Head direction cells in the rat postsubiculum fire in relation to the momentary directional heading of the animal, with each cell firing only when the animal faces in one particular direction. To understand how this signal might be generated, one useful step is to discover what other cell types, in addition to the head direction cells, may exist in the postsubiculum, since these cells might be involved in helping to generate the direction-specific activity.

Here, postsubicular cells were recorded as animals navigated in a cylindrical recording chamber. It was found that, in addition to head direction cells, the postsubiculum contains cells that show several other types of spatial/behavioral correlates, including angular velocity of the head, running speed, and location. Ten percent of the cells were classified as angular velocity cells, and they resembled vestibular afferent fibers, with antagonistic responses to clockwise versus counterclockwise turns. In addition, numerous other cell types were observed. These latter cells were harder to classify, but all showed a significant correlation with one or more of the above variables.

These findings suggest that the head direction cell signal may be at least partly based on the angular velocity, running speed, and locational signals observed here.

Cells throughout the hippocampal formation show striking spatial firing correlates as animals navigate through an environment (e.g., O'Keefe and Dostrovsky, 1971; O'Keefe, 1976; Muller et al., 1987; Barnes et al., 1990; Quirk et al., 1992; Taube et al., 1990a,b; Jung and McNaughton, 1993; Sharp and Green, 1994). These spatial firing patterns are thought to be critically involved in navigational behavior, since lesions to the hippocampus or related structures result in spatial learning deficits (e.g., O'Keefe et al., 1975; O'Keefe and Nadel, 1978; Olton et al., 1978; Morris et al., 1982; Sutherland et al., 1983; Taube et al., 1992).

One particular type of cell has been discovered in the postsubicular region of the hippocampal formation (see Fig. 1 for location of this region), and shows a firing pattern that is closely related to the animal's momentary directional heading (Ranck, 1984; Taube et al., 1990a,b; see Fig. 4). Each of these head direction cells fires only when the animal is facing in one particular direction (over an approximately 90° directional range), and it will do so any time the animal is facing that direction, regardless of where the animal is located within the environment, and (so far as has been examined at this time) regardless of what the animal is doing (Taube et al., 1990a). Each cell has its own preferred direction, so that together, the set of head direction cells appears to provide a continuous indication of the animal's momentary directional heading.

Since the initial discovery of these cells in the postsubiculum, similar directional cells have been discovered in other areas that are closely related anatomically to the postsubiculum, including the anterior thalamus (Taube, 1995), the lateral thalamic nucleus (Mizumori and Williams, 1993), and the posterior cingulate and parietal cortical areas (Chen et al., 1990; McNaughton et al., 1991). Thus, it appears that these areas may constitute a circuit that somehow constructs and maintains a directional signal based on relevant sensory information.

Analytical studies have shown that head direction cells in each of these areas are influenced by visual inputs, since rotation of a salient visual landmark results in an approximately equal rotation of the directional firing pattern for head direction cells (Taube et al., 1990b; McNaughton et al., 1991; Mizumori and Williams, 1993; Taube, 1995), and visual stimulation is necessary to "set" the directional pattern for latero-dorsal thalamic head direction cells (Mizumori and Williams, 1993). In addition, however, the cells are able to maintain accurate directional firing for some time even after removal of the single visual landmark (Taube et al., 1990b), or after the room lights have been turned off (Taube et al., 1988; McNaughton et al., 1991; Mizumori and Williams, 1993). Further, as animals travel from a familiar environment into a novel chamber, the cells are able to retain the directional preference established in the familiar environment (Burton and Taube, 1992; Sharp, unpublished observations). These results suggest that, in addition to utilizing visual landmarks (when they are available), the cells can also utilize movement-related information (about momentary angular velocity of the head) to maintain directional firing patterns through some kind of dead reckoning process (e.g., McNaughton et al., 1991; Wan et al., 1994). That is, after the removal of familiar environmental landmarks, the only available information for the directional signal must be that which results from the animal's own head rotations, since these would be the only ongoing indicator of momentary directional heading.

In order to obtain additional insight into the nature of the movement-related and other sensory inputs that might contribute to the generation of the directional signal, as well as the nature of the computations that may be involved, it is necessary to leave more of the other cell types (other than the head direction cells themselves), which may be part of the head direction circuit. As part of the work toward this goal, the present article provides a report on the firing properties of the general population of postsubicular cells. Thus, in the original Taube et al. (1990a) report, it was found that only 25.5% of all cells encountered were head direction cells. Another 15.1% were classified as theta cells (Ranck, 1973), because they showed an increased rate during the theta EEG pattern, and fired in phase with this rhythm, when present. The remaining 59.4% of the cells could not be classified, although some weak locational and directional modulation was observed for a few of these cells. In the Taube et al. (1990a) report, neither the theta cells nor the unclassified cells were formally recorded or analyzed. It seems reasonable to imagine that these other cells, although not showing obvious directional correlates themselves, might be critically involved in the neural calculations that ultimately generate the head direction signal. Data about the kinds of information these cells code, as well as the details of these signals, is necessary for construction of a theoretical framework to explain the direction-signaling abilities of head direction cells.
In this study, recordings were made from postsubicular cells as animals navigated in a cylindrical recording apparatus, similar to that which was used for the Taube et al. (1990a,b) reports on head direction cells. Throughout recording, the animals engaged in a pellet-chasing task (Muller et al., 1989), so that they were constantly active during the 20-30 min recording sessions. The animals were equipped with two light-emitting diodes that were rigidly attached their head, and the signals from these lights were used to provide a continuous indication of the animals' momentary directional heading and location. Each cell encountered (including head direction cells) was recorded from, and the firing patterns were analyzed for several possible types of behavioral correlates.

First, as mentioned above, there were theoretical reasons for suspecting that angular velocity of the head might play an important role in generating the head direction signal. Thus, the directional data from the light-emitting diodes on the animals' heads were used to determine momentary angular velocity of the head throughout the recording sessions. Cell activity was examined for correlates of this variable.

Another variable of interest was spatial location. It was expected that the postsubicular cells might show some location-specific activity patterns, since one of their major inputs is from the subiculum (e.g., Sorensen and Shipley, 1979; Witter et al., 1990), and cells in the subiculum are known to show locational correlates (Barnes et al., 1990; Sharp and Green, 1994). Also, it was reasoned that locational information might be useful under some circumstances, to help in the accurate calculation of the directional signal. For example, it is often possible to determine one's current directional heading by sighting an environmental landmark. This is only useful, however, if one knows roughly where one is located. Thus, if one is located north of a visual landmark that is currently straight ahead, then one is facing south. However, if the current location is to the south, then one must be facing north.

In addition, head direction was also examined as a possible firing correlate for all cells. As discussed elsewhere (e.g., McNaughton et al., 1991), there is reason to postulate that forms of directional signaling other than that shown by the head direction cells themselves might be of use in calculation of the head direction signal. In particular, it might be expected that there would be cells that would fire in relation to specific combinations of head direction and angular velocity, and there is preliminary evidence that cells of this type exist in the postsubiculum (Taube et al., 1990a; McNaughton et al., 1991). Cells of this type would be useful in predicting future directional heading (since any particular combination of current directional heading and current angular velocity results in a unique future directional heading), and thus cells of this type might be involved in helping to generate the directional signal.

Finally, many cells in the hippocampus (McNaughton et al., 1983; see below) and the subiculum (see below) show a positive correlation with running speed, so that the cells fire more rapidly with increasing speed of translational motion. These running speed correlates, as well as the hippocampal theta EEG pattern, which has been shown to accompany locomotor behavior (Vanderwolf, 1969), have been postulated to play an important role in the spatial functions with which the hippocampal formation is thought to be involved (e.g., O'Keefe and Nadel, 1978; McNaughton et al., 1983; O'Keefe 1991; Burgess et al., 1994). It was of interest to see whether the postsubicular cells would also show this correlate, and so the cells studied here were examined in relation to this variable.

One difficulty involved with analyzing the cellular activity in relation to each of these variables is that it could be expected that some of these variables might be confounded with one another (that is, might correlate with each other). Thus, for example, as has been discussed elsewhere (e.g., Taube et al., 1990a), location and head direction are not orthogonally distributed in relation to each other in this recording situation. One reason this is true is that it is not possible for the animal to face all directions along the edge of the cylinder, since the cylinder wall constitutes a mechanical barrier to the animal assuming certain headings when it is next to the wall. Thus, a cell with a strong directional preference might appear to also have locational preferences. It is possible, however, that these locational correlates could be generated just by the nonuniform distribution of directional heading at various locations. As another example, it is likely to be the case that running speed and any locational variables will co-vary, for on thing, it is probably impossible for the animals to generate angular head motion without also generating some translational motion of the head (since the rat's head does not have a central axis of rotation).

