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16. Because okadaic acid required long periods of bath application (>60 min) to block LTD, we did not repeat this two-pathway experiment using okadaic acid because any differential effect on synaptic transmission in the two paths would be difficult to distinguish from "drift" in the preparation.
17. We made whole cell voltage-clamp recordings with an Axoclamp 2A (Axon Instruments) using patch pipettes containing a cesium-based solution (*4*). Synaptic responses in the presence of CNQX (10 μM) and picrotoxin (25 μM) were recorded at holding potentials ranging from −80 to +40 mV. There were no significant differences in the current/voltage relation observed when recordings from control slices (n = 4) and calyculin A–treated slices (n = 4) were compared. The EPSC at −80 mV was 8 ± 4% (mean ± SD) and 11 ± 7% of the peak current in control cells and calyculin A–treated cells, respectively. At −30 mV the EPSC was 48 ± 9% and 47 ± 13% of the peak current in the two respective populations of cells.
18. In all experiments in which compounds were loaded directly into CA1 cells, an extracellular field EPSP was monitored simultaneously to ensure that the 1-Hz stimulation had elicited LTD in surrounding cells. Microcystin LR (10 μM in 0.5% ethanol) was added directly to the patch-pipette recording solution each day immediately before the beginning of experiments. Control cells were always examined on the same day with the same recording solution. In addition, the 1-Hz 6-min stimulation was always applied within 20 min of break-in, a period over which we have never observed washout of the ability to induce LTD. Only cells in which LTD was elicited in the simultaneously recorded field EPSP were included in the summary graphs.
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Dynamics of the Hippocampal Ensemble Code for Space

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Ensemble recordings of 73 to 148 rat hippocampal neurons were used to predict accurately the animals' movement through their environment, which confirms that the hippocampus transmits an ensemble code for location. In a novel space, the ensemble code was initially less robust but improved rapidly with exploration. During this period, the activity of many inhibitory cells was suppressed, which suggests that new spatial information creates conditions in the hippocampal circuitry that are conducive to the synaptic modification presumed to be involved in learning. Development of a new population code for a novel environment did not substantially alter the code for a familiar one, which suggests that the interference between the two spatial representations was very small. The parallel recording methods outlined here make possible the study of the dynamics of neuronal interactions during unique behavioral events.

The hippocampal formation is the highest level of association cortex (*1*) and is an essential component in memory encoding. Its role in the internal representation of space (*2*) is indicated by both neuropsychological studies (*3*) and the observation that its pyramidal cells ("place" cells) are selectively active in particular locations (*4*). At the computational level, the matrix-like organization of hippocampal circuitry has inspired the theory that it serves as a rapid autoassociative memory (*5*, *6*). Finally, its neurons exhibit potential substrates of learning in the form of cooperative, long-term synaptic enhancement (*7*). Thus, the hippocampus represents a key to understanding biological and computational mechanisms of associative memory and the structure of cognitive representations.

The spatial and mnemonic dependence of hippocampal neuronal activity has been well characterized at the level of single cells (*8*); however, complete understanding of hippocampal function will require knowledge of the dynamics of ensemble encoding (*9*) of information across many neurons during relevant behavioral tasks, particularly in view of both the involvement of the hippocampus in memories that are unique to a trial and the low firing rates and intrinsic variability of single hippocampal cells. In the only published study to address whether experience is required for the initial establishment of hippocampal spatial representations, single-unit recordings failed to detect differences in the firing of most place cells between the first and subsequent entries of a rat into a specific location (*10*). Here, we provide evidence to the contrary and describe the dynamics of ensemble encoding of space in the hippocampus during a single episode of exploration in a novel environment.

Three rats were implanted with microdrive arrays (*11*) containing 12 four-channel recording electrodes (tetrodes), each capable of resolving activity from 5 to 20 single hippocampal neurons (*12*). The rats were trained over 10 days to forage for small, chocolate pellets in half of a rectangular apparatus (box A) (*13*). The other half of the apparatus (box B) was obscured from view by a partition.

