Attention-like modulation of hippocampus place cell discharge: Supplemental Material
Supplemental Figure 1. Firing rate maps from a 53-cell ensemble. The standard (raw) firing rate map is depicted along with the state-specific firing rate maps and the shuffled state maps for each cell. The color-code is the same for each set of 5 maps. The median value of the firing rate in the peak red category is given below each map. The correlation between each shuffled or state-specific pair of maps is given above the corresponding pair of maps. The maps are sorted in ascending order of the state-specific correlation. Seven of these cells were shown in Figure 6 of the main text.

Supplemental Discussion
Relation to Prior Work on overdispersion

Published work characterized place cell overdispersion but did not lead to the conclusion that there is an attention-like modulation of place cell discharge. The overdispersion was first described at the level of single cells in rats foraging for randomly scattered food (Fenton and Muller, 1998). Analyses were restricted to passes through the center of firing fields. The statistics of overdispersion during foraging in a cylinder were corroborated in two subsequent papers (Olypher et al., 2002; Jackson and Redish, 2007), as well as the current study (Fig. 2B1). In the present study, a virtually identical level of overdispersion ($\sigma^2 \sim 5$) was computed for passes across firing fields that did not require the rat to cross the field center.

Both Olypher et al., (2002) and Jackson and Redish (2007) extended the initial finding by demonstrating overdispersion was reduced by taking into account goal-directed spatial behavior. Olypher et al. (2002) examined overdispersion in two groups of rats foraging for scattered food. Overdispersion was reduced in the group that had previously been trained to do a navigation task and was reduced even more when the rat was going to a goal. However, because navigation and attention were confounded, it was not possible to conclude that the reduced overdispersion was related to attention, even though in this case the rats with reduced overdispersion had received training that was identical to the navigate/variable group of the present study. Using essentially the same navigation task, Johnson and Redish (2007) also showed that goal-directed spatial behavior reduced overdispersion, but the confound of navigation and attention was not circumvented. Instead of attention, a parsimonious alternative account for the reduction in overdispersion reported was prior navigation training or navigation itself.

The present study is the first that attempted to disambiguate the contributions of navigation and attention to overdispersion. The navigate/stable and navigate/variable groups performed essentially identical navigation tasks but the attentional demands differed in the two groups. Overdispersion was compared while both groups did the same navigation task on a stationary arena. The arena was always stationary for the navigate/stable group but the arena would sometimes rotate for the navigate/variable group to condition them to preferentially use extra-arena, non-rotating cues for finding the navigation goal. Overdispersion was reduced in both groups compared to their respective control groups (forage/stable and forage/variable). The control rats had been exposed to the identical physical conditions and foraging behavior as the corresponding navigation-trained group, but they had not been trained to navigate to a goal. In addition to the influence of navigation, an additional influence of attention was revealed as a further reduction in overdispersion in the navigate/variable group compared to the navigate/stable group. Although the current study is not the first to investigate the influence of behavior on overdispersion, it is the first that attempted to distinguish the influence of navigation and attention on overdispersion.

Jackson and Redish (2007) extended the characterization of overdispersion to the level of the place cell population. They found a strong covariance of discharge variability in subpopulations of place cells, consistent with switching between two place cell ensemble states. While these states resemble what might be expected if two place cell subpopulations were modulated into distinct attention-related states, the relevance of this map-switching to current place information and attention was uncertain. The present work replicated the map-switching finding of Johnson and Redish (2007) and extended it by...
analysis of the place information that could be decoded from the state-organized ensemble discharge. This investigation demonstrated that each ensemble state corresponds to a more accurate representation of the rat’s location than can be obtained by ignoring the current state. This analysis provides the first direct evidence that each ensemble state contributing to overdispersion may have cognitive importance, as each state corresponds to enhanced information in the place code about current location. Thus, rather than being a nuisance source of noise, overdispersion appears instead to represent a refinement of the hippocampal place code that is momentarily active, consistent with the function of attention to enhance processing of relevant information by suppressing processing of what is currently irrelevant.

Supplemental References

Fenton AA, Muller RU (1998) Place cell discharge is extremely variable during individual passes of the rat through the firing field. Proc Natl Acad Sci U S A 95:3182-3187.