(1) MATERIALS AND METHODS

Animals

Twelve 5-mo. old, male, Long-Evans rats (Charles River, 575-636 g at time of surgery) were housed individually on a 12:12 h reversed light:dark cycle. Recordings were performed during the dark portion of the cycle. The rats were handled and weighed daily, maintained at 80-90% of their ad libitum weights, with ad libitum access to water. Animal care, surgical procedures, and euthanasia were performed in accordance with National Institutes of Health (NIH) and University of Texas Health Science Center at Houston IACUC guidelines.

Surgical procedures

Rats were initially anesthetized with ketamine (60 mg/kg i.p.) and xylazine (8 mg/kg i.p.) and maintained with isoflurane throughout the surgery. The scalp was incised and retracted from the skull, enabling the visualization of both bregma and lambda, which were then set in the same horizontal plane. After 7-8 stainless steel anchoring screws were embedded in the skull, a recording device allowing the independent manipulation of 14 recording probes was implanted over the right hemisphere in 10 rats. Twelve of the probes were tetrodes made of four lengths of fine nichrome wire (0.0005 inch diameter, gold-plated to a final impedance of ~250 kOhm at 1 kHz) twisted together (1,2). The remaining two probes were single channels that functioned as reference electrodes. The 14 probes were gathered into two bundles. The anterior bundle consisted of four tetrodes and a reference, while the posterior bundle consisted of the remaining eight tetrodes and reference. The anterior bundle of probes was aimed at the dorsal hippocampus, while the posterior bundle of probes was aimed at the LEC (5 rats) or MEC (5 rats). For 2 additional rats, a custom-manufactured recording device with 20 probes (18 tetrodes and 2 references) aimed at the entorhinal cortex (1 MEC and 1 LEC) was implanted. LEC bundles were centered at 7.5-7.7 mm posterior and 5 mm lateral to bregma, at an angle of 13-25º in the coronal plane. MEC bundles were centered at 8.6-8.75 mm posterior and 4.5-5.0 mm lateral to bregma, at an angle of 0-5º in the coronal plane. CA1 bundles were centered at 4.0-4.9 mm posterior and 2.0-3.5 mm lateral to bregma, at an angle of 0-25º in the coronal plane (equal to the EC bundle).

Once the recording device was in position it was fixed to the skull and anchoring screws using dental acrylic. The first layer of the dental acrylic was mixed with the antibiotic tobramycin (3% by weight) to assist in the prevention of infections (mixture was 30 mg tobramycin per gram of acrylic powder). Upon recovery from the anesthetic, rats were administered 26 mg of acetaminophen orally for analgesia, and subsequently received daily doses of tetracycline (50 mg/kg) or enrofloxacin (5 mg/kg) mixed in with their food until completion of the experimental procedures.
Recording techniques

After a 5-7 day recovery period, rats were habituated to sit quietly and/or sleep in a towel-lined dish mounted on a pedestal adjacent to the recording electronics and computer. Over the course of a number of days, tetrodes were slowly advanced to the CA1 pyramidal cell layer and to the entorhinal cortex. Neuronal signals were passed through a head stage composed of complementary metal oxide semiconductor operational amplifiers and were amplified between 2,000 and 10,000 times. The signals were filtered between 600 Hz and 6 kHz for hippocampal recordings and filtered between either 300 Hz or 600 Hz and 6 kHz for entorhinal recordings. Signals that crossed an amplitude threshold triggered a brief (1 msec) digitization at 32 kHz of all channels of that tetrode, and the waveforms were stored on a PC, using the Cheetah data acquisition system. Also mounted on the head stage was a circular array of light-emitting diodes (LEDs) to track the animal’s position during behavioral recording at 60 Hz.

Experimental protocol

Prior to surgery rats were habituated/trained over a minimum of 4 days to forage for chocolate sprinkles in a square, cardboard box (with the floor removed). The training box had no distinguishing characteristics on any of the walls and was placed in a number of brightly lit rooms for different rats with no attempt to mask the visual or auditory cues occurring outside the chamber. The floor of the chamber consisted of brown wrapping paper, which was changed every session. Initially, the chocolate sprinkles were distributed homogenously about the floor of the chamber and the rat was placed in the center and left for 20-45 min. Once the rat began to consume the food reward, the experimenter stood outside the rat’s view and tossed sprinkles into the chamber at random intervals and locations during the subsequent training sessions. By the end of this procedure rats were typically wandering around the chamber in search of food, pausing only to listen for the next scattering of sprinkles to hit the floor.