While the rat sat quietly or slept outside the apparatus, the electrodes were lowered until stable recordings of well-isolated cells in the pyramidal layer of CA1 were obtained on all tetrodes. Most hippocampal cells become active during these conditions, even if they exhibit little or no activity during the particular behavioral task under study (*14*, *15*). Eighty-two single units were identified in rat 1, 73 in rat 2, and 148 in rat 3. Of these, the numbers of pyramidal [complex spike (CS)] cells were 76, 71, and 141 for rats 1, 2, and 3, respectively. The remain-

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ing cells were "theta" cells (inhibitory interneurons) (*14*). Consistent with prior observations (*16*) and theory (*5*), the hippocampal representation was sparse—that is, the fraction of cells active in any particular location was small and the overall mean firing rates were low (0.96 Hz for cells with place fields). Of the CS cells from rats 1, 2, and 3, 34, 24, and 40, respectively, exhibited statistically significant spatial information content in their firing (*17*) in box A. The remaining CS cells were virtually silent there (Fig. 1).

Is the activity of a population of cells over a brief interval (population rate vector) a robust predictor of spatial location? If so, how does this prediction improve with the number of cells sampled and the time over which the activity is integrated? To answer these questions, we attempted to predict the movement trajectory of the rats in box A using the ensemble activity. We computed the expected rate vectors for each location using the mean rate of each cell at that location. The actual rate vector over each 1-s epoch was compared with each expected rate vector, and the site of maximal correspondence was assigned as the estimated location. The mean prediction error was corrected by subtraction of the approximate intrinsic tracking error (5 cm). The remaining error due to variations in cellular activity was approximately 5 cm for rats 1 and 2 (left panel of Fig. 2C) and 2 cm for rat 3.

The estimation procedure was repeated with 10 random samples of the CS cells from rat 1, at each of several sample sizes and integration times (Fig. 3A). As either the number of cells increased or the sampling interval increased up to about 1 s, the mean error was reduced. By extrapolation (Fig. 3B), 1-cm accuracy over 1 s would require about 130 cells. This is approximately what was found with the 141 CS cells from rat 3. For the same resolution of position on the time scale of the electroencephalogram theta rhythm (about 0.1 s), about 380 cells would be required. The error was not significantly reduced with longer sampling intervals, presumably because of the animal's motion.

We next assessed the effect of experience in a novel environment by removing the partition between boxes A and B. The specific questions that we had were (i) what effect would this have on established ensemble activity? and (ii) what are the dynamics of the process of forming new spatial representations in the novel region? After 10 min of exploration in box A, the partition was removed and the rats were allowed to explore both boxes. Rat 1 moved freely between the two regions. Rat 2 explored box B briefly and then paused in box A for over an hour before resuming exploration. Rat 3 hesitated for 5 min and then robustly explored for 12 min. After 20 min of exploration of both boxes, the partition was replaced, and all animals explored box A in a normal manner for an additional 10 min. The limited initial exploration by rat 2 precluded evaluation of the time course of its place field formation; however, its other data were consistent with the effects described below for rats 1 and 3 (*18*).

The session for rat 1 was divided into four phases: phase 1, the 10-min period in box A before partition removal; phase 2, the first 10 min with the partition between boxes A and B removed; phase 3, the second 10 min of this condition; and phase 4, the final 10 min in box A. For rat 3, phases 2 and 3 were each 6 min in duration. Trajectory reconstructions during a particular behavioral phase were performed with the mean spatial firing distributions for that phase. Therefore, the accuracy of reconstruction reflects the consistency of spatial firing over the phase.

During phases 2 and 3, the cells that were active during phase 1 (in box A) had spatial firing biases with a high degree of pixel by pixel correlation with phase 1 [rat 1, mean correlation coefficient (r) = 0.67 ± 0.26 (SD) and $P < 0.05$; rat 3, mean r = 0.62 ± 0.32 (SD) and $P < 0.05$], despite the altered sensory conditions attributable to the removal of the partition. Reconstruction error in box A did not increase (Fig. 2A). In contrast, during phase 2 error within the novel region (box B) was significantly greater in both rats 1 and 3, with only 17 and 31 CS cells, respectively, exhibiting robust spatial activity in the novel box. The spatial distribution of error during this period showed a clear transition at the boundary between boxes A and B (Fig. 2D). This transition was not due to differences in overt behavior between the two arenas. The behavior of rat 1 in each box was qualitatively and quantitatively indistinguishable during this time (average running speed was 17.3 ± 0.3 and 17.5 ± 0.2 cm/s in boxes A and B, respectively). The running speed of rat 3 was reduced by 15% in box B; however, error was not correlated with running speed ($r^2 = 0.002$).

