Concordant and Discordant Coding of Spatial Location in Populations of Hippocampal CA1 Pyramidal Cells

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Received 7 February 2002; accepted in final form 17 June 2002

Brown, Joel E. and William E. Skaggs. Concordant and discordant coding of spatial location in populations of hippocampal CA1 pyramidal cells. J Neurophysiol 88: 1605–1613, 2002; 10.1152/jn.00084.2002. Pyramidal cells in the rat hippocampus commonly show place-related activity, but it has been difficult to understand the factors that govern them. A particularly important question is whether individual cells have identifiable correlates that can be manipulated independently of the correlates of other cells. Recently Tanila et al. examined the activity of small ensembles of hippocampal cells in rats running on a plus-maze with distinct intra- and extramaze cues. When the two sets of cues were rotated 90° in opposite directions, some cells followed the intramaze cues, others followed the extramaze cues, and others “remapped” unpredictably; moreover, all possible combinations were seen within simultaneously recorded ensembles. In the current study, CA1 pyramidal cell population activity was recorded from four rats in a similar paradigm, using a recording system that permitted the analysis of ensembles of 4–70 simultaneously recorded units. The results were consistent with the data from the earlier study in showing an increase in remapping over time and in showing some place fields following one of the defined sets of cues while others remapped. When the possibility of random remapping was controlled for, however, the analysis did not show significant numbers of place fields following both sets of cues simultaneously. Furthermore, all rats initially showed fully concordant responses with all place fields following the local cues. For two rats, this pattern continued until a new configuration was introduced at which time all fields switched to follow the distal cues. Taken together, the results are difficult to reconcile with the hypothesis that individual hippocampal cells encode information about different subsets of cues in the environment.

INTRODUCTION

Currently a major controversy among investigators studying the hippocampus arises from the need to reconcile two substantial bodies of data. One suggests that the hippocampus is heavily involved in encoding the spatial location of an animal in its environment [the “cognitive map” hypothesis, supported by many neural recording, lesion and behavioral experiments (McNaughton et al. 1996; Morris et al. 1982; Muller et al. 1987; O’Keefe and Dostrovsky 1971; O’Keefe and Nadel 1978)]. The other suggests that the hippocampus plays a crucial role in certain types of memory [the “declarative memory” hypothesis, supported by many behavioral and lesion studies (Cohen and Eichenbaum 1993; Marr 1971; Squire 1992)]. These two hypotheses make different predictions on a variety of levels; in particular, they arguably make different predictions about the coding properties of hippocampal pyramidal cells. These have sometimes been called “place cells” because their spike activity in many experimental situations is strongly related to the animal’s current spatial location. As Eichenbaum has recently written, “If the [hippocampal] representation is a cohesive map, all of the elements should respond together to any manipulation. Alternatively, if place cells are merely memory elements that encode familiar places, they would also change their firing patterns to alterations in the environment but not necessarily in a cohesive way. The really interesting cases are when a large number of salient cues are changed and many others are not, or when the environmental stimuli are held constant while the task is changed, or when the animal moves between two adjacent environments composed of identical spatial cues. Can some place cells follow some of the cues, while other simultaneously recorded cells follow different cues? If so, the ‘map’ is not a cohesive spatial framework; rather the hippocampus contains a collection of representations that encode subsets of the cues” (Nadel and Eichenbaum 1999).

These predictions were examined in a recent study (Tanila et al. 1997a) in which rats were trained to run for brain stimulation reward on a plus-maze with local cues on the arms and distal cues on the curtains surrounding the maze. The rats were trained with all of the cues in a fixed (“standard”) configuration, and then the spatial firing properties of ensembles of 2–10 simultaneously recorded CA1 pyramidal cells were examined first with the cues in the standard configuration, then with the local and distal cues rotated by 90° in opposite directions. In response to this “double rotation,” some place fields were reported to follow the local cues, others followed the distal cues, others stayed fixed in the framework of the room, and others “remapped” in an unpredictable way. Within simultaneously recorded ensembles, the level of discordance (i.e., different place fields changing differently) was below chance, but nevertheless all possible combinations were observed, including instances where one field followed the local cues while another at the same time followed the distal cues. The authors’ interpretation of their results led them to conclude that hippocampal cells individually encode specific identifiable combinations of features in an environment.

