

1 **Egocentric boundary vector tuning of the retrosplenial cortex**

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3 Andrew S. Alexander, Lucas C. Carstensen, James R. Hinman, Florian Raudies, G. William  
4 Chapman, Michael E. Hasselmo

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6 Boston University, Center for Systems Neuroscience, Department of Psychological and Brain  
7 Sciences, Graduate Program in Neuroscience, 610 Commonwealth Ave. Boston, MA, 022215

8 Correspondence to: Andrew S. Alexander ([asalexan@bu.edu](mailto:asalexan@bu.edu)) and Michael E. Hasselmo  
9 ([hasselmo@bu.edu](mailto:hasselmo@bu.edu))

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31 **Abstract**

32 The retrosplenial cortex is reciprocally connected with a majority of structures implicated in  
33 spatial cognition and damage to the region itself produces numerous spatial impairments.  
34 However, in many ways the retrosplenial cortex remains understudied. Here, we sought to  
35 characterize spatial correlates of neurons within the region during free exploration in two-  
36 dimensional environments. We report that a large percentage of retrosplenial cortex neurons  
37 have spatial receptive fields that are active when environmental boundaries are positioned at a  
38 specific orientation and distance relative to the animal itself. We demonstrate that this vector-  
39 based location signal is encoded in egocentric coordinates, localized to the dysgranular  
40 retrosplenial sub-region, independent of self-motion, and context invariant. Further, we identify a  
41 sub-population of neurons with this response property that are synchronized with the  
42 hippocampal theta oscillation. Accordingly, the current work identifies a robust egocentric spatial  
43 code in retrosplenial cortex that can facilitate spatial coordinate system transformations and  
44 support the anchoring, generation, and utilization of allocentric representations.

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## 62 **Introduction**

63 Spatial cognition is a critical component of intelligent behavior. The ability to effectively recall  
64 and navigate between known goals relies on stored representations of spatial interrelationships.  
65 Further, episodic experiences can be thought of as situated within a stored mental map  
66 indicating the places in which events occurred (Tulving, 1972). Spatial representations that  
67 support both navigation and episodic memory are observed in many brain regions, including the  
68 hippocampus (HPC) and medial entorhinal cortex (mEC), where neurons exhibit receptive fields  
69 that are correlated with the position or orientation of the animal relative to the array of locations  
70 and cues that define the structure of the outside world. This viewpoint-invariant coordinate  
71 system is commonly referred to as the allocentric reference frame (O'Keefe and Dostrovsky,  
72 1971; Taube et al., 1990ab; Hafting et al., 2005).

73 Although it has been repeatedly shown that intact function of allocentric spatial circuits is critical  
74 for spatial memory and navigation (Morris et al., 1982; Taube et al., 1992; Steffenach et al.,  
75 2005), it is important to consider that all spatial information enters the brain via sensory organs  
76 and their corresponding processing streams. Accordingly, knowledge of the position of a  
77 prominent landmark and a neighboring goal location would be, at least initially, incorporated into  
78 a stored spatial map in egocentric coordinates relative to the animal itself (Andersen et al.,  
79 1983; Andersen et al., 1993; Andersen, 1997; McNamara and Rump, 2003; Burgess, 2006;  
80 Byrne et al., 2007; Bicanski and Burgess, 2018). Further, enacting navigational plans can be  
81 based upon stored allocentric representations but would ultimately require translation into  
82 sequences of actions anchored in an egocentric reference frame (e.g. one turns clockwise  
83 relative to their own previous orientation position; Byrne et al., 2007; Whitlock et al., 2008;  
84 Bicanski and Burgess, 2018).

85 Neural mechanisms by which egocentric and allocentric coordinate systems are interrelated are  
86 still the subject of intense examination. Computational models have predicted that cortical  
87 networks capable of integrating allocentric and egocentric information for either constructing or  
88 utilizing stored spatial representations require neurons with egocentric sensitivity to external  
89 locations (Byrne et al., 2007; Bicanski and Burgess, 2018). Most investigations into egocentric  
90 representations in unconstrained animals have focused on the neural substrates of path-  
91 integration, a navigational computation wherein self-location is approximated via continuous  
92 integration of angular and linear displacement (Mittelstaedt and Mittelstaedt, 1980; McNaughton  
93 et al., 2006). Neural correlates of these movement variables have been reported in several

94 structures (McNaughton et al., 1994; Cho and Sharp, 2001; Whitlock et al., 2012; Kropff et al.,  
95 2015; Alexander and Nitz, 2015; Hinman et al., 2016; Wilber et al., 2017).

96 Only recently have externally-anchored egocentric representations that extend beyond self-  
97 motion been reported (Wilber et al., 2014; Peyrache et al., 2017; Wang, Chen, et al., 2018;  
98 Hinman et al., 2019, LaChance et al., 2019). Egocentric representations of this nature may  
99 anchor to environmental boundaries. Boundaries present a unique intersection between  
100 egocentric and allocentric coordinate systems as they have fixed positions that define the  
101 navigable allocentric space and simultaneously restrict the egocentric affordances of the agent  
102 such as what can be viewed or what motor plans can be executed. Importantly, environmental  
103 bounds or walls extend along large regions of an environment, and thus enable extended  
104 interaction from multiple allocentric or egocentric perspectives. Egocentric neural responses  
105 have now been reported in multiple areas such as lateral entorhinal cortex (Wang, Chen, et al.,  
106 2018), dorsal striatum (Hinman et al., 2019), and postrhinal cortices (LaChance et al., 2019).  
107 However, none of these regions possess the reciprocal interconnectivity between egocentric  
108 and allocentric spatial circuitry that might mediate bidirectional reference frame transformations.

109 From a connectivity standpoint, the retrosplenial cortex (RSC) is an excellent candidate to  
110 examine egocentric representations during navigation. Further, theoretical work has posited that  
111 RSC forms a computational hub for supporting coordinate transformations (Byrne et al., 2007;  
112 Clark et al., 2018; Rounds et al., 2018; Bicanski and Burgess, 2018). RSC is composed of two  
113 interconnected sub-regions, dysgranular (dRSC) and granular (gRSC), which have slightly  
114 different connectivity with cortical and subcortical regions (Shibata et al., 2009). dRSC (in mice  
115 agranular RSC) is positioned along the dorsal surface of the brain and possesses biased  
116 interconnectivity with association, sensory, and motor processing regions that code in  
117 egocentric coordinates (Vogt and Miller, 1983; van Groen and Wyss, 1992; Reep et al., 1994;  
118 Shibata et al., 2004; Wilber, Clark, et al., 2015; Yamawaki et al., 2016; Olsen et al., 2016;  
119 Hovde et al., 2019). In contrast, gRSC has strong reciprocal innervation with the hippocampal  
120 formation and associated structures that are primarily sensitive to the allocentric coordinate  
121 system (van Groen and Wyss, 1990; Wyss and van Groen, 1992; van Groen and Wyss, 2003;  
122 Miyashita and Rockland, 2007; Sugar et al., 2011; Kononenko and Witter, 2012; Czajkowski et  
123 al., 2013; Olsen et al., 2017; Yamawaki et al., 2019ab; Haugland et al., 2019).

124 Despite possessing dense reciprocal connectivity with numerous regions known to support  
125 spatial cognition, few reports have examined spatial response properties of neurons within the  
126 RSC. Most assessments of functional properties of RSC neurons have occurred in rodents

127 performing track running tasks (Smith and Mizumori, 2012; Alexander and Nitz, 2015; Alexander  
128 and Nitz, 2017; Vedder et al., 2016; Mao et al., 2017; Mao et al., 2018; Miller et al., 2019). Track  
129 running experiments have revealed that RSC neurons exhibit spatial correlates with conjunctive  
130 sensitivity to allocentric and egocentric coordinate systems (among others) simultaneously  
131 (Alexander and Nitz, 2015). Conjunctive tuning of this type has been shown in modelling work to  
132 facilitate spatial coordinate transformations further supporting a role for RSC in the required  
133 transformation between these two spatial reference frames (Pouget and Sejnowski, 1997;  
134 Bicanski and Burgess, 2018). However, grid cells, head direction cells, place cells, and other  
135 forms of well-characterized spatial receptive fields have primarily been examined in two-  
136 dimensional (2D) environments. Only a few experiments have studied RSC in similar conditions  
137 and all such reports have focused on head direction encoding (Chen et al., 1994ab; Cho and  
138 Sharp, 2001; Jacob et al., 2017).

139 To examine externally-referenced egocentric representations in RSC capable of supporting both  
140 navigation and reference frame transformations we recorded from both RSC sub-regions while  
141 rats freely explored familiar two-dimensional environments. We report that subsets of RSC  
142 neurons exhibit a variety of spatially-stable activation patterns in egocentric and allocentric  
143 coordinate systems. These findings support predictions from computational modeling related to  
144 translation between spatial reference frames and highlight important navigation related variables  
145 encoded in association cortex (Byrne et al., 2007; Bicanski and Burgess, 2018).

## 146 **Results**

### 147 ***RSC neurons exhibit stable spatial activity during free exploration***

148 We recorded 555 neurons extracellularly in bilateral retrosplenial cortex (RSC) from male Long-  
149 Evans rats ( $n = 7$ ) during free exploration. To enable comparisons between functional properties  
150 of neurons recorded in dysgranular (dRSC) versus granular (gRSC) sub-regions of RSC, we  
151 estimated tetrode placement and depth for each session (**Figure 1a**,  $n = 130$  sessions, **sFigure**  
152 **1a-b**). Of the total population, 41.5% ( $n = 230/555$ ) were recorded from dRSC, 15.1% ( $n =$   
153  $84/555$ ) from the border between dRSC and gRSC, and 43.4% ( $n = 241/555$ ) within gRSC. For  
154 baseline sessions, rats foraged for scattered reward in  $1.25\text{m}^2$  square arenas with observable  
155 fixed distal cues.

156 RSC neurons exhibited complex firing rate fluctuations as rats randomly foraged within open  
157 arenas (**Figure 1b**). To assess the spatial stability of these representations for each neuron  
158 individually, we began by examining correlations between 2D spatial firing ratemaps constructed

159 from first and second halves of each experimental session (**Figure 1c**). Across the full  
160 population of RSC neurons, 47.0% of cells ( $n = 261/555$ ) had spatial correlations greater than  
161 the 99<sup>th</sup> percentile ( $\rho = 0.23$ ) of the distribution of correlations observed following 100 random  
162 shifts of the complete spike train for each neuron relative to spatial position (**Figure 1c**).

163 In some cases, RSC neurons with spatially anchored responses had slight differences in basic  
164 firing properties than those that were not spatially stable (**sFigure 2b**). Of particular interest and  
165 consistent with the presence of spatial receptive fields, RSC neurons with spatially reliable  
166 activity had significantly greater spatial coherence than non-stable cells (**sFigure 2b-c**).  
167 Spatially anchored firing patterns were also observed at more ventral recording sites where it  
168 was difficult to resolve whether the recording tetrode was in RSC or the cingulum bundle  
169 (**sFigure 2d**). Recordings from these sites were not included in the pool of RSC neurons for  
170 analysis.

### 171 ***Egocentric boundary vector responsivity of RSC***

172 Of neurons with stable spatial firing in the open field, several had receptive fields that were  
173 qualitatively proximal to environmental boundaries (**Figure 1b, right**). Inspection of the  
174 relationship between each spike and the movement direction of the animal revealed that these  
175 responses manifested when the animal was oriented in a similar manner relative to any wall,  
176 suggesting that the receptive field was defined in an egocentric manner. As such, these  
177 responses were reminiscent of egocentric boundary cells (EBCs) recently reported in the dorsal  
178 striatum (dStr, Hinman et al., 2019), lateral entorhinal cortex (LEC, Wang, Chen, et al., 2018),  
179 and postrhinal cortex (POR, LeChance et al., 2019). To test this explicitly we constructed  
180 egocentric boundary ratemaps (EBRs) using procedures previously described (Hinman et al.,  
181 2019; **Figure 1d**). Briefly, for each behavioral frame, the distance to the nearest wall in each 3°  
182 offset from the animal's movement direction was calculated (**Figure 1d**). The same process is  
183 repeated for the position of each spike from each neuron, and then ratemaps in polar  
184 coordinates were constructed by dividing the number of spikes by the total behavioral  
185 occupancy in seconds.

186 From each EBR, we computed the mean resultant length (MRL) of angular tuning as well as the  
187 absolute difference in angular tuning direction and distance between first and second halves of  
188 the baseline session. RSC cells were determined to exhibit significant egocentric boundary  
189 sensitivity if they met the following criteria: 1) they had a MRL for the first and second halves of  
190 the session that were greater than the 99<sup>th</sup> percentile of the distribution of resultants computed

191 following repeated shifted spike train randomizations, 2) had an absolute difference of mean  
192 directional tuning between halves of the baseline session that was less than 45 degrees, and 3)  
193 had an absolute difference in preferred distance tuning (described below) between halves that  
194 was less than 75% of the preferred distance tuning computed from the full baseline session.

