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Supplemental Notes

1. Supplementary Results

Object-vector cells have stable firing fields
Spatial tuning of object-vector cells was stable within individual trials, when the object was in the same position (odd-versus-even-minutes firing-rate map correlation: 0.76 ± 0.008, mean ± s.e.m).

Vector fields are similar for a wide span of objects
Mice were tested with 2-6 objects that were presented simultaneously in the recording box (Extended Fig. 2a,b). Similar vector fields emerged for each object. We measured the similarity of responses to simultaneously presented objects by first constructing vector maps around each object. Then we found the two fields in each pair of maps that had the nearest centre-to-centre distance and measured the difference in distance and orientation defined by the centres of these fields (Fig. 2b). As an alternative way of measuring the differences in the responses to different objects, we used as reference the vector field in the set of vector maps that expressed the median orientation and distance from the object. We then measured the differences between this reference and the most similar fields in the other vector maps. The differences were expressed as proportions of the maximum possible rotational offset (180 degrees) and a distance of 1 m. For orientation, we found a mean difference from this reference of 2.4 $\pm$ 0.25% across all object-cell pairs, and for distance we found a difference of 2.5 ± 0.3% (means ± s.e.m.). Taken together, the two sets of analyses suggest that object-vector cells fire at similar direction and distance from any object.

Object-vector cells maintain firing fields with different object shapes
We showed that object-vector cells retain their firing fields when discrete point-like objects are extended in a stepwise manner to become elongated rectangles or walls (Fig. 3a). In these experiments, peak and mean firing rates did not change across trials with different object lengths (Kruskal-Wallis test, peak firing rate: H = 2.1, P = 0.55; mean firing rate: H = 1.69, P = 0.64). Similarly, when object-vector cells were tested in the presence of a cylinder of increasing width, neither peak or mean firing rates nor field sizes changed significantly with object diameter (Kruskal-Wallis test, peak firing rates: H = 4.3, P = 0.23; mean firing rates: H = 1.99, P = 0.74; field size: H = 6.7, P = 0.15). Finally, when we changed the height of the object, mean firing rates were not significantly different across conditions, nor were peak firing rates or field sizes of object-vector fields (Kruskal-Wallis test, mean firing rate: H = 4.4, P = 0.22; peak firing rate: H = 6.0, P = 0.11; field size: H = 4.0, P = 0.26).

Object-vector cells are distinct from other functional cell types
Object-vector cells were distinct from grid cells and border cells as the vast majority of them lacked grid and border fields on trials with no objects (Extended Data Figure 4a,b). They could also be distinguished from head direction cells and speed cells, although a minor subset of the object-vector cells displayed conjunctive head-direction tuning (Extended Data Fig. 4b-d). Object-vector cells with two or more firing fields were not grid cells as they consistently had grid scores below

chance levels and no firing was observed in regions defined by a hexagonal matrix extrapolated from the two or three identified fields (Extended Data Fig. 4b,e,f).

Grid cells and head-direction cells maintained stable orientations across object and no-object trials (Extended Data Fig. 8a,b; spatial correlation of grid cells between object and no-object trials: 0.68 $\pm$ 0.02, mean $\pm$ s.e.m.; correlation of head-direction tuning curves for head-direction cells between object and no-object trials: 0.83 $\pm$ 0.02).

Object-vector cells are not boundary-vector cells

Object-vector cells in MEC can be distinguished from the boundary-vector cells of the subiculum. Subicular boundary-vector cells have been reported to fire at specific distances from specifically oriented boundaries of the environment[16,17,34,35], suggesting that these cells encode vectors with reference to the boundaries of the environment rather than merely the location of the boundaries. Visual inspection of hundreds of rate maps has suggested boundary-vector cells are not common in MEC[6,36,37], but these comparisons have lacked quantitative criteria for identifying cells with displaced firing fields that run in parallel to the boundaries of the environment. In the present study, we formalized qualitative criteria of previous studies[16,17,34] by defining boundary-vector cells as cells that have firing fields with a long axis corresponding to at least 70% of the length of one of the walls of the environment, in an orientation parallel to this wall (deviation of less than 10 degrees from the wall axis), at any distance away from the wall. We limited the quantification to recordings from square enclosures as boundary-vector fields are more poorly defined for circular environments. Twenty out of 860 recorded cells passed the criterion for boundary-vector cells (Extended Data Fig. 8c). Among these, 14 also passed the criteria for border cells, leaving only 6 cells with firing fields sufficiently wide or displaced from the walls to evade the criteria for border cells. Among these 6, only 1 had a field that did not at all impinge on the wall (Extended Data Fig. 8c; mean distance from wall to centre of field $\pm$ s.e.m.: 8.2 cm $\pm$ 0.7). The distance distribution of boundary-vector cells was thus clearly skewed towards low values compared to the distribution for object-vector cells (Extended Data Fig. 8d).

Object-vector fields in the absence of visual input

The fact that standing and suspended objects generated object-vector fields with equal efficiency (Fig. 4c,d) points to visual input as one likely source of location-specific firing in object-vector cells. We tested this further by comparing rate maps of object-vector cells in the presence of an object before and after the room lights were turned off while the animal was in the box (21 object-vector cells from 5 mice). Correlations between vector maps on light and dark trials were significantly decreased compared to correlations for pairs of light trials in the same cells (Extended Data Fig. 7d,e; Wilcoxon signed rank test, W = 207, n = 21, P = 0.0015). Spatial information and spatial coherence were also reduced (Extended Data Fig. 7f; spatial information content: Wilcoxon signed rank test: W = 227, n = 21, P = 1.1×10^{-4}, spatial coherence: W = 231, n = 21, P = 6.0×10^{-5}), although they remained above chance levels, possibly reflecting the continued use of path integration in darkness.

