

We developed a behavioral task which would allow us to show that rats are using idiothetic information exclusively to solve a spatial navigation problem. Following Mittelstaedt and Mittelstaedt (1980), the overall strategy was to observe the effects of manipulating rats' "sense of direction" on behavior. We used a homing task, where rats are trained to leave a home base (the location of which was varied on a trial-to-trial basis) to retrieve food chunks from the center of a large open field and return to the home base. Rats could be confined to the center of the open field to (a) allow an experimenter to clean the apparatus of cues which could guide homing, and (b) allow rats to be rotated slowly by an electric motor. The rats' response to this rotation allows us to distinguish whether they are using stable external cues or an internal sense to return home. If rats are using external cues, they should not be affected by rotation, since the cues have not moved relative to the home location. If they are using an internal sense (and the rotation is such that it cannot be compensated for) they should be affected. In the case where they are fully unaware of being rotated, their choice of return should correspond to the rotation. This idea is illustrated in Figure 1b.

Apparatus

The experimental apparatus, a modified Barnes maze (Barnes, 1979), was a large white circular table 185 cm in diameter, with 8 start locations (rectangular cut-away bays) spaced evenly around the perimeter (Figure 1a). The table surface, designed to minimise surface imperfections and be easy to clean, was cut from a single sheet of smooth, opaque white acrylic (Altuglas International) mounted on a MDF base. Black plastic home boxes (30 x 25 x 9cm) lined with sawdust could be placed securely into any of the start locations, such that rats could climb out onto the table and back into the box. In the center of the table, a grey plastic tube (25cm in diameter) could be raised and lowered electronically from the adjoining control room (this took about 2.8

seconds to raise or lower). The tube contained a central platform, level with the table surface and of the same material, which together with the tube could be rotated (independently from the table surface) by a geared-down stepping motor (Astrosyn, UK, model SST0040, step size 1.8° and gearbox ratio 50:1, for an effective step size of 0.036°) controlled from the adjacent room. The table was surrounded by floor-to-ceiling black curtains to minimise extramaze visual cues, and white noise (from a speaker positioned centrally above the apparatus) at 65dB was used to mask auditory cues. The curtains could be opened at four different locations to allow the experimenter to enter and exit the curtained enclosure at different points. The apparatus was lit from overhead by 4 DC lights and a monochrome video camera (Panasonic) was positioned above the center of the table so that all behavior could observed from the control room and recorded for reference and offline analysis.

Subjects

For behavioral testing, twelve naïve adult male Lister Hooded rats, weighing approximately 225g at the start of the experiment, were housed in cages of 4 in an animal room on a 12 hour light/dark cycle. All testing was carried out during the light phase of the cycle. From the first day of training, animals were food-deprived to between approximately 85%-90% of their free feeding weight and were maintained on this diet throughout the protocol. Rats were allowed ad-libitum access to water. From one week prior to training, rats were handled daily. Compliance was ensured with national (Animals [Scientific Procedures] Act, 1986) and international (European Communities Council Directive of 24 November 1986 [86/609/EEC]) legislation governing the maintenance of laboratory animals and their use in scientific experiments. For the electro-physiology experiments, three adult male Lister Hooded rats, weighing between 250-300g prior to recording electrode implant surgery, were housed in individual cages. Animals were allowed 1-week recovery period following surgery, after which training and screening for cells began. One recording subject (rat 4322) had been previously trained on a T-maze task in a different experimental room.

Training and testing

Training consisted of two stages, “fetching” and “raising”. The aim of the first (“fetching”) was to get rats to retrieve food chunks from the center of the apparatus and take them to their starting (or “home”) location to eat. The food chunks (“Wotsits”, Walkers, Leceister, UK) were cheese-flavored, baked corn puffs low in nutritional value cut up to approx. 5-10mm in length and 500mg in weight. As central-place foragers, rats naturally prefer to eat sufficiently large chunks of food in sheltered or perceived safe places rather than in a relatively exposed open field (Whishaw et al., 1990). Rats received 20-minute training sessions on alternate days, which were repeated until they successfully fetched at least 10 pellets per session for two consecutive sessions.