195 Using these metrics, 15.0% (n = 83/555) of RSC neurons were determined to be EBCs (**Figure**  
196 **1e-g**). When a speed threshold was applied (> 5 cm/s), a greater population of RSC neurons  
197 reached EBC criterion (22.9%, n = 127/555), which we utilize for further analyses. Overall,  
198 application of a speed threshold increased the mean resultant length for nearly all EBCs (**Figure**  
199 **1h**, median MRL difference = 0.02, IQR = 0.01-0.03; Wilcoxon Signed Rank, z = 7.73, p =  
200  $1.1 \times 10^{-14}$ ). This result suggested that the egocentric receptive field of EBC neurons is defined by  
201 the movement direction of the animal rather than head direction, which can be computed even  
202 when the animal is motionless. Indeed, when EBCs were assessed using head direction instead  
203 of movement direction the MRL significantly dropped (EBCs MRL with MD = 0.13, IQR = 0.10-  
204 0.18; EBCs MRL with HD = 0.10, IQR = 0.06-0.14, Wilcoxon sign rank test for zero difference, z  
205 = 8.04, p =  $8.75 \times 10^{-16}$ ).

#### 206 ***Properties of RSC egocentric boundary vector receptive fields***

207 Sub-populations of RSC EBCs exhibited either increased or decreased activation when the  
208 animal occupied a particular orientation and distance relative to environmental boundaries  
209 (**Figure 1e-g**). In accordance with prior literature, we refer to those neurons that were inhibited  
210 as inverse EBCs (iEBCs, **Figure 1g**) and neurons with excitatory receptive fields as EBCs  
211 (**Figure 1e-f**). K-means clustering on numerous EBC features (see methods) yielded four  
212 qualitatively coherent groupings of EBC receptive field sub-types that were characterized post  
213 hoc: 1) 24.4% (n=31/127) were animal-proximal with a small receptive field (**Figure 1e, blue**  
214 **border**), 2) 33.9% (n=43/127) were animal-distal with a larger and/or potentially noisier  
215 receptive field (**Figure 1f, orange border**), 3) 31.5% (n = 40/127) were animal-distal with a  
216 larger receptive field (**Figure 1f, yellow border**), and 4) 10.2% (n = 13/127) had large inverted  
217 EBC receptive fields (**Figure 1g, purple border**). Principal component analysis (PCA) on this  
218 same feature space showed that the first two components accounted for 55.6% and 10.8% of  
219 the variability, respectively. A comparison of PCA scores for these two components across all  
220 RSC EBCs clustered using K-means did not yield distinct boundaries between sub-populations,  
221 instead revealing a continuum of EBC receptive fields (**Figure 1j**).

222 Identification of the center of mass of EBC receptive fields revealed a bimodal distribution of  
223 preferred orientations that was best fit by a two component Gaussian mixture model (GMM) with  
224 means of 100° (L) and 239° (R) relative to directly in front of the animal (**Figure 1k**; Number of  
225 GMM components determined via minimizing AIC). Although EBCs were recorded in both  
226 hemispheres there was no obvious relationship between the preferred orientation and the  
227 hemisphere in which the neuron was recorded, indicating a lack of lateralization of EBC  
228 response properties (**Figure 1k**, inset). The distribution of preferred distances was best  
229 described by a four component GMM with means of 11cm, 21cm, 37cm, and 50cm centimeters  
230 (**Figure 1l**). The size of EBC receptive fields increased as a function of the preferred distance of  
231 the egocentric vector indicating that the resolution of the representation was dependent on  
232 proximity to boundaries (**Figure 1m**, Spearman's  $\rho = 0.37$ ,  $p = 2.57 \times 10^{-5}$ ). The presence of  
233 EBCs with preferred distances distal to the animal suggested that the EBC response property  
234 was neither dependent upon physical interaction with arena borders nor could be purely posture  
235 related which is known to modulate cortical neurons (Mimica, Dunn, et al., 2019).

### 236 ***EBC responses are localized within dysgranular RSC but lack topographic organization***

237 Egocentric boundary vector sensitivity was primarily observed in dRSC, where 37.0% (n =  
238 85/230) of neurons recorded were classified as EBCs (**sFigure 1c**). In contrast, EBCs were  
239 observed in 10.0% (n = 24/241) of gRSC and 21.4% (n = 18/84) of intermediary area cells  
240 between the two sub-regions (dgRSC, see methods and **sFigure 1a**). By and large, the  
241 distribution of EBCs amongst RSC sub-regions was consistent across animals (**sFigure 1c**).  
242 The EBC response property was observed across a wide range of A/P coordinates spanning a  
243 majority of RSC but possessed no further anatomical organization beyond sub-region specificity  
244 (range = 2.9 - 6.8mm relative to bregma, **sFigure 1d**). The distribution of spike waveform widths  
245 across all RSC neurons was bimodal with identified EBCs primarily found in the cluster of  
246 neurons with longer duration waveforms (**sFigure 1e**, K-means clustering on waveform width,  
247 cluster 1 median = 0.18s, IQR = 0.15 - 0.23s, EBCs in cluster 1, n = 15/127, 11.8%; cluster 2  
248 median = 0.31s, IQR = 0.21 - 0.34s; EBCs in cluster 2, n = 112/127, 88.2%). Further, EBCs had  
249 overall low mean firing rates (**sFigure 1e**, EBCs = 1.68Hz, IQR = 0.96 - 2.72Hz, not-EBCs =  
250 3.55Hz, IQR = 1.15 - 8.47Hz). Taken together, the EBC sub-population was determined to be  
251 primarily composed of putative principal neurons suggesting that the EBC signal is propagated  
252 across RSC sub-regions or into other brain regions.

253 EBCs could often be simultaneously recorded which enabled an analysis of potential  
254 topography in the distribution of preferred distance and orientation of the egocentric boundary

255 vector. Overall, 129 pairs of RSC EBCs were co-recorded across 31 sessions. Of these pairs,  
256 30.2% (n = 39/129) were recorded on the same tetrode (**sFigure 3a**), while the remaining  
257 69.8% of EBC pairs (n = 90/129) were concurrently recorded on different tetrodes (**sFigure 3b**).

258 To assess whether there was organization to preferred orientation and distance as a function of  
259 proximity of two EBCs (i.e. observed on same or different tetrodes), we next calculated the  
260 difference in receptive field center of mass for both angular and distance components for all  
261 pairs. Although the preferred distance of EBCs on the same tetrode was trending towards  
262 greater similarity (**sFigure 3c**), neither preferred orientation nor distance was statistically  
263 different for EBCs recorded on the same versus different tetrodes (**sFigure 3c-3d**, absolute  
264 difference in preferred distance (PD) same tetrode = 7.5cm, IQR = 5 - 21.88cm; absolute  
265 difference in PD different tetrode = 12.5cm, IQR = 5 - 22.5cm; Wilcoxon rank sum test, z = -  
266 1.16,  $p = 0.24$ ; difference in preferred orientation (PO) same tetrode = 33°, IQR = -43.5 -  
267 78.75°; difference in preferred orientation (PO) different tetrode = 34.5°, IQR = -6 - 111°;  
268 Wilcoxon rank sum test, z = -0.04,  $p = 0.97$ ). Accordingly, we conclude that there is a lack of  
269 topographic organization of egocentric boundary vector tuning in the RSC.

### 270 ***Egocentric boundary vector tuning in secondary motor cortex and posterior parietal*** 271 ***cortex but not medial entorhinal cortex***

272 In 3 animals, a subset of more anterior recording tetrodes were positioned in secondary motor  
273 cortex (M2, from bregma: AP: -1.1 to -2.9mm, ML:  $\pm 0.8$  to 1.2mm) and 56 neurons were  
274 recorded there (**sFigure 4a**). Of M2 neurons, 21.4% reached EBC criterion (n = 12/56, **sFigure**  
275 **4b**). Similarly, 95 neurons across 5 rats were recorded in posterior parietal cortex (PPC or V2,  
276 from bregma: AP: -3.7 to -5.9mm, ML:  $\pm 1.5$  to 2.4mm) and a sub-population of 9.5% (n = 9/95)  
277 reached EBC criterion (**sFigure 4c-d**). EBCs and iEBCs were observed in both structures and  
278 receptive fields had similar angular and distance distributions as those observed in RSC  
279 (**sFigure 4e-f**). In contrast, only 2.4% (n = 7/297) of medial entorhinal cortex (mEC) neurons  
280 recorded in similar conditions reached EBC criterion, indicating that the egocentric vector signal  
281 was generally not present within the region (**sFigure 4g**, Wang, Chen, et al., 2018).

### 282 ***EBC responsivity is not explained by self-motion correlates***

283 In free exploration, spatial locations near environment boundaries uniquely restrict the  
284 behavioral affordances of the animal. Many observed EBC receptive fields were proximal to the  
285 rat, firing only when the animal was close to boundaries and thus most limited in its possible

286 actions. We next tested whether the manifestation of egocentrically referenced boundary vector  
287 tuning was in actuality reflective of self-motion related firing that was stereotyped near borders.

288 We began by constructing self-motion referenced firing rate maps during open field sessions  
289 (Chen et al., 1994; Whitlock et al., 2012). The angular difference between movement direction  
290 ( $\Delta\theta$ ) and the Euclidian distance in two-dimensional location ( $\Delta d$ ) was calculated across a sliding  
291 100ms window for every position of the animal throughout a free exploration session (**Figure**  
292 **2a, left**). These displacement values were converted to Cartesian coordinates referenced to the  
293 previous location of the animal at each step, thus producing a map of the distance and direction  
294 of movement of the animal for all position samples within the exploration session (**Figure 2a,**  
295 **middle and right**).

296 Firing rate as a function of these displacement values are presented for example RSC neurons  
297 in **Figure 2c-f**. The zero-line intersection indicates the position of the animal at the beginning of  
298 each 100ms window and the x and y-axes reflect displacement in lateral and longitudinal  
299 dimensions, respectively. Thus, values to the right of the vertical zero line reflect the activity of  
300 the neuron when the animal moved to the right relative to the previous position and direction of  
301 its body axis and the distance that the action took the animal is reflected in the position of the  
302 value along the y-axis.

303 To quantify the stability of self-motion tuning, we correlated self-motion ratemaps for each  
304 neuron that were individually computed from interleaved temporal epochs (1s in duration) within  
305 the free exploration session. 15.3% ( $n = 85/555$ ) of RSC neurons exhibited self-motion related  
306 activity that had greater stability than the 95<sup>th</sup> percentile of the distribution of stability correlation  
307 values calculated following permutation tests (**Figure 2b**). Of this sub-population, 28.2% ( $n =$   
308  $24/85$ ) had firing rate modulation that was biased for leftward or rightward movements (**Figure**  
309 **2c**), while 34.1% ( $n = 29/85$ ) were sensitive to longitudinal movements consistent with speed  
310 tuning (**Figure 2d**). Of the EBC population, 19.7% ( $n = 25/127$ ) met the stability criteria,  
311 indicating that a small sub-population of neurons exhibiting egocentric boundary vector tuning  
312 had stable self-motion correlates (**Figure 2e**). However, the vast majority of RSC EBCs did not  
313 exhibit self-motion correlates confirming that egocentric boundary vector tuning was primarily  
314 not an epiphenomenon of movement related activity near borders (**Figure 2f**).

315 Beyond EBCs, the present analysis demonstrated overall limited self-motion tuning in RSC  
316 during free exploration. This observation shines new light on previously reported turn-sensitive  
317 neurons in RSC during track running tasks (Alexander and Nitz, 2015). In prior work, the

318 magnitude of clockwise or counterclockwise activation during track running was demonstrated  
319 to be generally insensitive to the magnitude of angular velocity on a trial-by-trial basis. In  
320 combination with the lack of self-motion tuning during free foraging observed here, the results  
321 collectively suggest that reported egocentric correlates in RSC are externally-referenced and  
322 unrelated to the speed of angular movement.

### 323 ***Generalized linear models demonstrate robust egocentric vector tuning of RSC EBCs***

324 Self-motion is necessarily conflated with egocentric boundary vector tuning because the  
325 response primarily manifested during movement (**Figure 1h-i**). An EBC may exhibit stable firing  
326 rate fluctuations as a function of self-motion that are driven by the egocentric boundary vector  
327 receptive field, not the action state of the animal. For example, an EBC with a receptive field to  
328 the animal's left may also show self-motion tuning for clockwise movements as a result of the  
329 animal being more likely to turn clockwise when there is a wall occupying the egocentric  
330 receptive field. Yet, the same neuron may not be activated when the animal turns clockwise in  
331 other locations within the environment that do not satisfy the egocentric boundary vector. Thus,  
332 although initially informative, a different approach was required to tease out the influence of self-  
333 motion and other potential spatial covariates on EBC activity patterns.

334 We next implemented a generalized linear model (GLM) framework to predict the probability of  
335 spiking at each time point as a function of the relative influence of multiple allocentric, self-  
336 motion, or EBC-related predictors (**Figure 3a**). Allocentric predictors included the movement  
337 direction of the animal and x- and y-position within the arena. Self-motion related predictors  
338 included linear speed and angular displacement (i.e. the differential of animal movement  
339 direction in 100ms windows).