During behavioral recording, the rats were run in a square chamber (67 x 67 cm, 51 cm high) with grey walls and a single white cue card (30 cm) the full height of the chamber mounted in the middle of the west wall (3). The experimental chamber was centered in a room adjacent to the recording equipment and surrounded by a circle of black curtains (275 cm diameter) that hung from ceiling to floor. Lighting was provided by a single 25W DC-powered bulb on the ceiling centered over the chamber. The light bulb was recessed in a 13-cm-diameter, black cylinder, which prevented the video camera, food dispenser spout, and motorized, 80-channel commutator from being illuminated. The ceiling was covered with an annulus of black curtains that extended from a 60-cm-diameter hoop centered in the room to the black curtains at the perimeter of the room. The ceiling panel on which the light, camera, commutator, and food dispenser were mounted was also painted black. During behavioral recording, white noise emanated from a small speaker centered directly below the small table upon which the experimental chamber rested. The food dispenser fixed in the ceiling automatically dropped a few chocolate sprinkles at fixed intervals of 30–60 s, which could be further supplemented by the experimenter’s manual triggering of the device.
The recording protocol consisted of a baseline session during which data were collected for 20-30 min while the rats slept or sat quietly in the same towel-lined dish in which the probes had been advanced. These data were collected to determine what units were present on which probes and to compare the stability of those units to similar baseline data collected after the behavioral recording. After the initial baseline period the rat was carried openly into the recording room without disorientation, the recording cable and head stage were connected, and the rat was placed in the chamber to forage for chocolate sprinkles. The experimenter exited quietly and started the behavioral recording from the adjacent room. After approximately 10 minutes the recordings were stopped and the experimenter re-entered the room, disconnected the rat, and returned it to the towel-lined dish adjacent to the electronic equipment for the second sleep baseline. Occasionally during the second baseline the rat was too active to sleep continuously and thus the behavior consisted of bouts of sleep mixed with periods of resting quietly. For two rats (115 and 123), a second behavioral session followed after 5-20 min, with fresh paper covering the floor of the chamber.

After four or five experimental sessions similar to those above, a number of the rats received additional behavioral trials in which the cue card was moved to different walls and/or the rat was placed inside a bucket and slowly rotated. (The results of these manipulations will be described in a separate report.) The main results of this report derive from the standard, 10-min sessions prior to any environmental manipulations.

Data Analysis

**Offline unit isolation.** The tetrode allows the isolation of single units based primarily on the relative amplitudes of signals recorded simultaneously at four slightly different locations. Additional waveform characteristics, such as spike waveform “energy” and spike width, were also used to supplement the identification based on relative amplitudes. Waveform characteristics were plotted as a scatter plot of one of the four wires versus another. Individual units formed clusters of points on such scatter plots, and the boundaries of these clusters were defined with the use of a custom interactive program running on a PC workstation. Isolation quality of the cell was rated on a subjective scale of 1 (very well-isolated) to 5 (poorly isolated), based on the size of the waveforms relative to background and on the closeness and degree of potential overlap between neighboring clusters. These ratings were made completely independent of the spatial firing characteristics of the cell. All cells rated 4 or 5 were excluded from further analyses. All cells with mean firing rates > 10 Hz were classified as fast-spiking and were not analyzed in detail. None of the fast-spiking neurons had visually obvious place fields or high spatial information scores. Finally, all cells that fired < 50 spikes during the 10-min session were removed from analysis (see below). Thus, of the 621 single units recorded from CA1, MEC, LEC, and surrounding cortical regions, quantitative analyses were performed on a total of 91 units from dorsal CA1, 93 units from the LEC, 66 units from the MEC, 31 units from the subiculum, 30 units from the parasubiculum, and 70 units from the perirhinal cortex.
Spatial selectivity measures and statistics. For each cell, firing rate maps were constructed by segmenting the environment into ~3 cm square bins and, for each bin, dividing the number of spikes fired by the amount of time the rat occupied that bin. The rate maps were then smoothed using the adaptive smoothing algorithm of Skaggs et al. (4) Spatial selectivity was measured by the amount of mutual information about the rat’s location in the environment (4) conveyed by the firing of a single spike (in bits/spike). Because this measure is robust if a cell fires > 50 spikes in a session, cells that fired less than this were considered too low-rate and were dropped from the analysis. For statistical purposes, a log10 transform was performed on the information score to normalize the distributions so that ANOVA tests could be run. To test the stability of spatial firing patterns within a session and between sessions, pixel-by-pixel correlations were performed on the firing rate maps. The correlations were transformed using the equation