In phase 3, the number of cells with spatial firing biases in box B increased from 17 to 27 for rat 1 (Fig. 2B) and from 31 to 37 for rat 3. Reconstruction error dropped correspondingly (Fig. 2D). In general, the cells allocated to box B were drawn from the pool that had not shown activity in phase 1 (box A). The average correlation of spatial firing distributions in box B, between phases 2 and 3, was low; however, there were only minor overall

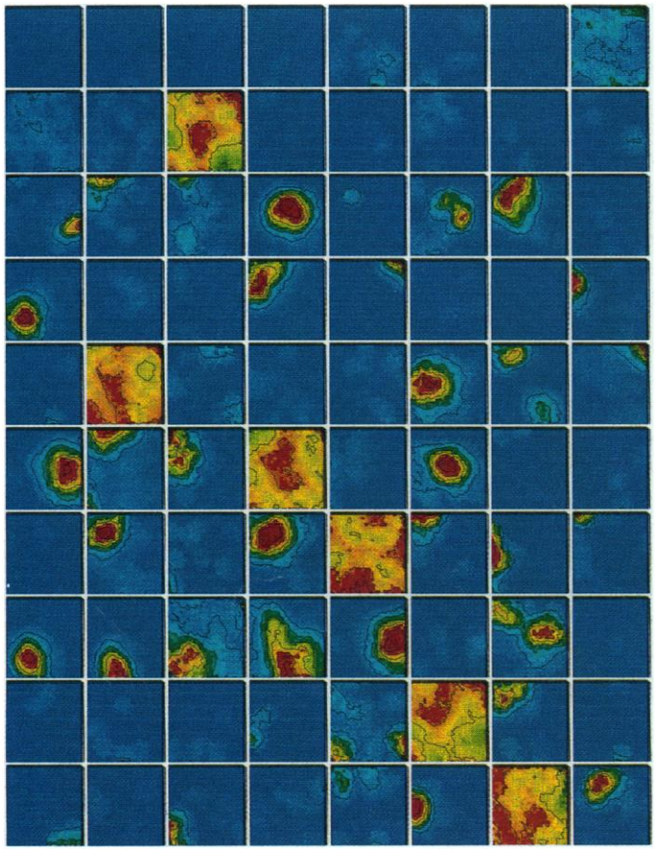

Fig. 1. Spatial firing distributions of 80 simultaneously recorded pyramidal and inhibitory neurons in the hippocampal formation of rat 1 during unrestrained exploration in the familiar half of the environment (box A). Each panel represents the spatial distribution of the firing rate for one cell. Maximal rates for cells with significant spatially related firing are indicated by red; no firing is indicated by dark blue. The inhibitory cells exhibit more dispersed firing. Many cells, which were active in other contexts, were virtually silent in box A; some of these became active in box B.

differences in the mean firing rate. Place fields were thus initially not stable in box B, and this variability was responsible for the increased reconstruction error during phase 2. Spatial firing distributions between phases 1 and 4 were highly correlated [rat 1, mean $r = 0.72 \pm 0.25$ (SD) and $P < 0.05$ (Fig. 2A); rat 3, mean $r = 0.65 \pm 0.29$ (SD) and $P < 0.05$], which confirms that the novel experience in box B had not substantially destabilized the representation of box A. Hippocampal spatial representations are thus not fully expressed at the time of the animal's first entry into the place field but improve rapidly with experience, which suggests that the synaptic modification mechanisms that are presumably involved are rapid. Incorporation of new spatial information has little effect on previously stored information, at least within the limits of this experiment.

During phase 2, there was a marked suppression (up to 70%) of 10 of the 15 inhibitory interneurons recorded. This occurred abruptly as the animal entered box B (Fig. 2E). Normal firing resumed abruptly when the animal crossed back into box A. These effects were characterized by a clear change in the relation between firing rate and running speed and hence were not due to running speed per se. The suppression of inhibitory interneurons during the development of a novel spatial representation suggests what possible dynamic processes may be involved. Inhibition by neurons containing γ-aminobutyric acid can powerfully regulate the efficacy by which a given excitatory input activates *N*-methyl-D-aspartate receptor–mediated synaptic enhancement (*19*). The suppression of inhibitory interneurons thus might facilitate the synaptic modification necessary to encode new spatial information.