340 EBC-related predictors were more complicated as a single position sample or spike possessed  
341 relationships to multiple locations along boundaries simultaneously. Accordingly, the EBC  
342 predictor could take many forms. To minimize the number of sub-predictors, EBC predictors  
343 were composed of the animal's distance and egocentric bearing to the center of the arena.  
344 Unlike arena boundaries, the center of the arena is a single coordinate that can be described as  
345 a function of individual angular and distance components or their conjunction for each position  
346 sample (**sFigure 5a**). Critically, EBCs were found to exhibit robust egocentric bearing and  
347 distance tuning to the center of the arena making the predictor a reasonable counterpart to  
348 referencing single unit activity to arena walls (**sFigure 5c-d**).

349 To test the impact of each predictor individually, we first generated a complete model fit using  
350 the full complement of predictors. Next, we dropped each covariate individually and assessed  
351 the decrement to model fit using the difference in Akaike information criterion and corresponding  
352 log-likelihood ratio tests (AIC, see methods). **Figure 3b** depicts the proportion of RSC neurons  
353 that had significant sensitivity to each individual predictor, split into the sub-populations of cells  
354 that were or were not classified as egocentric boundary sensitive using strength of bearing  
355 tuning and reliability as above and in previous work (Hinman et al., 2019). GLM output  
356 corresponded with the initial identification of EBCs using these metrics. Of EBCs, 81.9% (n =  
357 104/127) had significant decrements to model fit when conjunctive EBC predictors were  
358 removed from the model (**Figure 3b**).

359 Using the GLM, 70% (n = 89/127) of EBCs were significantly modulated by linear speed, more  
360 than doubling the percentage of neurons that were identified as velocity sensitive from self-  
361 motion ratemap analyses that utilized a 100ms temporal window (**Figure 2d**). GLM analyses  
362 yielded only 12.6% (n = 16/127) of RSC EBCs sensitive to angular displacement, thus further  
363 confirming that egocentric boundary vector sensitivity was not epiphenomenal to turning actions  
364 near arena bounds.

365 Although neurons previously characterized as possessing egocentric boundary vector tuning  
366 were accurately detected with the GLM, numerous other predictors were shown to also  
367 significantly co-vary with spiking activity (**Figure 3b**). A number of neurons that were initially  
368 characterized as non-EBCs had significant model decrements when the EBC-related predictors  
369 were excluded (38.8%, n = 141/363 after removing non-EBC interneurons that had mean firing  
370 rates > 15Hz; **Figure 3b**). However, as the GLM will zero-weight a non-contributing predictor,  
371 the removal of a single covariate can only serve to decrement model fit while adding a predictor  
372 can only improve model fit. Accordingly, a significant log-likelihood test following removal of a  
373 predictor does not fully demonstrate the relative impact of that predictor in the full model.

374 We next assessed the overall influence of each predictor class (allocentric, self-motion, and  
375 EBC-related) on model fit by constructing a nested GLM, dropping each predictor class, and  
376 then making comparisons between resulting model fits (Kraus et al., 2013). **Figure 3c** depicts  
377 the difference in model fit (dAIC) for both EBCs and non-EBCs between the full model and  
378 reduced models with all allocentric, self-motion, or egocentric boundary predictors removed.  
379 Larger dAIC values indicate greater impact of the predictor class within the full model. Models  
380 without all allocentric or EBC predictors had significant differences in fit between EBCs and non-  
381 EBCs (**Figure 3c**, Kruskal-Wallis,  $\chi^2 = 275.67$ ,  $p = 1.69 \times 10^{-57}$ , post-hoc Scheffe tests,

382  $p < 0.0001$ ). There was no difference between these sub-populations of RSC neurons for the  
383 removal of self-motion covariates from the model further supporting that EBCs were not more  
384 sensitive to speed or angular displacement than the remainder of the RSC population (**Figure**  
385 **3c**, Kruskal-Wallis w/ post-hoc Scheffe tests,  $p = 0.95$ ).

386 A clear divergence emerged in the importance of EBC-related predictors for the EBC and non-  
387 EBC sub-populations. As reflected in the difference in magnitude of dAIC, EBC predictors had  
388 greater impact than either allocentric or self-motion predictors for the EBC population (**Figure**  
389 **3d, blue**;  $dAIC_{EBC} - dAIC_{Allo}$  for EBCs = 203.5, IQR = 21 – 475.8;  $dAIC_{EBC} - dAIC_{SM}$  for EBCs =  
390 259.2, IQR = 65.6 – 541.1) than for the non-EBC population which had similar dAIC scores  
391 (near 0) for models lacking EBC predictors and other predictor classes (**Figure 3d, gray**;  
392  $dAIC_{EBC} - dAIC_{Allo}$  for non-EBCs = -14.9, IQR = -110.4 – 10.2;  $dAIC_{EBC} - dAIC_{SM}$  for non-EBCs = -  
393 1.33, IQR = -29.6 – 26.4). Overall, the impact of EBC-related predictors relative to other  
394 predictor classes was significantly greater for EBC versus non-EBC sub-populations ( $dAIC_{EBC} -$   
395  $dAIC_{Allo}$  for EBCs versus non-EBCs, Wilcoxon rank sum,  $z = -10.8$ ,  $p = 2.51 \times 10^{-27}$ ;  $dAIC_{EBC} -$   
396  $dAIC_{SM}$  for EBCs versus non-EBCs, Wilcoxon rank sum,  $z = -12.3$ ,  $p = 9.33 \times 10^{-35}$ ).

397 This result suggested that although models without allocentric or self-motion predictors could  
398 yield significantly decreased model fit, the vast majority of EBC neurons were significantly more  
399 impacted by EBC predictors. Two example EBCs in **Figure 3e** illustrate this point, wherein a  
400 spike train generated from the output of each model was used to construct trajectory plots and  
401 egocentric boundary ratemaps. In both cases, the model lacking egocentric orientation and  
402 distance information yields a trajectory plot and egocentric boundary ratemap that is  
403 substantially poorer at reconstructing the actual data than any other reduced model.

404 Although egocentric predictors were the dominant influence on EBC activation, nearly all EBCs  
405 (98.4%,  $n = 125/127$ ) were statistically impacted by the removal of more than one predictor  
406 category. In this manner the GLM analyses revealed that RSC EBCs were conjunctively  
407 sensitive to the position of arena boundaries in egocentric coordinates and allocentric heading  
408 or location simultaneously. This feature of EBC responsivity is consistent with theoretical work  
409 proposing a transformation between egocentric and allocentric spatial representations within  
410 RSC (Bicanski and Burgess, 2018).

#### 411 **GLM confirms vectorial representation**

412 Use of the GLM framework provided an opportunity to verify that RSC neurons with egocentric  
413 boundary sensitivity actually formed vector representations of the relationships between

414 environmental boundaries and the animal. By dropping out egocentric bearing and egocentric  
415 distance from the model individually, we were able to investigate the relative influence of the  
416 individual components of the egocentric boundary vector in isolation for each neuron.

417 Significant model decrements were observed in 100% ( $n = 127/127$ ) of EBCs following removal  
418 of the egocentric bearing component and 74.8% ( $95/127$ ) of EBCs were impacted by the  
419 removal of egocentric distance predictors. Overall, the magnitude of error to model fit was  
420 substantially greater when egocentric bearing was removed indicating that, although both  
421 distance and orientation components are critical for egocentric boundary vector responsiveness,  
422 the directional component more robustly drives neurons exhibiting this tuning preference  
423 (**Figure 3f**, difference in dAIC for egocentric bearing versus egocentric distance = 217.2, IQR =  
424 77.5 – 440.4; Wilcoxon signed rank test,  $z = 9.3$ ,  $p = 1.3 \times 10^{-20}$ ).

#### 425 ***EBCs respond to local not distal environmental features***

426 Characterization of EBC properties and self-motion correlates were conducted in baseline  
427 sessions in which the open arena remained in a fixed location relative to the experimental room  
428 and fixed distal cues therein. We next conducted a series of experimental manipulations of the  
429 relationship between the familiar arena and the testing room in order to confirm that EBC  
430 response properties were defined by the relationships between environmental boundaries and  
431 the animal itself.

432 First, we rotated the open field 45 degrees to maximally disrupt correspondence between arena  
433 walls and distal walls or cues present within the recording environment to verify that EBC  
434 responses were anchored to local boundaries and not the broader recording room. Under these  
435 conditions we recorded a total of 65 RSC neurons (across 4 rats and 14 sessions) of which 40%  
436 ( $n = 26/65$ ) had EBC sensitivity. Consistent with EBC responses being referenced to the rat,  
437 receptive fields in rotated arenas maintained the same orientation and distance with respect to  
438 the animal, even though arena boundaries now fell along completely different allocentric axes  
439 (**Figure 4a-c**; difference between baseline and rotated preferred orientation =  $1.5^\circ$ , IQR =  $-12 -$   
440  $18^\circ$ ; Wilcoxon sign rank test,  $z = 0.53$ ,  $p = 0.59$ ; difference between baseline and rotated  
441 preferred distance = 0cm, IQR =  $-3.75\text{cm} - 3.75\text{cm}$ ; Wilcoxon sign rank test,  $z = -0.26$ ,  $p =$   
442  $0.79$ ). Although vector tuning remained intact, there were slight but significant changes to  
443 ratemap coherence between baseline and rotation sessions which suggested that the quality of  
444 the egocentric boundary receptive field was decremented across conditions (**Figure 4d**;

445 difference between baseline and rotated ratemap coherence = 0.03, IQR = -0.02 – 0.06;  
446 Wilcoxon sign rank test,  $z = 2.27$ ,  $p = 0.02$ ).

447 Consistency in tuning could emerge if the allocentric map anchored to local boundaries rather  
448 than distal cues. This was not the case as a population of simultaneously recorded head  
449 direction cells (HD,  $n = 4$ ; **Figure 4a, right**) exhibited consistent mean tuning across the rotated  
450 and non-rotated conditions ( $n =$  median tuning difference =  $-6.6^\circ$ , maximum tuning difference -  
451  $12.4^\circ$ ). Accordingly, arena rotation experiments dissociated the directional component of EBCs  
452 from the allocentric reference frame of HD cells.

#### 453 ***EBC responsivity is anchored to boundaries not the center of the environment***

454 RSC EBCs exhibited egocentric vector sensitivity to both arena boundaries and the center of  
455 the environment which we utilized to our advantage in GLM analyses (**sFigure 5**). This occurs  
456 because arena boundaries have a fixed relationship relative to the center of the environment.  
457 Accordingly, an obvious question is whether the egocentric boundary response is in actuality  
458 defined as an egocentric vector to the center of the arena. We addressed this possibility by  
459 comparing preferred orientation and distance for 10 RSC EBCs (of 33 total RSC neurons from 4  
460 rats across 11 sessions) between baseline arenas and open fields expanded up to  $1.75\text{m}^2$   
461 (**Figure 4e**).

462 If EBC responses were anchored to boundaries, we anticipated that the orientation and  
463 preferred distance would remain consistent across both conditions. Conversely, if the receptive  
464 field was defined by a vector to the center of the arena then the distance component of the  
465 egocentric boundary vector would remain fixed to this point. In this scenario, the preferred  
466 distance would either move away from the animal in expanded arenas or potentially scale with  
467 the arena expansion. We observed that the preferred orientation, preferred distance, and  
468 ratemap coherence were not altered between baseline and expanded field sessions confirming  
469 that EBCs were indeed anchored to boundaries and not the center of the arena (**Figure 4b-d**,  
470 difference between baseline and expanded preferred orientation =  $-4.5^\circ$ , IQR =  $-24 - 6^\circ$ ;  
471 Wilcoxon sign rank test, signed rank = 19,  $p = 0.46$ ; difference between baseline and expanded  
472 preferred distance = 0cm, IQR =  $-7.5 - 5\text{cm}$ ; Wilcoxon sign rank test, signed rank = 13.5,  $p =$   
473  $0.56$ ; difference between baseline and rotated ratemap coherence = 0.01, IQR =  $-0.03 - 0.07$ ;  
474 Wilcoxon sign rank test, signed rank = 31,  $p = 0.77$ ).

#### 475 ***EBC responsivity is stable in novel environments***

476 Neurons within the broader neural spatial circuitry such as grid cells, head direction cells, and  
477 place cells, exhibit consistent, albeit remapped, spatial receptive fields in novel environments.  
478 We next questioned whether egocentric boundary vector tuned neurons of RSC would exhibit  
479 similar stability in their selectivity. We recorded 17 RSC cells including 8 EBCs in familiar then  
480 novel environment sessions (**Figure 4f**, 4 rats across 5 sessions). Neither distance nor  
481 orientation components of the egocentric boundary vector were altered in the novel environment  
482 relative to baseline illustrating that EBCs are not experience dependent and do not remap  
483 between environments (**Figure 4b-c**, difference between baseline and novel preferred  
484 orientation =  $6^\circ$ , IQR =  $-6 - 27^\circ$ ; Wilcoxon sign rank test, signed rank = 19,  $p = 0.47$ ; difference  
485 between baseline and novel preferred distance =  $-2\text{cm}$ , IQR =  $-20 - 0\text{cm}$ ; Wilcoxon sign rank  
486 test, signed rank = 2,  $p = 0.13$ ). Coherence of EBC receptive fields were unchanged between  
487 environments providing evidence that the resolution of the egocentric location signal was robust  
488 in both familiar and novel arenas (**Figure 4d**; difference between baseline and novel ratemap  
489 coherence = 0.02, IQR =  $0.00 - 0.08$ ; Wilcoxon sign rank test, signed rank = 27,  $p = 0.25$ ).