Individual training sessions started with a habituation/disorientation procedure, designed to (a) prevent the rat from carrying a sense of direction into the experiment, and (b) encourage the rat to become accustomed to its “home” box, a black plastic container lined with sawdust, which could be plugged into the apparatus. This procedure consisted of the rat being placed into a clean home box inside an opaque, covered holding box (30 x 40 x 22cm) located in the control room adjacent to the main experiment room. After 4 minutes (during which the rat was given a single “reminder” food pellet, the apparatus cleaned, its surface rotated to a new pseudorandom orientation, and a food pellet placed in its center) the experimenter carried the holding box into the experiment room and inside the curtained enclosure, and walked around the apparatus three times. Next, the holding box was placed on top of the tube mechanism of the apparatus, which allowed the holding box to be rotated 90° (direction chosen pseudorandomly for each session) over 60 seconds. Finally, the home box containing the rat was taken out of the holding box and plugged into a pseudorandomly chosen starting location, starting the training session.

During a training session, the experimenter monitored the rats’ behavior from the adjacent control room on a video monitor. When a rat fetched a food pellet from the center of the apparatus, the experimenter entered the curtained enclosure containing the apparatus from one of the four entry points to place a new food pellet. Some rats would occasionally attempt to eat a food pellet at a location other than their home box (usually in

the center); this was discouraged by taking the food pellet away from the rat and placing it and the rat back into the home box, after which rats quickly learned to discontinue this behavior. Some rats were initially reluctant to leave the home box; for those rats, outward excursions were encouraged by placing food pellets close to the home box.

Once a rat met the fetching stage criterion of at least 10 fetches per session for two consecutive sessions (this took less than two weeks for all but two rats), it was moved on to the second stage of training, "raising". The goal of this stage was to get rats used to being confined to the tube in the center of the apparatus before returning to their home box. The training protocol was similar to "fetching" (20-minute sessions on alternate days), albeit with the addition of several shaping techniques. To encourage rats to enter the tube completely (rather than just reaching into it with their snout or entering it with their front paws only) such that it could be raised, on some fetches a food pellet was only dropped once the rat entered the tube with all four of its paws. As rats became more comfortable entering the tube, the tube was raised briefly on some fetches, the frequency and duration of such "raises" gradually increasing. During raises later in training, the experimenter started cleaning the apparatus (a cloth wet with lemon-scented Fairy liquid solution) and replacing the start box with a clean one. To encourage rats to return to their home box after the tube was lowered, an additional food pellet was dropped into the tube just before lowering. Still, some rats tended to stay in the center after the tube was lowered; as before, this behavior was discouraged by increasing the white noise level temporarily and/or taking their food away. Once rats tolerated three 60-second raises in a 20-minute session and appeared motivated to leave the tube once lowered, they were ready for testing.

The testing protocol, from which behavioral data was taken, consisted of six days of three sessions per day for each rat. Each session was preceded by the habituation/disorientation procedure described above, and starting locations for each session were randomly generated. Each day contained two "probe" sessions with a "retraining" session in between, with the sessions at least three hours apart. A probe session, designed to provide minimal cues to the rat as to the location of its home, consisted of the rat fetching 3 pellets from the tube center. When a rat entered to fetch the 4^{th} pellet, the tube was raised, confining it to the center of the apparatus. During this confinement period, the home box was replaced by a clean one, and three additional

home boxes were inserted into the apparatus at 90° intervals relative to the original home location. Also, the apparatus surface as well as the top edge of the raised tube were cleaned with a cloth wet with Fairy liquid solution. Before the tube was lowered and rats could make their return choice, a food pellet was dropped into the tube for rats to carry home. Once rats made their return choice, defined as their snout being above one of the possible starting locations (which need not necessarily contain a home box), their choice was noted down and they were removed from the apparatus. A probe session could be a "no rotation" (no rotation of the tube during confinement) or a "rotation" session (90° clockwise or counterclockwise rotation of the tube): over 6 days, rats received 4 sessions of each type for a total of 12 per rat.

During probe sessions, rats received no particular reinforcement for choosing to return to their original home location instead of to one of the other open boxes, and thus may learn to search randomly for an open box. "Retraining" sessions were designed to encourage rats to return to the correct home location. Retraining sessions are similar to "no rotation" probe sessions, except that no additional home boxes were inserted (i.e. only the original box was replaced), and the tube was never rotated. Additionally, instead of the rat being removed after the first raise, the rat was allowed to keep retrieving pellets until four raises had been achieved, or the 20 minutes were up, whichever came first[2].

Data analysis (behavior only)

On all probe and retraining sessions, the rats' first home box location choice after lowering the tube was recorded. A choice was defined as the rat (viewed from above on the video monitor) "checking out", "investigating", or "visiting" a cutaway home box bay in the apparatus. Thus, first choice data is in 45° steps, where 0° is used to refer to the original home location, and positive numbers indicate the counterclockwise direction.