The successful recording and interpretation of neuronal ensemble activity in a behaving animal as demonstrated here opens the possibility, in principle, of the interpretation of neuronal activity in the absence of explicit behavior, such as during periods of sleep (*20*), motor planning (*21*), reasoning, and memory consolidation.

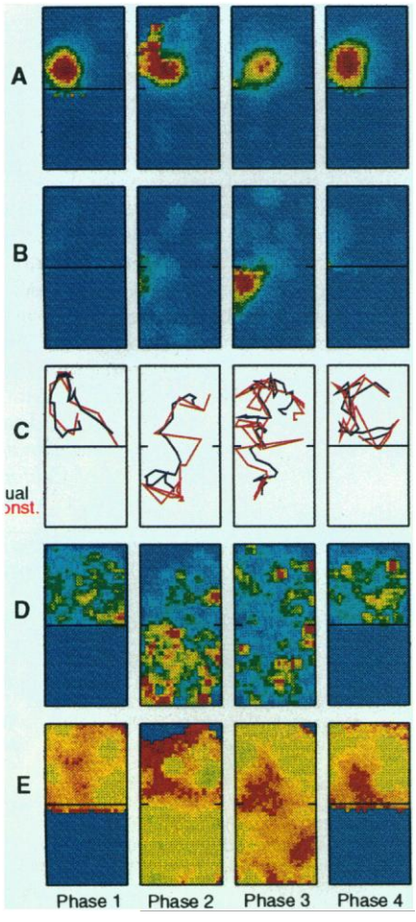

Fig. 2. (**A**) Typical place field in the familiar region (box A). (**B**) A place field that developed in box B during phase 2 and became more robust by phase 3 (the rate scale is as in Fig. 1). (**C**) Examples of the reconstructed (Reconst.) spatial trajectory (30 to 60 s) of the animal as estimated from the population firing rate vector. (**D**) Spatial distribution of reconstruction error (red indicates high error; blue, low error). (**E**) Average activity of inhibitory interneurons (theta cells). Each panel represents results for rat 1 for the full 124 by 62 cm arena, which was divided by a partition during phases 1 and 4. The top half of each panel represents box A; animal did not enter box B during phases 1 and 4.

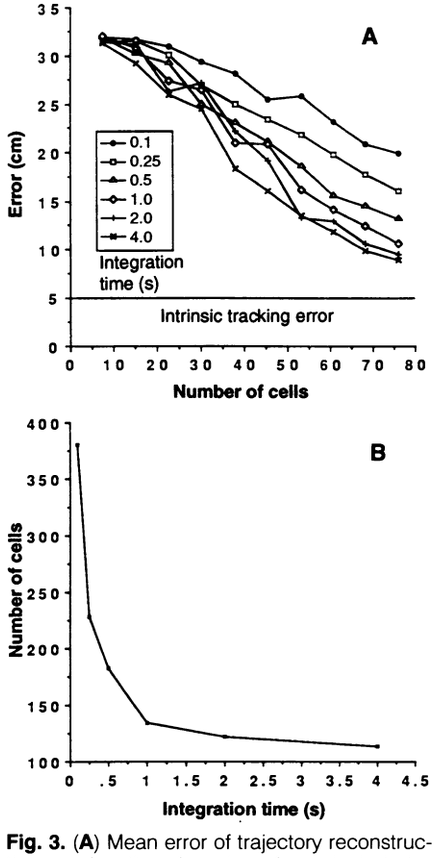

Fig. 3. (**A**) Mean error of trajectory reconstruction as a function of number of cells included in the population vector for sampling intervals from 0.1 to 4 s in the familiar environment (box A) before partition removal. Each point represents the mean error from 10 different random samples of the 76 CS cells from rat 1. After removal of the error component that resulted from the tracking system itself, these curves were roughly linear in a log plot for the data beyond about 30 cells. (**B**) Extrapolation of the log plots yielded estimates for the number of cells required for a resolution of 1 cm for different integration times.

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region 1.5 mm in diameter (250- to 300-μm spacing between adjacent electrodes). Each probe could be independently adjusted with a precision of approximately 10 μm. The array weighed about 10 g and did not significantly restrict the free movement of the animal. Neural signals were buffered with two miniature, 25-channel integrated preamplifiers, then passed to a set of six, custom-built, eight-channel filter-amplifier modules. Action potentials were digitized at 33 kHz per channel and stored by seven synchronized 33-MHz 80486-based computers running customized data acquisition software. Rat head position and orientation were tracked at 20 Hz. Surgery was according to NIH guidelines. The animals were male Fischer 344 (F344) rats, 9 months of age.