Because of these possible confounds, it was decided to use a multiple regression analysis, in which each consecutive data entry consisted of the momentary firing rate of the cell under study (as the dependent variable) and each of the head direction, angular velocity, running speed, and locational measures obtained from the same 100 msec time slice (as independent variables). This analysis yielded an overall $R^2$ value, which served as an estimate of the proportion of variance in the cell's moment-to-moment firing rate, which could be accounted for by all of the behavioral variables when considered simultaneously. Also, the square of the semipartial correlation coefficient ($sr^2$) value was obtained for each separate variable. This provides a measure of the proportion of the variance accounted for by that particular variable, beyond what is accounted for by the combination of the remaining variables. Thus, it is the unique contribution of that variable to the overall $R^2$ value. These same analyses were also conducted for the head direction cells themselves, in order to see whether these cells showed other behavioral correlates in addition to head direction.

It was also of interest to compare the results of the multiple regression analysis for the postsubicular cell population with those for other hippocampal areas. For this, data sets collected during studies on each of the subicular (Sharp and Green, 1994) and hippocampal (Sharp et al., 1995) regions were also processed using the multiple regression analysis developed here. The hippocampal and subicular areas also show spatial firing correlates for single cell activity, but they appear to have location, rather than direction, as a predominant correlate. Thus, they serve as interesting comparison areas, in order to gain insight about what kinds of correlates may be unique to the directional system.

In addition to these behavioral correlates, it was also thought useful to examine the local temporal firing patterns
of the postsubicular cells. Many cells throughout the hippocampal formation show a modulation of their firing rate at a frequency of about 8–12 Hz, so that there are periodic, sinusoidal fluctuations in firing rate at this frequency (Ranck, 1973, 1975; Mitchell and Ranck, 1980; Barnes et al., 1990; Stewart et al., 1992; Sharp and Green, 1994). As mentioned above, this theta modulation has also been reported for a minority of cells in the postsubiculum (Taube et al., 1990a). This 8–12 Hz pattern is within the frequency range of the hippocampal theta EEG pattern, and cells in the hippocampus have been shown to fire in relation to the phase of this EEG pattern (e.g., Fox et al., 1986; O'Keefe and Recce, 1993). As mentioned above, the theta EEG pattern in the hippocampus occurs during locomotor and exploratory behaviors (Vanderwolf, 1969) and has been postulated to play a role in behaviorally relevant spatial information processing. Theta frequency modulation was examined for the cells recorded here, to see what kinds of behavioral correlates could be observed for cells showing this pattern.

To examine the temporal firing patterns of the postsubicular cells, autocorrelation histograms were constructed. These show the probability of the cell firing over time, given the occurrence of an individual spike at time = 0.

Materials and Methods

**Experimental Subjects**

The subjects were 15 female, Long-Evans rats, weighing 200–250 gm at shipping. The animals were housed singly upon arrival, and had a 12 hr (0800–2000) light/dark schedule.

**Behavioral Apparatus**

All recording sessions were conducted in a 50.5 cm high, 74.0 cm diameter, cylindrical chamber, like that which has been used in earlier studies of postsubicular cells (Taube et al., 1990a,b). For eight of the animals, the cylinder was painted gray, and was equipped with a single white cue card that covered 100° of arc on the cylinder wall and extended from the floor to the top of the wall. For the remaining seven animals, the inner wall of the cylinder was painted to have a series of eight alternating black and white vertical stripes. The reason for this switch in visual cues had to do with a general change in behavioral methodology in the laboratory that took place over the time these data were collected. The details of the visual cues were not considered relevant here, and, as described below, the two types of visual environment did not influence any of the variables examined for the postsubicular cells. The floor of the cylinder was painted uniformly gray, with a water-resistant paint.

The entire cylinder was surrounded by a uniform, circular, black curtain that formed an enclosure 175 cm high and 137 cm in diameter at its widest, and then tapered off above this to a diameter of 57 cm, and a height of 213 cm. Illumination was provided by a single 100 watt overhead light (located in an inverted position above the curtain), which spread a diffuse, uniform light over the cylinder floor. Also located above the curtain was an automatic dispenser for the remote-controlled delivery of food pellets. Pellets dispensed in this way dropped to a position near the center of the cylinder floor and has been postulated to play a role in behaviorally relevant spatial information processing. Theta frequency modulation was examined for the cells recorded here, to see what kinds of behavioral correlates could be observed for cells showing this pattern.

To examine the temporal firing patterns of the postsubicular cells, autocorrelation histograms were constructed. These show the probability of the cell firing over time, given the occurrence of an individual spike at time = 0.

**Behavioral Training**

Prior to training, rats were placed on a food-deprivation schedule with which they were reduced to 80% of their ad libitum weight through limited daily feeding. They were then trained to search for 20 mg food pellets (BioServe, Frenchtown, NJ) that were thrown into a cylindrical apparatus (identical to the cylindrical chamber later used for recording) at pseudorandom locations, at approximately 15 sec intervals (Mulzer et al., 1987). A total of six training sessions were given, and during this period rats developed a pattern of nearly constant locomotion that lasted throughout the sessions and resulted in the rat covering the entire cylinder floor repeatedly throughout the session, in an apparently homogeneous fashion.

**Electrode Implantation**

The recording electrodes and surgical implantation have been described elsewhere (Sharp and Green, 1994). Briefly, after training, two driveable microwire recording electrodes (one per hemisphere), consisting of six wires each, were chronically implanted. The six separate wires, cut at an approximately 45° angle, consisted of formvar-insulated, 25 μm diameter, nichrome wire (California Fine Wire Co., Grover City, CA). The electrodes were placed stereotaxically (at coordinates 6.5 mm posterior and 2.5 mm lateral to bregma) while the rats were deeply anesthetized with pentobarbital. The electrodes were mounted within small microdrives (that could be used to lower the electrodes after recovery from surgery) that were permanently fixed to the skull with dental acrylic and securing screws. At surgery, the electrode tips were placed 2.0 mm below the brain surface, so that their tips were well above the postsubicular cell layers, and could be gradually lowered through these layers after recovery.

**Unit Isolation and Data Collection**

After recovery from surgery, animals were given screening/recording sessions during which the activity from the electrode wires was sampled while the rat performed the pellet-retrieving task in the cylinder. If no single cell activity was present, the electrode bundles were lowered slightly (between 0.022 and 0.044 mm) and the wires were checked again (up to four times of repeated lowering and checking activity per day). Upon isolation of activity from a single cell(s), a recording session (see below) was initiated. Two wires could be recorded from at the same time, and the signal from each was passed first through a field-effect transistor in source-follower configuration that was mounted on the pin attached to each electrode wire. This signal then passed through a cable (affixed to the connector on the animal's head) to an amplifier (gain between 5000 and 20,000) and filter (300 Hz, high pass, and 10 kHz, low pass), and then to a computer, for automatic data collection. The software used for data collection and cell discrimination (Brainwave Corporation) collected an epoch of the digitized analog signal for every event from the amplifier which exceeded a user-set threshold. These events were then separated into bins, each of which captured the waveforms generated by spikes from one individual cell, through a cluster analysis routine that utilized information from eight different parameters extracted from each waveform. In this way, it was often possible to collect data from more than one cell simultaneously. Each event, along with a time stamp, and indication of which bin it belonged to, was automatically stored. The waveforms from any one bin were considered as acceptable for inclusion in the data set if (1) there was judged to be a good signal-to-noise ratio at the time of recording, and the waveforms appeared uniform in shape; and (2) there was a refractory period of 1 to 2 msec between spikes.

The animals' moment-to-moment position in the cylinder was also sampled continuously throughout each session. For this, a video camera located above the cylinder monitored the location of two light-emitting diodes attached to the animal's head. One of these lights was aimed at the front, while the other was aimed at the back of the animal's head. The video signal was sent to a camera tracking system (Brainwave Corporation), which extracted a digitized representation of the location of each of the two lights for transmission to the computer at a rate of 60 Hz. This information was time stamped and automatically stored. During subsequent analysis, the animal's location at each sample time was calculated as the midway point between the front and rear headlights. The animal's head direction was calculated as the angle formed between a line that was horizontal to the video camera framework (and at a vertical level equal to the rat's rear headlight), and a line through the animal's front and rear headlight.

**Recording Sessions**

To begin each screening/recording session the animal was carried into the curtained enclosure (surrounding the cylinder) in an enclosed carrying cage, and the animal was attached to the recording cable while it was held on the experimenter's shoulder. The animal was then placed into the cylinder (in the same position each time), and automatic delivery of food pellets was initiated, while the signal from each recording wire was screened for single-cell activity. Upon isolation of single cell activity, a recording session, which typically lasted from 20 to 30 min, was begun. Throughout each session the animal continuously chased food pellets, and the cell activity, as well
as the position of the animal's headlights, was continuously recorded. At the end of the session, the animal was returned to its home cage in the enclosed carrying cage.

The floor and lower wall of the cylinder were wiped with a wet rag between each screening/recording session. These sessions were conducted on a daily basis for each animal until the electrodes had been lowered to a point at which cellular activity disappeared, indicating that the electrode tips were below the postsubicular layers.