[2]On all retraining sessions except one, rats achieved at least three raises, indicating they could perform the procedural aspects of the task well. The one session in which a rat failed to achieve three raises resulted in that rat being relegated to the "training" part of the protocol, until he met the raising criterion and testing was resumed.

To measure rats' homing performance, two measures were used: first, the ratio of first choices correct and total number of trials (where correct is defined as either the original location on a non-rotation trial and the rotated location on a rotation trial). Second, a "homing vector" was constructed by taking the vector mean of individual return choices, i.e. each individual return choice contributes a vector of length 1 in the direction of the choice relative to the home location, and the sum of these choices is then divided by the number of choices to yield a mean homing vector. This homing vector, conventionally indicated as r, contains two independent quantities of interest: firstly its direction, which indicates the rats' mean homing direction, and secondly its length $|r|$, which is a measure of homing strength. A mean vector length of 1 indicates rats always made the same response; a mean vector length of 0 indicates they had no preferred homing direction (although this does not imply their responses were uniformly distributed: a statistically devious rat might go one way half the time and the opposite way the other half of the time). A correction to $|r|$ was applied because data were spaced with 45° intervals (Batschelet, 1981). Rayleigh's test for uniformity was used to test whether rats had a significant homing preference against responses not being distinguishable from randomness (Batschelet, 1981). Confidence intervals for the mean homing direction were computed (Fisher, 1993) and used to establish whether homing directions deviated from a reference direction (e.g. the home location at 0°) or to compare conditions (e.g. non-rotated and rotated). To test whether two response distributions were different, Watson's Y_r (Watson 1983, cited in Fisher 1993 pp. 115-117) was used, which tests for a common mean direction.

Recording sessions

Recording sessions were similar to the "probe" sessions described above. Once a unit with directional firing was identified, a baseline recording session (for use in assessing recording stability) on the screening dish was collected before the experimental session on the apparatus commenced. The screening dish was located outside the curtained enclosure containing the apparatus, with the experimenter and recording equipment in the adjoining room. After the baseline session, the rat was placed in an opaque holding box and transported by the experimenter into the curtained apparatus enclosure whilst remaining plugged in to the recording

system. Then the disorientation procedure and testing protocol (probe trials described in section "training and testing", above) began. Rats were allowed to fetch a few food chunks from the center of the apparatus, returning to a home box to eat. After a couple of such "fetches", when the rat next entered the center, a tube was raised to confine the rat to the center for 60 seconds. During this time, the apparatus was cleaned, the home box replaced with a clean one, and three additional boxes inserted at 90° intervals. In some ("rotation") trials, the tube was rotated 90° over 60 seconds. After the rat made a return to one of the home boxes, at least 5 minutes of data was collected before it was returned to the holding box, to be put back on the screening dish for another baseline session. This sequence was repeated for as long as recording stability could be maintained and rats remained interested in performing the task.

Electrodes and surgery

Recording assemblies, built with a modified tripod design (Kubie, 1984), contained 4 tetrodes of Formvar-coated 25μm NiCr wire (California Fine Wire, Grover Beach, CA). Tetrodes were threaded through a 27Ga thin-wall stainless steel cannula, with the recording tip extending 2-3 mm beyond the cannula at one end, and individual wires affixed to the pins of a MillMax plug (MillMax, Oyster Bay, NY) at the other. Together with three screws (80 threads per inch) secured into tapped Amphenol sockets (Wallingford, CT), the plug and cannula with tetrodes were made into a single advanceable unit using dental acrylic. The recording tip of the assembly was coated in paraffin (polyethylene glycol, Sigma) to prevent the tetrodes from bending during surgery.

Anesthesia was induced and maintained using halothane (Merial Animal Health, UK) as rats were placed in a stereotaxic frame (Kopf Instruments, Tujunga, CA), and bilaterally implanted with recording electrodes. After craniotomy, dura was pierced and electrodes were lowered to the target site (rat 6225: anterodorsal thalamic nucleus, coordinates AP -1.8 mm, ML $\pm$ 1.3 mm, DV -3.9 mm relative to bregma; rat 0304: postsubiculum, AP -7.0, ML $\pm$ 2.8, DV -1.7 mm; rat 4322: hippocampal CA1, AP 3.5, ML $\pm$ 2.5, DV -1.5 mm). Electrode assemblies were affixed to the skull using small screws (Fine Science Tools) and dental

acrylic. Each assembly was connected to a skull screw using copper wire, allowing the animal to be grounded through the recording system. Analgesia was administered in oral form (Large Animal Rimadyl, Pfizer, UK) in the animals' water supply. This analgesic solution was freely available to all animals from 24 hours pre-surgery until 48 hours post-surgery. Rats were allowed 1 week recovery time before screening for cells began.