#### 490 ***Stability of EBC sub-populations requires physical boundaries***

491 Sensory information originating from multiple modalities likely underlies the egocentric nature of  
492 the RSC boundary vector responses. There are two reasons to believe that somatosensation  
493 may inform the preferred orientation and distance of a subset of EBCs. First, many RSC  
494 neurons with egocentric boundary vector tuning had preferred distances that were proximal to  
495 the animal and within or near whisker range (Preferred distance  $<12\text{cm}$ ; 16.5%,  $n = 21/127$ ;  
496 **Figure 1l**). Secondly, the preferred orientation of EBCs spanned all egocentric bearing angles  
497 but were biased laterally perhaps reflecting whisker interaction with borders (**Figure 1k**). As  
498 such, we questioned whether the presence of a physical boundary was required for EBC spatial  
499 tuning and/or particular subsets of EBC receptive fields.

500 To this end, baseline sessions were compared to recordings in environments that were  
501 bordered by drop offs with no arena walls ( $n = 35$  neurons from 7 sessions across 3 rats). 29  
502 neurons recorded under these conditions exhibited EBC sensitivity in the baseline session  
503 (**Figure 5g**). EBCs detected in the baseline session had similar preferred orientations but more  
504 distal preferred distances in sessions with no physical walls (**Figure 4b-c**, difference between  
505 baseline and no walls preferred orientation =  $-6^\circ$ , IQR =  $-70.5 - 19.5^\circ$ ; Wilcoxon sign rank test,  $z$   
506 =  $-0.41$ ,  $p = 0.68$ ; difference between baseline and no walls preferred distance =  $-11.3\text{cm}$ , IQR =  
507  $-28.8 - 2.5\text{cm}$ ; Wilcoxon sign rank test,  $z = -2.4$ ,  $p = 0.02$ ). Additionally, the overall coherence of  
508 the egocentric receptive field was significantly decreased in the absence of physical walls and

509 fewer EBCs were detected in these sessions (**Figure 4d**; difference between baseline and no  
510 walls ratemap coherence = 0.10, IQR = -0.00 – 0.23; Wilcoxon sign rank test,  $z = 3.6$ ,  $p =$   
511 0.0003; EBCs with no walls = 51.4%,  $n = 18/35$  versus  $29/35$ ). Collectively, these results  
512 suggest that the EBC population signal is degraded in the absence of explicit borders.

513 Despite this fact, numerous EBCs sustained their preferred egocentric vector across conditions.  
514 To investigate why some neurons were disrupted and not others we next examined the  
515 difference in receptive field coherence as a function of baseline preferred orientation and  
516 distance. There was no relationship between the preferred orientation of the neuron and the  
517 magnitude of degradation of the spatial signal with no physical walls (**Figure 4h**, Circular-linear  
518 correlation,  $\rho = 0.32$ ,  $p = 0.23$ ). In contrast, the more proximal the egocentric boundary receptive  
519 field was to the animal at baseline the more decreased the tuning was in an arena with no  
520 physical walls (**Figure 4i**, Spearman's correlation,  $\rho = -0.39$ ,  $p = 0.04$ ). Taken together, these  
521 results support the idea that the subset of animal-proximal egocentric boundary cells (**Figure**  
522 **1e**) may rely on somatosensory interaction with borders, while EBCs with more animal-distal  
523 receptive fields (**Figure 1f**) are preserved in environments with no physical walls because they  
524 rely on other sensory modalities.

525 ***RSC EBCs are insensitive to environmental geometry which yields a directional***  
526 ***representation of environment shape***

527 Boundaries are unique environmental features in that they both restrict navigational affordances  
528 and define the spatial structure of the broader environment. Accordingly, the presence of  
529 boundary sensitive neurons within RSC indicates that the region is capable of detecting features  
530 of environmental geometry. In a square open field like the one utilized for baseline experimental  
531 sessions there are two primary defining features of environmental geometry: 1) conjunctions of  
532 walls forming 90° corners and, 2) boundaries that are orientated along two-axes of allocentric  
533 environmental directions. As such, we questioned if EBCs would maintain their preferred tuning  
534 in circular environments that excluded both of these geometric features.

535 We recorded 23 RSC EBCs as animals free foraged in square and circular environments across  
536 two experimental sessions each day (**Figure 5a**, total RSC neurons recorded under these  
537 conditions = 32 across 4 rats and 8 sessions). As with most other environmental manipulations,  
538 EBC boundary vectors were unchanged when the geometry of the environment was altered  
539 (**Figure 5b**, difference between square and circle preferred orientation = 5.5°, IQR = -33 – 18°;  
540 Wilcoxon sign rank test,  $z = 0.10$ ,  $p = 0.92$ ; difference between square and circle preferred

541 distance = 2.5cm, IQR = -2.5 – 7.5cm; Wilcoxon sign rank test,  $z = 1.92$ ,  $p = 0.054$ ; difference  
542 between square and circle ratemap coherence = 0.002, IQR = -0.03 – 0.08; Wilcoxon sign rank  
543 test,  $z = 0.41$ ,  $p = 0.68$ ).

544 A striking feature of many EBCs (**Figure 5a, left**), but not all (**Figure 5a, right**), was the  
545 structure of movement direction tuning between square and circular environments. As a  
546 consequence of consistent egocentric boundary vector tuning in environments of different  
547 shapes, EBCs would typically possess four-pronged directional tuning that aligned with the  
548 orientation of the walls in square environments (**Figure 5a, left top**). In contrast, the same  
549 consistency in EBC tuning yielded directionally uniform tuning in circular environments (**Figure**  
550 **5a, left bottom**).

551 **Figure 5c** depicts movement direction tuning plots for the full population of RSC neurons  
552 recorded in square and circular arenas. When the mean population movement direction tuning  
553 was examined, distinct peaks fell at the four cardinal directions in square arenas but no such  
554 peaks were observed in their circular counterparts (**Figure 5c, bottom plots**). We hypothesized  
555 that differences between directional tuning, as a consequence of the presence of EBCs, would  
556 allow downstream regions to disambiguate environments of different geometries.

557 To test this, we trained a linear classifier on a random 80% of the directional tuning curves from  
558 both environments and attempted to predict which environment the other 20% of movement  
559 direction tuning curves were recorded within (**Figure 5d**, Linear discriminant classifier,  $n =$   
560 10,000 iterations). Consistent with the hypothesis that geometry could be decoded from a  
561 population with EBC tuning, the arena could be identified correctly with 67.7% accuracy (IQR =  
562 55.6 – 72.2%) which was statistically significant from both statistical chance (Wilcoxon sign rank  
563 with 50% accuracy median,  $z = 78.7$ ,  $p = 0$ ) and a classifier ran with arena identity randomized  
564 (randomized arena identity = 50%; IQR = 44.4 – 55.6%; Wilcoxon rank sum test,  $z = 76.6$ ,  $p =$   
565 0). We conclude that regions possessing egocentric boundary vector tuning may provide  
566 punctate directional signals to downstream regions such as the medial entorhinal cortex that  
567 can be compared to other directional inputs to inform circuits about environment geometry.

#### 568 **A sub-population of RSC EBCs are theta modulated**

569 In building off of geometry detection in RSC EBC ensembles, a natural next question is how  
570 might these egocentric positional signals be integrated within the broader spatial circuitry.

571 Previous work has demonstrated that RSC local field potentials feature a prominent theta  
572 oscillation during active movement that is strongly coherent with theta rhythms observed in the

573 dorsal hippocampal formation (Borst et al., 1987; Colom et al., 1988; Talk et al., 2004; Koike et  
574 al., 2017; Alexander et al., 2018). Spatial representations in regions with strong theta  
575 rhythmicity, such as MEC or HPC, are strongly influenced by boundaries and environmental  
576 geometry (Muller and Kubie, 1987; Gothard et al., 1996; O'Keefe and Burgess, 1996; Kenaith et  
577 al., 2017; Kinsky et al., 2018; Solstad et al., 2008; Krupic et al., 2015; Krupic et al., 2018). We  
578 next questioned whether RSC neurons exhibiting egocentric boundary vector sensitivity were  
579 potentially synchronized with these areas via theta oscillations.

580 Consistent with previous work, we observed a strong RSC theta oscillation and that individual  
581 RSC neurons engage with the theta oscillation in two primary modes (**Figure 6a-b**). First, a  
582 small sub-population of RSC neurons exhibit theta rhythmic spiking (as revealed by  
583 autocorrelations of their spike trains) and are phase locked to the locally recorded theta  
584 oscillation (**Figure 6b**; 4%,  $n = 22/555$ ). Second, a larger subset of RSC neurons do not  
585 possess consistent theta rhythmic spiking but are phase locked to the theta oscillation (**Figure**  
586 **6c**; 27.6%,  $n = 153/555$ , see methods). In order to be phase modulated without firing at a theta  
587 rhythm, this latter population may transiently engage with the theta oscillation by firing at  
588 particular phases after skipping random theta cycles.

589 No EBCs exhibited intrinsically theta rhythmic spiking, but 24.4% of EBCs ( $n = 31/127$ ) did  
590 phase lock to RSC theta oscillations (**Figure 1d**). The strength of theta modulation (mean  
591 resultant length, MRL) was significantly greater for theta-modulated non-EBCs than EBCs  
592 (**Figure 6e**, non-EBCs MRL = 0.13, IQR 0.10 – 0.19; EBCs MRL = 0.11, IQR = 0.09 – 0.13,  
593 Wilcoxon rank sum test,  $z = 2.09$ ,  $p = 0.04$ ). Although not significantly different, non-EBC theta-  
594 locked RSC neurons were biased to firing during the rising phase of the theta rhythm whereas  
595 theta-locked EBCs preferred the falling phase (**Figure 6f**, non-EBCs phase = 3.6 rad, IQR = 1.9  
596 – 4.8 rad; EBCs phase = 2.3 rad, IQR = 1.7 – 5.3 rad; Kuiper two-sample test,  $k = 1134$ ,  $p = 1$ ).  
597 These results confirm that a sub-population of RSC EBCs are phase-locked to theta oscillations  
598 present in RSC, consistent with recent modelling work suggesting periodic modulation as a  
599 mechanism for comparing current sensory input about the environment against stored spatial  
600 representations (Byrne et al., 2007; Hasselmo et al., 2012; Bicanski and Burgess, 2018).

### 601 ***RSC spatial sensitivity in the open field and during track running***

602 RSC spatial responses have been primary examined during track running paradigms (Smith and  
603 Mizumori, 2012; Alexander and Nitz, 2015; Alexander and Nitz, 2017; Vedder et al., 2016; Mao  
604 et al., 2017; Mao et al., 2018; Miller et al., 2019). Accordingly, we questioned whether there was

605 any relationship between stable firing correlates in free exploration and route running. To this  
606 end, a subset of RSC neurons (n=87 neurons across 3 rats) were recorded in both open field  
607 exploration and on track running paradigms (**sFigure 6a**).

608 Consistent with previous work, we observed RSC neurons with activation anchored to track  
609 locations associated with turning, start and end locations associated with reward, and non-  
610 specific patterns associated with a particular route during track running (**sFigure 6b-c**).

611 Although there was no clear relationship between EBC responsivity and activation during track  
612 traversals, there was a strong positive correlation between spatial stability in these two  
613 navigational conditions, suggesting a possible sub-circuit within RSC for reliable spatial  
614 representation (**sFigure 6d**, open field stability ( $\rho$ ) = 0.41, IQR = 0.27 - 0.60; track-running  
615 stability ( $\rho$ ) = 0.07, IQR = -0.01 - 0.20; Spearman's rho,  $r = 0.68$ ,  $p = 0$ ).

## 616 **Discussion**

### 617 ***RSC spatial representations facilitate reference frame transformations***

618 The current data support and extend the functional role of RSC in reference frame  
619 transformations. Specifically, the RSC population exhibits sensitivity to multiple spatial  
620 coordinate systems, an essential characteristic of circuitry capable of generating such  
621 translations. In the current work we report a large subset of spatially reliable neurons that  
622 encode the position of boundaries in egocentric coordinates. Referred to as egocentric  
623 boundary cells or EBCs, these neurons robustly encoded a vectorial representation of the  
624 distance and orientation of any boundary relative to the animal itself (i.e. in an egocentric  
625 reference frame; Wang, Chen, et al., 2018; Hinman et al., 2019; LeChance et al., 2019).  
626 Egocentric boundary representations are predicted to form a critical component of the  
627 coordinate transformation circuit, as the response property could function to inform the broader  
628 spatial circuitry about the position of external landmarks in a viewpoint-dependent manner  
629 (Byrne et al., 2007; Bicanski and Burgess, 2018).