**Comparison Data Sets**

As mentioned above, it was of interest to examine firing patterns in other hippocampal regions using the same analytic methods employed here. For this, data collected in the context of other work was utilized. The data for hippocampal cells came from a study that examined the effects of movement-related cues on hippocampal place cells (Sharp et al., 1995), while that for the subiculum came from a study of the basic spatial properties for cells in that area (Sharp and Green, 1994). In general, the methods for each of these studies were very similar to those used here, in that animals (of the same species, gender, and weight used here) performed the pellet-chasing task in the same apparatus, and the electrode construction, cell screening, and data collection methods were the same. One point which should be made is that during the subicular study the cylinder wall was gray, with a single white card (covering 100° of arc) on the wall, while for the hippocampal animals, the cylinder was equipped with vertical black and white stripes. Recall that in the present study there were some animals studied in each of these two conditions, and this variable made no difference to the data for these postsubicular cells (see below). Thus, it seems that the subicular (Sharp and Green, 1994) and hippocampal (Sharp et al. 1995) data sets can serve as appropriate comparison sets for the postsubicular cells, even though the two were collected under somewhat different stimulus conditions from each other.

**Data Presentation and Analysis**

**Firing Rate Maps**

In order to visualize any locational patterns for the cell activity, the time of occurrence for the spikes of a given cell, along with the position data, were used to construct a firing rate map for each cell (Muller et al., 1987). For this, the cylinder floor was divided into 2.9 by 2.9 cm pixels, and the total amount of time spent in each pixel, along with the total number of spikes that occurred when the animal was in that pixel, were used to calculate an average rate for each. The relative rate in each was then indicated in the map using a gray scale, the value of which was chosen based on the mean and standard deviation of the pixel rates for that cell (see Fig. 4 legend for details). A diagonal line was used to indicate pixels that the animal visited, but in which the cell did not fire. A blank pixel means that the animal did not visit that location during the session.

**Examination of Firing Rate in Relation to Head Direction, Angular Velocity, and Running Speed**

For this, the data from each session were placed into 100 msec bins (thus changing the effective sampling rate from 60 to 10 Hz), and for each of these bins (from the beginning of the session to the end) a determination was made of (1) the firing rate of the cell under study (in spikes/sec); (2) the directional heading of the animal during that bin, taken as the midpoint of the animal's directional heading at the beginning and the end of the bin; (3) the angular velocity during that bin (taken as the difference between the head direction at the beginning and the end of that bin, in degrees/sec, with clockwise changes coded as positive values, and counterclockwise changes coded as negative values); and (4) the running speed (taken as the change in location from the beginning to the end of the bin, in cm/sec). These values were used to determine the average firing rate over the session for each value of head direction, angular velocity, and running speed. They were also used for the multiple regression analysis described below. Also, it should be noted that, for the purpose of the multiple regression analysis, the animals' momentary location was taken as the midpoint of its location at the beginning and the end of each 100 msec bin.

**Overall Average Firing Rate**

The overall rate (in Hz) for each cell was calculated by dividing the total number of spikes in the session by the total session time (in seconds).

**Multiple Regression Analysis**

The multiple regression analysis was conducted using software developed by the author. The analysis employed four independent variables, those being head direction, location, angular velocity, and running speed. The dependent variable was firing rate. For the angular velocity, running speed, and rate variables, the values for each data point in the analysis were simply the numerical values calculated on the basis of the 100 msec bins, as described above. This could not completely be true for head direction and locational variables, however, since it was not expected that firing rate would be a linear function of either head direction (as measured in degrees) or locational variables (using x and y coordinates). Rather, directional and locational firing patterns in the hippocampal formation tend to be quite idiosyncratic, so that each cell that codes direction has its own unique preferred direction, and each cell that signals location has its own preferred location(s). Thus, for these two variables, the point of the analysis was to ask if the cell showed a reliable locally graded influence of either of these variables so that information about the cells' own average firing rate in a given range of directional headings (or spatial locations) would assist in prediction of the cell's momentary rate. Thus, for example, if a cell shows consistent, graded modulation of its firing rate as a function of head direction, then it should be possible to predict firing rate at a particular moment, when the animal is facing a particular direction, by using the cell's average firing rate in the immediately adjacent directions. For this, it was necessary to initially make a first pass through the data, in order to obtain average values for the entire session for firing rate as a function of both head direction (averaged into 6° bins) and location (averaged into 2.9 cm square locational pixels, as described above for the rate maps). Then, during the subsequent multiple regression analysis, the data point for each 100 msec time bin for the directional variable was the mean of that cell's average firing rate in the two directional bins on either side of the animal's current directional heading. Thus, if, for a given sample, the animal was facing at a 90° angle of head direction (relative to the video camera framework), then the value for head direction as an independent variable in the multiple regression analysis would be the mean of the average rate for that cell in the directional bin to the left (at 84°) and in that to the right (at 96°) of the animal's current heading. Thus, the cell's average firing rate in the neighboring head direction bins was used as a predictor for its current momentary rate. Similarly, the value for the locational variable was the mean of that cell's average rate in the eight pixels surrounding the pixel in which the animal was located during that sample. In this way, if the cell showed a reliable tendency to make local graded variations in its firing rate as a function of either head direction or spatial location, this could be detected by using values of its own average rate in neighboring regions (directions).

This analysis was run for the data from each session of each cell, and it allowed determination of (1) the R² value, which is a measure of what proportion of the cell's total variance in firing rate can be removed by taking into account all four of the independent variables, and (2) the square of the correlation coefficient for each of the independent variables. This latter value can be taken as a measure of the amount of the total variance which one particular variable, alone, accounts for. Each of these values can be tested for statistical significance, using an F test.

It should be noted that the validity of this F test is not dependent on whether the cell's firing rate distributions (as a function of the behavioral variables) are normally distributed. This is true because in this case the test is not being used to examine differences in firing rate distributions. Rather, the test is used to assess whether or not the R² and s² values are significantly different from zero. Thus, the relevant consideration is whether or not the population of correlation coefficients (over the session) for firing rate as a function of head direction is an approximately normal distribution for correlation coefficient values of samples taken from a population whose true correlation coefficient is zero, this means that the F test is valid in this case (Roscoe, 1975). It was also possible to examine the interaction terms for any or more of the variables, when this seemed appropriate.

**Spike Train Analysis**

Autocorrelation histograms were constructed by summing the number of times in which a spike occurred within each 1 msec bin from zero to 300, giving the occurrence of a spike at time 0. These sums were then divided by the total number of spikes, to yield the prob-
ability of occurrence for each interval. These autocorrelation histograms reveal any rhythmic modulation of cell firing probability.

**Analysis of Firing Rate during Clockwise versus Counterclockwise Turns as a Function of Head Direction**

For this, data samples were divided into those that took place during clockwise versus counterclockwise turns. The samples for each turning direction were then displayed in a graph of firing rate as a function of head direction.

**Histological Examination and Reconstruction of Cell Location**

After recording, animals were perfused transcardially under deep anesthesia with a formyl saline solution. Prior to this a small current (30 mA X 5 sec) was passed through one wire of each electrode, in order to mark the location of the electrode tips. The brains were then sectioned in the coronal plane at 40 µm intervals, mounted, and stained with both cresyl violet and Prussian blue. For the present purposes, the postsubiculum was defined as it was in the Taube et al. (1990a,b) reports, as the area in the dorsal portion of the hippocampal formation that is lateral to retrosplenial cortex, medial to the subiculum, and dorsal to the presubiculum (see Fig. 1).

**Results**

Data were collected from a total of 71 postsubicular cells in 21 hemispheres of 15 rats. The average firing rate for the population was 19.14 (± 2.48) spikes/sec, while the average spike width (between the initial departure from and subsequent return to baseline) and spike height (from the initial negative, to the subsequent positive peak) were 292.95 (± 15.2) msec and 263.08 (± 17.79) µV, respectively.

The $R^2$ value for the multiple regression analysis, utilizing head direction, place, running speed, and angular velocity as independent variables (as described above) was significant ($df = 4, \alpha, F > 4.62, p < 0.001$) for every cell, with the average value being 0.19. This suggests that simultaneous consideration of these variables can account for a significant (approximately 20% on average) portion of the variance in the momentary firing rate for the general population of postsubicular cells.