At the end of the experiment animals were terminally anesthetized with sodium pentobarbitol (Euthatal, Merial Animal Health, UK). Small electrolytic lesions were made on the electrode tips (electrode positive, using a 9V battery for 10 sec.) and animals were perfused intracardially with 0.9% saline followed by 4% formalin. The brains were removed and stored in Formalin for a minimum of 24 hours. Brains were then placed in a solution of 2% potassium ferrocyanide made from 10% formalin in saline for 24 h. Coronal 30μm sections were cut on a cryostat with every fifth section recovered for histological analysis. These recovered sections were mounted on gelatine subbed slides, stained with 0.1% cresyl violet acetate and coverslipped using DPX. The location of the electrode tips was then assessed by examining each section under a microscope (Wild M420, Switzerland). For display purposes, images of selected sections were transferred to a computer using a slide scanner (Epson F-3200) at 3200 dpi.

Recording electronics

After post-surgical recovery rats were screened for unit activity using an Axona (St. Albans, UK) 32-channel recording system equipped with a two-spot tracking system as rats sat on a paper towel-lined screening dish 25 cm in diameter. Each electrode assembly was connected to a recording headstage, one of which contained two clusters of infrared light-emitting diodes (LEDs), one small (2 LEDs) and one large (4 LEDs), 6 cm apart. The output of a monochrome CCD camera (Panasonic, 50Hz frame rate) mounted overhead fed into a two-spot tracking system which outputs time-stamped positions of the largest and second-largest cluster of pixels exceeding an adjustable luminance threshold. These points usually correspond to the small and large LED clusters on the headstage, with the position of the rat defined as the average and the head direction as

the angle between the these two points.

Neuronal activity was amplified through unity gain buffer amplifier chips on the headstages, relayed through a flexible tether connected to a ceiling-mounted commutator, amplified 1000-fold, and band-pass filtered between 600 and 6000Hz. The amplified signals were digitized at 50KHz, further amplified (10-30 times) and displayed on a personal computer monitor. Signals were monitored visually for unit activity above noise and background activity levels, and custom analysis software was used to plot the firing characteristics of putative cells. When directional firing was found, the recording protocol began (see below). When no suitable units were found, the electrodes were advanced 20-80 μm and the screening procedure repeated no less than 6 hours later. During recording sessions, tracking data was recorded continuously at 50Hz, and neural data stored when any signal channel exceeded an amplitude threshold defined by the experimenter: for every such event, 1 ms of neural activity (from 0.2 ms before to 0.8 ms after when threshold was reached) was timestamped and stored for the four channels on the corresponding tetrode.

Training

Unlike the behavioral protocol described above, recording rats did not receive controlled training to criterion. At the time of the recording sessions reported here, rats had varying degrees of experience with the experimental apparatus. Rats 6225 and 0304 were experienced subjects who would complete a session (i.e. make a couple of fetches, tolerate a tube raise, and make a return choice) within 10 minutes. Rat 4322 only had two habituation sessions on the apparatus and at the time of recording would not enter the center of the apparatus voluntarily on all sessions except the first one. On those sessions, the rat was gently picked up and slowly placed in the raised tube, whereupon the trial proceeded as normal, the rat apparently motivated to return to the home box.

Data analysis

It was of interest to determine whether neural activity recorded from head direction (HD) cells shifted in preferred firing direction following confinement, and whether such shifts correlated with spatial behavior (the rats' chosen return).

Unit isolation. All of the data acquired during baseline and recording sessions were analyzed off-line. Using the timestamped neural data, single units (putative cells) were isolated based on the relative amplitudes of signals recorded simultaneously from a tetrode. Waveform characteristics were plotted as a scatter plot of one of the channels versus another. Individual units formed clusters of points on such scatter plots, the boundaries of these plots were manually defined using the MClust cluster cutting package (A. D. Redish, University of Minnesota; Axona file format loader, M. van der Meer). For each cluster, interspike interval histograms, auto-correlograms, and plots of spike amplitude on each channel over time were generated and inspected for suspicious activity.