630 RSC neurons also exhibited multiple forms of allocentric modulation that could be integrated  
631 with EBCs or other forms of egocentric information within theta timescales. Nearly half of RSC  
632 neurons exhibited reliable and spatially-anchored responses during free foraging behavior.  
633 Spatially stable cells had complex 2D spatial representations that in some cases were  
634 reminiscent or possibly descended from spatial non-grid cells observed in mEC (Diehl et al.,  
635 2017), allocentric boundary vector cells and axis-tuned neurons of dorsal subiculum (Hartley et  
636 al. 2000; Lever et al., 2009; Olson et al., 2017), and/or location modulated head direction cells

637 of post-subiculum (Peyrache et al., 2017). A second form of allocentric response was observed  
638 in a subset of RSC neurons that exhibit allocentric head direction sensitivity. These forms of  
639 allocentric spatial information may be processed or compared with egocentric boundary vector  
640 information within theta timescales. Both subsets of neurons exhibited theta phase modulation  
641 which is well known to synchronize information processing throughout the broader allocentric  
642 spatial circuit.

643 When paired with the unique anatomical connectivity of RSC with both egocentric and  
644 allocentric processing regions, the presence of neurons, such as EBCs, that are sensitive to one  
645 or more spatial coordinate systems signifies that the region is capable of interrelating external  
646 and internal spatial information for the initial construction and use of stored spatial  
647 representations. This fact may explain the diversity of impairments observed in spatial  
648 navigation, learning, and memory that occur following damage or lesion to the area (Valenstein  
649 et al., 1987; Takahasi et al., 1997; Harker and Whishaw, 2002; Vann et al., 2003; Vann and  
650 Aggleton, 2004; Vann and Aggleton, 2005; Pothuizen et al., 2008; Keene and Bucci, 2009;  
651 Hindley et al., 2014; Elduayen and Save, 2014).

652 ***The RSC egocentric boundary vector code is context-independent which generates a***  
653 ***directional code that reflects environment geometry***

654 EBC spatial receptive fields were activated when the animal was positioned with both a specific  
655 orientation and distance from an environmental boundary. EBCs maintained their preferred  
656 vector tuning preference in rotated arenas, expanded arenas, and novel arenas (**Figure 4**).  
657 Accordingly, the EBC signal does not remap across environments, thus providing a stable,  
658 context invariant, positional metric.

659 This stability can be contrasted to the vast majority of allocentric representations, such as place  
660 cells, grid cells, or head direction cells, that are known to either show global or rate remapping,  
661 translations, or rotations between environments (Muller and Kubie, 1987; Bostock et al., 1991;  
662 Leutgeb et al., 2005; Yoganarasimha and Knierim, 2006; Fyhn et al., 2007; Leutgeb et al., 2007;  
663 Hoydal et al., 2019). In contrast, border cells of mEC and boundary vector cells of dorsal  
664 subiculum maintain similar tuning preferences in a context invariant manner analogous to that  
665 observed in the EBCs shown here (Solstadt et al., 2008; Lever et al., 2009). It remains to be  
666 seen what interactions exist between cells possessing these different types of boundary  
667 anchored receptive fields, however the current data suggest that boundary sensitive neurons

668 may provide a foundational map upon which other spatial representations can be situated  
669 (Bicanski and Burgess, 2016).

670 Like border and boundary vector cells, RSC EBC vector representations did not remap in  
671 environments of different geometries (Solstadt et al., 2008; Lever et al., 2009). However,  
672 because EBCs respond in a directionally-dependent manner along every environmental border,  
673 the mean directional tuning of the RSC population reflected the shape of the environment  
674 (**Figure 5**). Here, we demonstrated that this directional signal could be utilized to distinguish  
675 arena shape. Relative positions of boundaries have repeatedly been shown to alter or anchor  
676 allocentric spatial representations, especially in mEC grid cells and HPC place cells (Muller and  
677 Kubie, 1987; Gothard et al., 1996; O'Keefe and Burgess, 1996; Keinath et al., 2017; Keinath et  
678 al., 2018; Kinsky et al., 2018; Solstadt et al., 2008; Krupic et al., 2015; Krupic et al., 2018; Julian  
679 et al., 2018). mEC receives excitatory projections, both directly and indirectly, from RSC and  
680 projects into HPC (Kononenko and Witter, 2012; Czajkowski et al., 2013). We hypothesize that  
681 the RSC arena-geometry-related directional signal may serve to provide excitatory drive at  
682 specific allocentric head directions to inform the circuit about the relative angles amongst  
683 borders.

#### 684 ***Egocentric vector tuning may support route-centric representations of RSC and PPC***

685 Consistent with previous work in dorsal striatum, RSC EBC tuning was strongest during motion  
686 and the directional component of egocentric boundary receptive fields was more robustly driven  
687 by the movement direction of the animal rather than head direction (Hinman et al., 2019). Taken  
688 together, these properties of EBC sensitivity suggest that the positional signal is related to  
689 active navigation and the relationship of trajectories through the environment relative to  
690 environmental boundaries.

691 RSC and the reciprocally connected PPC have been shown to exhibit activity patterns during  
692 track running paradigms that are anchored to the shape of the route itself (Nitz, 2006; Nitz,  
693 2012; Alexander and Nitz, 2015; Alexander and Nitz, 2017). Route-referenced activity in these  
694 regions could be potentially explained by EBC tuning or in part arise from the integration of EBC  
695 responsivity with other spatial covariates. Consistent with this hypothesis, we showed that the  
696 sub-population of spatially stable neurons in 2D free foraging (which included large numbers of  
697 EBCs) were more likely to exhibit spatially stable representations during track running (**sFigure**  
698 **6**).

#### 699 ***EBCs are primarily restricted to the dysgranular RSC***

700 A striking anatomical feature of the EBC population was that it was primarily localized to the  
701 dysgranular sub-region of RSC (dRSC). dRSC has connectivity weighted towards egocentric  
702 coordinate systems, as it is reciprocally innervated by cortical regions important for processing  
703 sensory and motor information as well as association areas such as PPC wherein  
704 egocentrically-referenced spatial responses have been observed (McNaughton et al., 1994;  
705 Whitlock et al., 2012; Wilber et al., 2014; Wilber et al., 2017). Further, the concentration of EBCs  
706 in dRSC is consistent with theoretical work posing a circuit for translating between egocentric  
707 and allocentric coordinate systems that includes posterior parietal cortex (PPC), RSC, and the  
708 extended hippocampal formation as primary hubs (Byrne et al., 2007; Oess et al., 2017; Rounds  
709 et al., 2018; Clark et al., 2018; Bicanski and Burgess, 2018).

710 Of note, dRSC is also known to possess bidirectional head direction cells (BDHD) that respond  
711 to local reference frames in multi-compartment environments with distinct contextual cues  
712 (Jacob et al., 2017). This sensitivity ultimately yields allocentric directional tuning plots that are  
713 bimodal. In the current work, strongly tuned EBCs commonly exhibited quad-modal allocentric  
714 directional tuning that was aligned with the four walls of square environments. This similarity in  
715 directional tuning response of EBCs and BDHDs and their co-localization in dRSC raises  
716 questions as to the nature of the relationship or interactions between these functional sub-  
717 populations.

718 One possibility is that neurons in dRSC are prone to represent the locations of spatial  
719 landmarks using egocentric vectors and that EBCs and BDHDs are both special cases  
720 constrained by their respective experimental setups. In the case of EBCs reported here, the  
721 vector may anchor to boundaries because borders are the only landmarks present in the open  
722 field that can cause activation of the receptive field. In the work of Jacob et al., the egocentric  
723 vector may respond to borders as well as local visual landmarks or doorways between two  
724 compartments. The bimodal directional tuning in the latter experiment may arise from  
725 constrained egocentric sampling along two-axes as a consequence of the multi-compartment  
726 environment segmenting two opposing walls. This proposed egocentric vector encoding of  
727 environment features in RSC may underlie functional correlates of local heading orientation,  
728 scene processing, or goal location in RSC in humans (Maguire, 2001; Epstein et al., 2007;  
729 Epstein et al., 2008; Marchette et al., 2014; Chrastil et al., 2015; Patai et al., 2019).

730 ***A network of vector-based egocentric spatial representation***

731 In addition to RSC, EBCs were also observed in both posterior parietal (PPC) and secondary  
732 motor cortices (M2) but not mEC which is commonly thought to represent space in allocentric  
733 coordinates. The presence of EBCs in PPC converges nicely with previous work demonstrating  
734 egocentric bearing sensitivity of PPC neurons to visual cues positioned along boundaries  
735 (Wilber et al., 2014). Computational models exploring circuitry for reference frame  
736 transformations and spatial imagery initially predicted EBCs to exist in PPC (Byrne et al., 2007).  
737 However, egocentric responses were initially reported in lateral entorhinal cortex, dorsal  
738 striatum, and postrhinal cortex, and now here in RSC, PPC, and M2 (Wang, Chen, et al., 2018;  
739 Hinman et al., 2019; LeChance et al., 2019; see also, Gofman et al., 2017). Accordingly, a  
740 picture of a distributed network of interconnected regions with egocentric vector representations  
741 is beginning to emerge. Given the presence of EBCs in several midline structures, it is possible  
742 that EBCs are also present in the anterior cingulate cortex as well as thalamic structures that  
743 innervate midline associative cortex (Weible et al., 2012; Matulewicz et al., 2019). Future  
744 investigations should focus on dependencies amongst the regions currently implicated, as the  
745 EBC network may possess functional and anatomical connectivity resembling the well-  
746 characterized extended head direction cell network (Taube et al., 2007).

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#### 754 **Author Contributions**

755 A.S.A., L.C.C., J.R.H., and M.E.H designed the study. A.S.A and L.C.C. conducted all  
756 experiments. A.S.A., F.R., and G.W.C. analyzed the data. A.S.A. and M.E.H wrote the paper. All  
757 authors assisted with revision of the manuscript.

#### 758 **Declaration of Interests**

759 The authors declare no competing interests.

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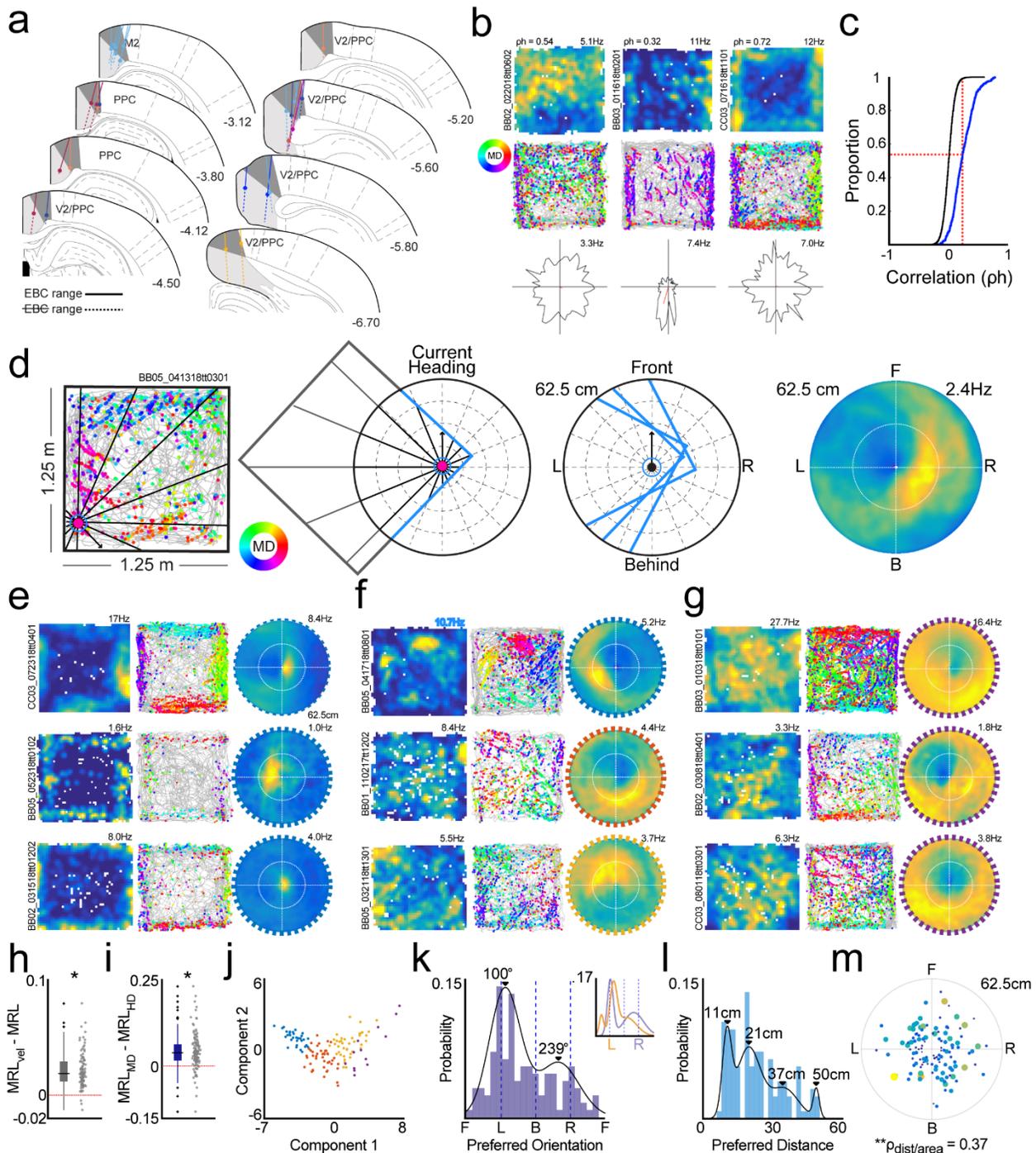
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1077 **Figures**