Examination of the $sr^2$ (the square of the semipartial correlation coefficient) values for each of the independent variables, however, revealed that the cell population was quite diverse, so that most cells showed a significant relationship to only a subset of the independent variables. Figure 2 shows a summary of the behavioral correlates for the total postsubicular sample, as well as for the subset of postsubicular cells in each of the categories described below. The histograms on the left show the values for the overall $R^2$ and each of the $sr^2$ values for the individual variables. The histograms on the right show the percentage of cells in each category for which a significant correlation was found for the overall $R^2$ ($df = 4, \alpha, F > 4.62, p < 0.001$) and for each of the $sr^2$ ($df = 1, \alpha, F > 10.8, p < 0.001$) values. Figure 3 shows the same information again for the postsubicular cells, as well as for the cell populations collected in each of the hippocampal and subi-
cylindrical regions, with the hippocampal cells divided into complex spike and theta cell (Ranck, 1973) categories. Most (63 out of 71) of the postsubicular cells showed a significant correlation with head direction, as might be expected. The proportion of variance (s²) accounted for by head direction was quite variable (range = 0.00006 to 0.45), however, and the average s² for this variable was 0.12. Most of the postsubicular cells (58 out of 71) also showed a significant correlation with running speed, although the magnitude of this effect was generally quite small (average s² = 0.01; range = 0.000003 to 0.15), indicating that an average of only about 1.0% of the variance in momentary firing rate could be accounted for by this variable alone. For most (49 out of 58) of the cells showing running speed as a significant correlate, the correlation was positive, so that as running speed increased, cells fired more quickly (see, e.g., Fig. 9D). For 9 of the 58 cells for which running speed was a significant correlate, however, the correlation was negative (as was the case for the cell shown in Fig. 11D). A significant influence of place was also observed for most of the cells (69 out of 71), although, again, the proportion of variance accounted for by this variable was small (average s² = 0.02; range = 0.0007–0.23). Finally, a significant influence of angular velocity was found for 24 out of 71 of the cells, and again, the proportion of variance accounted for was relatively small (average s² = 0.006; range = 6.1 × 10⁻⁸ to 0.16).

There were no detectable differences in any of these measures in relation to the two versions of the cylinder (recall that for eight of the animals the cylinder was equipped with one white card against a gray background, while for the remaining seven animals the walls were painted with black and white stripes). No significant differences were seen for either the R² or any of the individual s² measures as a function of this variable (df = 69, t < 1.67, p > 0.10).

Examination of the data pattern for individual postsubicular cells revealed that many of the cells could be placed clearly into one of two categories. These two categories are (1) head direction cells, as originally described by Ranck (1984) and Taube et al. (1990a,b), and (2) angular velocity cells, which showed a characteristic function (described below) of firing rate with angular velocity, and for which angular velocity was the predominant correlate. For the remaining cells (those that did not fit clearly into either the head direction or angular velocity categories) it was difficult to arrive at a clear categorization scheme. Thus, each of these cells showed significant s² values for some particular subset of the variables examined, with the relative portions of variance accounted for by each being quite idiosyncratic. Although clear categories did not seem to be present for these remaining cells, some general tendencies could be discerned, and so, for the purpose of presentation, these cells have been tentatively placed into categories that are described, along with the head direction and angular velocity categories, below.

**Head Direction Cells**

Twenty-six of the 71 cells could be clearly classified as head direction cells like those described previously (Ranck, 1984; Taube et al., 1990a,b). These cells were characterized by a single, triangular peak (Taube et al., 1990a) in firing rate as a function of head direction, with each cell having its own, unique, single preferred direction. Figure 4A shows the firing rate maps for a typical cell in this category. The central map (showing firing rate as a function of location in the cylinder) shows that the cell fired at almost all locations throughout the cylinder. In the circular array of maps surrounding this, the firing rate data are divided into direction-specific categories, with each map in the circular array showing the firing rates for only those samples taken when the animal was facing (within a 22.5° range) in the direction shown by the accompanying arrow. It can be seen that, in general, cell activity was present only when the animal was facing in the approximately 225° to 270° range of head directions. Figure 4B shows a plot of firing rate as a function of head direction. This cell showed its highest rate at 254°, and the rate decreased linearly and symmetrically around this peak, as has been previously described (Taube et al., 1990a). This cell was typical of most observed, which showed similar triangular functions, with the average peak firing rate (the rate at the peak of the preferred direction) across cells being 24.97 (± 3.32), and the average directional tuning width (measured as the width of the triangular function at the point halfway between the peak and the baseline firing rates) being 57.12 (± 4.18). The multiple regression analysis revealed a s² value of 0.38 for head direction for this cell. Thus, 38% of the moment-to-moment variance in the cell's activity could be accounted for by using the average firing rate in the adjacent directional headings (those to the immediate right and left of the direction being sampled) as a predictor (as described in Materials and Methods).

All of the cells in the head direction cell category showed a highly significant s² value for head direction (df = 1, t > 10.5, p < 0.001), and the average s² value was 0.27 (see Fig. 2).

The central map in Figure 4A makes it appear that there could also be a strong locational correlate for this cell, since the cell did not fire much in the upper right quadrant of the cylinder, while showing high rates in the lower left portion.
Figure 4. Behavioral correlates and temporal firing pattern for a typical postsubicular cell in the head direction category. A, Firing rate maps to show cell activity as a function of location (central map) and both location and direction (circular array of maps). For construction of the central map, the cylinder floor was divided into 2.9 by 2.9 cm pixels, and the firing rate for each pixel was obtained by dividing the total number of spikes that occurred when the rat was in that location by the total time spent in that location. These values were then used to compute a mean and standard deviation over all the pixel rates. The relative rate for each pixel is depicted using one value of a five-valued gray scale, so that pixels that are more than two standard deviations above the mean pixel rate for that cell are given the darkest value, those between one and two standard deviations above the mean have the next highest value, those within one standard deviation above the mean use the next value, those within one standard deviation below the mean receive the next value, and those that are one or more standard deviations below receive the lowest value. Pixels that the animal visited, but in which the cell did not fire, are indicated by a
It seems likely that part of this impression of strong locational bias is artifactually generated by the fact that the animal did not randomly distribute its directional heading in relation to location, so that the animal spent more total time facing in the cell's preferred head direction in some locations than in others. Thus, for example, it was not possible for the rat to face in the 234° direction (the cell's preferred direction) when positioned along the upper right quadrant, since the rest of the animal's body would have to protrude through the wall in order to do this. Examination of the circular array of direction-specific maps confirms this idea, since firing rates for samples taken for the 225 and 270° rate maps show quite uniformly high rates throughout the cylinder, for almost all adequately sampled locations. Nonetheless, the multiple regression analysis revealed a significant place correlate (df = 1, F = 243.09, p < 0.001) for this cell, suggesting that there was, in fact, a locational influence, although the percent variance accounted for was quite small (sr² = 0.01). In the total sample of head direction cells, 96% showed a significant place correlate (df = 1, F > 10.8, p < 0.001), suggesting that these cells tended to have a slight locational influence, although the average sr² value was only 0.01.

Figure 4C shows firing rate for this same cell, plotted as a function of angular velocity. In this graph, average firing rate during counterclockwise rotation is shown on the left portion of the abscissa, on a scale which ranges from 0°/sec (in the center of the abscissa) to −600°/sec (at the left-most end of the abscissa). Firing rates during clockwise rotation appear on the right half of the graph, over a range of 0°/sec (in the center of the abscissa) to 600°/sec (at the right-most end). This cell was typical of most head direction cells in that it showed little apparent correlation with angular velocity (though there was some tendency for higher velocities in either direction to be associated with higher rates). Only six of the head direction cells showed a significant angular velocity correlate (df = 1, F > 10.8, p < 0.001), and for these, the average sr² was 0.0004. Figure 4D shows firing rate for this same cell as a function of running speed. This cell showed little detectable influence of this variable, and this result was typical for the general set of head direction cells, for which the average sr² for running speed was 0.0004.

Finally, Figure 4E shows the autocorrelation histogram for this cell. It can be seen that there was no tendency for this cell to show a rhythmic (theta-like) pattern, such as is observed for theta cells in the hippocampus (e.g., Ranck, 1973; Fox et al., 1986) and most cells in the subiculum (Barnes et al., 1990; Sharp and Green, 1994). Rather, firing probability first peaked (after an initial refractory period) and then decreased linearly as a function of time after a spike. This type of histogram was observed for all of the cells in the head direction category.

Results from the analysis of direction-specific firing during clockwise versus counterclockwise turns revealed little effect of this variable, although subtle effects were observed for a few of the head direction cells (data not shown). These effects have been examined in detail in a related paper (Blair and Sharp, 1995).

Angular Velocity Cells

Seven of the 71 cells showed angular velocity as their predominant correlate. An example of this kind of cell is shown in Figure 5. Figure 5C shows firing rate as a function of angular velocity, just as it was shown for the cell depicted in Figure 4C. It can be seen that this cell showed a steep (slope, −0.047 Hz/degree), nearly linear relation to angular velocity. This cell preferred counterclockwise turns, so that its rate increased linearly with increasing velocity for counterclockwise turns and decreased with increasing velocity for clockwise turns. Surprisingly, the multiple regression analysis for this cell revealed that only 16% of the variance could be accounted for by angular velocity. Thus, although the average (over the entire recording session) firing rate at each value of angular velocity shows a very clear angular velocity correlate (as observed in Fig. 5C), the multiple regression analysis shows that only a small portion of the moment-to-moment firing pattern can be accounted for by this variable. This was true for other cells in this category as well, so that the average sr² value for angular velocity was 0.06 for these cells. As discussed below (see Fig. 13), it is likely that these surprisingly low sr² values are due to the fact that the 100 msec time bins used for the multiple regression analysis did not allow for an accurate estimate of the cell's momentary rate, given the average firing rate of these cells.

