Path shape impacts the extent of CA1 pattern recurrence both within and across environments

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Abstract

Similarities and differences in the visual content, scale, and shape of environmental boundaries for two environments have been extensively examined for their impact on the recurrence of spatially-specific hippocampal firing patterns across environments and across multiple regions of a single environment. While the shapes of paths taken through an environment are known to impact hippocampal firing patterns within any single region of a single environment, it is not known to what extent path shape and scale can impact firing pattern recurrence across two environments and across multiple regions of a single environment. This question was addressed in the present work where the spatial firing patterns of hippocampal CA1 neurons were examined as rats traversed differently-shaped spiral paths centered on the same position within a visually-observable curtained enclosure. On such tracks, firing fields for CA1 neurons were found to recur across multiple sub-regions of a single path and across similarly-positioned regions of different paths. Both within and across different spiral tracks, the extent of such pattern recurrence was strongly influenced by similarity in the specific sequences of movement directions and locomotor behaviors engendered by different path shapes. The findings demonstrate that the shapes of paths taken through an environment can robustly and dynamically alter both the scale of spatially-specific CA1 firing fields and the extent to which they recur across environments.

Keywords: Hippocampus, Place, Rat, Generalization, Discrimination, CA1
Introduction

In rats freely moving within an environment, hippocampal neurons exhibit firing restricted to specific sub-regions of their environment (O'Keefe and Dostrovsky, 1971; Muller et al., 1987; McNaughton et al., 1983). However, firing specific to any given sub-region may, in turn, be strongly modulated in magnitude by the overall path or route taken through that sub-region (Frank et al., 2000; Wood et al., 2000; Ferbinteanu and Shapiro, 2003; Nitz, 2006; Ainge et al., 2007). That is, hippocampal spatially-specific activity is modifiable according to the series of experiences that accompany traversal of particular routes through space. Such data are consistent with recent findings indicating that the hippocampus is necessary for memory of the order with which sub-regions of an environment are visited (Hunsaker et al., 2008). Taken together, behavioral and electrophysiological findings suggest that spatially-specific, but route-dependent firing may directly reflect a mechanism by which the hippocampus generates episodic memories and, more generally, that the spatial firing patterns of hippocampal neurons shed light on the character of episodic memory formation (Eichenbaum et al., 1999; Shapiro et al., 2006).

Theoretically, the spatial firing patterns of hippocampal neurons could strongly favor a discrimination process wherein an environmental sub-region common to otherwise different paths is mapped differentially depending on which path has been taken. Alternatively, hippocampal firing patterns could favor a generalization process wherein the path-dependency of firing within a given sub-region is minimal and distinct memories for different paths through a given space are not generated. Convincing evidence for both strong and weak route-dependence of firing has been published (compare, for example, Wood et al., 2000; Ferbinteanu and Shapiro, 2003; and Nitz, 2006 with Frank et al., 2000; Bower et al., 2005).
Notably, generalization could also take another, very different form wherein firing patterns persist over extensive, adjoined sub-regions of an environment or recur across two or more spatially separate sub-regions of a single path. The key distinction here is that firing pattern generalization is distributed across sub-regions as opposed to recurring in the same position associated with two different paths. Presumably, firing pattern generalization of this type would be enhanced by similarity among different sub-regions in the makeup of other variables known to modulate hippocampal spatially-specific firing. A list of such variables would certainly include type of behavior (e.g. execution of a left or right turn), movement direction, and the presence or absence of specific sensory stimuli (McNaughton et al., 1983; Markus et al., 1995; Shapiro et al., 1997).

Currently, little evidence is available to clearly support the contention that generalization can take the form of recurrence of firing patterns across extended or different sub-regions of space. In published work involving random foraging patterns within an arena, partial overlap in firing patterns has been observed for two environments sharing the same shape (Muller and Kubie, 1987; Skaggs and McNaughton, 1998; Leutgeb et al., 2005). Partial overlap is also seen under conditions wherein two environments have different shapes (e.g., circular versus square), but are similar in size, their positioning in an experimental room, and in the arrangement of a single prominent visual cue defining the allocentric space (Lever et al., 2002). Such data demonstrate that similarities in the shape and appearance of boundaries that define an allocentric space can yield partial recurrence of firing patterns. Note, however, that in these studies, recurrence of firing patterns pertains to individual sub-regions of two environments that are identical in their positioning relative to the environment’s boundaries (e.g., the northwest edge of two environments). That is, the spatial firing patterns observed in these studies do not extend across multiple sub-regions of a single environment. Furthermore, in two studies, such pattern recurrence across environments was shown to be temporary in nature with complete differentiation.
of the environments achieved after only a few days of experience (Muller and Kubie, 1987; Lever et al., 2002).

In other work, the spatially-specific firing fields of some hippocampal neurons were indeed found to adapt in size to the changing dimensions of an environment or to variations in the distance between prominent visual cues that define the allocentric space (Gothard et al., 1996; Muller and Kubie, 1987; O'Keefe and Burgess, 1996; Fenton et al., 2000). Nevertheless, the features that define a route taken through space, combinations of movement directions and turns, were not systematically investigated for their role in inducing recurrence in firing patterns across space. Thus, the factors determining the extent to which hippocampal firing patterns recur across different spaces remain incompletely defined. Specifically, it remains to be determined whether similarity in movement direction and type of locomotor behavior can induce pattern recurrence across sub-regions of space in the same way that differences in these variables can induce pattern differentiation within individual sub-regions of space. Also in question is whether pattern recurrence can persist when the environment is highly familiar and stable in shape.

To address these questions, the spatial firing profiles of hippocampal CA1 neurons were examined during uninterrupted traversals of spiral tracks. Each track was composed of five repeating loops each composed of the same set of trajectories through an easily observable, unchanging, and highly familiar allocentric space. Trajectory repeats covered widely spaced regions of allocentric space and were associated with temporally distal epochs of uninterrupted path traversals. Individual tracks differed both in shape (squared versus circular) and in the required turn behavior (left versus right). Using this design, it was possible to determine the extent to which firing pattern recurrence could be induced by similarity in the sequences of movement directions and locomotor behaviors that compose routes taken through an environment.
Materials and Methods

All procedures fell within the guidelines of the National Institutes of Health and approved Institutional Animal Care and Use Committee protocols.

Subjects/Behavior

Recordings were obtained from 4 adult, male Sprague-Dawley rats. Animals were trained to traverse each of four spiral tracks centered on the same position in the recording room (figure 1). All tracks were composed of 5 individual ‘loops’ defined by short (4 cm) walls which permitted visualization of the full recording area and its attendant distal spatial cues. Trajectories differed in shape (squared vs. circular), direction of movement through any given room position, and behavior (left- vs. right-turning). Inbound (center-going) and outbound (perimeter-going) path-running on each track was motivated by food restriction. Food reward was presented at the center of each spiral for inbound trajectories and at the spiral origin (on the perimeter) for outbound trajectories. During training, all animals also experienced track running under conditions of complete darkness and under conditions where tracks were rotated 180 degrees relative to their normal position in the room. Prior to surgery and recordings, experience on all tracks was extensive with daily training occurring over the course of 1-2 months.