Inclusion criteria. Isolated units were assessed for inclusion in the analysis based on how coherently they expressed a single preferred firing direction (PFD, i.e. to what extent they behaved like a "classical" head direction cell with a Gaussian or triangular tuning curve). It is possible for cell firing to contain information about head direction without having a clear single PFD (e.g. Johnson et al. 2005), but for the purposes of this experiment we were interested in observing PFD changes in single cells. For each recording session, spikes from a cell were separated into "pre-confinement" and "post-confinement" segments. For each segment, a directional tuning curve was constructed by summing spikes and time spent for each angular bin of direction θ_i (bins were 1° wide); firing rates F_i were obtained by dividing number of spikes by amount of time spent for each bin. A measure of the cell's directional consistency was obtained by computing the "tuning vector length" r of the vector mean of these bins weighted by their firing rates (van der Meer, 2007; Yoder and Taube, 2009):

$$C = \frac{1}{\sum_{i=1}^{n} F_i} \sum_{i=1}^{n} F_i \cos\theta_i, \quad S = \frac{1}{\sum_{i=1}^{n} F_i} \sum_{i=1}^{n} F_i \sin\theta_i, \quad r^2 = C^2 + S^2 \tag{1}$$

This measure, the length of the circular mean or population vector of the cell's directional tuning curve, expresses how coherently a cell expresses a single PFD: a cell not tuned for direction or a directional cell with opposing bimodal PFDs would have r approaching 0, while a well-isolated head direction cell can exceed 0.9. If a cell had a tuning vector length $r \geq 0.3$ for both pre- and post-confinement segments as well as the pre- and post-recording baseline sessions, it was included for analysis. For all cells included this r value was sufficient to be indicative of a nonrandom distribution of firing rate along the directional range (Rayleigh test for uniformity); factors contributing to low r values include poor cell isolation, suboptimal tracking quality, and preferred direction drifts over time. It seems likely some of the cells recorded are not "classic" head direction cells (Taube et al., 1990; Taube, 1995), but since they were stable and had a significant single directional preference, they were considered relevant and included in the current analysis. The tuning curves shown in Figures 2–S2 plot the firing rates against the corresponding bin's direction θ_i in polar coordinates, after smoothing by taking the circular mean of a 11-bin window around each bin (i.e. $G_i = \frac{1}{11} \sum_{i-5}^{i+5} F_i$, where i wraps around from 359 to 0 and vice versa and G_i are the smoothed firing rates).

Preferred firing directions. Cell PFDs were computed for pre- and post-confinement using Equation 1 and extracting the direction of the vector resultant:

$$\bar{\theta} = \begin{cases} \tan^{-1}(S/C) & (\mathrm{S} > 0, \mathrm{C} < 0) \\ \tan^{-1}(S/C) + \pi & (\mathrm{C} < 0) \\ \tan^{-1}(S/C) + 2\pi & (\mathrm{S} < 0, \mathrm{C} > 0) \end{cases}$$

This method for determining PFDs, although different from previously reported methods which involve fitting a triangle or a Gaussian to the cell's tuning curve (Taube et al., 1990; Blair et al., 1997), yields comparable results to the Gaussian fit method for cells that have approximately Gaussian tuning curves, but

makes no assumptions about tuning curve shape. This has the effect of being more accurate in cases where the tuning curve isn't strictly Gaussian, but is also noisier, since "stray" spikes are able to influence the PFD instead of being excluded by the fitting process. Because the sliding window tuning curve analysis (below) relies on computing tuning curves based on limited data where often tuning curves were incomplete and definitely not Gaussian, this method was preferred.

Comparison of the pre- and post-confinement PFDs is sensitive to PFD shifts over time. To ensure that PFDs were obtained when the cell had a stable PFD, fine-timescale PFDs were plotted as a function of time by computing the PFD in a sliding window of 240s in length (not shown except in Figure S2. This enabled visual inspection and selection of appropriate time intervals to reflect the cell's true PFD as close before and after confinement as possible. As an indication of how coherent each data point indicated a single PFD, 90% confidence intervals around the mean were computed (Fisher, 1993). Note that tight PFD confidence intervals do not always indicate an accurate estimate of the cell's true PFD: in particular, limited directional sampling can bias the PFD estimate, for instance when the rat faces a constant direction at the "tail" of a given cell's directional tuning curve throughout the PFD estimation window. Furthermore, when there is a genuine PFD change, the time course over which this is reflected in PFD window analysis depends additionally on the width of the window and the relative spike counts from the old and new PFDs. Because of these limitations, conclusions based on this analysis require careful examination of the circumstances for individual cases.