Figure 5, A and B, shows that this cell was active throughout the area of the cylinder, and that there were no apparent large effects of either location or head direction, although the place sr² value was statistically significant (df = 1, F = 315.64, p < 0.001), suggesting an influence of location on this cell. Surprisingly, all of the angular velocity cells showed place correlates that were statistically significant (df = 1, F > 10.8, p < 0.001), but low in magnitude, so that the average sr² was 0.017.

Two of the angular velocity cells showed a significant correlation with head direction (df = 1, F > 10.8, p < 0.001), although the magnitude of this effect was very small (average sr² for those cells for which it was significant = 0.0053). Figure 5D shows firing rate as a function of running speed for this cell, and it can be seen that there was little detectable effect of this variable. In general, the angular velocity cells showed a tendency to have a small (average sr² = 0.0029) but significant relationship to running speed. The angular velocity cells were quite variable in their average firing rate (range = 5.28 to 93.82 spikes/sec), with the average rate being 31.80 spikes/sec. Examination of the autocorrelation histograms showed that two of the seven angular velocity cells showed a pronounced theta-frequency modulation in their
Figure 5. Behavioral correlates and temporal firing pattern (as in Fig. 4) for a postsubicular cell in the angular velocity category. This cell showed a pronounced correlation with angular velocity, so that faster turning in the counterclockwise direction was associated with higher firing rates, and faster turning in the clockwise direction was associated with lower firing rates. There was little obvious effect of head direction, running speed, or location for this cell. Also, there was no indication of theta frequency modulation of firing rate. For this cell, $R^2 = 0.21$, and the $s^2$ values are as follows: head direction, 0.0006; angular velocity, 0.16; place, 0.016; running speed, 0.0025.
firing rate (like that shown for a different cell type in Fig. 11F), while the remaining angular velocity cells showed patterns more similar to that shown in Figure 5E. Finally, examination of the directional firing properties for clockwise versus counterclockwise turns revealed that these cells showed a turn preference throughout the directional range that was not detectably influenced by directional heading (data not shown).

One troublesome aspect of the data for the angular velocity cells is that six of the seven cells were collected from one electrode track in one animal (see Fig. 12). The remaining cell was collected from a different animal. The fact that so many of the angular velocity cells were from one electrode track raises, first, the question of whether each of the reported cells were really separate cells, or whether there were some cases in which the same cell was recorded over more than one session, and was accidentally thought to be a different cell each time. This seems particularly possible, given the fact that all of these cells preferred left turns (that is, showed high rates during left turns and lower rates during right turns).

Because of this concern, the data from each session were carefully examined with respect to several criteria, in order to determine whether the data were from a different cell than had been previously recorded. Specifically, for the data from any two sessions to be judged as being from two different cells, it was necessary that they differ from one another in (1) overall firing rate; (2) details of the function relating firing rate to angular velocity; (3) overall temporal firing pattern, as viewed in the autocorrelation histogram; and (4) the spike waveform shape and size. Figure 6 shows an example of a recording made from the same electrode track as the cell shown in Figure 5. This data set was judged to be from a different cell than that in Figure 5, because it differed from that one on each of the criteria listed above. First, Figure 6B-D shows a higher overall firing rate for this cell than for the cell shown in Figure 5. Also, the autocorrelation histogram in Figure 6E shows that this cell reached its peak average firing rate at a shorter postspike latency than did the cell shown in Figure 5E. Also, comparison of Figures 5C and 6C shows that the two cells were somewhat different in their function of firing rate versus angular velocity. Thus, for example, the cell depicted in Figure 6 shows a single, nearly linear gradient of firing rate in relation to angular velocity throughout the entire angular velocity range, while that shown in Figure 5 shows a relatively steep gradient over the range from approximately ~500 to approximately 150°, and then shows a relatively shallow gradient to the right of this.

It should also be noted that there were several cases in which repeated sessions were judged as having been taken from the same cell; in these cases the data from the repeated sessions showed nearly identical patterns for each of the criteria listed above. Thus, it appears that there actually was a set of angular velocity cells located along the same electrode track, and all showing a preference for counterclockwise turns. This suggests that there may be a columnar organization for these cells (see discussion below). It should be noted that the one angular velocity cell recorded from a different animal showed a preference for clockwise turns, thus showing that both turning preferences can be observed. This angular velocity cell was the only cell of any kind observed for that hemisphere.

Another problem with the fact that almost all of the angular velocity cells came from just one electrode track is that it raises the possibility that an error was made in the histological examination of this track, so that the electrode for this hemisphere was somehow mistakenly identified as having been in the postsubiculum. This would explain why angular velocity cells were otherwise so rare in the postsubiculum. Indeed, histological examination revealed that the track, in this case, was very close to the border between the postsubiculum and the subiculum. (Alternatively, the track from the other animal that yielded an angular velocity cell was not close to this border, but was, instead, in the more medial portion of postsubiculum.) Thus, it is conceivable that the true location of the electrode tips at the time recordings were made was somehow misjudged, and the angular velocity cells were actually located in the subiculum. This seems unlikely, however, since, of the 85 cells recorded in the subiculum (see Fig. 5) only four showed a significant $s^2$ value for angular velocity, and the magnitude of these effects was very low (average $s^2$ value for these four cells = 0.0015).

Another possibility is that these cells were actually located in the presubiculum region. The pre- and postsubicular areas are difficult to distinguish visually, and the anatomical methods used here could not provide confident discrimination between the two, using cytological criteria alone. However, examination of the electrode track for these cells showed that it was located in a position further anterior than that at which the presubiculum can be observed. Thus, altogether, it looks as if rare columns of angular velocity cells can be found in the postsubiculum.

**Head Direction Cells with Multiple Peaks**

The 12 cells in this category were like the head direction cells described above, in that their predominant behavioral correlate (that yielding the largest $s^2$ value) was head direction. These cells were different from the head direction cells, however, in that they tended to be tonically active, and to show multiple, irregular peaks in the plot of firing rate as a function of head direction. These cells also showed lower average $s^2$ values for head direction (average $s^2$ = 0.05) than did the head direction cells described above.

An example of a cell of this type is shown in Figure 7. The multiple peaks in firing rate as a function of head direction can be seen in Figure 7B. The rate map (7A) shows that the cell was active in all parts of the cylinder, and showed a significant influence of location on firing rate ($df = 1, s, F = 264.93, p < 0.001$). This cell, like most cells in this category, showed a significant effect of running speed ($df = 1, s, F = 515.84, p < 0.001$), although the magnitude of the effect was small ($s^2 = 0.04$). There was also a very small, but significant, effect of angular velocity on this cell ($df = 1, s, F = 59.216, p < 0.001$), with $s^2 = 0.004$.

The autocorrelation histogram for this cell shows a subtle, rhythmic modulation of its firing rate at a frequency of approximately 9 Hz, which is within the frequency range shown by the hippocampal theta EEG pattern. Four of the cells in this category showed this theta-frequency modulation, while the remaining cells showed a pattern like that shown, for example, in Figure 4E.

These multiple peak head direction cells tended to have relatively high average firing rates (average rate = 33.66 spikes/sec) when compared to the head direction cells described above (average rate = 4.84). This was due, in part, to the fact that the former class of cells were tonically active (in contrast to the head direction cells described above, which are silent throughout much of the directional range). However, even when the peak rates (the rate of firing when the animal was facing in the direction associated with the highest average firing rate) for these two cell classes are compared, there is still a large difference (average peak rate for head direction cells = 24.97 ($\pm$ 3.23), while that for head direction cells with multiple peaks was 56.74 ($\pm$ 9.21)) and this difference was statistically significant ($df = 36; t = 4.07, p < 0.001$).