\[ z = 0.5 \times \ln\left(\frac{1 + r}{1 - r}\right) \]

in order to normalize the distribution for ANOVA tests. Although statistical tests were performed on transformed scores, the means of the raw values for spatial information and spatial correlation are reported in the manuscript, along with the standard error of the mean. If the ANOVA reported significant main effects or interactions, the Tukey test was performed to determine which groups differed.

Histology and tetrode track reconstruction

At the end of the experiment, small electrolytic marker lesions were made on a subset of the tetrode tips by passing 10 µamp of anodal current for 10 seconds. The animal was perfused transcardially with 4% formal saline the following day. The head was removed and allowed to soak in the same perfusate overnight, after which all the probes were raised and the brain extracted ventrally and placed in a 30% sucrose formalin solution. After the brain sank, it was encased in gelatin, cut in serial coronal sections (40 µm) on a freezing microtome, mounted, and stained with cresyl violet. Sections were magnified and photographed with a digital camera.

Reconstruction of the electrode tracks and assignment of each track to a tetrode was a multi-step procedure. Because the brain sections were usually cut at an angle that was somewhat oblique to the tetrode track, the tracks had to be traced through several sections. With the aid of photo prints of the sections and a light box, each tetrode track was followed and marked from the brain surface to the end of the penetration. In most cases, the tetrode tracks were straight and parallel with each other all the way down to the entorhinal cortex. (For 3 additional rats, however, damage to the overlying cortex or crossed electrode tracks made it impossible to identify the tracks with certainty, and the data from these rats were subsequently not included in this report.) For each track in a section, the anterior-posterior level and distance from midline of the track were plotted on a two-dimensional representation of the cortical surface. This graph was compared with a diagram of the geometric configuration of the tetrodes as they exited the bundles, created before the drive was implanted. By comparing the geometric arrangement of recording
tracks with the known geometry of the recording bundle, each track was confidently assigned to a tetrode. This assignment was further assisted by matching the ends of the tracks with the recorded end depths of the tetrodes and by identifying those tetrode tracks with small electrolytic lesions.

Once the electrode tracks were identified, individual recording sites had to be located along the length of each track to identify the brain region recorded. Careful records of the recording depth were kept each time the tetrode was moved. These recording depths were mapped onto the digital photographs of the sections by multiplying the depth by the magnification factor of the photo and by a histological processing shrinkage factor. In some cases, this shrinkage factor was measured explicitly for a given rat because we had made 4 marker lesions, spaced 1 mm apart, along the track of one tetrode (5). In most cases, however, we used an average shrinkage factor of 85%. The accuracy of the magnification and shrinkage factors was tested by measuring the length of representative tetrode tracks from brain surface to end and comparing with the known total advancement of the tetrode. Additional checks came from comparing the calculated depths on the photographs with the depths of known electrophysiological landmarks recorded during tetrode advancement (such as the transition from neocortex to white matter and the transition from white matter to deep layers of entorhinal cortex). With these calculations, we were able to identify the depth of each recording site on the digital photographs. Because some uncertainty still remained with these measures (e.g., different tissue sections may shrink different amounts, individual sections may shrink inhomogeneously), recording sites that were judged too close to the borders of two regions (e.g., LEC and perirhinal cortex; superficial and deep layers) were classified as ambiguous locations (e.g., LEC/peri; mid layers) and were analyzed separately.