Behavioral responses. The rat's choice of return post-confinement was defined as the crossing point of the rat's path with an imaginary circle, concentric with the table and covering the innermost point of the home box bays. This method is more accurate than merely recording the choice of home box as in the behavioral experiment, enabled by the tracking system.

Recording session examples

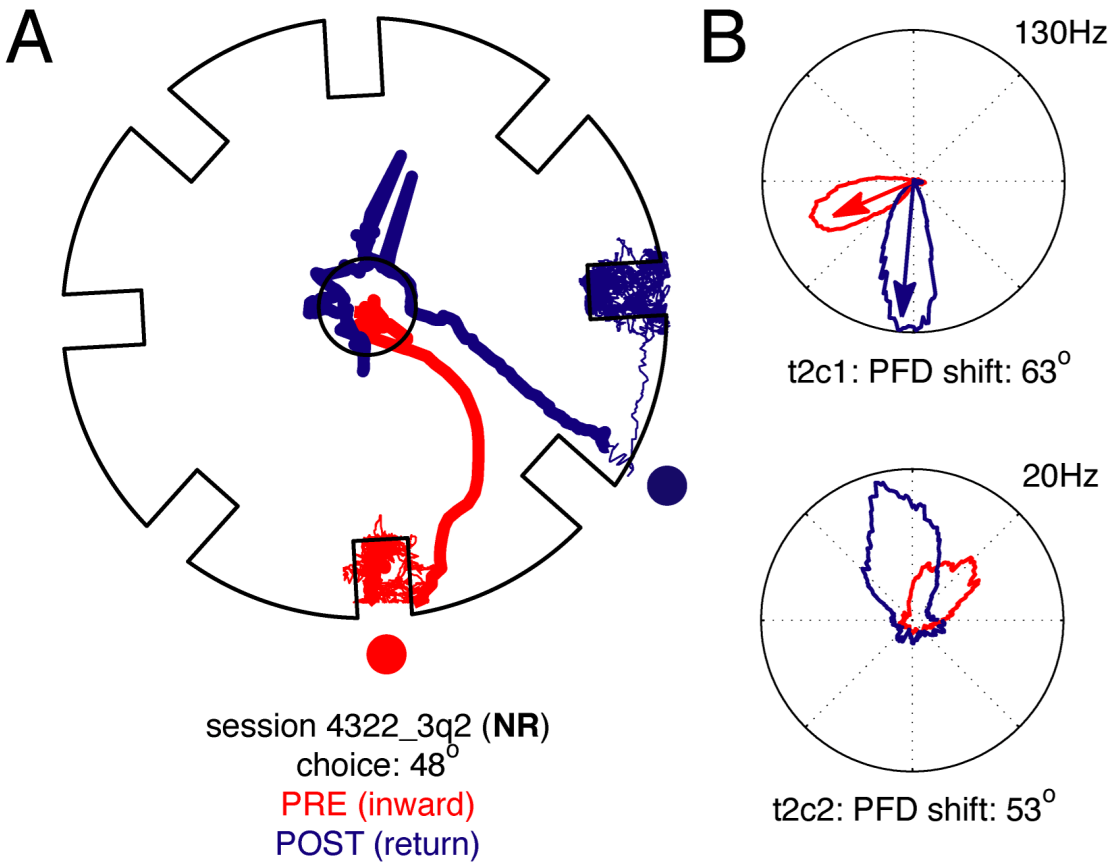

Figure S1: An example of spontaneous PFD drift during a non-rotation session. As in Figure 1 in the main text, panel A shows the rat's path before (red) and after confinement (blue), and panel B shows the tuning curves of two simultaneously recorded HD cells before (red) and after (blue) confinement. The rotation of the cells' preferred firing direction (63° and 53°) matched the rat's behavioral choice (48°) in this case.

