
Locating ego-centers in depth for hippocampal place cells

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Abstract

A hippocampal place cell in a freely moving rat fires vigorously only when the rat's head is inside a two-dimensional region in the environment called its place field. The location and distribution of a place field is determined by a fixed light-emitting diode attached to the rat's head. If place fields are truly correlated with a "center of self" in space, then the least variable and the most compact place fields should occur when the animal's position is represented by that center instead of the diode, which is at an arbitrary location near the head. By using two diodes, the position as well as the tilt angle of the head can be estimated, which allows any point on the sagittal plane to be used to represent the animal's position. We have analyzed 25 place cells from a freely moving rat in a figure 8 maze and found that for each cell there is indeed a unique point for which the place field becomes most compact. However these points are different for different cells even when recorded simultaneously and they are scattered in an oblique and elongated region around the animal's eyes. Hence the "center of self" is not a unique geometric point. This method provides a new way to characterize a place field in a coordinate frame localized relative to the animal rather than to the environment and provides the first evidence that place cells code the location of an animal's head above the ground as well as its two-dimensional location in space.

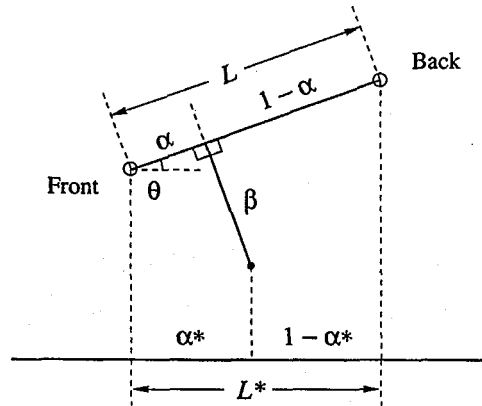


Figure 1: Rigid geometry of tilt. As seen from above, the position of any presenting point is completely determined by the positions of the front and back diodes.

1 Tilt of the head

The automatic position tracking system uses a video camera mounted on the ceiling to detect the positions of the two infrared diodes fixed on the head of a freely moving rat. As shown in Fig. 1, since the length L between the front and back diodes is known (15 cm), the tilt angle θ can be determined by the measured length L^*

$$\tan \theta = \sqrt{(L/L^*)^2 - 1}. \quad (1)$$

The roll angle cannot be determined here, and is ignored. Although there exist two possible solutions for tilt, either down or up, we only need to consider the down solution as shown in Fig. 1 because this corresponded to the natural postures for the animal in our data. This can be verified by checking how the apparent distance between the two diodes varied. If the posture changed from down to up, there should exist a transient moment with maximum distance, which never occurred in our data segment. Moreover, observation of the animals' behavior during such tasks indicates that they rarely, if ever, assume a nose-up posture.

An arbitrary point in the sagittal plane can be specified by two dimensionless variables α and β so that the unit length corresponds to L (Fig. 1). Once a representing point is chosen with given α and β , its position projected on the floor can be determined as a combination of the measured positions of the two diodes using the ratio

$$\alpha^* = \alpha + \beta \tan \theta. \quad (2)$$

Both α and β can be either positive or negative, with $\alpha < 0$ for "ahead of the front diode" and $\beta < 0$ for "below the two diodes" (see the coordinates of Fig. 4, where $X = \alpha$ and $Y = \beta$). In particular, $\alpha = 0$ and $\beta = 0$ is the front diode, and $\alpha = 1$ and $\beta = 0$ is the back diode.

2 Defining an ego-center for a place cell

A place field is constructed from a spike train recorded from a single cell by projecting the instantaneous position of a point near the head of the rat on the floor for each spike. This distribution is called a place field, which represents how the firing probability of that cell varies in space. As shown in Fig. 2, the place field distribution depends on the choice of the representing point.