To determine the location of recording sites relative to the dorsolateral projection bands of Dolorfo and Amaral (6), two-dimensional, unfolded cortical maps of the entorhinal cortex were constructed for each rat (6,7). Briefly, a 1-in-4 series of sections through the full rostrocaudal extent of the entorhinal cortex was digitally photographed. The fundus of the rhinal sulcus was identified and the margins of the lateral and medial divisions of the entorhinal cortex were noted (6,8-10). The pial surface of the cortex from each digital image was then traced, noting the divisions and landmarks identified above using a custom interactive program. The two-dimensional unfolded maps were constructed by straightening the contours and aligning them to the fundus of the rhinal sulcus. Tetrode locations were plotted by marking the location of the tetrode tip projected onto the pial surface.
(2) Fig. S1
Figure S1. Firing rate maps from all cells in the sample. LEC and MEC cells were divided into superficial (layers II and III), deep (layers V and VI), and mid layers (too close to superficial-deep border to identify with certainty). Only superficial cells (which constitute the hippocampal afferents) were included in the quantitative analysis of the paper. The hippocampus sends its output to the deep layers (layers V and VI) of entorhinal cortex. The mean spatial information score of the 11 cells recorded from the deep layers of LEC was 0.35 ± 0.07 and from the 13 cells recorded from the deep layers of MEC was 0.25 ± 0.06. Although the deep MEC cells had less spatial information than the superficial cells, the deep cells were recorded from locations biased toward the intermediate projection band (Fig. S3). Because of this bias and the small number of deep cells, we cannot make any statements about differences between deep and superficial MEC. Deep LEC cells had slightly higher information scores than superficial, but again the small number of deep cells recorded makes any interpretation tenuous. Neither parasubiculum nor perirhinal cells showed any difference between deep and superficial layers. A 2-factor ANOVA with area and layer as factors showed a main effect of area [parasubiculum > perirhinal, F(1,80) = 30.0, P < 0.0001] with no main effect of layer [F(1,80) = 1.3, P = 0.26] and no interaction [F(1,80) = 0.0, P = 0.98], so the cells from the different layers within each area were grouped together. Finally, the ventral subiculum cells showed very little spatial tuning. For all 31 subiculum cells, the mean spatial information score was 0.12 ± 0.04; for the 18 subiculum cells that fired < 10 Hz, the mean spatial information score was 0.19 ± 0.06.
(3) **Figure S2.** Individual unfolded flat maps for each rat. Following procedures described in Dolorfo and Amaral (6,7), we created unfolded flat maps of the entorhinal cortex for each rat and plotted on these maps the location of the tetrode tips at the end of the experiment. Tips located to the right of the LEC were in the perirhinal cortex. Tips located to the left of the MEC were in the parasubiculum. Because the tetrodes often passed through the cortical layers at oblique angles (especially near the rhinal sulcus and parasubiculum; see Fig. 2), the final tip locations did not always denote the exact recording sites of all cells in the penetration (see Fig. S3). These figures demonstrate the general recording regions for each rat, and were used to create the average map shown in Figure 2A. Also shown are the number of cells from each rat that contributed to the analysis (peri: perirhinal cortex; para: parasubiculum; subic: ventral subiculum).
Figure S3. Recording sites for MEC and LEC. Although the flat maps of Fig. S2 show the general locations of the recording sites in a way that can be compared with the tracer injections of Dolorfo & Amaral (6), some information is lost regarding the precise localization of each site due to the oblique nature of many penetrations. For each cell in the MEC and LEC data sets (superficial, mid, and deep layers), we plotted the recording site on the relevant sections from the atlas of Paxinos and Watson (11). (Because the rats used in the present study were larger than those of the Paxinos and Watson atlas, the coordinates of the recording sites relative to bregma do not match precisely the coordinates of the corresponding sections of the atlas.) These data show that many cells were recorded from superficial LEC in regions very close to the rhinal sulcus (the dorsolateral projection band), although other cells were recorded from the intermediate band. No differences were seen between these regions in the spatial information scores (see Fig. S4-D). Many superficial MEC cells were recorded from the dorsolateral band, although perhaps slightly rostral to the region that projects to the most septal hippocampus. Nonetheless, most cells do appear to originate in regions that project to the dorsal half of the hippocampus, within the dorsolateral band as defined by Dolorfo & Amaral (6).
(5) **Figure S4.** Factors that might influence MEC vs LEC spatial information difference. (A) Recording isolation. On average, spikes recorded from superficial LEC were smaller than those recorded from superficial MEC [LEC = 168 ± 10 µV, MEC = 260 ± 12 µV, \( t(11) = 5 \times 10^6, P << .0001 \)]. Because spike height is generally correlated with unit isolation (although background activity and cell density are important factors as well), this difference raises the possibility that the lack of spatial tuning in LEC was the result of poor unit isolation. To address this issue, we plotted the spatial information as a function of spike height for MEC and LEC. It is shown that MEC cells had higher spatial information than LEC cells regardless of spike height, suggesting that the smaller extracellular spikes in LEC do not account for the difference in spatial tuning between the areas. (B) To further address the unit isolation issue, cluster isolation rankings were compared between the superficial MEC and superficial LEC samples. As described in
the Methods supplement, cells were classified into 5 categories during the manual cluster-cutting procedure. These rankings were assigned completely independent of any response correlate of the cell, and were based solely on the experienced user’s subjective estimate of how well isolated the cluster was from background firing and from other clusters. Cells were ranked from 1 (excellent isolation) to 5 (poor isolation); only cells that received a rank of 3 or higher were used in this paper. Although there was an overall difference among the three areas in cluster isolation quality \( \chi^2 = 18.5, P < .001 \), there was no difference between LEC and MEC in the proportions of these rankings \( \chi^2 = 2.2, P = 0.33 \). Similarly, a 2-factor ANOVA (cluster ranking vs. EC area) on spatial information scores showed a main effect of EC area \( F(1,116) = 41.1, P < .0001 \) but no significant effect of cluster ranking \( F(1,116) = 2.1, P = 0.15 \) and no significant interaction \( F(1,116) = 1.0, P = 0.33 \). Furthermore, the spatial information of the Category 3 MEC cells was larger than that of the combined Category 1 and 2 LEC cells \( 0.58 \pm 0.07 \) vs. \( 0.23 \pm 0.04, t(49) = 3.3, P < .005 \). These data demonstrate strongly that the differences between MEC and LEC are not the result of poor unit isolation in LEC.