Recordings

Polyimide-insulated tungsten wire (25 micrometers, California Fine Wire) was twisted and fused to form ‘stereotrode’ recording wire pairs. Stereotrode tips were gold-plated to impedances of 200 kOhms and mounted within custom-made microdrives. At the point of connection to a recording tether, signals were current-amplified by an array of field-effect transistors built into the connector assembly (NBLabs, Denison, TX). Action potentials and local field potentials were amplified (Neuralynx, Tucson, AZ), then digitally recorded using custom-made software courtesy of Matt Wilson (MIT) and Loren Frank (UCSF).
The animal's position in the room was obtained by tracking head position via an overhead camera which detected LED lights fitted into the recording headstage. Position on the track was then determined by fitting such tracking data to track templates (see, for example, supplemental figure 2).

Single unit discrimination was carried out as described extensively in prior publications (Nitz, 2006; Wilent and Nitz, 2007). Subsequent to surgical implantation of microdrive/stereotrode assemblies above the dorsal hippocampus (AP -3.5, ML 2.2), recordings were obtained within the overlying posterior parietal cortex for more than one week. Stereotrodes were then lowered slowly (approximately 40-80 micrometers per day) until reaching the hippocampus. Stereotrode locations within field CA1 of the hippocampus were verified by the presence of sharp-wave/ripple events within local field potential recordings. Such in-vivo localization was later confirmed by histological analysis of recording wire tracks.

**Template matching procedure**

The fitting of positional tracking data to track templates is described in supplementary figure 2A. Track templates were composed of a series of evenly-spaced points (0.6 cm separation). Tracking data from uninterrupted traversals was shifted and/or rotated to best fit a given track template. Subsequently, individual tracking points were assigned template points by determining the most proximal track template point.

**Firing field localization**

Place fields were identified and their start, center, and end-points determined as described in supplementary figure 2B. Briefly, following Mehta et al. (1997; see also Lee, Rao, and Knierim, 2004), firing fields were defined as spatially isolated increases in firing rate resulting in peaks exceeding 5 Hz and persisting at rates of 10% peak rate or better for at least 15 pixels (7.5 cm). The start and end points of firing fields were defined as the positions where firing rate dropped below 10% the peak firing rate. Firing rates over the range of pixels defined by
this method were used to determine the center of mass (COM) of each firing field. To permit comparison of field positions across tracks, it was necessary to also calculate the angle, relative to the recording room, of the COM of firing fields. Note that the use of firing field angles for this analysis presumes that firing field sets bear an allocentric frame of reference as opposed to one based upon the start and end-points of the track itself. The experiments described in supplementary figure 1 confirm this.

Field length ratio determination

Firing field sets dominated the present dataset and were composed of 3-5 firing field repeats which occurred on adjacent loops and were aligned across the same range of angles relative to the curtained borders of the recording room (e.g., top panels of figure 1C). The lengths of each individual field were determined. Subsequently, field length ratios for all possible combinations were calculated. For example, a neuron with analogous fields across loops 2, 3, and 4 of a given track would yield 3 ratios (loop 2 length vs. loop 3 length, loop 2 length vs. loop 4 length, and loop 3 length vs. loop 4 length). Neurons with 4-field and 5-field sets yielded 6 and 10 ratios, respectively. As this procedure normalizes differences between the mean cross-loop field lengths of individual neurons, such ratios were pooled for comparison in figure 1D. Expected field length ratios were determined by simply taking all possible ratios of the physical lengths of individual loops as determined by the number of assigned template points.

For neurons (74%) bearing field sets as opposed to isolated fields, the analysis of field lengths across the 5 loops of squared tracks was complicated by the presence of neurons (N=32) whose firing fields quite obviously did not change in size to match differences in the overall size of the individual loops (e.g., figure 1C, lower left ratemap and figure 2A rightmost ratemap). As shown, most of these neurons exhibited firing fields localized to track corners (figure 2D, see supplementary figure 2C for explanation of assignment of fields to corners versus straight-aways). The complication arose from the fact that neurons with firing field lengths which did adapt to overall loop length did, sometimes, exhibit
significant firing across track corners. Thus, it was not possible to first assign a
given field set to a corner or straightaway and then compare the degree to which
each group’s field lengths matched loop-to-loop differences in physical length.
Instead the opposite approach was employed. Neurons which statistically
showed very little sign of field length adaptation (<10% than expected based on
physical loop lengths) were identified followed by an examination as to whether
their firing fields were or were not randomly distributed.

Results

Animals learned to make uninterrupted inbound (i.e., center-going) and outbound
traversals of 4 different spiral-shaped tracks. Each track demanded different
locomotor action sequences (i.e., series of left or right turns and straight runs,
figure 1A). All tracks were composed of 5 individual ‘loops’ defined by short (4
cm) walls permitting visualization of the full recording area. Loops were
numbered 1-5 (largest-smallest) and defined as shown in figure 1B. Tracks
differed in shape (circular versus squared), the direction of travel associated with
any given space, and/or type of turn behavior (all left versus all right). As such, it
was possible to compare CA1 firing patterns across different, partially-
overlapping combinations of spatial, temporal, directional, and behavioral
context.

Overview of CA1 firing patterns on spiral tracks

The exact nature of the spatial firing patterns observed across spiral-shaped
tracks was somewhat unexpected. With few exceptions, dorsal CA1 neurons
having significant discharge on any given track exhibited either isolated spatial
firing fields (23%, N=82) or, much more often, firing field ‘sets’ (77%, N=238,
figure 1C). Firing field sets were composed of 3-5 firing field repeats which
occurred on adjacent loops and were aligned across the same range of angles
relative to the curtained borders of the recording room (supplemental figure 1).
To determine the spatial frame of reference for such firing fields, spatial firing patterns before and after 180-degree rotations of spiral tracks (relative to the curtained enclosure) were compared. From such experiments, the allocentric space defined by the positioning of visual objects along the curtained enclosure, as opposed to the spiral track itself, was found to constitute the spatial frame of reference for firing field sets (supplemental figure 1).