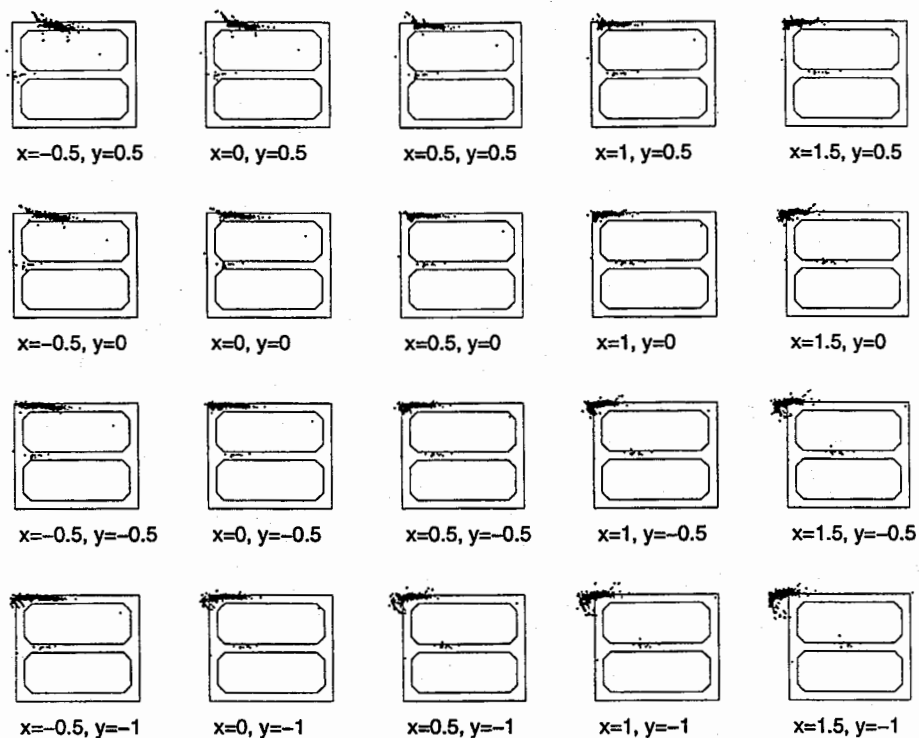


Figure 2: For a given cell, the location and compactness of its place field depends crucially on which point is used to represent the animal's position. This cell is cell 19 in Fig. 3, and the X-Y coordinates are identical to those in Fig. 4. The data were collected while a rat run continuously for 16 min on the elevated track of the figure-8 maze.

The basic idea of this paper is as follows. First, the majority principal neurons in the rodent hippocampus carry information related to the animal's current position in space. A natural question to ask is which point should be used to represent the current position of the animal. For example, one may choose either the front or the back diode, but this choice appears arbitrary.

Imagine that there is a place cell that represents the center of the animal's eyes. If a "wrong" point, say, the back diode, is chosen as the representing point, the resultant place field should become more blurred or more variable than the real one. This is because even when the eyes remain at the same spatial location, the animal may be looking at different directions or tilting its head with different angles, which leads to highly variable position of the back diode. If this scenario is true, then from existing data we can systematically vary the representing points and find the location that yields the most compact or the least variable place field.

We used both variance and entropy measures on the place field distribution to quantify the compactness of a place field. The results were similar although not identical. The spatial grids for place field had 256×256 pixels (111×111 cm), with the distribution slightly blurred by convolving with a Gaussian with a standard deviation of 1.5 pixels. No additional smoothing was used anywhere. All results shown in this paper were obtained using the variance of the spike distribution across