There were two issues that motivated further investigation of
made using a “Cheetah” parallel recording system (Neuralynx) consisting of eight 8-channel amplifiers with software-configurable high-and low-pass filters feeding their output to a custom-made controller and A/D processor, which sampled the signals at 32 kHz per channel. This fed a formatted stream of data to a Sun Ultrasparc 2 workstation running custom-written acquisition and control software. Each time the signal on one of the tetrode channels crossed a specified threshold, a 1-ms sample of data was saved from all four channels of the tetrode and written to disk. At the same time, position records containing information about the distribution of light across the video image were acquired at 60 Hz and written to disk.

**Behavioral task and training**

The apparatus used in this experiment was intended to be similar to that used in a set of recent papers, including Shapiro et al. (1997) and Tanila et al. (1997a,b): an elevated, plus-shaped maze with a uniquely textured insert on each arm (Fig. 1, top left). The recording room contained a 2-m square region surrounded by dark blue ceiling-to-floor curtains. The maze was constructed of wood and consisted of an octagonal central platform (30 cm) and four arms (45 × 10 cm). The ends of each arm tapered to a point and held a small aluminum food cup. The central platform was covered with a fitted, removable sheet of aluminum, and the entire maze was painted flat gray. The maze arms were also covered by removable aluminum inserts to which texture cues were attached.

The experimental apparatus, and the entire environment visible from it, were designed to be symmetric with respect to rotations by any multiple of 90° with the exception of two sets of specific cues, designated “local” and “distal.” The local cues consisted of four

![FIG. 1. Top left: layout of the environment in which training and recording were performed. Rats were trained to run for food reward on a plus-shaped maze with distinctive inserts on each arm, surrounded by curtains with distinctive objects attached on each side (see text for details). Door at lower left leads to adjoining room containing recording equipment. Remaining plots: arrangement of local and distal cues in each of the 5 configurations used in the experiment. The standard configuration was used for training and for the 1st and last sessions on each day of recording; the double rotation configuration had the local cues rotated 90° clockwise while the distal cues were rotated 90° counterclockwise; the local split configuration had the distal cues unchanged while 2 of the local cues (1 and 3) were rotated clockwise and the other 2 rotated counterclockwise; the rotated local split was identical to the local split except that all controlled cues (local and distal) were rotated by 180° with respect to the room; and the alternate double rotation (used as a probe for rat 1) had the local cues rotated 180° while the distal cues were rotated 90° clockwise.](http://jn.physiology.org/doi/fig/10.1152/jn.00026.2001)
uniquely colored and textured inserts placed on the arms of the plus-maze (coarse plastic mesh, metal screen, ridged plastic, sandpaper). No specific olfactory cues were used. The distal cues consisted of four unique objects suspended from the center of each of the curtains surrounding the maze (aluminum foil, striped card, 2 paper bags, white towel). Room illumination was provided by four 25-W lights recessed symmetrically into the ceiling within the curtained enclosure. A video camera used to track the animals’ movements was suspended from the ceiling directly above the center of the maze.

Training began prior to electrode implantation with a gradual adaptation to the recording environment. Initially, each rat was placed on the central platform of the maze once a day and allowed to explore freely for 30 min, after which it was returned to its home cage and fed. Pellets of rat chow (20 mg) were present at the ends of the arms and were replaced once the rat had eaten them and exited that arm. Once the rat was regularly running to the ends of the arms to obtain the food reward (3–4 days), a training paradigm was used to encourage the rat to quickly and completely sample the entire maze. The rat was hooked up to the headstage cables for the rest of the sessions. (The rat was not disoriented or displaced in a high-walled cardboard cylindrical container so that it could not observe cue manipulations. (The rat was not disoriented or displaced in a high-walled cardboard cylindrical container so that it could not observe cue manipulations.) The rat was then removed from the maze and the rat was allowed to explore for 30 min without entering a previously visited arm more than once per trial. This took between 7 and 10 days per rat. All training was done with the cues in the same “standard configuration.”

