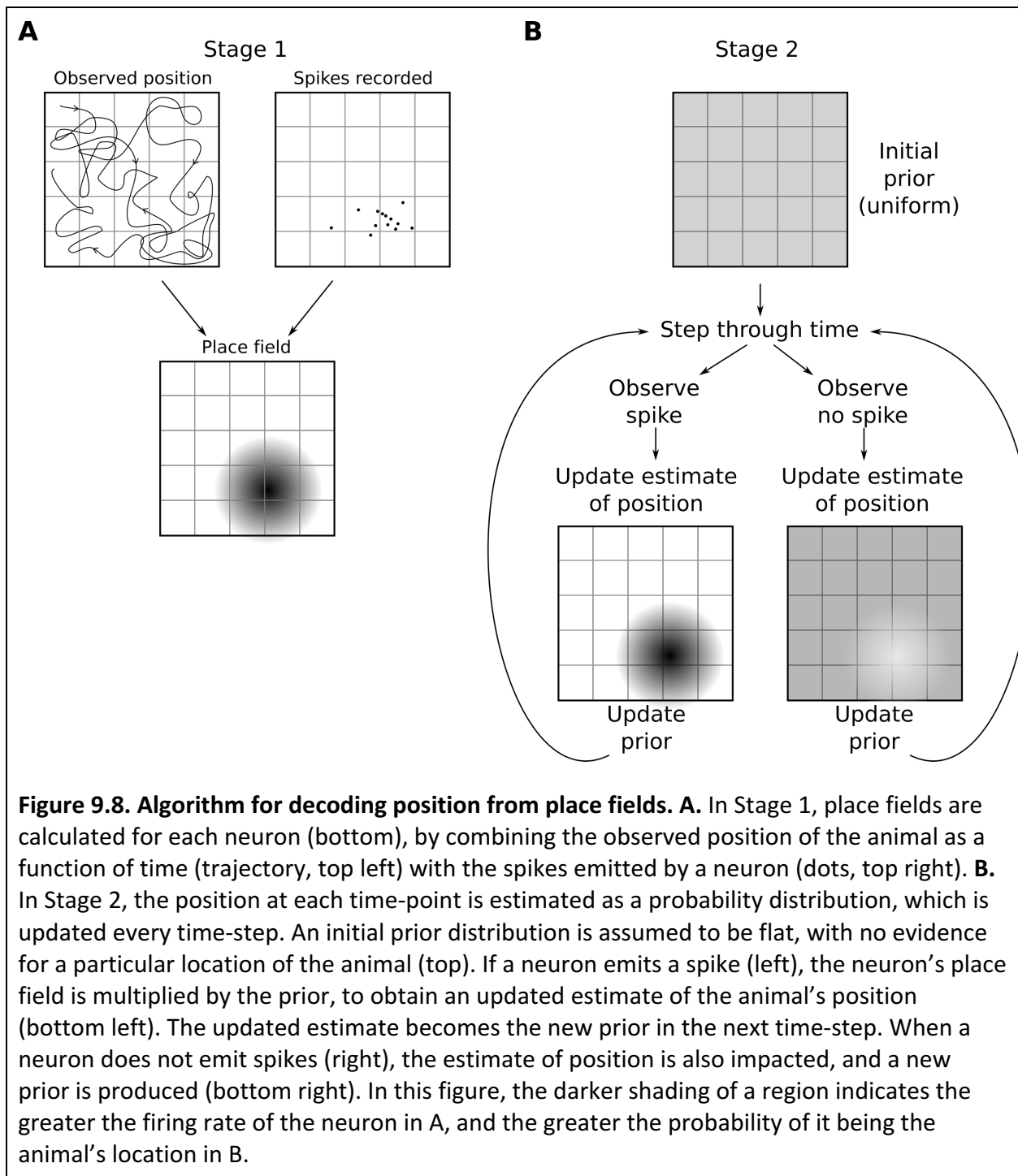


## 9.7. Decoding position from multiple place fields



Neurons in the hippocampus have firing rates that depend on the spatial location of an animal. Within a particular environment, the place fields—meaning the set of locations at which a neuron fires—are reliable for periods ranging from a few hours or days, possibly up to several weeks<sup>26</sup>, and are compact, peaking at a particular location in space and

decreasing monotonically with distance away from the peak. Cells with such responses are called place cells.