13. For rats 1 and 2, the environment was a rectangular box 124 cm long by 62 cm wide by 62 cm high. The walls of the apparatus were covered with a variety of distinct visual and tactile cues. The apparatus was located within a curtained-off partition of the room containing the electrophysiological recording equipment. A slightly smaller apparatus was used for rat 3.
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TECHNICAL COMMENTS

Photochemistry in the Primitive Solar Nebula

In his recent article (*1*), J. Kasting refers to a paper by Prinn and Fegley [reference 21 in (*1*)] that discusses the blocking of solar ultraviolet (UV) light by dust in the primitive solar nebula and the effect this might have had on hydrodynamic escape. Although the reasoning used by Prinn and Fegley (*2*) is valid for most of the UV spectrum, it is not valid for the brightest UV feature—the HI 1216 Å line, which is known as the Lyman α line (Lyα).

In their currently accepted theory for the chemical evolution of the primitive solar nebula, Prinn and Fegley argue that photochemistry is unimportant and that thermochemistry controls the relative abundances of molecular species throughout the planet-forming region (*2*). They provide useful estimates of the chemical energy available to the solar nebula from several sources and establish that even the small photolysis rate resulting from starlight is more important than the photolysis rate from direct sunlight. For Lyα, however, this calculation does not include the contribution from backscattering of solar Lyα by hydrogen atoms in the interplanetary medium (IPM). The current brightness of the IPM in the vicinity of the Earth is about 400 Rayleighs (*3*) or, equivalently, about 4×10^8 photon cm^{-2} s^{-1} over the entire sky. For comparison, the direct Lyα flux from the sun is currently about 3 to 5×10^{11} photon cm^{-2} s^{-1} at the Earth (*4*). Although the direct flux is a more important source in the inner solar system, the IPM source falls off much more slowly (*3*) than the direct flux, so that the two sources are of comparable strength at the orbit of Neptune (*5*).

In the primitive solar nebula, the disk opacities were large enough that no direct solar Lyα could penetrate more than a few tenths of an astronomical unit from the protosun (*2*), even though the protosun, if comparable to a T-Tauri star, would be emitting up to 10^4 more Lyα photons than the current sun (*6*). However, because Lyα emissions are observed coming from T-Tauri stars, it seems plausible that the nondisk regions of the primitive solar nebula may have been relatively free of opacity. If so, then both sides of the nebular disk could have been bathed by a flux of up to 10^4 times more Lyα than is present in the IPM today. Furthermore, because the density of atomic hydrogen in the primitive IPM was probably much higher than it is today [the backscattering reflectivity of the IPM is currently only about a tenth of a percent or less (*7*)], there may have been an additional amplification factor in the early days of the solar system. At 10^4 times its current brightness, the IPM flux of Lyα available to the upper atmosphere of the Earth would have been about 10 times the current solar HI 1216 Å irradiation. So perhaps it is not necessary to assume that the solar nebula must have been dissipated before blowoff and isotopic fractionation could have occurred in the atmospheres of the terrestrial planets (*8*). The effects of IPM-backscattered Lyα are also pronounced for the outer regions of the primitive solar nebula. The photodissociation rates of, say, CH_4 or NH_3 near Neptune's orbit would have been comparable to the photodissociation rates these molecules experience today in the vicinity of the Earth. This scenario would favor the formation of strongly bonded molecules such as CO and N_2 over the more easily photolyzed CH_4 and NH_3 in all regions of solar system. Contrary to the statements of Prinn and Fegley (*2*), it seems that solar photochemistry *was* important in the early solar nebula and that the IPM-backscattered source of Lyα should be represented in future chemical models of solar system formation.

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Kasting reiterates (*1*) a traditional view that the global Archean atmosphere and ocean [Stage I, before about 2.4 billion years ago (Ga)] was a reducing environment without free O_2. Relevant data (*2*) and geochemical and biochemical arguments (*3*) that support alternative views are not mentioned by Kasting, who addresses two items. (i) Some O_2 should have been available to generate a minimum ozone screen