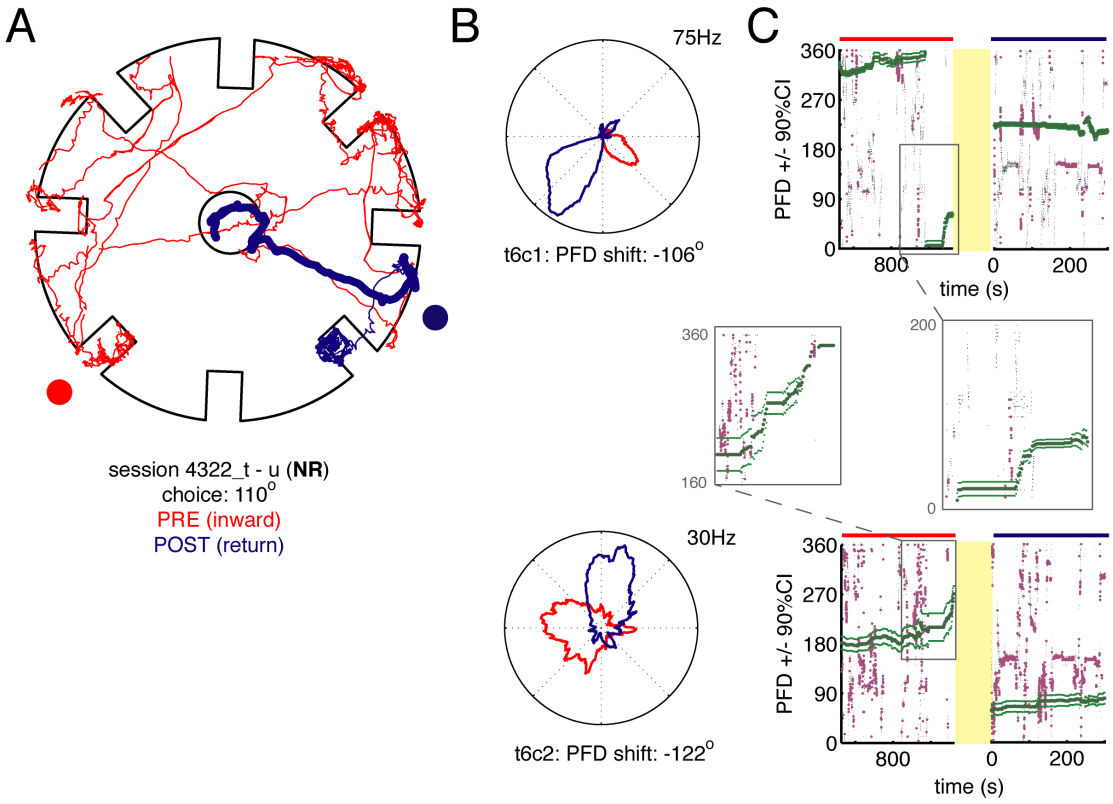

Figure S2: Apparent mismatch no rotation session, where HD cells seemed to shift preferred directions one way, yet the rat chose to return the opposite way. **A**: Position tracking indicates the rat choosing to return to 110°. **B**: Tuning curves shifted by the opposite amount (-106° and -122° for the two cells respectively), however, this might be obscuring some fine-timescale changes. **C**: Sliding window analysis reveals a possible preferred firing direction shift just before confinement. The two inset plots show a magnified view of the 100s before confinement, using a smaller time window (120s instead of the 240s used for the main panels). If instead of computing pre-confinement tuning curves over the time indicated by the colored bars (as in panel **B**), preferred firing directions are estimated from this analysis, return choice and HD signal shift are in agreement (see main text).