The very presence and prevalence of firing field sets (or ‘field-set’ neurons) opened the dataset to two qualitatively different forms by which partial overlap in firing pattern could be analyzed. The first form involves comparison of firing field sets across different tracks. Here, firing pattern overlap is assessed as the tendency for neurons to fire across the same positions in allocentric space despite differences in the directions of movement and/or types of behavioral sequences dictated by the shapes of two different tracks. As will be discussed, this form of firing pattern overlap was measured both by determining the extent to which neurons discriminated two tracks by exhibiting firing fields on one, but not the other, track, and, subsequently, by determining whether those neurons having firing fields on both tracks exhibited those firing fields across the same allocentric space. This form of partial overlap in firing pattern might also be referred to as ‘partial remapping’ as the similarities and differences in activity are described for the identical regions of allocentric space. However, since the term ‘remapping’ implies an active reorganization of an existing spatial mapping and since the present experiments examine stable firing patterns on highly familiar tracks, the more generic term ‘pattern recurrence’ will be maintained.

The second form of analysis considers firing patterns within single tracks. Here, the term ‘pattern recurrence’ (of a firing pattern) will again be used, but is meant to refer to pattern recurrence across different spaces and different episode epochs which nevertheless share the same or similar combination of locomotor behavior and directional heading. As cross-track analysis of firing pattern overlap necessitated initial evaluation of single-track firing characteristics, the
results of such ‘pattern recurrence’ analyses for individual tracks will be
presented first.

Within-track pattern recurrence of CA1 firing patterns

Figure 1C depicts firing rate maps for four different CA1 neurons. Three of these
exhibited firing field sets, a pattern which defined the majority of neurons having
significant discharge on any of the tracks utilized. The firing pattern of such
neurons can be said to recur or generalize across both time (or loop number) and
across multiple sub-regions of the track. This effect is quantified in the analyses
described below. The fourth firing rate-map (bottom-right of figure) exhibits an
isolated firing field pattern more like that observed in a very large number of CA1
recording studies.

Across the full population of neurons exhibiting firing field sets on circular spiral
tracks, comparisons of field lengths on individual loops matched comparisons of
overall loop lengths (e.g., figure 1C, top right). To quantify this effect, the ratio of
each neuron’s firing field lengths for all possible pair-wise combinations of loops
1-5 was obtained (figure 1D, upper plot). Mean cross-loop ratios for field lengths
of circular spirals (red lines) closely matched the ratios expected by comparing
physical loop lengths (gray bars). Accordingly, a very high correlation value ($r =
0.98$) was obtained by correlating mean field length ratios across all cells with
ratios of actual (physical) loop length ratios (i.e., correlating the values given by
the red bars of figure 1D with the gray bar values). Strong correlations were also
observed at the level of single neurons where mean correlations across all cells
were high for data obtained from circular spiral tracks (mean $r = 0.72 +/- 0.35$)
and from squared spiral tracks (mean $r = 0.66 +/- 0.44$).

The adaptation of firing field lengths to loop lengths appeared to arise as a
lengthening of field sizes on outer loops. As shown in supplemental figure 3,
only loop firing fields for such neurons were inordinately long (mean, 62.5 cm)
compared to those observed on both smaller and larger non-spiral tracks placed 
in the same room (20-27 cm; t-test, p<0.001 for both comparisons), compared to 
the firing field sizes of loop 1 neurons with isolated fields (42.37 +/- 21.5 cm; t-
test, p<0.01), and compared to those of other laboratories recording from 
approximately the same dorsal region of CA1 (Mehta et al., 1997; Maurer et al., 
2005). In contrast, field lengths on non-spiral tracks were of similar length to 
those found along loops 4 and 5.

Similar results were observed on squared spiral tracks (e.g., figure 1C upper left 
rate map). Longer loops were associated with proportionately longer field 
lengths for those neurons exhibiting field sets (figure 1D, lower, red bars). 
However, a subset of 32 neurons (23.5% of squared-spiral field-set neurons) 
exhibited firing fields whose lengths clearly did not adapt to the much larger sizes 
of outer loops (e.g., figure 1C - lower left image, figure 2A – leftmost image). For 
such neurons, field length ratios for larger/smaller loops averaged less than 10% 
the expected value (figure 1D, lower, black bars).

The presence of field-set neurons with non-adapting firing field lengths strongly 
suggests that overall loop length is, in and of itself, not directly related to the 
cross-loop differences in firing field lengths. An alternative possibility is that field 
length adaptation occurs whenever type of locomotor behavior is held constant 
and allocentric position and direction of travel are held within certain ranges. 
This likely explains the non-random distribution of non-adapting firing field sets 
across circular (3%) versus squared spiral tracks (23.5%). Type of locomotor 
behavior on circular spiral tracks is unchanged while squared spiral tracks 
demand rather sharp transitions between forward running and left or right turning 
(e.g., supplemental figure 4). As a consequence, across all paths considered in 
the present dataset, the corners of squared spiral paths represent the only 
instances where type of locomotor behavior (execution of a turn) and movement 
through 90° of directional headings occur over the same lengths of space 
irrespective of overall loop length.
Accordingly, closer examination revealed that firing fields for non-adapting field sets were not distributed randomly across the space of squared spiral tracks. Rather, for the large majority of such neurons, firing fields occurred with proximity to the corners of squared spiral tracks (84%, or 27 of 32, figure 2D). To test the statistical significance of this bias, the position of firing fields on loop 3 for a given non-adapting field set was categorized as lying on either a straight-run section or corner section (see supplemental figure 2C for detail). Straight-run and corner sections occupied equal proportions (0.5) of the total track. As such, the expected distribution of corner vs. straight-run fields was taken as the number of fields divided by 2 (i.e., 32/2, or 16). A chi-square test comparing the expected and actual distribution revealed a strong bias for non-adapting field sets to lie along corner sections ($\chi^2=15.1$, $p<0.001$). Thus, the spatial expansion and compression of the combined behavioral, positional, and directional context inherent to the structure of the squared spiral track was mirrored in the field lengths of CA1 neurons bearing field sets.

The final set of within-track analyses examined whether subtle differences between the five loops of a track also impact the degree of pattern recurrence exhibited by hippocampal CA1 neurons. The middle 3 loops of the 5-loop spirals used here are those most similar to each other. Each covers the same set of movement trajectories and each is flanked by another loop. Loops 1 and 5 are the most different. The 4-cm wall forming the outermost border of loop 1 is flanked by a 1 meter drop-off to the floor and, in addition, is associated with the initiation of locomotion. The innermost border of loop 5 is flanked by the reward zone and precedes the abrupt end of locomotion as well as the delivery of reward.