As can be seen in Figure 2, the angular velocity $s^2$ values...
Figure 6. Behavioral correlates and temporal firing pattern (as in Fig. 4) for another postsubicular cell in the angular velocity category. This cell was recorded from the same electrodes track as the cell depicted in Figure 5, and, like that cell, showed a pronounced correlation with angular velocity, so that faster turning in the counterclockwise direction was associated with higher firing rates, and faster turning in the clockwise direction was associated with lower firing rates. The overall shape of the function was somewhat different from that in Figure 5, however (see text). This cell showed a slight, positive correlation with running speed, while there was little obvious effect of head direction or location. Also, there was no indication of theta frequency modulation of firing rate. For this cell $R^2 = 0.12$, and the $r^2$ values are as follows: head direction, 0.00009; angular velocity, 0.04; place, 0.019; running speed, 0.018.
Figure 7. Behavioral correlates and temporal firing pattern (as in Fig. 4) for a postsubicular cell in the head direction-multiple peaks category. This cell showed graded, gradual fluctuations in firing rate as a function of head direction. There was also a positive correlation with running speed, as well as a tendency to show higher rates as a function of clockwise turning speed. Also, there was a slight indication of theta frequency modulation of firing rate. For this cell, $F_P = 0.14$, and the $r^2$ values are as follows: head direction, 0.046; angular velocity, 0.0049; place, 0.022; running speed, 0.042.
for these cells tended to be quite small (average $r^2 = 0.0018 \pm 0.0005$), suggesting that there was little effect of this variable on these cells. Examination of these cells using the analysis of directional firing for clockwise versus counterclockwise turns, however, revealed that three of these cells showed a significant effect of angular velocity over a part of the directional range. Figure 8 shows the results of this analysis for two of these cells, as well as for a cell in the place-like category (see below), which also showed this effect. Firing rate is shown as a function of head direction for clockwise (thin line), versus counterclockwise (thick line), turns, and the small circles located in the upper portion of the graph indicate the locations at which the rate during the two turning directions was significantly different ($df$ variable, $p < 0.01$). Each cell shows a selected directional range(s) over which there is an increase in firing rate during turns in one direction, but not the other.

For the remaining cells in this category the turn-specific analysis of directional firing showed that the pattern of multiple peaks was very similar for clockwise and counterclockwise turns (data not shown).

**Place-Like Cells**

Seven of the 71 postsubicular cells were categorized as place-like cells, because they showed location as the predominant behavioral correlate (that yielding the highest $r^2$ value), and showed relatively little influence of other of the variables tested. Figure 9 shows an example of a cell in this category. This cell showed a region of relatively high firing along the lower right edge of the cylinder (Fig. 9A). Cells in this category were similar in appearance to subicular cells recorded in the same behavioral paradigm (Sharp and Green, 1994), in that they tended to fire over a large portion of the cylinder, showing gradual modulation of their rate as a function of location. This pattern of spatial firing is different from that of hippocampal place cells, which tend to show a single, circumscribed region of high firing (e.g., Muller et al., 1987), while showing near zero rates in other portions of the environment.

Examination of the circular array of direction-specific maps in Figure 9, as well as the graph of direction-specific firing (Fig. 9B), suggests that there was also a large, graded effect of head direction on the firing rate of this cell, so that the cell fired at relatively lower rates when the animal was facing in the direction range from approximately 90 to 180°. At least part of this apparent directional bias was generated artificially, however, due to the fact that the animal could not face in the 90-180° directional range when it was located in the region of the cell's highest firing rate (due to the mechanical boundary imposed by the cylinder wall), as indicated by the blank pixels in this region for the direction-specific maps at the 135° and 180° orientations (Fig. 9A). The results of the multiple regression analysis also support this interpretation, since the $r^2$ value for head direction for this cell was very small ($r^2 = 0.004$, though significant ($df = 1, \alpha, F = 56.36, p < 0.001$).

Also, this cell showed no detectable effect of angular velocity ($df = 1, \alpha, F = 0.0009, p > 0.25$), and this was typical for cells in this category (see Fig. 2). Finally, this cell showed a reliable positive correlation with running speed ($df = 1, \alpha, F = 71.2, p < 0.001$), as was typical of many of the cells in this category (see Fig. 2).

Only one cell in this category showed rate modulation in the theta frequency range, while the others showed an initial refractory period, followed by a relatively high probability of spike occurrence which decreased linearly over time (as in Fig. 9E). The average firing rate for cells in this category was 6.14 (± 2.43). Analysis of directional firing for clockwise versus counterclockwise turns revealed one cell in this category that showed a direction-specific influence of turning direction (see Fig. 9C).

**Place by Head Direction Cells**

The 14 cells in this category showed clear modulation of firing rate as a function of both head direction and location, with relatively little influence of the other variables. An example of a cell like this is shown in Figure 10. This cell fired predominantly when the animal was in the lower right portion of the cylinder, and then only when the animal was faced at an approximately 45° directional heading. The $r^2$ values for this cell were highly significant for both place ($df = 1, \alpha, F = 121.94, p < 0.001$) and head direction ($df = 1, \alpha, F = 885.02, p < 0.001$). Since the firing pattern of this cell appeared to depend on an interaction between the place and head direction variables, it was decided to run a version of the multiple regression analysis that included the place by direction interaction term. As expected, this interaction term was highly significant ($df = 1, \alpha, F = 445.88, p < 0.001$), yielding an $r^2$ value of 0.029. Thus, it appears that this cell (as well as others in this category) was influenced by both place and directional information, which combined to generate a place signal that was conditional on directional heading.

It should be noted that many of the cells in this category...
Figure 9. Behavioral correlates and temporal firing pattern (as in Fig. 4) for a postsubicular cell in the place-like cell category. This cell showed a region of high firing in the lower, right portion of the cylinder. There was also some fluctuation in rate as a function of head direction, though this may have been largely related to unequal distribution of directional heading within the place field (see text). There was also a small, positive correlation with running speed, and little obvious influence of angular velocity. Also, there was no indication of theta frequency modulation of firing rate. For this cell $P = 0.002$, and the $sr^2$ values are as follows: head direction, 0.0039; angular velocity, $6.1 \times 10^{-4}$; place, 0.038; running speed, 0.0049.
Figure 10. Behavioral correlates and temporal firing pattern (as in Fig. 4) for a postsubicular cell in the place by direction cell category. This cell showed a region of high firing in the lower, right portion of the cylinder, but only for directional headings between approximately 0 and 90°. There was also an influence of angular velocity, with higher rates for counterclockwise turns and lower rates for clockwise turns. There was also a positive correlation with running speed. There was no indication of theta frequency modulation of firing rate. For this cell, $\Phi = 0.079$, and the $s^2$ values are as follows: head direction, 0.059; angular velocity, 0.0043; place, 0.0081; running speed, 0.0029.
did not show a spatially circumscribed firing field like that seen in Figure 10. Rather, many of the cells fired throughout the area of the cylinder, so that they were tonically active, but showed reliable, graded modulation of rate as a function of location. For these cells, the directional preference was also graded throughout the directional range, so that the cells fired throughout the entire range of head direction, but showed graded, reliable modulation of rate as a function of directional heading. For these cells, then, there was a location-related firing pattern that could be observed at each directional heading, and that was generated by higher overall firing rates in some directional headings than in others.

Figure 10C shows that there was also a relationship between firing rate and angular velocity for this cell, and this function appeared similar to that shown by the angular velocity cells described above, in that firing rate increased with increasing velocity for counterclockwise turns, and decreased during clockwise turns. The $s_r^2$ value for angular velocity for this cell ($s_r^2 = 0.004$) was quite small, however, compared to that for the angular velocity cells described above. One possible explanation for this low $s_r^2$ value is that the relationship that is suggested so strongly by Figure 10C is actually an artifactual result of the place by directional firing pattern shown by this cell, in combination with the behavioral patterns induced by the cylindrical shape of the recording apparatus. Thus, it was probably the case that the animal generated relatively more counterclockwise turns in the cylinder when in the cell’s preferred location and directional heading, since the animals have a tendency to circle along with the contour of the wall (which would result in left turns when facing in the 45° direction in the lower left portion of the cylinder). If this idea provides the entire explanation for the angular velocity effect observed in Figure 10C, then the inclusion of the place by direction interaction in the multiple regression analysis should have removed the significance of the angular velocity $s_r^2$ value entirely. That is, if consideration of the conditional effects of place and directional heading can completely explain the apparent association of higher firing rates with counterclockwise turns, then angular velocity should no longer yield a significant $s_r^2$ value. The results from this analysis revealed that, in fact, inclusion of the place by direction interaction did reduce the $s_r^2$ value for angular velocity (from 0.004 to 0.003), as expected. The latter value, however, was still statistically significant ($df = 1, \alpha = 30.36, p < 0.001$) and head direction ($df = 1, \alpha = 44.95, p < 0.001$) did reach statistical significance. Figure 11D reveals that this cell was unusual in showing a negative correlation of firing rate with running speed, so that faster running was associated with slower firing. All other cells in this category showed a positive correlation between these two variables.

Three of the cells in this category showed a pronounced theta-frequency modulation of firing rate, like that shown in Figure 11E. One of the cells in this category showed a very unusual temporal firing pattern, in that there was a very long (> 50 msec) refractory period, followed by a peak firing probability at about 110 msec, which was then followed by a gradual linear decrease in average firing rate. The remaining cell in this category showed a more typical postsubicular cell pattern, like that shown, for example, in Figure 6E. The average firing rate for cells in this category was quite high (44.54 spikes/sec).