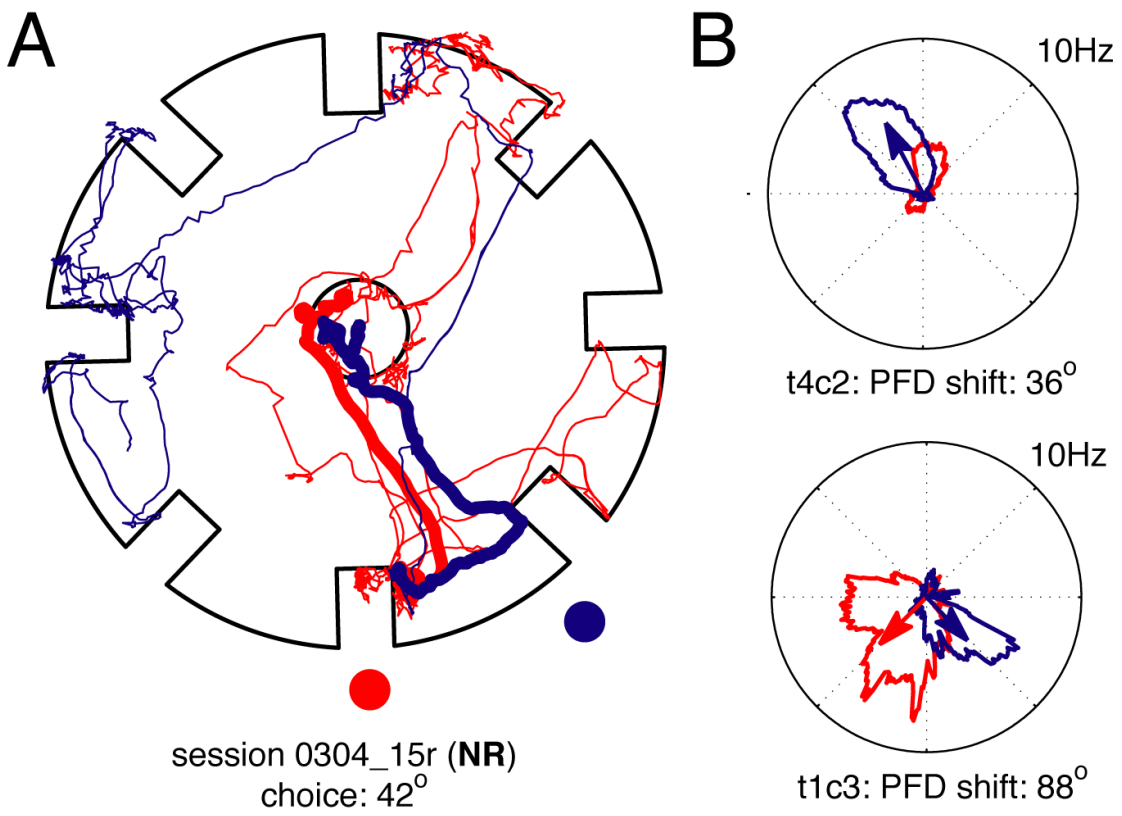

Figure S3: An example of two simultaneously recorded HD cells from a different subject. Panel layout as in Figure S1.

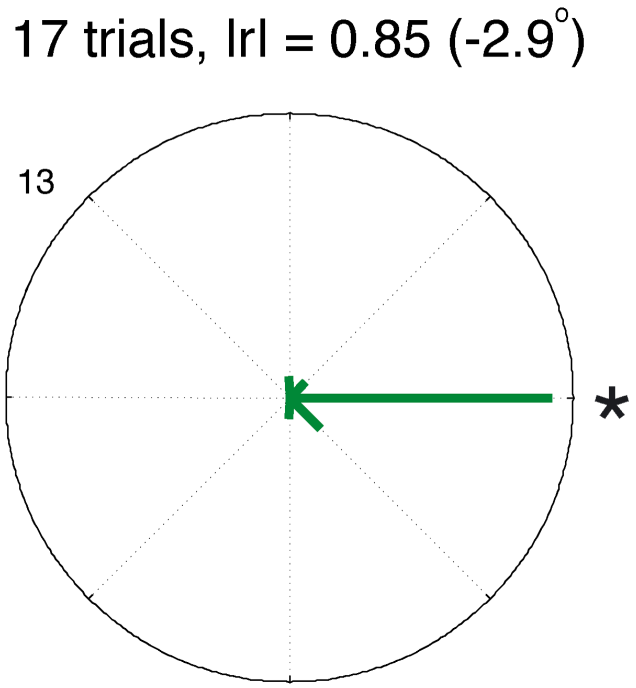

Figure S4: To assess whether limitations on homing performance during probe trials were due to issues not related to path integration, we maximized the allocentric spatial cues available to the rats by adding cues to the environment (on the apparatus as well as on the surrounding curtain), and always starting rats from the same location. Other than these changes, trials were run exactly as in the path integration version of the task (that is, 60 seconds of confinement, maze cleaned, 4 boxes opened). This experiment was only run with 3 of the subjects. Figure shows the circular histogram of first choices; rats homed significantly to the starting location (-2.9° $\pm$ 19.9°, Rayleigh test: $r = 0.85$; $p < 0.001$). This high directionality value of 0.85 suggests that this version of the task was easier than the path integration version, and thus that the relatively low homing performance was not due to insufficient motivation to return to the home location.

Supplementary video

Video shows the overhead camera view of a 90-degree counterclockwise rotation trial recorded from rat 0304. LED clusters on the recording headstage are indicated by the horizontal lines. The rat starts from the "south" box, but returns close to the "east" box following rotation (with a slight underrotation that is representative of the data, see Figure 1d in the main text). Note the replacement of the original start box, insertion of new boxes, and cleaning of the table by the experimenter in the 60-s confinement interval. Video was speeded up by a factor 2.

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