Three different features of CA1 activity patterns mirrored these between-loop similarities and dissimilarities. First, isolated fields (figure 2A, middle image), whose activity clearly distinguishes between loops, were not distributed evenly
Across loops but were most numerous on loops 1 and 5 (figure 2C). Second, 61% of neurons characterized as having field sets exhibited fields on only 3 or 4 of the 5 loops (e.g., figure 2A – left image); on the remaining loop(s), there was very little or no activity. That is, the expected fields were ‘missing’ thereby distinguishing these loops from those containing firing field repeats. As for isolated fields, ‘missing’ fields predominated on loops 1 and 5 (figure 2B). For both isolated and ‘missing’ fields, the ‘expected’ distribution across loops was assumed to be the total number of such fields divided by the number of loops (e.g., the number of ‘expected’ isolated fields per loop was 82/5 or 16.4). For both isolated and ‘missing’ fields, chi-square tests comparing expected to actual cross-loop distributions were highly significant (isolated fields $\chi^2=98.0$, $p<0.001$; ‘missing fields $\chi^2=256.7$, $p<0.001$). Finally, in a related analysis, the greater overall similarity among loops 2, 3, and 4 was paralleled by greater overall pattern recurrence of CA1 activity. Neurons with sets of 3 repeating fields across loops 2, 3, and 4 (N=28) were twice as numerous as 3-field sets across loops 1, 2, and 3 (N=14) and 14 times more numerous than 3-field sets across loops 3, 4, and 5 (N=2). Setting the expected distribution of 3-field firing field sets across loops 1-5 as the number of such sets divided by the number of possible loop combinations (3) on which they could occur (loops 1, 2, 3, loops 2, 3, 4, or loops 3, 4, 5), the observed distribution of 3-field sets was found to be significantly biased toward loops 2-4 ($\chi^2=22.2$, $p<0.001$).

**Cross-track partial overlap of CA1 firing patterns**

The degree of overlap between spatially-specific firing patterns of CA1 hippocampal neurons varied as a function of the similarity between the trajectories taken on different spiral tracks. Trajectory similarity varied according to a combination of variables which were allocentric position, directional heading, and two different features of locomotor behavior (circular-spiral-running versus squared-spiral running and left-turning versus right-turning). Figures 3A and 3B depict the activity of two representative neurons across four different trajectories.
Figure 3C depicts the percentage of neurons exhibiting firing field sets across different types of track pairings. For the same set of track pairings, figures 3D-3G depict the spatial orientation (in allocentric space) of firing field sets for those neurons exhibiting field sets under both conditions.

Leaving only the allocentric (i.e., room-centered) positions encountered as the feature common to two experiences, CA1 firing patterns are near maximally different (figures 3C,3G). Little evidence of partial overlap in CA1 firing patterns was observed when the trajectories taken: 1. differed in shape (circular vs. squared); 2. occurred on physically different tracks; 3. involved opposite movement directions across any given environmental position; and, 4. required different locomotor behaviors. Under these conditions, locomotor behavior varies not only by turn type (left vs. right), but also by obvious differences in the meter of changes in speed across circular and squared tracks (supplemental figure 4). All these variables differed across, for instance, outbound traversals of circular, left-turning and inbound traversals of squared, right-turning spiral tracks. Of 74 neurons recorded across two such conditions, the large majority (55, or 74%) discriminated the two experiences by exhibiting a significant firing field on only one of the two tracks (figure 3C, rightmost condition). To determine whether the remaining 19 neurons exhibited firing fields in the same or different positions within the environment, the center of mass (COM) for each firing field was determined and their angles, relative to track center, were calculated (supplemental figures 1,2). Between the two conditions, the mean difference in firing field angle was 108.2° (+/- 53.3°, SD) which is not significantly different than the 90° difference expected by chance (one-sample t-test). Furthermore, the correlation between field angles was not significant (r = -0.27, figure 3G).

Similarly, little evidence for overlap in firing patterns was observed for any given allocentric position when the trajectories taken differed in directional heading and type of turn behavior (left vs. right), but with type of spiral (circular vs. squared) held in common. As shown in figure 3C (3rd condition from left), 81.1% of
neurons exhibited firing fields in only one of the two conditions for track comparisons of this type. Furthermore, for those neurons with field sets in both conditions (18.9% of all), the positioning of those field sets relative to the allocentric space differed (figure 3F).

In contrast, a high degree of recurrence in firing patterns was detected in comparisons across trajectories which differed only by the physical track on which the animals were run. For instance, inbound trajectories of the track schematized in figure 1A (top left) and outbound trajectories along the track schematized in figure 1A (top right) both involve left-turning behavior along a circular spiral path. In addition, the directions of movement through any given environmental position differ only slightly. Here, in contrast to the aforementioned set of comparisons, a higher percentage of CA1 neurons (59 of 104, or 56%) exhibited firing fields on both spiral tracks. ($\chi^2 = 8.3$, $p<0.01$, figure 3C leftmost condition). Moreover, those neurons with significant firing fields on both tracks, maintained those fields within very similar regions of the recording room (figure 3D). Two such examples are given in figures 3A and 3B. In each figure, the lower left versus upper right heat-mappings of firing rate across space reveal field sets in very similar allocentric positions. A counter-example is given by the same neuron in figure 3A which differentiated the trajectories shown in the upper left and lower right plots. Across experiences, the angles of firing field COMs, relative to track centers, were tightly correlated (figure 3D, $r = 0.82$, $n=59$, $p<0.001$). The mean difference in COM angle was $36^\circ$ ($\pm 49^\circ$ SD) which was significantly less than $90^\circ$ mean difference expected by chance ($p<0.001$, one-sample t-test). Thus, across two different time periods associated with traversal of two different spiral tracks, a high degree of CA1 firing pattern similarity is observed when the type of locomotor behavior and directions of movement through space are maintained.

Finally, a moderate level of firing pattern overlap was observed when the direction of movement through any given space varied only slightly, but
locomotor behavior differed (compare, for instance, figure 1A top-left and bottom left inbound runs). As already noted, circular and squared spiral tracks that shared left-turning or right-turning behavior were associated with different temporal patterns of movement speed. Simply put, squared spiral tracks demand decelerations into each 90° turn. This difference alone greatly reduced, but did not eliminate, partial overlap in activity patterns. While 81% (161 of 198) of CA1 neurons discriminated two such experiences by firing significantly only on one track, those with significant activity on both tracks often exhibited fields over similar allocentric positions. Firing field COM angles between such path-running experiences were significantly correlated ($r=0.49$, $p<0.02$, figure 3E) and 16 of 37 neurons exhibited firing field COM angle differences of less than 45° ($\chi^2 = 9.9$, $p<0.01$). Note that the expected distribution for this analysis assumed that the distribution of angular differences between field sets would be random with 25% expected to fall in each of the following ranges: 0°-45°, 46°-90°, 91°-135°, and 136°-180°).