Object-vector fields can be elongated rather than circular

We modelled object-vector fields as a function of Euclidian distance from the preferred vector (see Methods). Firing rate functions corresponding to either a Gaussian circle or an ellipse were fitted to the unsmoothed firing rate maps. As expected when parameters are added, most of the cells showed a slightly better fit to the elliptic model (Extended Data Fig.3a,b); however, in most cases, the fit was only moderately improved using the elliptic model instead of the circular (median improvement of elliptic model: 0.7%, 25-75th percentiles: 0.3 – 1.8%). The median aspect ratio of the best fit across all cells was 1.6 (1.0 would correspond to a perfect circle), suggesting that object-vector fields can be quite well described by a Gaussian model in many instances, but yet tend to be modestly elongated on average.

2. Supplementary Discussion

Our experiments identify a new category of MEC neurons – object-vector cells – characterized by allocentric firing fields with specific distances and directions from salient landmarks. Object-vector cells may underlie animals' ability to use vectors from objects, in an allocentric framework, to guide their local navigation[8-10,38]. These cells may account for the tendency of some non-grid MEC neurons to respond at fixed distances from repeating landmarks in a linear virtual environment[39], and may provide the input to cells with similar properties in CA1[40].

Three types of vector coding have been reported in the hippocampal system previously. First, in the LEC, a class of cells represent egocentric bearing to nearby items[25], and in CA1 of the hippocampus, 'goal-vector cells' are tuned to the animal's egocentric direction towards a goal[24]. The present object-vector cells differ from these cells in that the object-vector cells represent the animal's allocentric direction and distance from the object, i.e. their firing fields are fixed in room coordinates, independently of the animal's body orientation. Their firing preferences are maintained even when the animal is facing away from the object, suggesting that some of the positional code is retained as memory.

A second group of cells, with allocentric vector coding, has been reported in a study of CA1 cells in which place cells were found to intermix with a sparse population of cells that fired at specific distances and directions from a subset of objects placed in the recording compartment[15]. Earlier work has similarly shown that some cells in this region have firing fields that follow the location of a landmark array when the array is moved in a test arena[41], or fire at some distance away from wall inserts in the compartment[42]. CA1 cells have also been shown to fire at fixed distances from salient landmarks during virtual navigation on a linear track[40]. While allocentric vectorial relationships, with both distance and direction tuning, were either not investigated or not quantified in these studies, the cells do seem to have properties in common with the object-vector cells of the MEC. But there may also be important differences, over and above the mere abundance of vector-coding cells in MEC. Object-vector cells in MEC developed fields unconditionally at every single object the mouse encountered, in contrast to their hippocampal counterparts, which often responded only to a subset of the objects[15]. Moreover, while object-vector cells in MEC emerged instantly during foraging in the box, not requiring any extended experience with the environment or the object, the firing fields

of the hippocampal cells often developed over multiple trials[15]. The apparent slow emergence of object-vector representations in the hippocampal population points to instantly-appearing object-vector representations in MEC as a possible source for training hippocampal cells secondarily to form vectors between often-visited goals and stable landmarks for subsequent storage in memory. Such a training process would be reminiscent of how odour-selective cells in the LEC can, over many trials, entrain odour-selective cells in the CA1[43].

The third type of vector coding previously proposed for the hippocampal system is mediated by boundary-vector cells. In early theoretical models of spatial coding[13,14,34], boundary-vector cells were suggested to fire at specific distances and directions from boundaries in the local environment such as the peripheral walls of the recording box. Cells with such properties have since been reported in the subiculum[17,35] but the majority of these cells fire preferentially along the boundaries of the environment and only rarely at long distances away from the boundaries, out in open arena space. Using quantitative criteria (Extended Data Fig. 8c,d), the present study confirms previous qualitative reports[6,36,37] suggesting a near absence in MEC of cells with elongated firing fields at specific distances from lengthy background boundaries such as the peripheral walls of the compartment. Our study shows instead that the MEC has a high density of object-vector cells, which define positions anywhere in the local space based on vectors to point locations from discrete free-standing objects in the arena space. Such objects may take on a variety of shapes and may include extended surfaces such as wall inserts. By varying systematically the geometry of objects in the arena space, we found that point-like objects and free-standing lengthy boundaries have similar effects on activity of object-vector cells, with boundary inserts forming a subset of objects within a larger space of widths, lengths, heights, shapes, and identities. However, in experiments with extended wall inserts, object-vector cells often developed multiple point-like fields, often anchored to the ends of the wall insert, rather than extended fields parallel to the boundary, much like place fields in the hippocampus split up in similar parametric experiments[13]. This might suggest that object vectors are not generally referenced to the entire wall but rather to points of contrast on the wall, such as its edges and corners. When points of contrast are present on the background walls, such as when an object is attached to it (Fig. 4c; Extended Data Fig. 10a), object-vector responses may be evoked from points on the external walls too. The breadth of object features and object geometries that can evoke vectorial responses, and their bias towards point-like objects, may enable MEC networks to perform positional vector calculations at high accuracy across a wide variety of naturalistic environments where extended environmentally bounding surfaces comprise only minor components of the environment's structure.

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