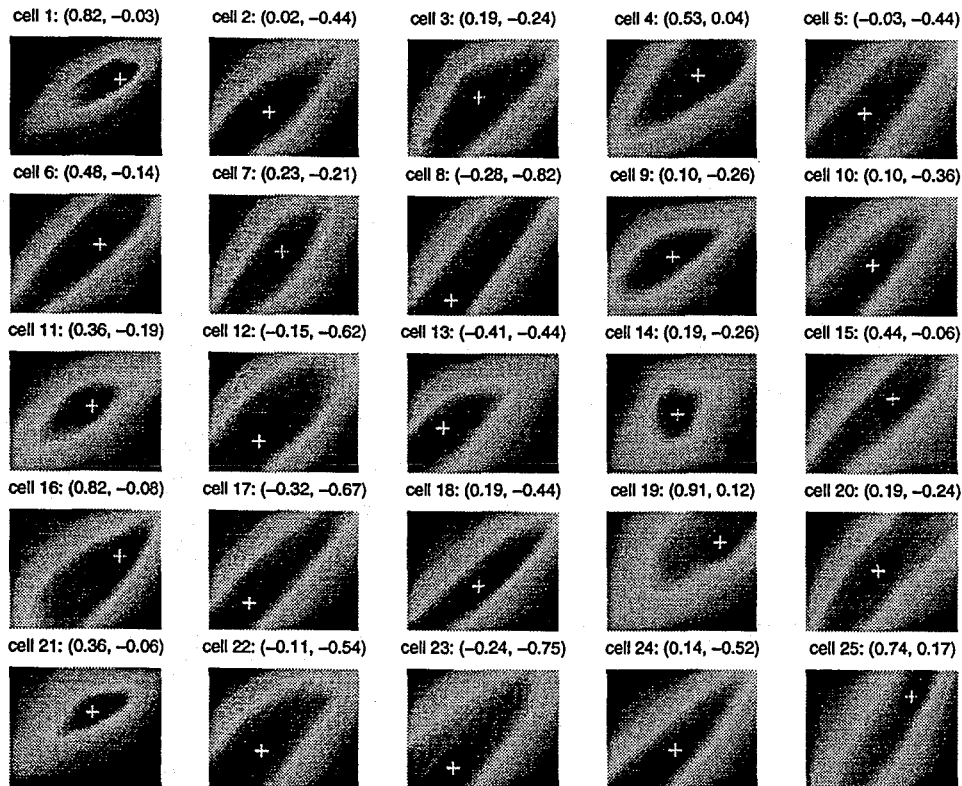


Figure 3: Compactness of the place fields of 25 simultaneously recorded cells for systematic shifts of representing point. The light cross in each panel indicates the representing point (ego-center) that yields the most compact place field. The parameter region is identical to that in Fig 4 (from -1 to 1.5 for X , and from -1 to 0.5 for Y).

all pixels.

3 Results

As shown in Fig. 3, each cell indeed had a representing point that yielded most compact place field. We call this point the ego-center for the place cell. The existence of such a center without local minima confirms the assumption that each cell has a preferred ego-center as well as a place field.

For simultaneously recorded cells, the ego-centers do not coincide but are scattered around an elongated region (Fig. 4). Thus the activity of the place cells cannot all represent the location of the same geometric point, or a single point for "center of self". This raises the possibility that the neural representation of self location might be somehow distributed in a region of space around the animal's head.

The elongated scattering of ego-centers appeared to be a robust feature, although factors such as the exact choice of smoothing, measure of compactness, or data segment could cause some errors in locating the ego-center of an individual cell.

We have also tested how time-shift may affect the compactness of place fields, in

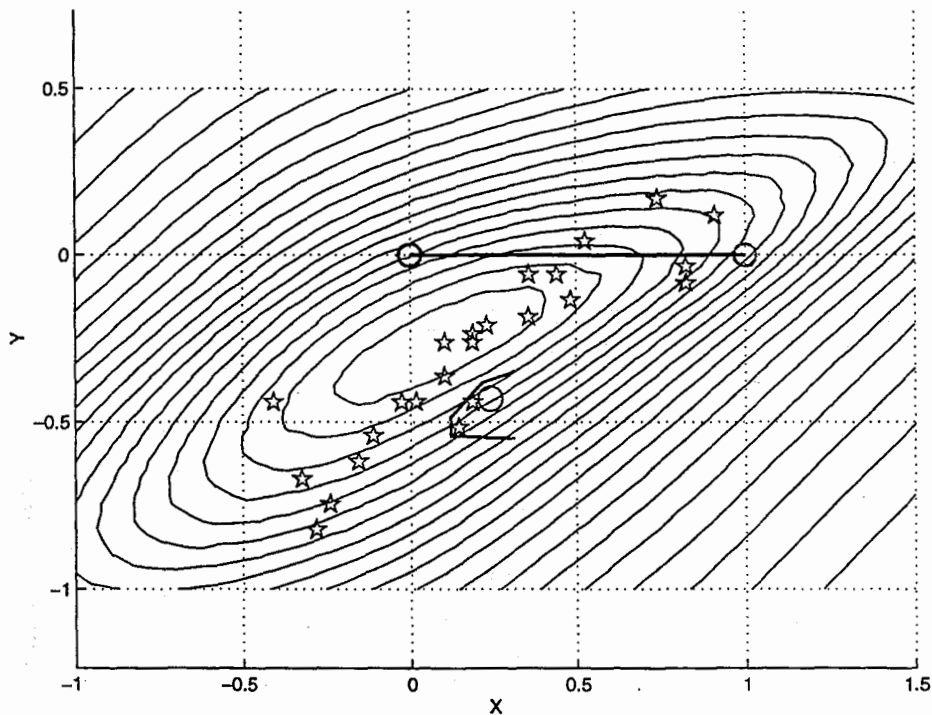


Figure 4: Ego-centers (stars) of the 25 cells as in Fig. 3 in the sagittal plane. The contours indicate the variance distribution averaged over all cells. The coordinates of the front and back diodes are $(0, 0)$ and $(0, 1)$, respectively, with the unit length corresponding to ~ 15 cm. The schematic profile of the rat's head is a rough estimate. All of the ego-centers are clustered along an elongated region surrounding the head of the rat.

addition to the choice of representing point. Our preliminary study did not reveal a clear pattern.