Discussion

The spatially-specific firing patterns of dorsal hippocampal CA1 neurons were examined during uninterrupted traversals of differently-shaped spiral tracks (figure 1B). A small, but significant, proportion of neurons exhibited the isolated, place-specific firing fields of the type typically observed in CA1 recordings. However, such fields were largely limited to the first and final loops of the five-loop tracks (figure 2C). In contrast, the large majority of CA1 neurons (~75%) exhibited firing patterns that recurred across multiple sub-regions of space and across temporally distal epochs of individual spiral tracks. Specifically, such within-track pattern recurrence took the form of repeating firing fields across analogous sub-sections of the five differently-sized loops composing each spiral track (figure 1C).
A second form of pattern recurrence was observed in comparisons of firing patterns across differently-shaped spiral tracks. Here, some neurons exhibited firing fields over those portions of two tracks that occupied the same space in the recording room while others fired on only one track or exhibited fields in different places (figure 3). Both within-track and across-track pattern recurrence was maximized by similarity in movement direction and the specific type of turning and straight-run behaviors utilized in path traversal. In this way, the results extend the findings of prior work showing that the similarity in shape of environmental boundaries and visual appearance of environmental boundaries can strongly influence the extent to which pattern recurrence within or across environments is observed. Furthermore, the present results demonstrate that pattern recurrence can be observed even following extensive experience. The relevance of the work to understanding the dual role of the hippocampus in mapping spatial position and generating episodic memories is discussed below.

Adaptation of firing field sizes within individual spiral tracks

Within individual spiral field tracks, a large majority of neurons exhibited firing field repeats. Field lengths on each loop for a set of repeating firing fields closely matched size differences in the loop lengths themselves (figure 1D). Given the structures of the tracks, loop lengths were also proportional to the distances over which type of locomotor behavior (i.e., left turns, right turns, straight runs) and movement direction were held in common, suggesting that the observed firing field lengths mirrored the distances over which behavior and movement direction were unchanged. Experiments with squared spiral tracks were especially critical in revealing this adaptive feature of CA1 neuron spatially-specific firing patterns. Squared spiral tracks feature discontinuous changes in movement direction and type of locomotor behavior such that parallel straight-run sections for different loops vary in size, but not in the type of locomotor behavior utilized or in movement direction. In contrast, adjacent corners of squared spiral tracks are associated with turning behavior and transitions through 90-degrees of
movement direction that occupy equally-sized spaces across all loops. Accordingly, neurons with firing fields along straight-run sections exhibited adaptation in the firing field lengths; concurrently, neurons with firing field repeats that did not adapt to loop size were positioned almost exclusively along the corners of squared spiral tracks (figures 1D, 2D).

Together, the presence of firing field repeats and the relation of their field lengths to track geometry provide strong evidence that the specific sequences of movement direction and locomotor behaviors that compose paths can induce persistence of firing fields across multiple, adjoined environmental sub-regions. This result forms a natural counterpart to the demonstration that firing pattern changes for a single sub-region may be induced by changing either the movement direction or overall path taken to reach that sub-region (McNaughton et al., 1983; Frank et al., 2000; Wood et al., 2000; Ferbinteanu and Shapiro, 2003; Nitz, 2006; Ainge et al., 2007). Furthermore, the results complement those of prior studies demonstrating that environmental shape and the spacing of visual cues at boundaries can alter the space over which hippocampal spatially-specific firing is observed (Muller and Kubie, 1987; O'Keefe and Burgess, 1996; Fenton et al., 2000). Finally, the extensive pattern recurrence associated with path similarity in the present study can be contrasted with the findings of Frank et al., (2000) where 'path equivalence' was not found for the majority of CA1 neurons. The differences between this study and the present may derive from differences in the shapes of those paths that preceded and followed two paths of the same shape. Alternatively, differences in CA1 firing patterns across same-shaped paths may have been related to differences in their temporal positioning within the working memory component of the task used by Frank et al..

Given that CA1 firing fields on spiral tracks were positioned according to the stable frame of reference given by the curtained enclosure, the variation in firing field lengths for neurons recorded in CA1 is remarkable and suggests that the observed scale at which hippocampal neurons map space can be highly
dynamic. While firing field sizes have previously been shown to correlate positively with the position of neurons along the septo-temporal axis of the hippocampus (Jung et al., 1994; Maurer et al., 2005; Kjelstrup et al., 2008), the specific positioning of recording electrodes in the present study is unlikely to explain, in particular, the long firing fields of neurons along loop 1 of spiral tracks. Such fields were much longer than those observed for CA1 neurons recorded from the same hippocampal sub-region and in the very same curtained enclosure but on non-spiral tracks (supplemental figure 3). Loop 1 field lengths were also significantly larger than those reported for the very same sub-region of CA1 in experiments that specifically examined field size (Mehta et al., 1997; Maurer et al., 2005). Finally, for the same population of animals (and, thus, the same recording sites), loop 1 field lengths for neurons with repeating fields were significantly longer than loop 1 field lengths for neurons with isolated firing fields. Field sizes for the latter were intermediate to loop 3 and loop 4 field sizes. While the neural mechanisms permitting adaptation in firing field size cannot be determined in the present work, several possible explanations are worth consideration. First, it is possible that long and short firing fields arise from dynamics in the responsivity of CA1 neurons to different sets of dorsomedial entorhinal ‘grid’ neurons having narrowly-spaced versus widely-spaced activation nodes (McNaughton et al., 2006; Hafting et al., 2005). Notably, entorhinal ‘grid’ cell firing nodes themselves can increase in size in response to the changing size of an environment, though the permanence of such changes remains to be established (Barry et al., 2007).

A second possibility is that, with some modification, the boundary vector model for hippocampal spatially-specific firing (Hartley et al., 2000; Barry et al., 2006) may provide an explanation for the observed firing patterns. Here, firing for a given CA1 neuron is thought to depend greatly on inputs from boundary vector cells. The latter are thought to fire according to a combination of the animal's proximity to a boundary and its head-direction relative to that same boundary.
Considering the short walls defining the track as the relevant boundaries, the animal's proximity to them and its head direction remain constant across parallel straight-run sections of the squared-spiral tracks. Thus, it is possible that boundary proximity and the type of locomotor behavior that it entails is combined with head direction to result in elongated firing fields. However, in another study carried out in the very same curtained enclosure (Nitz, 2006), hippocampal firing fields did not elongate in response to extensions in track segments despite persistence of head direction and boundary proximity. In the latter study, as compared to the present work, those sections of the full path that shared allocentric positioning, boundary proximity and head-direction were embedded within otherwise differently-shaped paths demanding different locomotor behavior sequences. On spiral tracks, of course, such sections are embedded within identically composed paths (i.e., the five loops of each track). Thus, overall route shape constitutes a controlling variable which the boundary vector model would need to incorporate in order to explain the present findings. Notably, this conclusion is also consistent with the finding that ‘missing’ fields for neurons bearing less than the 5 possible firing field repeats were largely confined to the beginnings and endings of the behavioral sequences composing full track traversals. Here again, boundary proximity and head-direction are shared between loops 1 and 2 and between loops 4 and 5, but loop 1 begins with initiation of the route traversal and loop 5 ends with a full stop at the reward site.