(C) In many rats, parts of visual cortex sustained damage as the result of the tetrode arrays being driven into the brain. One possibility is that the lack of spatial tuning in LEC was the result of this damage. To explicitly test this possibility, rats 115 and 123 were implanted and added to the set of subjects. Rat 115, which produced the greatest number of superficial LEC cells in the dorsolateral band, sustained no obvious damage to the visual cortex, and its spatial information scores \( 0.21 \pm .03, n = 36 \) were not different than the other LEC rats \( 0.19 \pm .02, n = 32; t(66) = 0.72, P = 0.48 \). Rat 123 sustained some visual cortex damage, but it was mild compared to the other MEC rats. Its spatial information scores \( 0.54 \pm .07, n = 22 \) were significantly larger than Rat 115 \( t(56) = 5.36, P < .0001 \). These results, along with the observation that MEC rats tended to sustain more damage than LEC rats yet had more highly specific place fields, make it highly unlikely that the difference between MEC and LEC was the result of visual cortex damage. (D) To test whether the lack of spatial tuning in LEC was the result of an overabundance of recordings from the intermediate projection band, we compared the spatial information from the cells judged to be located nearest the rhinal sulcus \( 0.20 \pm .03, n = 41 \) with the cells that were judged to be located in the intermediate zone \( 0.20 \pm .02, n = 27 \). There was no difference in spatial information between these two groups \( t(66) = 0.90, P = 0.37 \), suggesting that LEC cells lacked strong spatial tuning in both dorsolateral and intermediate projection bands under the recording conditions of this experiment. The two cells in the dorsolateral band that had spatial information scores > 0.8 are shown as cells 1 and 2 of Fig. 1B. It is clear from that figure that, although the spatial information scores were high, neither cell displayed the robust, spatially selective firing of CA1 and some MEC cells.
Figure S5. Differences among CA1, MEC, and LEC in stability of spatial firing patterns. (A) In the 2 rats with tetrodes in either MEC (rat 123) or LEC (rat 115), we systematically recorded two sessions each day in order to compare the stability of firing patterns across sessions. Stability was assessed by performing pixel-by-pixel correlations on the firing rate maps of the 2 sessions. Superficial MEC cells had much higher spatial correlation scores than superficial LEC cells between sessions [0.626 vs. 0.305, t(43) = 4.17, P < .0001], showing that the spatial firing of MEC cells was consistent across sessions.
sessions and suggesting that many LEC cells with significant spatial information scores were not reproducible across sessions. (B) For all cells of all rats, we compared the spatial firing patterns of the first half (5 min) of each session with the second half. Firing rate maps for each split session for the 10 cells shown in Figure 1 are shown here. In general, CA1, MEC, and parasubiculum rate maps were similar across the two halves of the session, whereas LEC, perirhinal, and ventral subiculum were less similar (with some marked exceptions). LEC cell 4 fired in the same restricted location in both halves of the session. It is noteworthy that this location corresponded to one edge of the white cue card on the wall. Other cells with apparent place fields were not consistent. For example, cell 8 initially fired sparsely for the first half of the session (maximum firing rate = 0.05 Hz) and then developed a broad “place field” slightly southwest of the center of the environment in the second half (maximum firing rate = 0.08 Hz). This rat demonstrated a strong bias for this particular location over many days of recording, however, perhaps because the chocolate sprinkle reward tended to drop at this site. In follow-up sessions that day, the cell continued to fire at the same location. Finally, the same cell is believed to have been recorded the following day, and on this day it displayed no spatial bias at all. Thus, it is possible that the spatial bias of this cell was related to some local quality of that location or to a learned association between a spatial location and the local cue. (C) To quantify the differences in stability of spatial firing patterns, histograms of spatial correlation scores between the two halves of a session for CA1, superficial MEC, and superficial LEC were constructed. There was an overall difference between the 3 areas [F(2,207) = 27.4, P < .0001]. Posthoc tests showed that CA1 (mean = .49) had greater correlations than both MEC [mean = .32; q(207,3) = 10.4, P < 0.001] and LEC [mean = .17; q(207,3) = 5.2, P < 0.005] and MEC had greater correlations than LEC [q(207,3 = 4.2, P < 0.05]. (D) A scatter plot of spatial information for the whole session vs. spatial correlation between session halves showed that for CA1 and superficial MEC, there was a strong relationship between cells with higher information scores having highly stable firing patterns between the two session halves [CA1: r = .51, P < .001; MEC: r = .66, P < .001], whereas the relationship in LEC was significant but much weaker [r = .26, P < .05].
(A) MEC cells in the dorsolateral band have been reported to display multi-peaked, highly specific firing locations (12). Although we saw some cells with multi-peaked fields (e.g., cells 4, 5, and 9 in Fig. 1B; other examples in Fig. S1), many of the place fields in our sample were single-peaked and resembled standard, CA1 place fields. The most striking example of multi-peaked firing in our sample came from a cell that we could not localize with certainty, as it was in a caudal region where the MEC, parasubiculum, and retrosplenial cortex converge (cell 1). Interestingly, 4 days later, we recorded another cell ~0.45 mm deeper that had the exact same pattern of multi-peaked firing; however, the centers of each peak were displaced approximately 14 cm to the right of the peaks of the previous cell (cell 2). The displaced peaks between the two cells may indicate a role for these cells in representing displacement of the rat as it moves about in its environment, which may be useful for computations of path integration.