1078 **Figure 1. Ego-centric boundary vector representations of RSC neurons during free**  
 1079 **exploration.** **a.** Locations of RSC tetrode tracts where neurons with ego-centric boundary  
 1080 sensitivity were observed. For each tetrode, solid lines indicate range where EBCs were  
 1081 recorded and filled circles indicate most ventral location of EBC observation. **b.** Example two-  
 1082 dimensional rate maps (top), trajectory plots (middle), and head direction tuning plots (bottom)  
 1083 for three RSC neurons with significant stability in spatial firing. For trajectory plots, the position  
 1084 of the animal throughout the entire experimental session is depicted in gray. The location of

1085 individual spikes are shown with colored circles which indicate the corresponding movement  
1086 direction of the animal according to the legend on the left. **c.** Cumulative density function depicts  
1087 Spearman's rho calculated after correlating 2D ratemaps taken from the first and second halves  
1088 of each experimental session (blue). In black, distribution of spatial stability scores after  
1089 randomly shifting spike trains relative to position. Red vertical line shows 99<sup>th</sup> percentile of  
1090 randomized distribution and its intersection with the real distribution of spatial stability.  
1091 Percentage of neurons above red horizontal line have significant spatial stability. **d.** Schematic  
1092 for construction of egocentric boundary ratemaps (EBRs). Left and middle panels, an example  
1093 spike is mapped with respect to egocentric boundary locations in polar coordinates. Left, the  
1094 movement direction of the animal is determined for each spike (vector with arrow) and the  
1095 distance to wall intersections for all 360° are determined (sub-sample shown for clarity). Middle  
1096 left, boundaries within 62.5cm are referenced to the current movement direction of the animal  
1097 for a single spike. Middle right, example boundary positions for three spikes. Right, example  
1098 egocentric boundary ratemap (EBR). **e.** Two-dimensional ratemaps, trajectory plots, and  
1099 egocentric boundary ratemaps for 3 example RSC EBCs with animal-proximal receptive fields.  
1100 **f.** Same as in e, but for 3 RSC EBCs with animal-distal receptive fields. **g.** Same as in e and f,  
1101 but for 3 RSC EBCs with inverse receptive fields. **h.** Difference in strength (mean resultant  
1102 length, MRL) of EBC tuning when a speed threshold was applied ( $MRL_{vel}$ ) versus no speed  
1103 threshold (MRL). **i.** Difference in strength of EBC tuning when egocentric bearing was  
1104 referenced to movement direction ( $MRL_{MD}$ ) rather than head direction ( $MRL_{HD}$ ). **j.** For neurons  
1105 with significant egocentric boundary vector tuning, a scatter plot of first two principal component  
1106 (PCA) scores calculated on multiple features of egocentric boundary ratemaps. Colors show 4  
1107 subsets of EBCs determined from K-means clustering on the same feature space as PCA and  
1108 correspond to the colored boundaries around EBRs in e-g. **k.** Histogram of preferred orientation  
1109 of receptive field across all RSC EBCs. Black line, probability density estimate from two-  
1110 component Gaussian mixture model (GMM) on distribution of preferred orientation. Black  
1111 triangles indicate peaks in GMM estimate. **l.** Same as k, but for preferred distance of all RSC  
1112 EBC receptive fields. **m.** Polar scatter plot of preferred orientation versus preferred distance for  
1113 the full RSC EBC population. Circle size indicates the area of the egocentric boundary vector  
1114 receptive field.

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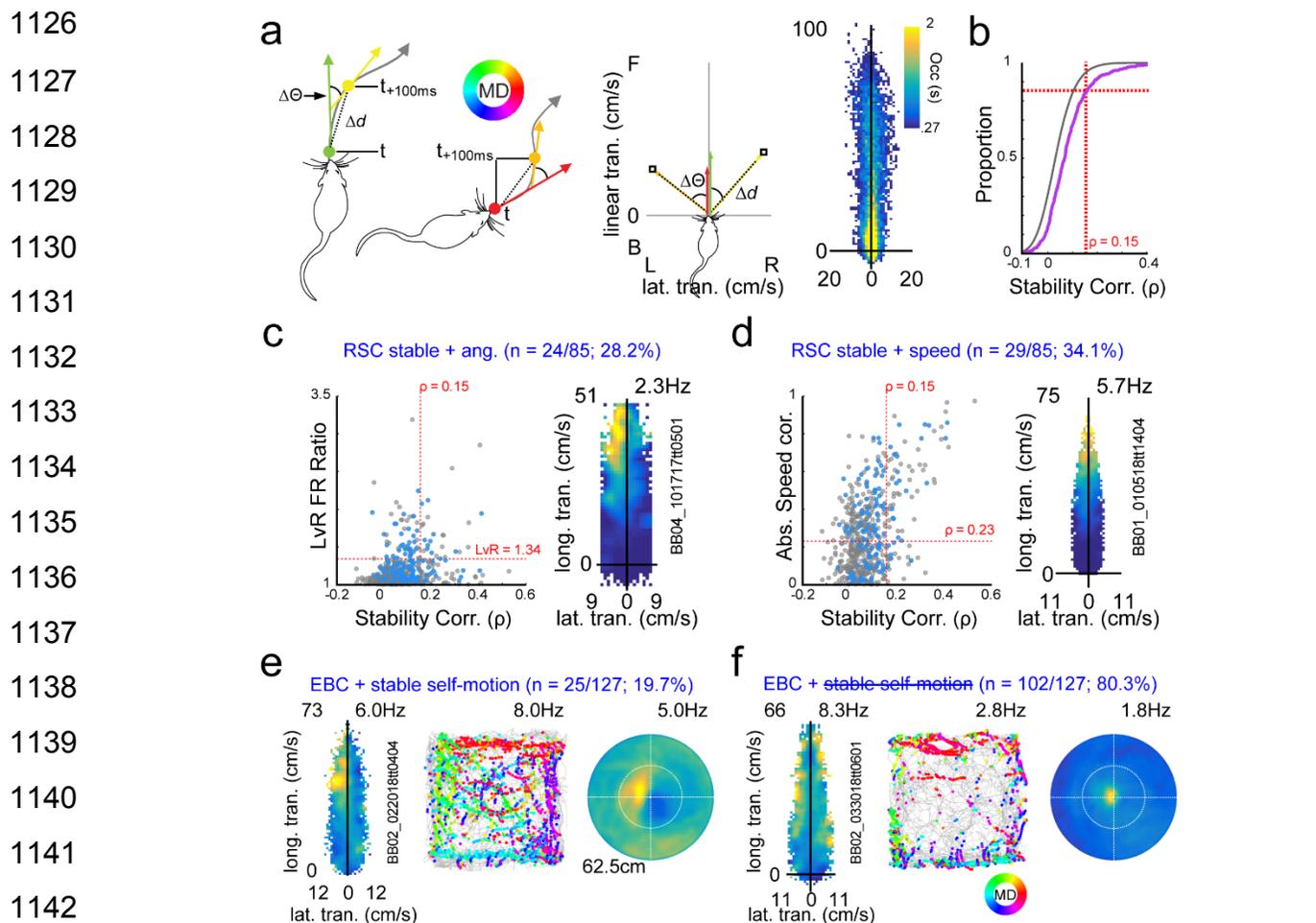
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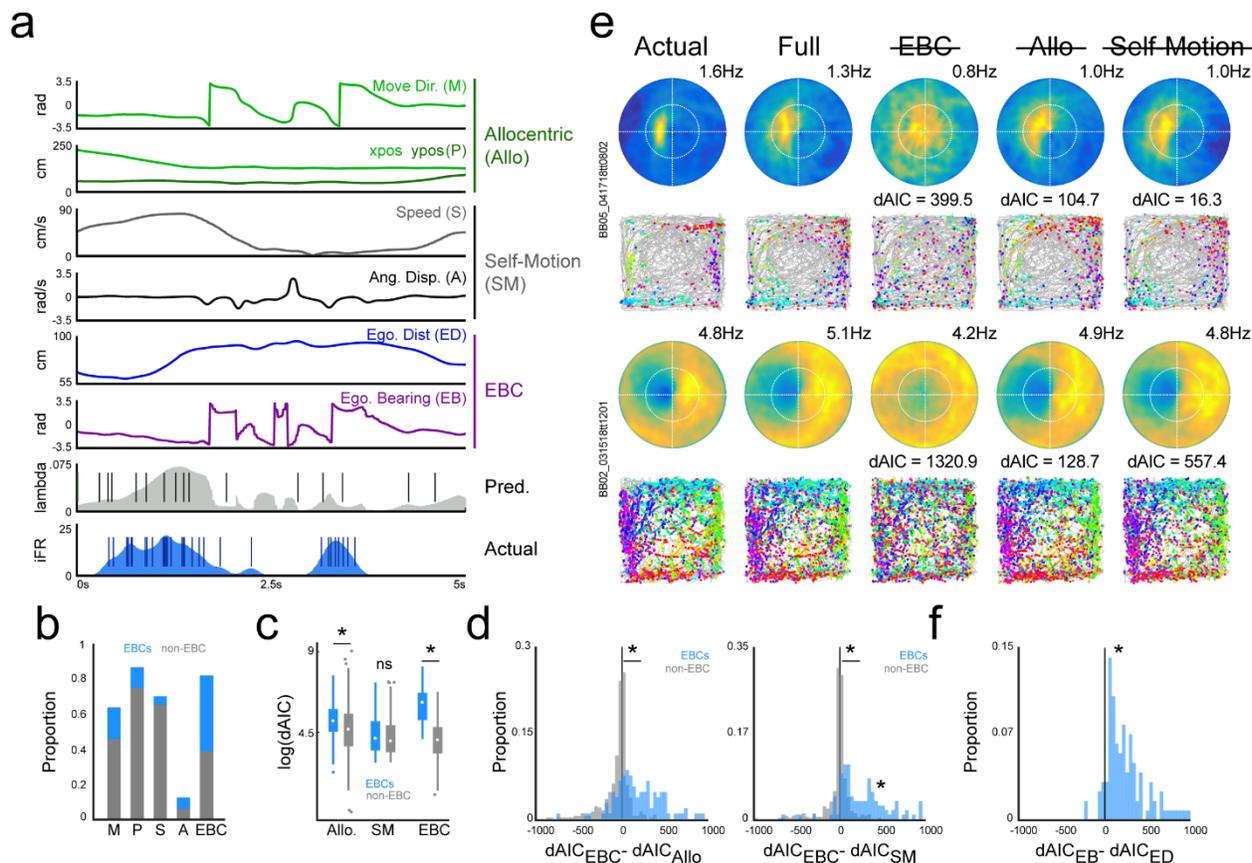
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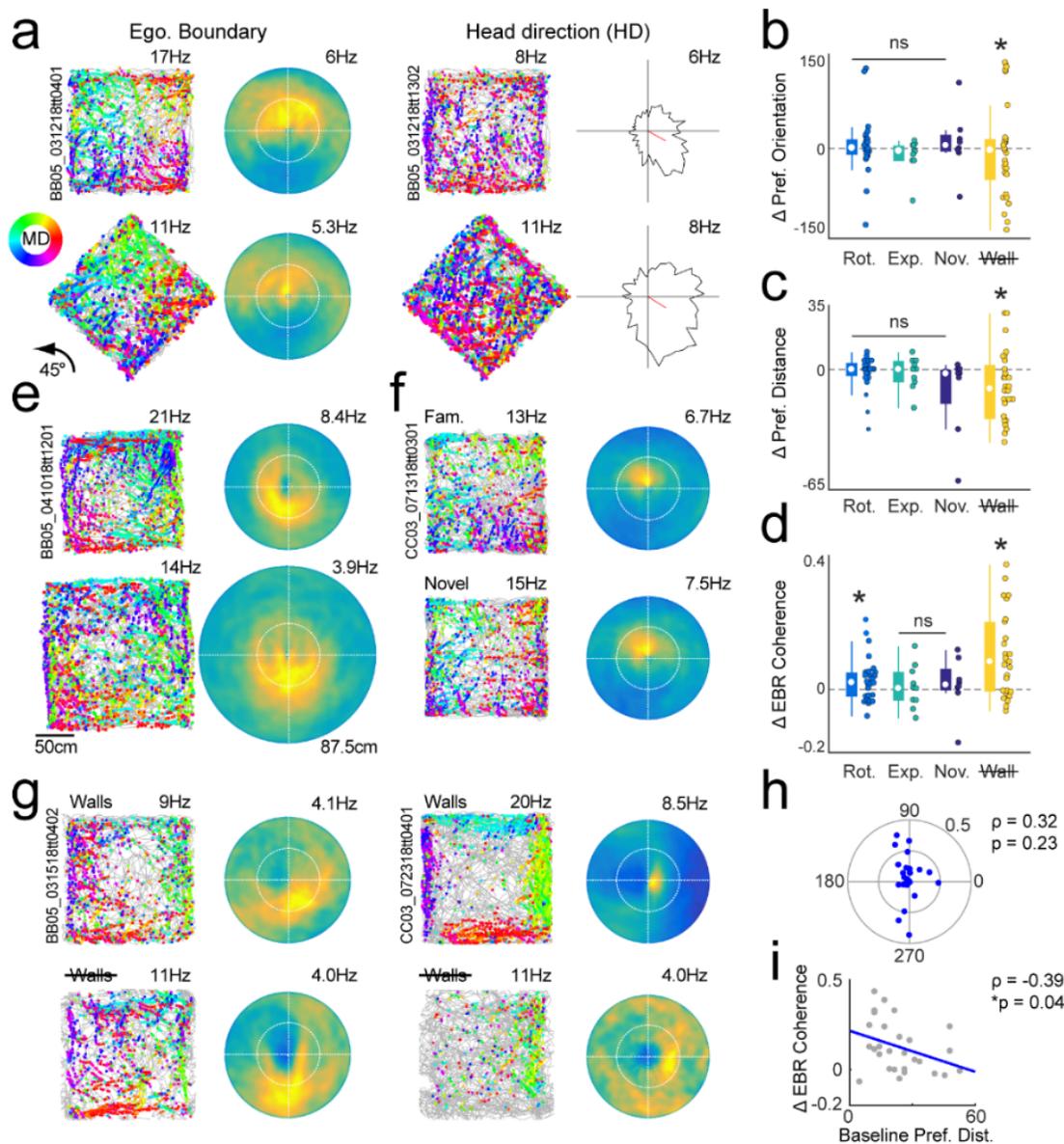
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**Figure 2. RSC egocentric boundary vector representations cannot be explained purely by self-motion correlates.** **a.** Schematic of generation of self-motion referenced ratemaps. Left, example angular and distance displacements across 100ms temporal windows for two hypothetical position samples. Middle, corresponding lateral and longitudinal displacement for left examples in self-motion referenced coordinates. Right, heat map depicting mean occupancy in seconds for lateral and longitudinal displacement combinations across a complete experimental session. **b.** In pink, cumulative density functions for self-motion ratemap stability values (Spearman's  $\rho$ ) for all RSC neurons (randomization in gray). Red vertical line shows 95<sup>th</sup> percentile of randomized distribution and its intersection with the real distribution of spatial stability. Percentage of neurons above red horizontal line have significant spatial stability. **c.** Left, spatial stability score (x-axis) versus absolute ratio of activity on left versus right halves of self-motion ratemaps (y-axis) for all RSC neurons. Blue dots correspond to identified RSC EBCs. Red lines and corresponding values correspond to 99<sup>th</sup> percentiles of randomized distributions for both metrics. Neurons with values in upper right region were determined to have significant angular displacement tuning. Right, example RSC neuron with significant firing rate modulation for counterclockwise movements. **d.** On left, same as in **c**, but for spatial stability score versus absolute correlation between mean firing rate and animal speed. Right, example RSC neuron with significant firing rate modulation as a function of animal speed. **e.** Example RSC EBC with stable self-motion correlates. **f.** Example RSC EBC with non-stable self-motion correlates.