**Incidence rate of firing pattern recurrence for analogous positions of two tracks**

In a multitude of studies, the spatial firing patterns of hippocampal neurons during random foraging within open-field environments has been examined. From such studies, it is clear that environment shape, size, and the arrangement of prominent distal visual cues are strong determinants of both spatially specific firing and the degree of similarity between spatial firing patterns for two environments (Muller and Kubie, 1987; Wilson and McNaughton, 1993; O'Keefe
and Burgess, 1996; Fenton et al., 2000; Lever et al., 2002; Nitz and McNaughton, 2004;). Yet, despite strong evidence that integration of movement direction and speed is a strong contributor to spatially specific firing (e.g., Markus et al., 1994; Sargolini et al., 2006; Skaggs and McNaughton, 1998), relatively little work has directly addressed the impact of locomotor sequences in determining overlap in spatial firing patterns for different experiences (Markus et al., 1995).

In the present work, the walls defining spatial paths were short allowing the animal to track its position relative to stable visual cues arranged across the curtained enclosure. The results of track rotation experiments (supplemental figure 1) consistently revealed these more distal cues to be the spatial frame of reference for hippocampal firing patterns. As such, it was possible to ascertain the extent to which locomotor behavior itself (i.e., the sequencing of movement directions and locomotor behaviors such as turning) impacts overlap between two different experiences.

Overlap in firing patterns for different spiral tracks occupying the same allocentric space was found to depend on the similarity in the movement directions and locomotor behaviors across those tracks. For example, high similarity is given by comparing outbound (center-to-perimeter) runs along squared spiral paths demanding right turns with inbound runs along squared spiral paths also demanding right turns; the two conditions yield identity in behavior and direction for any given allocentric position in the recording room. What differs is the increasing versus decreasing space between turns from beginning through end. Such comparisons revealed high cross-track firing pattern overlap for the subset of neurons that exhibited significant firing fields on both tracks (figure 3D). Still, pattern recurrence was incomplete in that approximately 40% of all neurons discriminated the two track-running experiences by firing significantly on only one track (figure 3C). The latter result presumably reflects the impact of context
given by ‘inbound’ versus ‘outbound’ travel as all other variables are held in
common.

At another extreme, association of any single allocentric position with different
movement directions and different locomotor behaviors yielded negligible overlap
in cross-track firing patterns (figures 3F,3G). Thus, even within an allocentric
space (the curtained enclosure) whose dimensions and spatial distribution of
visual cues are unchanged, the influence of position can be fully negated by
differences in movement direction and type of locomotor behavior. The observed
changes in spatially-specific firing are consistent with prior work demonstrating
that movement direction can, by itself, determine whether a single CA1 neuron
fires within a given sub-region of space (McNaughton et al., 1983). The result
also extends prior work showing that the presence or absence of local cues can
enhance the percentage of neurons exhibiting direction-dependent firing
(Battaglia et al., 2004).

A more subtle manipulation of locomotor behavior was considered by examining
firing pattern overlap for conditions where allocentric position, movement
direction, and turning direction (left versus right) were all held in common, but
turning itself differed in that it was continuous (circular spirals) or discontinuous
(squared spirals). By exhibiting appreciable discharge along only one or the
other of two such tracks, a significant number of neurons discriminated the
allocentric spaces occupied by the two tracks (figure 3C). Thus, even subtle
manipulations of behavior (constant versus sharp turning) can negatively impact
the degree to which recurrence of firing patterns across conditions is observed.
Nevertheless, a significant proportion of those neurons with spatially-specific
firing on both tracks exhibited such firing over the same allocentric positions.
That is, a small, but significant degree of pattern recurrence remains when
allocentric position and direction of travel are held constant (figure 3E).
Taking together the results obtained in cross-track comparisons, it appears that the continuum of differences in movement direction and type of locomotor behavior across all possible track pairings was paralleled by a continuum of pattern recurrence in CA1 firing field positions. This result is consistent with work demonstrating that gradual morphing of environment shape (e.g., from a circle to a similarly sized square) is paralleled by a graded alteration in the allocentric positioning of CA1 place-specific firing fields (Leutgeb et al., 2005). The hippocampal sub-region differences in degree of pattern recurrence identified in the latter study remain to be tested with respect to pattern recurrence induced by similarity in movement direction and locomotor behavior.

**Possible implications of pattern recurrence for episodic memory generation**

Three pieces of evidence favor the idea that spatially-specific firing patterns of hippocampal neurons can shed light on the character of episodic memory generation. First, the order in which even widely separated sub-regions of allocentric space are visited is robustly registered on short timescales (<200ms) in the firing order of hippocampal neurons (O'Keefe and Recce, 1983; Kjelstrup et al., 2008; Huxter et al., 2008). Second, as previously stated, the ordering of positions encountered in an environment may also be given by differences in the magnitude of spatially-specific firing; different paths through a single space may yield different firing patterns for that space (Frank et al., 2000; Wood et al., 2000; Ferbinteanu and Shapiro, 2003; Nitz, 2006; Ainge et al., 2007). Finally, the hippocampus itself has recently been shown to be necessary for memory of the order of positions visited in an environment (Hunsaker et al., 2008).

To the extent that the character of episodic memory generation depends on the firing order of spatially specific hippocampal CA1 neurons, the character of firing field distributions on spiral tracks indicates that temporal epochs of episodic memories are irregular in their duration. This conclusion can be reached
irrespective of whether one takes completion of a single loop as representing a single ‘episode’ or, instead, the full spiral track traversal (which, notably, is supported by the uninterrupted nature of the full traversal).

Considering the space of any full spiral track, the present results demonstrate that firing pattern differences are much greater for the first and last loop as compared with the middle three loops (i.e., nos. 2-4). A primary reason for this is that isolated fields and the ‘missing’ fields of CA1 neurons with firing field repeats occurred much more often on the first and last loops. Firing patterns across loops 2 through 4 are very similar to each other. As a result, if one considers distinction in firing pattern as a requirement for distinguishing epochs of time, then traversal of the five loops composing a full spiral track can be broken down into 3 temporal epochs, traversal of loop 1, traversal of loops 2-4, and traversal of loop 5. Notably, differences in the time durations associated with each epoch are extensive.