After the rats recovered from surgery, daily sessions included a search for cells followed by additional training. Over the course of 2–10 days the tetrodes were slowly lowered into the CA1 layer of the hippocampus. As the tetrodes approached the cell layer, they were moved less than 100 µm/d. Once all of the tetrodes had been moved for the day, the rats were subjected to additional training without being hooked up to the headstage and cables. In this case, the task was identical to the subsequent recording sessions: the confinement procedure was no longer used and the arms were kept baited with food pellets at all times. The rat would find a food pellet at the end of an arm, and that arm would be rebaited immediately upon the animal’s exit. After 2–3 days of running freely on the maze in this manner, each rat was hooked up to the headstage cables for the rest of the sessions. This was the final stage of training and generally coincided with the tetrodes’ arrival at the CA1 layer. Recording sessions began once a rat was willing to run for at least 15 min on the maze and CA1 pyramidal cells had been identified on most of the tetrodes. Daily recording procedures began with a limited search for cells, an opportunity for fine adjustments to be made prior to recording. Tetrode movement prior to recording generally decreased stability during recording and was minimized.

**Double rotation task**

Each daily recording consisted of three sessions. In the first session, the rat ran on the maze for 5 minutes with the cues in the standard configuration. (All of the configurations used in the experiment are illustrated in Fig. 1.) The rat was then removed from the maze and placed in a high-walled cardboard cylindrical container so that it could not observe cue manipulations. (The rat was not disoriented or disconnected from the recording cable except in a few cases where the cable had become badly twisted during the session.) The local cues were rotated 90° clockwise, and the distal cues were rotated 90° counterclockwise. The rat was then returned to the maze for a second session with the cues arranged in the “double rotation” condition (Tanila et al. 1997a). After 5 min, the rat was removed and placed in the box again. The cues were returned to the standard configuration, and the rat was returned to the maze for a third and final 5-min recording session. The cue arrangements in the first and third sessions were identical. During recording, each arm was rebaited once the rat had exited that arm. Each animal participated in one recording per day until the number of simultaneously recorded cells fell to less than 10 per ensemble for several consecutive days.

**Local split task**

A variation on the double rotation task was introduced if the unit responses to the double rotation configuration remained concordant over the first 7–10 days of recording (as happened for 2 of the 4 rats). For the remaining days, instead of the double rotation these rats were exposed to a “local split” cue arrangement in the middle recording session between the two standard sessions. In the local split session, the NW and SE local cues were rotated 90° clockwise, and the NE and SW local cues were rotated 90° counterclockwise. This manipulation was used to examine whether the control exerted by the local cues could be disrupted by perturbing their arrangement with respect to each other. (Note that the local split is formally equivalent to a double rotation of the local cues, leaving the distal cues fixed. The local split arrangement could also be described as a mirror-image flipping of the local cues.)

**Probe trials**

Two special cue-arrangements were used in small numbers of recording sessions to investigate questions that arose during the course of the study: an alternate double rotation in which the local cues were rotated 180° while the distal cues were rotated 90° clockwise. This was used for several days on one of the rats to test whether a small group of cells that appeared to be following the distal cues would continue to do so for a different cue arrangement. A rotated local split configuration, identical to the local split except that all controlled cues—both the local and distal cues—were rotated by 180° with respect to the room, was used on 1 day for one of the rats to examine whether cells whose fields stayed fixed in the room/distal-cue frame would be controlled by room cues or by the distal cues if the two were dissociated.