1163 **Figure 3. Egocentric vector tuning is more robust than allocentric or self-motion**  
 1164 **correlates using a generalized linear modelling framework.** **a.** Example GLM predictors  
 1165 composing allocentric, self-motion, and egocentric vector classes with corresponding actual and  
 1166 predicted firing rates and spike trains over a five second window. **b.** Proportion of non-EBC RSC  
 1167 neurons (gray) and EBC RSC neurons (blue) exhibiting significant sensitivity to each predictor  
 1168 individually. M, movement direction; P, x- and y- position; S, speed; A, angular displacement;  
 1169 EBC, egocentric boundary. **c.** Boxplots depicting median and quartiles of log-transformed  
 1170 difference of Akaike information criteria scores (dAIC) for models with all allocentric, self-motion,  
 1171 or egocentric vector predictors removed (blue bars, EBCs; gray bars, non-EBCs). Larger dAICs  
 1172 indicate greater error in model fit with removal of a predictor class. **d.** Comparison of dAIC  
 1173 scores for models with egocentric vector versus allocentric predictors removed (left) or  
 1174 egocentric vector versus self-motion predictors removed (right) for EBCs (blue) and non-EBCs  
 1175 (gray). Rightward shifts indicate greater error in model fit for models with removed egocentric  
 1176 vector predictors. **e.** For two example RSC EBCs, predicted GLM spike trains from all models  
 1177 were utilized to construct egocentric boundary ratemaps and trajectory plots. Left column, actual  
 1178 egocentric boundary ratemap and corresponding trajectory plot. Second column, for the same cell,  
 1179 an egocentric boundary ratemap and corresponding trajectory plot for the generalized  
 1180 linear model constructed using all egocentric vector, allocentric, and self-motion predictors.  
 1181 Final three columns, egocentric boundary ratemaps and trajectory plots for each reduced model  
 1182 and corresponding dAIC scores. **f.** Comparison of dAIC scores for models with the egocentric  
 1183 bearing versus the egocentric distance removed reveal greater impact of egocentric bearing for  
 1184 EBCs.



1185 **Figure 4. EBCs are anchored to local boundaries, respond in novel environments, and**  
 1186 **lose sensitivity in arenas without explicit borders.** **a.** Left, trajectory plot and egocentric  
 1187 boundary ratemap (EBR) for an example EBC with similar egocentric boundary vector tuning in  
 1188 baseline experimental session (top) and a second session in an environment rotated 45°  
 1189 (bottom). Right, example head direction neuron sustains directional tuning across both  
 1190 conditions. **b.** Preferred orientation of EBC receptive fields in all arena manipulation sessions  
 1191 subtracted from preferred orientation in baseline sessions. **c.** Preferred distance of EBC  
 1192 receptive fields in all arena manipulation sessions subtracted from preferred distance in  
 1193 baseline sessions. **d.** EBC receptive field coherence in all arena manipulation sessions  
 1194 subtracted from receptive field coherence in baseline sessions. **e.** Trajectory plot and EBR for  
 1195 an example EBC with similar egocentric boundary vector tuning in baseline experimental  
 1196 session (top) and a second session in an expanded arena (bottom). **f.** Trajectory plot and EBR  
 1197 for an example EBC with similar egocentric boundary vector tuning in baseline experimental

1198 session (top) and a second session in a novel arena (bottom). **g.** Trajectory plot and EBR for  
1199 two example EBCs between baseline session (top) and session with walls removed (bottom).  
1200 Left EBC has a more distal receptive field and exhibits similar egocentric boundary vector  
1201 tuning. Right EBC has a more proximal receptive field and has disrupted tuning in arena with no  
1202 walls. **h.** For EBCs recorded in arenas without walls, the preferred orientation at baseline plotted  
1203 against the change in EBC receptive field coherence between the two sessions. **i.** Same as **h**,  
1204 but for change in coherence as a function of baseline preferred distance.

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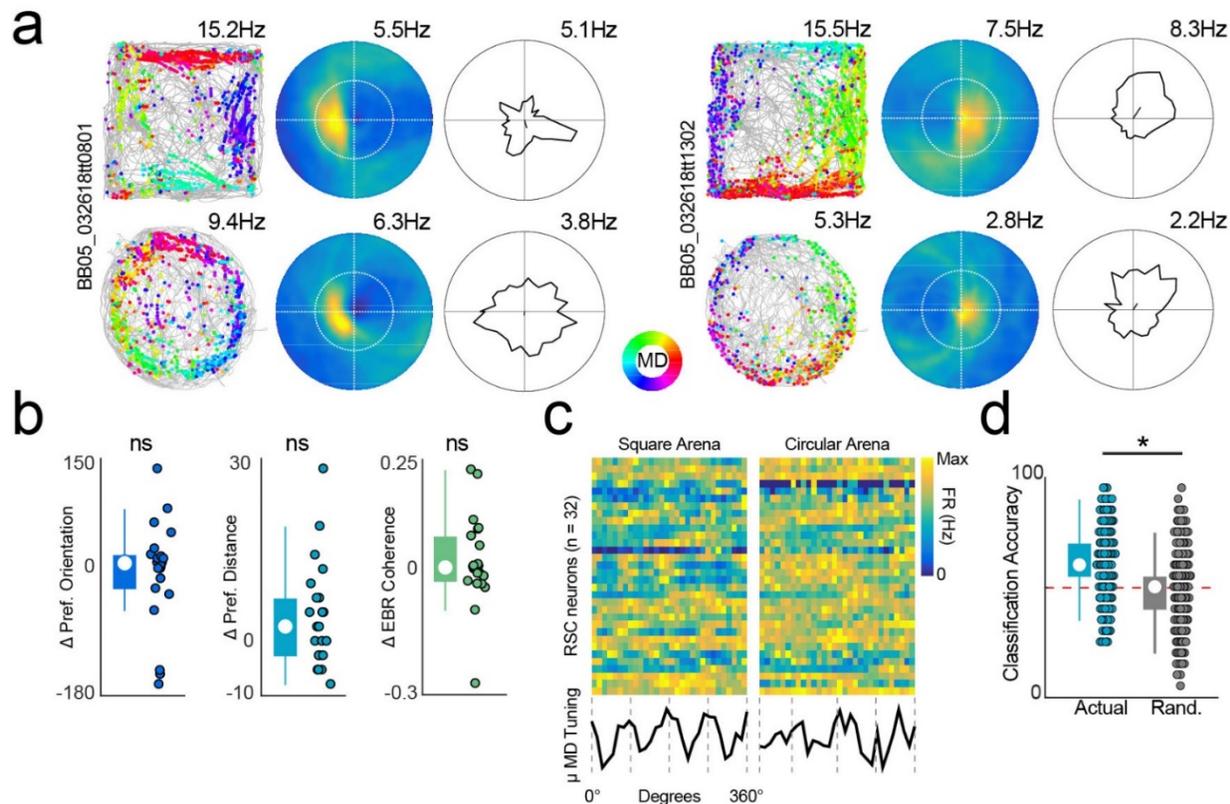
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1215 **Figure 5. RSC EBCs are insensitive to environmental geometry which generates a**  
 1216 **directional representation of environment shape.** **a.** Trajectory plots, egocentric boundary  
 1217 ratemaps (EBR), and movement direction tuning plots for two example RSC EBCs for  
 1218 experimental sessions in a square (top) and circular environment (bottom). **b.** Preferred  
 1219 orientation, preferred distance, and EBC receptive field coherence from recording sessions in  
 1220 the circular arena subtracted from the corresponding metrics in baseline sessions. **c.** Movement  
 1221 direction tuning plots for all RSC neurons in the square arena (left) and circular arena (right).  
 1222 Color depicts intensity of activation (blue is zero firing rate, yellow is maximum firing rate).  
 1223 Bottom in black, the average movement direction tuning across the full population of RSC  
 1224 neurons for the square and circular environments. Gray dashed lines depict 90° axes. **d.** Arena  
 1225 classification accuracy for linear discriminant analysis on movement direction tuning from **c.** In  
 1226 teal, actual classification. In gray, classification after randomizing arena identity. Red dashed  
 1227 line is statistical chance.