If episodes are instead considered at the level of individual loop completions, irregularity in the time-frame over which CA1 patterns change is also observed. Particularly for loops 2-4, firing patterns for individual neurons tend to persist along straight-run sections of squared spiral tracks. Such pattern stability over long stretches of space and time are broken by abrupt alterations in hippocampal firing patterns at the corners of squared spiral tracks when neurons with firing field repeats specific to corners begin firing. From this view, the completion of a loop breaks down into 8 different epochs of two distinct durations, long duration straight run sections and short duration turn points.

Finally, the high degree of pattern recurrence both within individual tracks and across some pairs of spiral tracks, suggests that the firing patterns of hippocampal CA1 neurons are adaptive in ways that can favor generalization of episodic memories for different experiences. Event sequences, such as those of a path traversal, compose different episodes. The degree of overlap in the event
content and event ordering of any two episodes can be expected to vary continuously. The present data strongly suggest that the CA1 region registers commonalities among otherwise different episodes. In doing so, the CA1 region may generate episodic memories in a way that permits memories to be examined for similarities and differences (Eichenbaum et al., 1999). Ultimately, this may permit the subsequent extraction of rules by which events often proceed and support behavioral planning under analogous conditions. This interpretation is consistent with recent findings correlating human hippocampal fMRI data during exposure to different pairings of visual items with later performance on a generalization task utilizing different pairings of the very same stimuli (Shohamy et al., 2008).

Summary

Across the space of individual spiral-shaped routes through an environment, hippocampal CA1 neurons exhibited adaptation in their firing fields that closely followed specific variations in movement direction and locomotor behavior sequences. Adaptations took the form of pattern recurrence across multiple sub-regions of the environment, across widely separated temporal epochs of route traversals, and across experiences on differently-composed spiral tracks. The results identify route shapes and the movement directions and behaviors required for their traversal as robust variables driving adaptations in CA1 firing patterns. The results also suggest that the CA1 region of the hippocampus plays a critical role in generating episodic memories that link common elements of temporally displaced experiences.
Figure Legends

**Figure 1:** Most CA1 neurons form firing field ‘sets’ on spiral tracks. Within such sets, individual field lengths adapt to the spaces associated with like context. **A.** Animals made inbound (black arrows) and outbound (blue arrows) traversals of 4 different spiral-shaped tracks centered on the same position within the space of an easily-observable curtained enclosure. Trajectories differed in shape (squared vs. circular), direction of movement through any given room position, and behavior (left- vs. right-turning). **B.** Representative tracking data for individual inbound, right-going trajectories taken on a squared and a circular spiral track. Each was composed of 5 individual loops. **C.** Spatial firing ‘ratemaps’ of 4 different CA1 neurons. For each ratemap, a light blue schematic of the path trajectory is given. All data shown here were for inbound (center-going) runs. Three basic forms of spatial firing were observed from a sample of 349 neurons. Upper left and right: Neurons with adapting field sets (N=238) exhibited repeating fields over approximately the same trajectories of 3-5 individual loops of the full spiral track; field lengths ‘adapted’ in that they matched differences in the size of individual path loops. Lower right: isolated firing fields (N=82) were predominantly observed on outer or inner loops. Lower left: ‘non-adapting’ neurons exhibited repeating fields which clearly did not adapt to individual loop lengths. Most (27 of 32) were observed on or near the corners of squared spiral tracks. **D.** Actual (red lines) versus expected (gray bars) firing field length ratios for all possible combinations of loops 1-5 (x-axis) for all neurons exhibiting firing field sets. Expected ratios are based on the ratio of the physical lengths of each individual loop. Upper: On circular spiral tracks (N=135), the ratios of firing field lengths across individual loops closely follows the values expected based on the physical length of each loop. Lower: The firing fields of most neurons recorded on squared spiral tracks also adapted to loop-to-loop differences in size (red lines, N=103). A subset of CA1 neurons, primarily localized to corners of squared
spiral tracks, exhibited similarly-sized firing fields across all loops (black lines, N=32).

**Figure 2:** Non-random distribution of ‘missing’ fields, isolated fields, and non-adapting field sets. A. Spatial firing ratemaps. Left: Inbound, left-going traversal of a circular spiral track. This neuron exhibited firing field repeats on individual loops 1-4, but is ‘missing’ a firing field for the innermost loop (#5). Middle: Inbound, right-going traversal of a circular spiral track. An isolated firing field is observed on the innermost loop. Right: Inbound, right-going traversal of a squared spiral track. This neuron exhibited a non-adapting field set with proximity to the northwest corner. B. Total number of ‘missing’ fields across loops 1-5. C. Total number of isolated fields observed on loops 1-5. D. Total number of non-adapting field sets on circle spirals (C), straightaway segments of squared spirals (SS), and corner segments of squared spirals (CS). Missing and isolated fields predominate on loops 1 and 5 while non-adapting field sets predominately occur along corner segments. Each distribution is non-random as determined by a chi-square test (p<0.001 or better).

**Figure 3:** Comparison of field positions across different spiral tracks. A. Spatial firing ratemaps for a single CA1 neuron during inbound and outbound traversals of two different circular spiral tracks. Left-turning inbound and left-turning outbound firing patterns (upper right and lower left maps) correspond to different tracks, but are nevertheless very similar presumably owing to the similarity in spatial positions, type of behavior (circle- vs. square-running), and directions of movement. In contrast, the same neuron discriminated equally-similar experiences on right-turning inbound and right-turning outbound trajectories (upper left and lower right maps) by exhibiting a field set only for the former trajectory. B: Spatial firing ratemaps for a non-adapting ‘corner’ neuron with a similar discharge pattern across two squared spiral tracks at the points of each where left turns are made in the SE quadrant of the room. White arrows indicate mean angle of firing fields relative to the room. C. For each type of track
comparison, the percentage of neurons having significant firing fields on both
tracks is graphed. Note that there are actually 4 path combinations for each
comparison type, but only 1 combination is depicted. For comparison type 1
(leftmost bar), data from inbound and outbound left-turning paths on squared
spirals is included as the type of behavior and directions of travel are the same.
For comparison 2, the type of turn behavior (L/R) and directions of travel are the
same, but all combinations are of circular vs. squared spirals. For comparison
type 3, the only similarity between paths is that they are of the circular or squared
type of spiral. For comparison type 4 (rightmost bar), all variables, except of
course allocentric position, are different.  

D. Comparison of firing field angles for trajectories on two different tracks which share the same directions of movement and types of behavior (maze schematics below depict one of two possible trajectory comparisons). Out of 104 possible cases, firing fields in both conditions were observed 59 times (57%). Most points (N=59) line up close to the red line which corresponds to identical firing field angles in the two conditions. Accordingly, the correlation between field angles was very high (r = 0.82).  