In this section, we will consider how information from the spike trains of multiple place cells can be combined to provide an estimate of an animal's position that is more precise than one might expect given the number of neurons and size of their place fields. The method requires the multiplication together of probability distributions, where each information source can provide one such distribution. For a review of combining probabilities, see Section 1.4.3. Two main principles are required in these methods:

- 1) When combining information from multiple sources, the probability of an occurrence is calculated by multiplying together the contributions from the separate information sources.
- 2) The sum of probabilities over all possible occurrences yields one. When decoding an animal's position, an occurrence means the animal being at a particular location, so the probability distribution means the probability of the animal being at any point in space. This second principle means that the sum over all locations of the probability distribution is one—that is, the animal cannot be in two places at once and it must be somewhere.

An important aspect of the approach used here is the incorporation of the most recent estimate of an animal's position as a probability distribution in the calculation of the estimate of its position at the next time-point. Specifically, the latest estimate of position produces the prior probability at each location for the next estimate, as shown in Figure 9.8B. The prior probabilities need not be identical to the previous position estimate, because the rat is known to move and its typical movements—how much it shifts position between time-points—can be taken into account in the update (see below). Therefore, three distinct sources of information are combined together to update the estimate of the animal's position:

- 1) The probability distribution produced for the previous estimate of position.
- 2) A model of the animal's typical movements to update the previous estimate of position into a prior for the next estimate of position.
- 3) A probability distribution for each cell, proportional to the place field of each cell that spikes, or with a dip at the place field of each cell that does not spike. These probability distributions are multiplied together with the prior to produce a new position estimate.

These methods, called Bayesian filtering<sup>35</sup>, were developed by Emery Brown, Uri Eden, and colleagues<sup>36,37</sup> and are similar to a method called Kalman filtering (see, *e. g.*,<sup>38</sup> for an example and see<sup>39</sup> for an introduction).

When decoding position from neural activity in this manner, two stages are required (Figure 9.8):

**Stage 1:** The position must be observed while spikes from each cell are counted. The firing rate of a cell in each position can then be calculated as the number of spikes produced while in a position divided by the total time spent in that position. For such a calculation, one can split the continuous environment into a square grid. The resulting set of spike counts will be quite noisy, so a smooth function should then be fit to the data. The most common function is a two-dimensional Gaussian, which has a maximum at a particular

location and a spread whose standard deviation can vary as a function of direction to define an ellipse, whose long axis can have any direction. For the code used to produce Figure 9.9, we just assume circular two-dimensional Gaussians, such that the standard deviation is the same in all directions. These two-dimensional Gaussians define the place-fields of each neuron.

Stage 2: The estimated place-fields are used to decode the position of the animal using the subsequent spike trains. The firing rates can be converted to a probability of a spike in a small time-bin. These probabilities can be subtracted from one to obtain the probability of no spike in a small time-bin. Bayes' theorem must then be used to obtain the probability of the animal being in a particular location given a spike (or no spike) in a time-bin using the probability of a spike (or no spike) when in that location calculated in Stage 1. For example,

$$P(\text{position}|\text{spike}) = \frac{P(\text{position})}{P(\text{spike})} P(\text{spike}|\text{position}) \quad \text{Eq. 9.1}$$

where

$$P(\text{spike}) = \sum_{\text{all positions}} P(\text{spike}|\text{position}). \quad \text{Eq. 9.2}$$

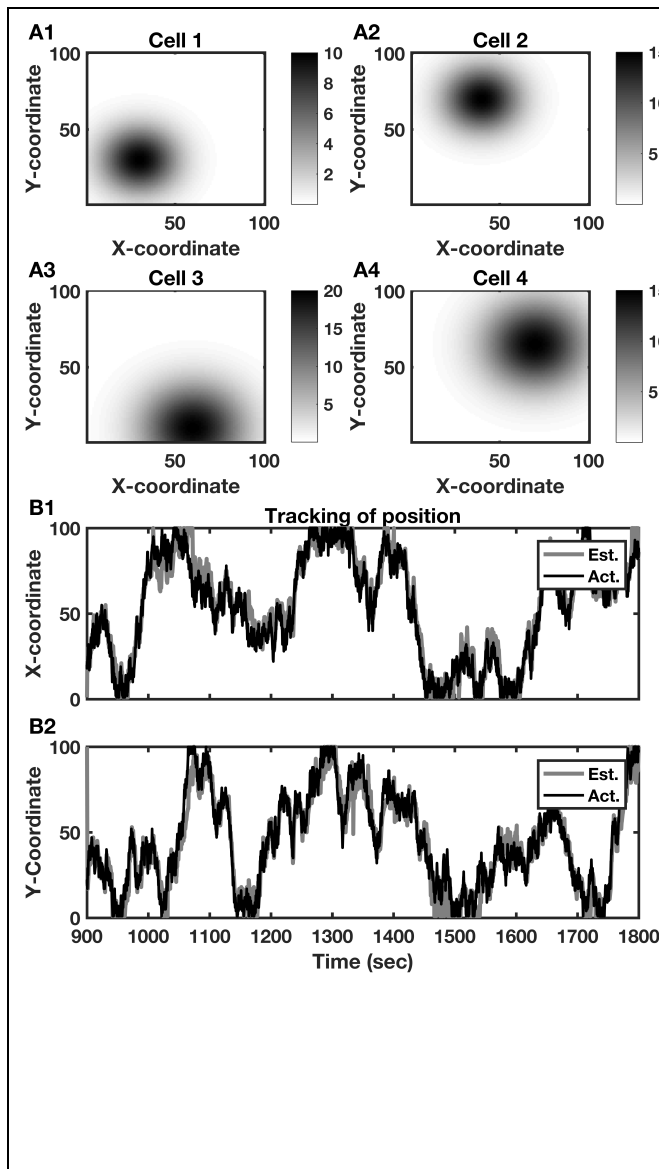
Use of Bayes' theorem (Eq. 9.4) for each neuron's place-field is then akin to normalization, so that each probability distribution for location given a spike (or no spike) from a cell sums to one.