**Data analysis**

Unit discrimination was performed offline based on the assumption that each recorded neuron would show a different pattern of spike waveform amplitudes across the four channels of a tetrode (McNaughton et al. 1983; O’Keefe and Recce 1993). Units were discriminated using an interactive program (xclust, M. A. Wilson) that plots each spike as a point in two-dimensional (2D) space, according to its amplitudes on two selected tetrode channels. Spikes from an individual neuron tend to form clusters when plotted this way. The user draws polygons to define the edges of clusters. When the process is complete, a unit is defined by a conjunction of polygons drawn in several 2D projections.

The main data analyses for this study were based on correlation coefficients for spatial firing rate maps. The methods used to construct firing rate maps have been described in detail in earlier papers (Skaggs and McNaughton 1998; Skaggs et al. 1996). Briefly, the position data were initially binned in a 64 × 64 grid, and the total occupancy time and total number of spikes fired were counted for each pixel in the grid. An “adaptive smoothing” algorithm was then used to calculate an estimated mean firing rate for each pixel by expanding a circle centered on the pixel until the total occupancy within the circle met a specific numerical criterion and then setting the estimated firing rate equal to the number of spikes divided by the occupancy time. Corre-
lation coefficients between firing rate maps for two sessions were calculated using all pixels having nonzero occupancy for both sessions. Correlations between firing rate maps for the first and last standard sessions on a given day were used as a measure of the quality and stability of spatial firing. For most purposes, a correlation coefficient greater than 0.5 was deemed to indicate a sufficiently reliable place field to be used for analysis of cue manipulations. Cells showing correlation coefficients less than zero were considered to have remapped. This is a rather conservative criterion but probably does not produce a large number of misclassifications. [See Skaggs and McNaughton (1998) for examples of the statistical distribution of correlations between unrelated place fields.] In any case, counts of remapping cells are only used in a comparative way in the current study and never assigned any absolute significance.

180° rotation control

The most important question in this experiment was whether there were sessions in which some fields were controlled by the local cues while others were controlled by the distal cues. Place field rotations can be observed as high correlations between firing rate maps from session 1 and appropriately rotated firing rate maps from session 2. Operationally, the question was whether there were, within a single session, some cells showing high correlations for a rotation of 90° while others showed high correlations for −90°.

There is, however, a difficulty with this formulation, arising from the possibility of random remapping. If some fraction of fields remap unpredictably, then some subset of these will, just by chance, remap approximately to locations rotated 90° or −90° from their original locations. The expected incidence of this sort of "coincidental" rotation is not easy to calculate from first principles. There is a simple way to control for the incidence of coincidental rotations based on the structure of the apparatus. There were three sets of cues that a field might in principle be controlled by: the fixed room cues (producing a rotation of 0°); the distal cues (producing a rotation by 90°); and the local cues (producing a rotation by −90°). There were no cues that rotated by 180°. Therefore, if a place field appeared to rotate by 180°, onto the opposite arm of the apparatus, it can be assumed that this must have been an coincidental rotation. Conversely, the number of fields rotating onto the fourth arm can serve as a control for the expected number of coincidental rotations onto each of the other arms.

Thus the main question in this experiment was framed operationally as follows: define the rotation (0, 90, or −90) leading to the highest mean correlation as the "dominant" rotation for the session. This leaves two "non-dominant" rotations. The question was: did either of the two non-dominant rotations show significantly higher correlations than the 180° rotation? If so, then at least two subsets of cues (the dominant and 1 other) are deemed to have exerted significant control over place fields during the session. Conversely, if the non-dominant rotations did not differ significantly from the 180° rotation, there was considered to be no evidence in the data for anything more than the dominant rotation plus random remapping.

RESULTS

General observations

Data were obtained from four rats, which, for purposes of describing individual differences, will be designated rat 1 through rat 4. All rats learned to sample the entire maze equally well during training. Each rat developed a stereotypic pattern of movement on the maze (e.g., always running clockwise or counterclockwise), but there were no other obvious behavioral differences between rats during recordings. The number of recording days per rat ranged from 11 to 25, and the number of well-isolated pyramidal cells recorded ranged from 4 to 70 per ensemble. A typical session lasted 5 min and included 15–20 trials.