E. A wider, but non-random, distribution of firing field angles was found across conditions in which directions of movement through any given space and turn-behavior (left vs. right) were held constant, but type of behavior (circle- vs. square-running) differed. Firing fields in both conditions occurred in only 19% (37 of 198) of all possible cases. For these neurons, the correlation of field angles was significant, but lower (r = 0.49).  

F. 18.9% of neurons exhibited firing fields across conditions in which directions of movement and turn-behavior were opposite, but type of behavior (circle- vs. square-running) was the same. Here, the correlation of field angles was minimal and statistically non-significant.  

G. Comparison of firing field angles for trajectories on two different tracks which differ in two forms of locomotor behavior (left- vs. right-going, circle- vs. square-running) and directions of movement through any given space (maze schematics below depict one of four possible trajectory comparisons). Only 19 of 74 neurons exhibit field sets in both conditions and the angular positions of those fields (relative to center) were unrelated (r=-0.27).
Supplementary figure 1: Allocentric reference frame of CA1 spatial firing patterns. A. 180-degree spiral track rotations were used to determine whether CA1 spatial firing patterns were anchored to local maze cues or to distal room cues. The track center was kept constant across conditions. The track sat atop a table in the middle of a curtained area of the recording room. The curtain was adorned with fabric shapes of different sizes and colors which served as distal cues of room position. The curtain was open to the rest of the recording room on one side. Animals rested in a cushioned bowl between track running sessions (orange circle). B. Spiral track rotation unavoidably produces a slight offset of track positions. Because of this, it was not possible to examine correlations between 2D firing ratemaps. Instead, for individual firing fields, the center of mass and its angle relative to the room was determined. For neurons with repeating fields, the mean angle of all fields was taken as the overall firing angle. If spatial firing patterns correspond to track position, one would expect the angle difference between the normal and rotated configuration to be near 180-degrees. If spatial firing patterns are anchored to room cues, one would expect the firing angle to be unchanged between conditions. Note that maintenance of allocentric positioning of firing fields means that those fields, across the two conditions, occur at quite different phases of the full inbound or outbound track traversal. C. Between conditions, firing angle was largely unchanged. Plotted for 30 neurons from 3 animals (red, green, blue) are the firing angles (relative to the room) for the normal and rotated configurations. Firing angles were distributed evenly. Most points fall close to the diagonal line which represents identical field angles for the two configurations. A strong correlation between normal and rotated firing angles was observed ($r=0.71, p<0.001$) supporting the conclusion that firing fields are anchored to distal room cues (i.e., they take an allocentric frame of reference).

Supplementary figure 2: Template matching of position points, firing field measurements, and ‘straightaway’ vs. ‘corner’ segments of squared spiral tracks.
A. Position points for each inbound and outbound traversal along circular (top) and squared (bottom) spiral tracks were matched to a template. A custom-made Matlab GUI (Mathworks-Natick, MA) was used to scan all tracked points in order to identify the point at which the animal began a ballistic path toward the center reward site (an ‘inbound’ run) and to identify the exact point just preceding the point at which the animal stopped within the center reward site. Outbound path traversals were treated similarly. Only position points associated with uninterrupted path traversals were used for analysis. Left: representative inbound path traversals (light blue points) of circular-left (upper) and squared-left (lower) tracks overlaid by their associated path template (black points). All tracking points were easily matched to the closest template position. Black points and red points depict pre-run and post-run points not considered in analyses. Right: each spiral track was composed of 5 analogous ‘loops’ whose beginnings are depicted by colored ovals. Template matching permitted firing rates in two-dimensional space to be considered along a single vector. B. Following Lee, Rao, and Knierim (Neuron, 2004, vol. 42(5), pgs.803-15), firing fields were defined as spatially isolated increases in firing rate peaks exceeding 5 Hz and persisting at rates of 10% peak rate or better for at least 15 pixels (7.5 cm). The start and end points of firing fields were defined as the positions where firing rate dropped below 10% the peak firing rate. Center of mass (COM) was determined based on positional firing rates between start and end. C. For the purpose of examining the spatial distribution of ‘non-adapting’ firing field sets, squared spiral tracks were divided into ‘straightaway’ (blue) and ‘corner’ (red) segments as shown. As all non-adapting neurons exhibited a firing field on loop #3, only the COM of the loop 3 firing field for each neuron was utilized.

Supplementary figure 3: Increased firing field sizes on the outer loops of spiral tracks. In separate animals, neurons from the same region of CA1 were recorded as animals traversed two different (i.e., non-spiral) mazes. The maze depictions given above match the sizes of these mazes relative to each other (scale bar applies to all). During recording, each maze was centered on the same point in
the same room with the exact same distal cue configuration. Single unit
discrimination was performed by the same person and field sizes were
determined by the same method as used for spiral track firing fields. Left: On the
‘TT’ maze, animals proceeded upward from the center-bottom point of the maze
and made three L/R choices to reach one of eight goal sites. One of the eight
paths is given in red. On the ‘MS’ maze, animals shuttled back and forth between
goal sites in the NW and SE corners along paths such as the one given in red.
Firing fields for CA1 neurons on the ‘TT’ and ‘MS’ mazes averaged, respectively,
20.0 and 27.1 cm in length (N=64,62, +/- SD). The field sizes from these
experiments were in good agreement with work from other laboratories (e.g.,
Maurer et al., 2005, Hippocampus; Mehta et al., 1997, PNAS). Middle and right:
mean firing field sizes (+/- SD) observed along loops 1 through 5 of the circular
and squared spiral tracks. On the outermost loop (#1, N=136) of squared spiral
tracks, firing fields were twice the size observed on the ‘TT’ and ‘MS’ mazes. On
circular spiral tracks, loop 1 firing fields (N=99) were 2.74X the size of those on
‘TT’ and ‘MS’ mazes. ANOVA with Fisher’s PLSD post-hoc tests revealed
significant differences in field size for spiral track loops 1 and 2 versus field sizes
for ‘TT’ and ‘MS’ mazes (all comparisons p<0.001).

Supplementary figure 4: Running speed dynamics differ between traversals of
circular and squared spirals. A. Shown are representative examples of running
speed for two different animals (top and bottom). Traversal of circular spiral
mazes demands only gradual changes in turning angle. Nevertheless, in most
cases, mean running speed on circular spiral paths (left graphs) varied within
individual loops. On squared spiral paths (right graphs), running speed maxima
and minima were related to each of the 90-degree turns that comprise individual
loops (black arrows mark a few of the turns). As a result, the spatial frequency of
running speed dynamics is higher for traversal of squared paths. B. Mean
running speed as a function of loop number. Outermost to innermost loops of
spiral tracks were numbered 1-5. Bar graphs depict mean running speed (+/- SD)
for each loop for circular and squared spiral paths.
References


Figure 1
Figure 2
Figure 3