(B) An open question is whether the predominantly single-peaked place cells recorded from MEC of the present experiment represents a different class of spatially selective neurons than the multi-peaked cells, or whether the two types of cells are fundamentally the same. A preliminary report by Fyhn et al. (13) demonstrated that these multi-peaked firing fields form a grid-like representation of the surface of the recording chamber. This figure presents a conceptual model of how such grids at different spatial scales may account for the variety of place fields seen in the superficial MEC (Fig. 1, Fig. S1). At a fine scale, multiple spots appear inside the walls of the box (black square), showing the patterns of Fig. S6A. Different cells represent similar grids that are displaced relative to each other (red and green “fields” of Fig. S6B correspond to cells 1 and 2 of Fig. S6A). At a medium-grade scale, only 2-3 spots would fit inside the box, resulting in spatial firing patterns such as cells 5 and 9 of Fig. 1B. At a coarse scale, some cells would tend to fire in single, large fields (such as the red cell of Fig. S6B, right, similar to MEC cell 10 of Fig. 1B) or in smaller, highly specific fields along the walls (such as the green cell of Fig S6B, right, similar to MEC cells 1-3 of Fig 1A). These single- and multi-peaked firing fields may thus represent a set of purely spatial inputs into the hippocampus, representing a grid of the environment at different spatial scales, as has been previously suggested for a gradient of spatial scaling along the septotemporal axis of the hippocampus (14). Evidence that grid cells represent space at different scales has been obtained in another laboratory (15), lending support to the idea that the MEC firing properties shown in the present study may be consistent with the spatial grid phenomenon.
(8) SUPPORTING REFERENCES

(4) W. E. Skaggs, B. L. McNaughton, M. A. Wilson, C. A. Barnes, Hippocampus 6, 149 (1996).