The cue manipulation performed for the first days of testing consisted of three 5-min sessions: standard configuration; double rotation configuration; and standard configuration. For all four rats, the result for the first day of testing was that all stable cells (i.e., cells that maintained the same spatial firing pattern in sessions 1 and 3) followed the local cues in the double rotation session (Fig. 2). For two of the rats (2 and 4), all cells continued to follow the local cues as long as the double rotation manipulation was continued (7 and 10 days, respectively). For rat 1, the second through fourth double rotation sessions were unusable due to a bad ground connection and/or electrode instability. From the fifth double rotation session onward, the place fields showed a combination of remapping and control by the distal cues. For rat 3, the first seven sessions showed complete control by the local cues, and all sessions thereafter showed a combination of distal cue control and remapping (Fig. 3).

The conclusion that all fields initially followed the local cues, for all four rats, is drawn on the basis of correlation plots of the sort illustrated in Fig. 4, in which firing rate maps in the standard configuration are correlated with rotated firing rate maps derived from the double rotation session. The x axis in these plots shows the correlation between firing rate maps from two standard configuration sessions and therefore represents a measure of the reproducibility of correlations. The y axis shows the correlation between the firing rate map from a standard session and the rate map from the double rotation session, rotated by 0°, 90°, or 180°. In the illustrated example, all cells with large x coordinates also show large y coordinates for the 90° rotation, which corresponds to the local cues; therefore it is concluded that all reproducible fields rotated concordantly in this data set. Quantitatively, a field was deemed to remap if it produced an x coordinate greater than 0.5 and a y coordinate less than 0 (for the 90° rotation). By this definition, no fields remapped in any of the four rats in the initial sessions, and for rats 2 and 4, no fields ever remapped at all. It cannot be ruled out, however, that the properties of place fields may have changed in a more subtle way in response to cue manipulations.

As stated, the ensembles of two rats, 1 and 3, eventually began to both follow the distal cues and partially remap (Fig. 5). This accords with the observations by Shapiro et al. (1997) and Bostock et al. (1991) that the probability of remapping increases as a function of experience in a novel environment. It is not clear whether the level of remapping continued to increase gradually or switched abruptly at one time and remained constant thereafter. Figure 4B shows a plot of correlations for each of the possible rotations, from rat 1. The majority of cells showed high correlations for a rotation of −90°, corresponding to the distal cues. Several cells, though, did not. Note that three of the cells showed high correlations for a rotation of 90°, corresponding to the local cues. This exemplifies the observation, by Tanila et al. (1997), that a fraction of place fields may rotate in the opposite direction from the majority. In this particular data set, no place fields showed high correlations for a rotation of 180°. Fields that did so were, however, observed in other data sets. A statistical comparison of the numbers of fields rotating in discordance from the majority, versus the number rotating by 180°, is presented in the following text.
For rat 1, there was a surprising aspect about the distribution of cue control among tetrodes. In this rat, following the switch from local cue control to distal control plus remapping, a number of cells recorded from tetrode 2 had place fields that rotated with the distal cues, while the remaining cells from tetrode 2 remapped unpredictably. None of the cells from the other eight tetrodes, though, showed anything except complete remapping. This discrepancy between tetrodes continued without change from days 7 through 19, which was the final day of recording. The number of usable cells on each tetrode varied considerably over this time. The largest ensemble for tetrode 2 contained seven usable cells of which four had fields that rotated with the distal cues (this is the session shown in Fig. 3). Distal cue control was confirmed by adding an additional 5-min session on days 15 and 17, in which the cues were configured in the alternate double rotation (see METHODS). Across days, there were a minimum of 59 distinct cells recorded from other tetrodes, all of which had fields that remapped. Strictly speaking, it is not legitimate to perform a statistical test on these numbers because of their post hoc
nature, but a $\chi^2$ test shows a significant difference with $P < 10^{-8}$, without any correction for multiple comparisons. For rat 3, there were no significant differences between tetrodes in the level of distal cue control.