4 Reconstruction of position vs. tilt

Do place cell activity also carry information about the tilt of the head? Using the same 2-step Bayesian method discussed in Zhang, Ginzburg, McNaughton & Sejnowski (1998), we reconstructed the position of both the front and the back diodes separately, based on the spikes of 25 cells collected in a sliding time window of 1 sec. Since the information about the tilt is completely determined by the apparent distance between the two diodes as seen from above, we only need to estimate how well this distance can be reconstructed. In the preliminary result shown in Fig. 5, the tilt reconstruction was much less precise than the high accuracy of position reconstruction. In the reconstruction, different cells were assumed to be independent. It is possible that tilt information might be contained in correlation of cells. Further work is needed to explore this possibility, compensate for behavioral bias, and to quantify the amount of information contained in the population.

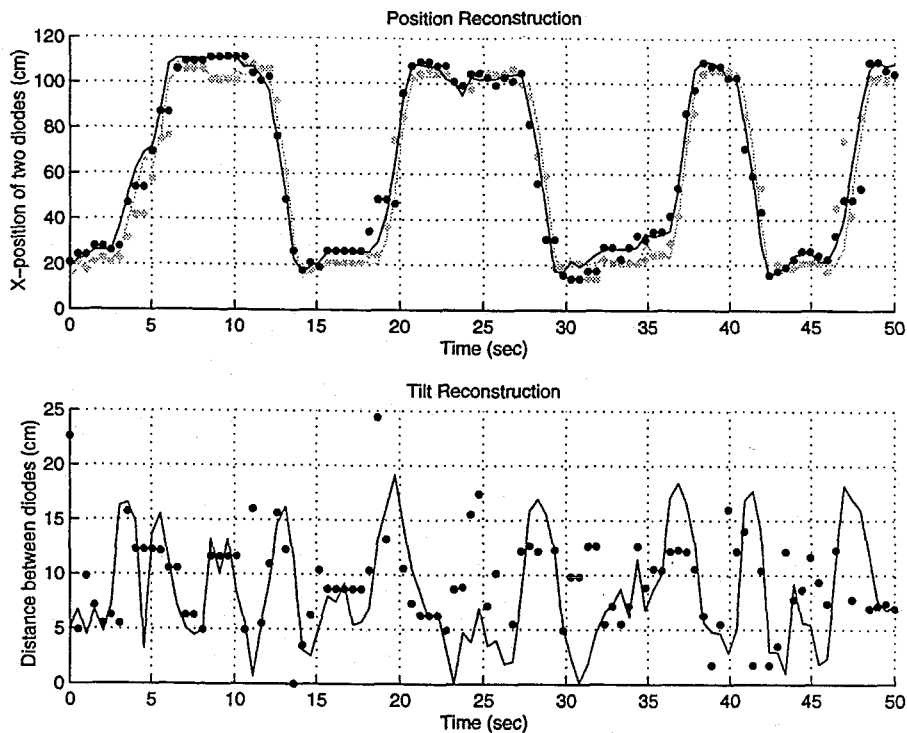


Figure 5: The floor positions of the two diodes can be reconstructed very accurately from the instantaneous firing rate of 25 place cells (upper panel: dark plot—front diode; light plot—back diode). The reconstruction of the distance between the two diodes, which determined the tilt of the head, was less precise but still correlated ($r = 0.36$, in contrast to $r = 0.98$ for position reconstruction). In all cases, curves are true values, and dots are reconstructed values.

5 Discussion

We have defined the three-dimensional point that yields the most compact place field as the ego-center of the place cell. This provides a new egocentric (centered to self) measure of a place cell in addition to the allocentric (centered to environment) measure of a place field (O'Keefe & Dostrovsky, 1971; Wilson & McNaughton, 1993). Muller & Kubie (1989) first reported an effect of time-shift on the compactness of place fields. In that study only a single diode was used so that time-shift was confounded with where the diode was attached to the head. Skaggs, McNaughton, Wilson & Barnes (1996) studied the case with two diodes with their linear combination as the representing point. This paper is the first report of locating an ego-center in depth, using nonlinear combination of two diodes and taking account of the tilt angle and rigid geometry.

At least three diodes are required in order to locate an ego-center in three-dimensional space. The current results apply only to the two-dimensional sagittal plane so that possible variability related to roll angle has been effectively averaged out. Additional refinement by correcting geometric distortion for position tracking and increasing video speed should lead to more accurate results. Since the definition of ego-centers is quite general, it may provide useful information in other

experimental settings for the neural representation of space.

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