The procedure then is to step through time. First, take the previous probability distribution for the animal's location. Alter that distribution as necessary to indicate how the animal could change its location from one time-bin to the next, to produce a prior. Then, for each neuron, successively multiply the prior either by its probability distribution for location given a spike (when it spikes, Figure 9.8B bottom left) or by its probability distribution for location given no spike (when it does not spike, Figure 9.8B bottom right). Finally normalize the resultant distribution so that it sums to one.

The whole procedure can be called Bayesian filtering, because the method of combining the prior probability distribution with the incoming information is an implementation of Bayes' rule. That is, we can expand Eq. 9.4 for the whole process and write it as Bayes' theorem:

$$P(\text{position}|\text{set of spikes}) = \frac{P(\text{position})P(\text{set of spikes}|\text{position})}{P(\text{set of spikes})}. \quad \text{Eq. 9.3}$$

In Eq. 9.6, the term  $P(\text{position})$  is the prior, based on the probability of a position at the previous time-point and on the model of the animal's movement. The terms  $P(\text{set of spikes}|\text{position})$  and  $P(\text{set of spikes})$  are both produced by multiplying together the corresponding probabilities for each neuron.



**Figure 9.9. Decoding of position using the spikes produced by place-cells. A1-A4.** Circular place fields of simulated cells with the neurons' firing rates peaked at a particular location (higher firing rate is indicated by the darker shading—see color bars). **B1-B2.** An adaptive decoder allows spikes from the four cells represented in A) to update *estimates* of the position (gray curves, Est.), tracking the *actual* position (black curves, Act.) with a high degree of accuracy. Indeed, the error between estimates and actual position is generally a lot lower than the standard deviations of the mostly non-overlapping place fields shown in A. **B1.** Estimate and actual value of the x-coordinate as a function of time. **B2.** Estimate and actual value of the y-coordinate as a function of time. The second half of a trial was used for decoding (Figure 9.8B), while the first half was used for estimation of the place fields (Figure 9.8A). This figure was produced by the online code `place_decoding.m`. If you run the code, you will see the two-dimensional probability distribution for the estimate of position evolve over time.

In the online code (`place_decoding.m`) used to produce Figure 9.9, we simulated a random walk for the animal's movement in Stage 1. We can then use the random-walk assumption in the model needed to update the prior on the animal's position across time-steps. For example, if we knew the animal's location precisely at a previous time-point, then, without any information from neural activity, we would expect the animal to be within a small distance of that prior position, with equal likelihood in any direction. Therefore, without information from spikes, the estimate of position gets less certain—the peak of high probability spreads out—as time goes on. In Stage 2 of the code, therefore, with possible positions given as grid-squares, we take the probability distribution of the previous time-point and allocate a fraction of the probability on each grid-square equally to neighboring grid-squares. In this manner, we update the position estimate in terms of the animal's movement.

Alternatively, in a more sophisticated method, one could select specific directions based on the prior movement of the animal and the observed tendency to keep going in the same

direction. In general, any observed regularity in motion can be incorporated by modifying the update from the previous probability distribution when producing the prior. Similarly, any preference for certain positions in the environment can be incorporated by multiplying by an additional prior proportional to the relative preferences for each position. In general, any prior information can be translated into a probability distribution, which multiplies any current estimate of position. By incorporating more information, such priors tighten the estimate of position, but they could lead to errors, in particular if a probability of zero is given to any location. For example, one might be tempted to provide a probability of zero to any location where the animal has not been observed, but this would be an error—just because the animal has not done something in the past does not make it impossible in the future, yet a probability of zero implies impossibility.