The ensembles of the other two rats, 2 and 4, continued to follow the local cues as long as the double rotation was used. Once 2 and 4 had completed 7 and 10 recordings, respectively, it was deemed unproductive to continue this manipulation, and these rats were switched to the local split manipulation. For both of these rats, the local split caused all reliable place fields to stay fixed with respect to the distal/room cues, thus showing no influence of the local cues (which on the previous day had exerted 100% control; Fig. 6). Local split sessions were repeated for 17 and 5 days (respectively), and throughout this time showed no recognizable remapping whatsoever.

For rat 2, to clarify whether control was being exerted by the distal cues or fixed room cues (whose relative locations did not change in the local split configuration), on the 14th day of recording (7th local split session), a probe was performed in which the controlled cues (local and distal) were arranged in the local split configuration but rotated 180° with respect to the room. In this case, all place fields rotated with the distal cues, none staying fixed in the room frame. This suggests that in the local split sessions, it was the distal cues, rather than the room cues, that exerted control over the place fields. For the same rat, after 14 local split sessions, the rat was subjected to another double rotation session to test whether the local cues had lost their influence in the interim. In this session, as in the earlier double rotation sessions, all reliable place fields rotated with the local cues.

**Discordance analysis**

For the sessions in which there was less than complete concordance (11 data sets from rat 1 and 4 data sets from rat 3, together constituting all of the data from these rats after they had switched from fully concordant to partially discordant responses), the data were examined to see whether there was any significant evidence of fields rotating discordantly from the dominant rotation for the session. (In all of these cases, the dominant rotation was $-90^\circ$, following the distal cues.) This
was done by correlating spatial firing rate maps for the standard configuration with rotated firing rate maps for the double rotation configuration. As a control, the distribution of correlations for the non-dominant rotation (90°) was compared with the distribution of correlations for a rotation of 180° (the rationale for this is explained in Data analysis). Figure 7 shows the correlations for the pooled data. There was no significant difference between the distributions; the mean correlation for the 180° rotation was actually larger than for the non-dominant rotation (0.032 vs. −0.007), though neither was significantly different from zero. Comparing the shapes of the distributions using a Kolmogorov-Smirnov test yields a difference measure of $D = 0.142$, which is not significant though nearly so ($P = 0.067$). Thus, there is no real indication of above-chance numbers of fields following the non-dominant rotation in this experiment.

**DISCUSSION**

The present experiment was designed to replicate what were considered the essential features of the experiment of Tanila et al. (1997a) with two important additions: first, a control was added for the possibility that random remapping could give rise to the “coincidental” appearance of place fields rotating in other locations.
synchrony with a set of controlled cues; second, larger populations of neurons were recorded from so that more quantitative information on the level of discordance could be obtained.

One of the most striking results of the experiment was the very high level of concordance observed in the majority of data sets. All rats showed what appeared to be complete concordance in the initial double rotation sessions, with all high-quality fields following the local cues; and two of the four rats showed complete concordance throughout the entire experiment even after the local split manipulation was introduced. This high level of concordance was clearly not a consequence of the rats “ignoring” the distal cues: two of the rats spontaneously switched to distal cue control (plus remapping) after several sessions, and the other two switched to distal cue control when placed in the local split configuration. Thus all four of the rats demonstrated some degree of distal cue control.

The second striking result is that no statistically significant evidence of discordant control by the local and distal cues could be shown. The only discordant responses were combinations of distal cue control and random remapping. This is in contrast to the conclusion reached in Tanila et al. (1997a). It is important to emphasize, however, that the data from the current experiment were not in any important way inconsistent with the data reported by Tanila et al. Both studies observed simultaneously recorded cells responding in discordant ways. Both observed partial random remapping, in which some place fields followed one set of cues while other fields disappeared or shifted unpredictably; moreover, both found that the level of remapping tended to increase over time. Both observed instances in which some fields appeared to rotate with the distal cues while other fields appeared to rotate with the local cues. The essential difference is that the current experiment controlled for the possibility of “coincidental” rotations, whereas Tanila et al. considered all rotations to be meaningful.