**Evidence about Possible Columnar Organization of Behavioral Correlates in the Postsubiculum**

The chronic recording method used here is somewhat limited in its ability to provide information about whether cells are organized into a columnar arrangement in terms of their behavioral correlates. This is true because only one vertical penetration is made in each hemisphere for each animal. Thus, if cells of a particular type are located along one particular electrode track, it is not clear whether that cell type is specific to a particular column that the electrode traveled along, or whether there was a more general concentration of that cell type in that hemisphere, or that animal. Also, the plane along which the postsubiculum is organized is not exactly perpendicular to the trajectory of the electrode track, so that the electrode tips would not be expected to follow the exact vertical orientation of any existing column. Nonetheless, some inferences can be suggested by examination of the clusters of cell types located along individual electrode tracks.

Figure 12 shows the distribution of cell types along each electrode track, in the vertical order in which they were encountered, with cells recorded at the same time shown parallel to one another. The label in the upper left corner of each rectangular area shows the animal number and hemisphere (right, R; left, L) for the electrode track depicted. There is some suggestion that there could be a columnar arrangement of cell types in that, for two of the tracks (70-L and 98-R) several cells of the same type were recorded. Most of the other tracks, however, yielded a heterogeneous set of cells, and even in cases in which cells were recorded simultaneously, there was often discordance in the cell types. Interestingly, even in cases in which several head direction cells were recorded in a row, the directional preferences were not likely to be similar.

**Comparison with Other Parts of the Hippocampal Formation**

From Figure 3 it can be seen that, as expected, the postsubicular cell population showed the highest percent of cells that were significantly related to head direction, and also showed
Figure 11. Behavioral correlates and temporal firing pattern (as in Fig. 4) for a postsubicular cell in the running speed-related cell category. This cell showed a strong negative correlation with running speed, while there was little influence of any other behavioral variable. There was also strong theta frequency modulation of firing rate. For this cell $R = 0.09$, and the $s^2$ values are as follows: head direction, 0.0038; angular velocity, 0.00026; place, 0.026; running speed, 0.052.
the highest average $s^2$ values for this variable. Postsubiculum also showed the highest percent of cells with a significant angular velocity correlate, as well as the highest $s^2$ value for this variable.

All cell categories showed a reasonably large number of cells with a significant running speed correlate, though the average $s^2$ values for this variable were negligible for all groups except the hippocampal theta cell category. Finally, cells in the subicular and hippocampal region showed the highest $s^2$ values for place, as might be expected. However, these values were surprisingly small, given the apparent robustness of the place cell signal when average firing rates as a function of location are examined (e.g., Muller et al., 1987).

**Relationship between Rate Sampling Accuracy and Percentage Variance Accounted for by Multiple Regression**

One surprising aspect of the results from the multiple regression analysis is that the $s^2$ values are generally quite small, even when examination of average firing rate functions reveals obvious, strong effects. For example, data for the head direction cell shown in Figure 4 reveals that the average firing rate for this cell was strongly determined by directional heading (Fig. 4B). Nonetheless, only 38% of the moment-to-moment variance in firing rate could be accounted for by the head direction variable (head direction $s^2 = 0.38$). Similarly, the angular velocity cell shown in Figure 5C showed a strong influence of angular velocity, yet the $s^2$ value for this variable was only 0.16.

A possible reason for these low $s^2$ values is that the momentary rate was always estimated over a 100 msec time bin (see Materials and Methods) for the purpose of the multiple regression analysis. Given the average firing rates shown by the postsubicular cells studied here, it could be that these time bins are too short to provide an accurate estimate of firing rate for any one bin. Thus, for example, a cell that fires at an average rate of 5 spikes/sec would have a roughly 50% chance of firing during any one 100 msec time bin. This means that its rate would fluctuate considerably from one time sample to another, even if the cell consistently fired at 5 spikes/sec, when averaged over a longer time span. Thus, it is possible that a large portion of the variance in momentary rate has to do with local temporal variability in firing probability.

To test the validity of this explanation, “dummy” cells were constructed to try to replicate the salient overall firing characteristics of each of the cells in the head direction and angular velocity categories. Each “dummy” cell fired probabilistically, but in a way that was related to the head direction or angular velocity function being replicated.

Thus, for each head direction cell, a companion “dummy” cell was created that showed a similar directional tuning curve, in terms of peak firing rate (the rate at the optimal direction) and preferred direction and directional range. For this, the behavioral data (obtained from the two lights on the animal’s head) from the session in which the real head direction cell was recorded, was used to help determine, from moment to moment, the probability that the dummy cell would fire. For each 4 msec interval throughout the session the dummy cell was created to fire to replicate the animal’s head direction or not fire with some probability, and that probability was based on the real cell’s average rate for the current directional heading. For example, the cell depicted in Figure 4B shows a peak firing rate of approximately 20 spikes/sec when the animal is facing in the preferred direction of 234°. Thus, for any 100 msec behavioral sample during which the animal happened to be facing 234°, the probability of the cell firing during any 4 msec period within this sample was set at 0.08. Since there are 250 4 msec time bins in a second, and $250 \times 0.08 = 20$, this yields an average firing rate of 20 spikes/sec. Whether the dummy cell actually fired during any particular 4 msec interval was determined by the results of a random number generator in this way, a “dummy” cell was created that fired with a probability related to the animal’s head direction, but that showed variability in rate for different samples at the same direction. These dummy cells did, in fact, show directional tuning curves (data not shown) that were very similar to those shown by the real cells.

Figure 13 (upper half) shows the percent variance ($s^2 \times 100$) that was accounted for by the head direction variable for each of the real and dummy head direction cells. The data are displayed as a function of the cells’ peak firing rates (the

---

**Supplementary Figure 1**

Illustration of the cell types located along each electrode track in each hemisphere. Animal number and hemisphere (right—R, left—L) are provided in the upper left portion of each rectangular area, within which the cells for the electrode track in that hemisphere are shown. Each circular symbol represents the relative vertical location of a cell recorded from that hemisphere. The category to which the cell belonged is indicated by the symbol type (see key on right), and for head direction cells, the preferred direction is indicated by the direction of the arrow within the symbol. Cells that were recorded simultaneously are displayed next to one another, at the same vertical level.
expected that the $sr^2$ if very high peak rate values were used to create the dummy cells, and this suggests that, as might be expected, the real head direction cells was consistently lower than that for the dummy cells. To test this prediction, a dummy cell was created that had a peak rate of 200 spikes/sec. The multiple regression analysis for this cell yielded $sr^2 = 0.80$ and $R^2 = 0.96$. The $sr^2$ values for the other behavioral variables (speed, location, and angular velocity) were, as expected, very low, and did not approach statistical significance. This means that at this high rate, consideration of the head direction variable can account for 80% of the variance, while another 16% of the variance can be accounted for by the complete multiple regression analysis, but cannot be ascribed to the unique contribution of head direction, since this variable is confounded (in the animal’s behavior) with the other variables (see the introductory paragraphs).

Another interesting observation is that the percent variance accounted for by head direction for the head direction cells is higher on the average than that accounted for by the angular velocity variable for the angular velocity cells. This is true even for the comparison between the dummy head direction and Angular Velocity cells. One possible explanation for this is that the head direction cells have a large number of time bins for which the expected (and actual) firing rate is zero. This is true, since the cells are virtually silent over much of the directional range. These zero rates would not be influenced by poor sampling (except in unusual cases in which the cell spuriously fires when the animal is facing the “wrong” direction), since there is no local temporal variance over long intervals during which the cell does not fire. Thus, the large portion of samples that are not affected by poor sampling might lead to overall higher $sr^2$ values for the head direction cells.

Discussion

The major finding of this report is that, in addition to the directional signals originally described by Ranck (1984) and Taube et al. (1990a,b), there are also several other types of spatial/behavioral correlates for cells in the postsubiculum. These include angular velocity, running speed, and location. Each cell examined showed a significant correlation with at least one of these variables (head direction, angular velocity, running speed, and place), and most showed some combination of these influences.

One new type of cell, here named angular velocity cells, showed a linear relationship to the angular velocity of the head, so that the firing rate increased with increasingly faster turns in one direction, and decreased as a function of turning rate in the other direction (Figs. 5, 6). This response pattern is remarkably similar to that which has been observed for primary afferents in the vestibular system, in that the cells have a resting discharge, and show increases in rate to acceleration in one direction, and decreases in rate to accelerations.
in the opposite direction (e.g., Goldberg and Fernandez, 1971). Thus, these data suggest that the postsubiculum receives information from the vestibular system about angular rotation of the head. It is not clear what anatomical projections could be responsible for this, although cells that show this same pattern of response to angular velocity have been observed in areas 17 and 18 of cat visual cortex (e.g., Vanni-Mercier and Magnin, 1982), and, in the rat, these regions have been found to send projections to the postsubiculum (Vogt and Miller, 1983). Also, cells related to angular motion have been observed in sensorimotor and posterior parietal cortices in the rat (McNaughton et al., 1994), and these areas are indirectly connected to the hippocampal formation.