Certainly there were significant methodological differences between the current study and the experiment of Tanila et al.: one used brain-stimulation reward and the other used food reward; one used odor cues and the other did not; the relative sizes of the local and distal landmarks may have differed; training procedures may have differed; etc. There is no way to ascertain that these differences could not cause differences in the amount of discordance in the hippocampal representation. It is not, however, at this point necessary to postulate an explanation of this sort, because the data from the two experiments were generally consistent. Nevertheless, it must be clear that the inability to detect significant local-distal discordance in the current study does not imply that discordance could not be observed in other situations, or even in a replication of the same situation. A negative conclusion can only be established by a large body of evidence collected in a wide variety of different situations.

Even so, the data from this experiment are in several ways difficult to reconcile with the idea that individual hippocampal cells convey specific information about different subsets of cues in an environment. In particular, for the two rats subjected to the local split manipulation, both showed the same pattern of results: while the double rotation was used, all place fields rotated with the local cues; the first day the local split was introduced, all fields stayed with the distal/room cues and seemed to completely ignore the local cues. It seems unlikely that all of the cells were “local cue cells” on 1 day and “distal cue cells” on the following day; rather, it seems more probable that the population as a whole was controlled by the global configuration of all of the landmarks in the environment. Indeed, one scenario that might account for the data would be to conjecture that the influence of the landmarks was mediated largely by the head-direction system, which is thought to respond to landmark information in a unified, “winner-take-all” manner (Knierim et al. 1995; Taube et al. 1990).

It is remarkable that two of the rats switched from local cue control to distal cue control after several days of experience, even though there were no apparent changes in behavior or in the contingencies of the task. A number of previous studies have found that in many situations distal cues exert a stronger influence than local cues over place fields and/or spatial navigation behavior (e.g., Cressant et al. 1997; Olton and Samuelson 1976), but to our knowledge no such delayed shift in control has previously been reported, and the cause of it is unclear.

What is the theoretical significance of these results? In light of the way the issue was framed in the INTRODUCTION, they might be taken to support the cognitive map hypothesis over the declarative memory hypothesis. There is, however, a different way of looking at the matter. There are reasons for expecting unified, non-factorable representations in a cognitive mapping system, but there are reasons for expecting such representations in a memory system as well. In most theoretical models of one-trial memory systems, such as the Hopfield network or various modifications of it (Amit 1989; Hertz et al. 1991), performance depends strongly on orthogonality between the patterns that are to be memorized. It is difficult to have orthogonality in a system where each unit’s activity depends on a limited subset of features of the environment, because an environment containing a mixture of features from two other environments will then be represented by a hippocampal activity pattern partially overlapping with the representations of the other environments. In the most thoroughly studied models, this will cause interference between memorized patterns, interference that is undesirable. Thus it is not necessarily the case that the results of the current experiment go against either the memory theory or the spatial theory, but rather, that the opposite outcome would have presented difficulties for both theories.

It might be objected that partial remapping, which has clearly been demonstrated in several studies [e.g., Skaggs and McNaughton (1998) as well as the current experiment and the Tanila et al. experiment that motivated it], presents the same difficulties. One possible response might be that partial remapping has thus far only been demonstrated in environments that have minimal differences from each other. It could, therefore, be a pathological behavior of the system, rarely seen in the ordinary life of an animal. This hypothesis suggests the prediction that, in a properly designed experiment, the incidence of partial remapping would be correlated with the level of interference between memories formed in two different, but similarly structured, environments.

We thank D. Touretzky and J. L. McClelland for valuable suggestions for improvement. This work was supported by National Science Foundation Grant...
NOTE ADDED IN PROOF

While this article was in press, an article appeared by Knierim (2002) that provides strong evidence for discordant responses to cues by simultaneously recorded hippocampal pyramidal cells.

REFERENCES