The total number of angular velocity cells identified in this sample was relatively small, constituting only 7 of the total set of 71 postsubicular cells. Also, six of these cells came from just one electrode track. Thus, it appears that the angular velocity cells are quite rare, and this preliminary evidence suggests that they may be organized in a columnar arrangement (though it should be noted that there is little evidence for a columnar arrangement for the other cell types, as shown in Fig. 12). Interestingly, all six of the cells from the single electrode track preferred left turns, while the one cell from a different animal preferred right turns. This suggests that both right- and left turn-prefering cells can be found, and that this preference may also be column specific.

The discovery of angular velocity correlates in the postsubiculum has interesting theoretical implications (e.g., McNaughton et al., 1991; Blair and Sharp, 1995). As mentioned in the introductory paragraphs, it has been found that head direction cells in the postsubiculum can retain their directional preference even after removal of salient environmental orienting cues (Taube et al., 1990b). Also, head direction cells in the laterodorsal nucleus (which is closely connected anatomically with the postsubiculum) can retain a stable directional preference over a few minutes of navigation in the dark (Mizumori and Williams, 1993). Thus, there is evidence that the directional signal in the postsubiculum can be maintained even in the absence of environmental landmarks. It seems that this ability must be based on internally generated cues about angular movement of the head. Thus, as has been suggested elsewhere (e.g., McNaughton et al., 1991; Blair and Sharp, 1995), it could be the case that the accurate signaling of current momentary directional heading (as an animal navigates through space) is based on information about the last directional heading, along with information about recent angular motion of the head. Any particular combination of initial directional heading and subsequent angular velocity would generate a calculable new directional heading, and neural network architectures based on this idea have been developed (McNaughton et al., 1991). The data presented here suggest that the postsubiculum may constitute a neural network device that contains the necessary information to perform this calculation.

One caveat that must be made about these angular velocity cells is that, since most of the cells were located along just one track, it is possible that this track was actually located in an anatomical region that was different from those of the other electrodes, but that was somehow mistakenly identified as being in the postsubiculum. This seems especially possible since the postsubiculum is notoriously difficult to distinguish from the adjacent presubiculum, and, in fact, there is disagreement as to whether the pre- and postsubiculum should actually be considered to be two separate areas. Careful comparison of this track location with published photos of this region (van Groen and Wyss, 1990) make it appear that this track was, in fact, in postsubiculum; however, future examination of behavioral correlates for cells in both the pre- and postsubiculum will be necessary to further comment on this question. It should be noted, however, that this issue does not significantly affect the theoretical considerations mentioned above in relation to the calculation of directional signals from angular velocity information, since the postsubiculum receives inputs from the presubiculum (van Groen and Wyss, 1990).

In addition to the obvious angular velocity correlate observed for the angular velocity cells, many of the postsubicular cells in other categories also showed influences of angular velocity, though these were more subtle than those for the angular velocity cells. Approximately one-third of the postsubicular cells showed a significant correlation with angular velocity, and this percentage was much higher than that observed in either of the subicular or hippocampal regions.

In order to further investigate these subtle effects of angular velocity, an analysis was conducted in which firing rate as a function of head direction was examined for data samples taken during clockwise versus counterclockwise turns. This analysis revealed that some cells showed differences in rate as a function of turning direction, but only over a restricted portion of the range of head directions, and this is compatible with earlier preliminary observations (Taube et al., 1990; McNaughton et al., 1991). Thus, these cells seemed to act as angular velocity detectors which operated only over a limited range of head directions. Cells of this type have been postulated as possibly playing a role in helping to generate the head direction cell signal (McNaughton et al., 1991), since any particular angular velocity/direction combination predicts the next directional heading, and thus could play a role in establishing the next appropriate firing pattern in the head direction cells.

The running speed correlates observed here were similar to those that have been reported in the hippocampus (McNaughton et al., 1983) and that were demonstrated in the present study for subicular cells (see Fig. 3). Thus, running speed information seems to be present throughout much of the hippocampal formation. It is not clear what role this signal plays in spatial information processing in the hippocampal formation. One possibility for running speed information in the hippocampus proper is that it is involved in integration of distance traveled in order to update current location, as has been discussed elsewhere (McNaughton et al., 1983). It seems less clear what role the information could play in the postsubicular circuitry. One general consideration about the set of correlates observed here is that, taken together, they constitute a complete set of information necessary for determination of future location and heading in space. Thus, the information about current location, head direction, running speed and angular velocity would, in principle, allow for exact calculation of future position in space at some exact future time. It seems conceivable, then, that the overall population activity of the postsubiculum could be used by downstream areas, such as the hippocampus, where it could help update the hippocampal place cell representations, or motor control areas, where it might play a role in guiding spatial behavior.

It is not surprising that locational correlates were observed for cells in the postsubiculum, since the postsubiculum receives a major projection from the subiculum (Sorenson and Shipley, 1979; van Groen and Wyss, 1990), which is also known to show locational firing correlates (Barnes et al., 1990; Sharp and Green, 1994; see Fig. 3). For many of the cells in the postsubiculum, this information was combined with directional information, so that, within any one location, firing rate was strongly influenced by head direction. These place by direction cells provide an interesting contrast to hippocampal place cells, which are typically not strongly influenced by head direction when recorded in this type of cylindrical
apparatus (Muller et al., 1987; see Fig. 3). It is not clear what role these place by direction cells play in the postsubiculum, although units of this type have been postulated in a neural network model of maze learning, in which place by direction units drive a set of locomotor movements that lead to the reward (Brown and Sharp, 1995). These locomotor movements are dependent on cells that signal both place and direction together, since neither piece of information alone is sufficient to specify the correct behavior. Thus, for example, if the rat is east of the goal and heading north, it should turn left to obtain the goal, while if it is in that same location and facing south, it must turn right.

Examination of the temporal firing patterns for the postsubicular cells revealed that 17% of these cells showed a rhythmic modulation of their firing probability at a frequency range between 8 to 12 Hz, and this observation is compatible with that of Taube et al. (1990a). This modulation is within the frequency range of the theta modulation observed for cells in the hippocampus (e.g., Ranck, 1973; Fox et al., 1986) and most cells in the subiculum (Barnes et al., 1990; Sharp and Green, 1994). It is interesting that such a small percentage of the postsubicular cells show this theta pattern (as opposed to the hippocampal and subicular regions, where it is ubiquitous). It is also surprising that none of the head direction cells showed this theta modulation, even though each of the other postsubicular cell categories had at least one theta modulated cell. It is interesting to speculate whether the theta modulated cells might participate in different information processing circuitry than the cells that do not show this pattern.

One aspect of the data that should be stressed is that, aside from the head direction and angular velocity cells, the remaining cells did not fall into clearly demarcated categories (though they were placed into tentative categories for the purpose of discussion). Rather, each cell in the remaining categories showed a unique, idiosyncratic combination of spatial/behavioral correlates, suggesting great diversity within this population of cells. It is possible that some of the multiple correlates could have resulted from less than perfect electrical isolation of the cells at the time of recording. Thus, even though we were taken to ensure that each "cell" used in the study showed a refractory period (which would not be possible for multiple cells), a uniform waveform for its spikes, and a large signal-to-noise ratio, it remains possible that, in some cases, the records were contaminated by signals from more than one cell. This could lead to an overestimate of the number of correlates for any one cell, and could obscure the identification of some clear categories, if they existed (as opposed to the animals' behavior (directional heading or angular velocity). Each dummy cell was made to replicate either a head direction cell or an angular velocity cell from the current set of postsubicular cells (see results section). It was seen that these dummy cells also showed low $r^2$ values (see Fig. 13). These values (as well as those for the real cells) were systematically related to the peak firing rate of the cell for head direction cells, and to both firing rate and the slope of the rate-by-angular velocity function, for the angular velocity cells.

These results, along with the high levels of statistical significance obtained for many of the $r^2$ values in this study, suggest that, in general, the cells in this study were, in fact, very strongly related to the behavioral variables identified here, but that local temporal variability in spike trains also had a strong impact on the total amount of moment-to-moment variance which could be accounted for. It might seem that one way to correct for this rate sampling problem would be simply to increase the sample time. However, there can be considerable change in the relevant behavioral variables (such as head direction and angular velocity) within each time bin as the bins are lengthened. This means that these behavioral variables might be inaccurately sampled if the sample time were increased.

In summary, the postsubicular cell population constitutes a diverse set of cells, which, as a group, show salient correlates with each of the head direction, angular velocity, running speed, and place variables examined here. Detailed analysis of the spatial correlates for these cells suggests that the postsubicular cortex, in addition to containing the head direction cells themselves, may also contain cells whose firing patterns constitute some of the building blocks used for computation of this directional signal.

Notes

I thank H. T. Blair for many helpful discussions and editorial comments, as well as computer assistance. Thanks to Catherine Green for help in manuscript preparation. This work was supported by NSF Grant 9120131 to P.E.S.

Address correspondence to Patricia E. Sharp, Department of Psychology, P.O. Box 208205 Yale Station, Yale University, New Haven, CT 06520-8205.

References


Goldberg JM, Fernandez C (1971) Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. I. Resting