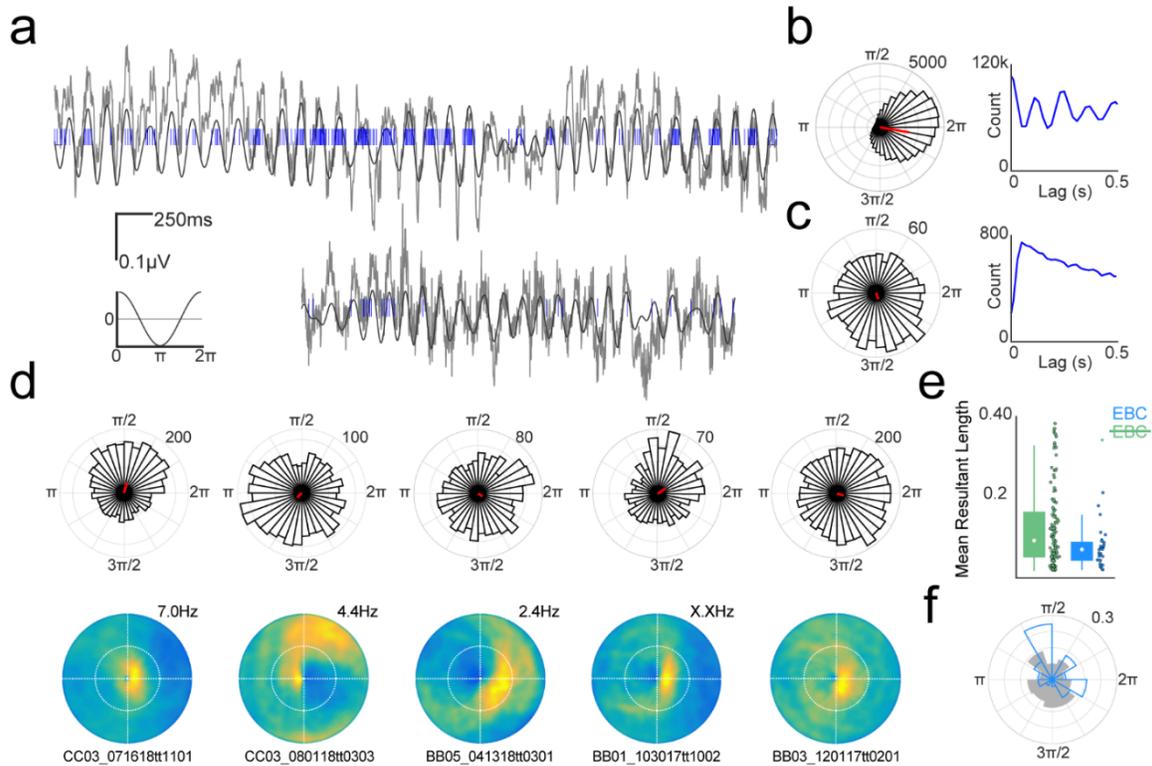
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1234 **Figure 6. A subset of RSC EBCs are theta modulated.** a. Two examples of RSC theta  
 1235 oscillation (gray) and spike train of simultaneously recorded neurons (blue). Bottom left, scale  
 1236 bar and schematic depicting correspondence between oscillation and theta phase. b. Left,  
 1237 circular histogram depicting spike counts as a function of theta phase for the neuron in the top  
 1238 row of a. Density of spikes near  $2\pi$  indicates that the neuron is locked to the peak of the theta  
 1239 phase. Right, spike train autocorrelogram for the same neuron shows theta rhythmic spiking. c.  
 1240 Same as in b, but for the neuron depicted in the bottom row of a. This neuron is significantly  
 1241 theta phase modulated but does not exhibit theta rhythmic spiking. d. Example theta phase  
 1242 modulated EBCs. Top row, circular histogram of spike counts versus theta phase. Bottom row,  
 1243 corresponding egocentric boundary ratemaps. e. Strength of theta phase modulation as  
 1244 measured by the mean resultant length for non-EBCs (green) and EBCs (blue). EBCs have  
 1245 significantly weaker theta modulation than non-EBCs with significant phase relationships. f.  
 1246 Preferred theta phase for all EBCs (blue) and non-EBCs (gray). EBCs tended to prefer the  
 1247 falling phase of the theta oscillation while non-EBCs preferred the rising phase but this  
 1248 difference was not significant.

1249 **Supplemental Figures**

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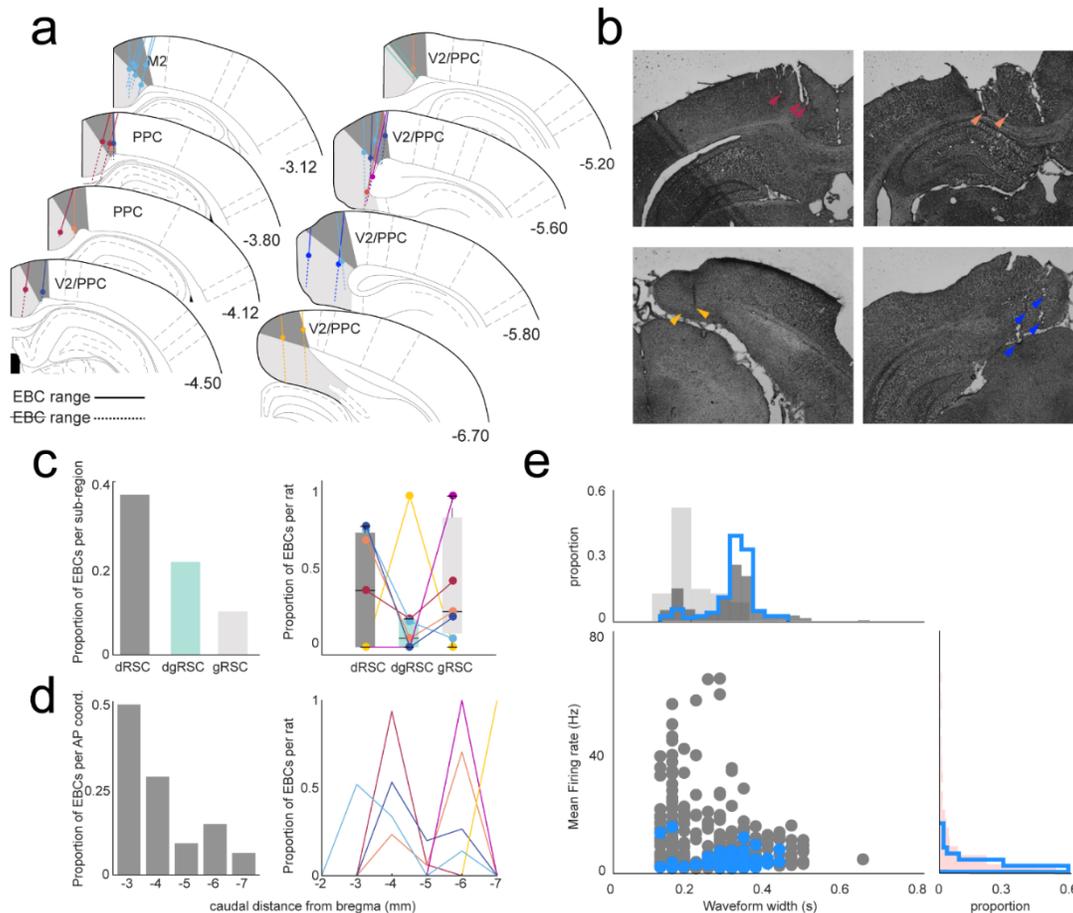
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1263 **Supplemental Figure 1. Locations of RSC egocentric boundary cells and identification as**

1264 **putative principal cells. a.** Schematic depicting location of tetrodes where EBCs were

1265 recorded. Each color corresponds to a different animal. Dark gray indicates dRSC and light gray

1266 indicates gRSC. Circles indicate the approximate dorsal-ventral (D/V) position of the wire for the

1267 last recording with EBCs on each tetrode. The dashed line indicates span of recordings in D/V

1268 axis that did not yield EBCs. Solid line indicates span of recordings in D/V axis that did yield

1269 EBCs. EBCs were also observed in secondary motor cortex (M2) or parietal cortex (V2/PPC)

1270 and these regions are noted. **b.** Example histology showing tetrodes in RSC. Tetrode locations

1271 are indicated with colored triangles which correspond to individual animals in **a.** **c.** Left,

1272 proportion (out of 1.0) of EBCs relative to all RSC neurons recorded in each RSC sub-region.

1273 Right, proportion of EBCs relative to all RSC neurons recorded in each sub-region for each

1274 animal (colored dots and lines). **d.** Same as for **c.**, but for approximate anterior-posterior location

1275 of EBC. **e.** Bottom left, scatterplot depicting mean firing rate versus width of spike waveform for

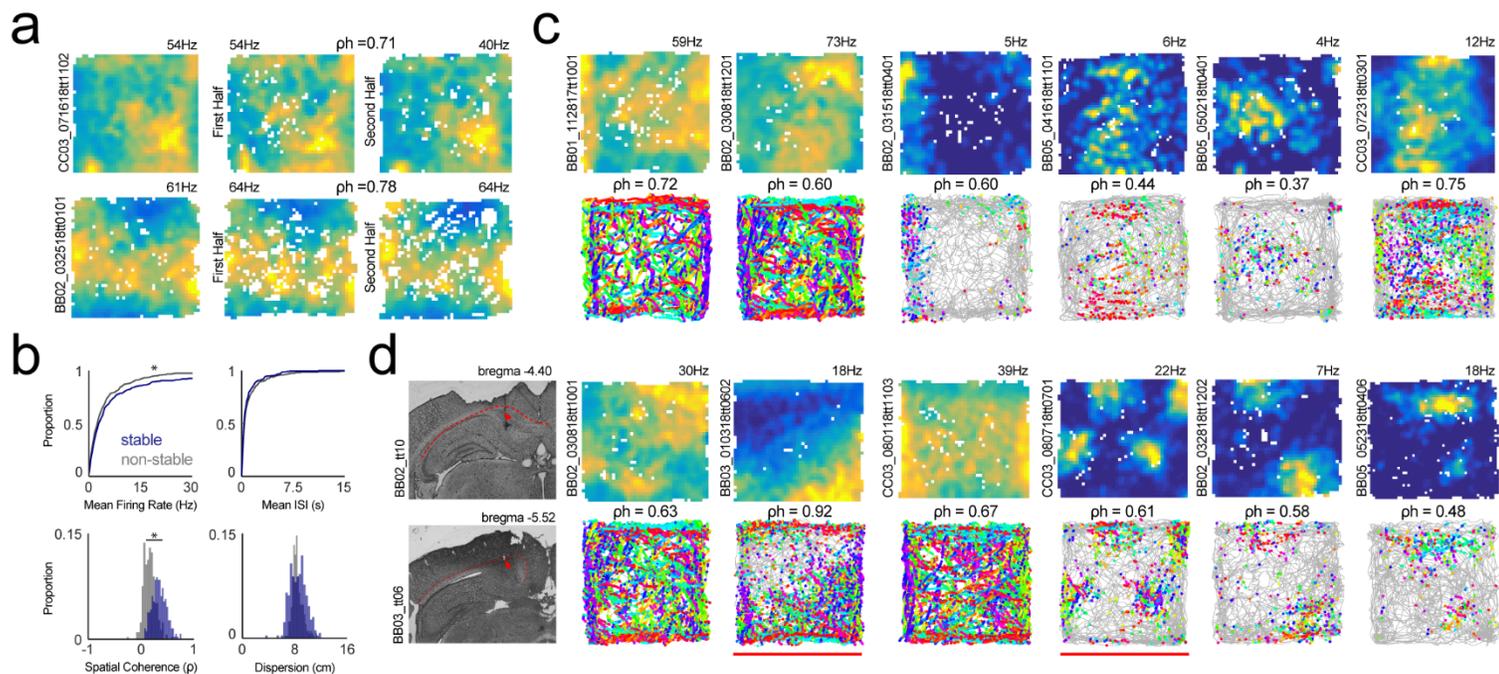
1276 all RSC neurons in gray and EBCs in blue. Top, histogram of waveform width clustered into fast

1277 (light gray) and slow waveforms (dark gray). Blue histogram corresponds to distribution of

1278 waveform width for all EBCs which have wider waveform widths. Right, histogram of mean firing

1279 rate (light pink). Blue histogram corresponds to distribution of mean firing rate of all EBCs

1280 demonstrating overall low mean firing rate.



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1282 **Supplemental Figure 2. RSC spatial stability during free foraging. a.** Two-dimensional (2D)

1283 firing ratemaps for two neurons (rows) showing process for determining spatial stability. Left

1284 column, 2D ratemap for full session. Middle and right columns, 2D ratemaps for the first and

1285 second halves of each session. Above ratemaps, corresponding spatial correlations between

1286 the two halves of the session. **b.** Properties of spatially stable (blue) versus non-stable (gray)

1287 RSC neurons. Top left, spatially stable cells had slightly lower mean firing rates than those that

1288 did not have spatial reliability (**sFigure2b**; stable = 3.02, IQR = 1.23 - 7.25Hz; not-stable = 4.93,

1289 IQR = 0.95 - 5.56Hz; Wilcoxon rank sum,  $z = -1.06$ ,  $p = 0.04$ ). Top right, mean inter spike

1290 intervals were not different between stable and non-stable neurons (stable = 0.36, interquartile

1291 range (IQR) = 0.15 - 0.99; non-stable = 0.41, IQR = 0.19 - 1.15; Wilcoxon rank sum,  $z = 1.89$ ,  $p$

1292 = 0.06). Bottom left, RSC neurons with spatially reliable activity had significantly greater spatial

1293 coherence than non-stable cells (stable Spearman's  $\rho = 0.33$ , IQR = 0.25 - 0.43; not-stable

1294 Spearman's  $\rho = 0.16$ , IQR = 0.08 - 0.23; Wilcoxon rank sum,  $z = -14.448$ ,  $p = 2.6 \times 10^{-47}$ ).

1295 Bottom right, spatial dispersion of the top 90% of firing rate bins in centimeters for stable and non-stable

1296 neurons (stable = 21.3cm, interquartile range (IQR) = 18.8 - 23.3cm; non-stable = 20.6cm, IQR

1297 = 19.7 - 22.2cm; Wilcoxon rank sum,  $z = 1.89$ ,  $p = 0.06$ ). **c.** 2D ratemaps and trajectory plots for

1298 example RSC neurons with significant spatial stability. **d.** Example 2D firing rate maps and

1299 trajectory plots for neurons recorded at or near the cingulum bundle. Left column shows two

1300 such recording locations with neurons recorded at each site demarcated with a horizontal red

1301 line. In some cases, recordings from the cingulum bundle resembled grid cells.

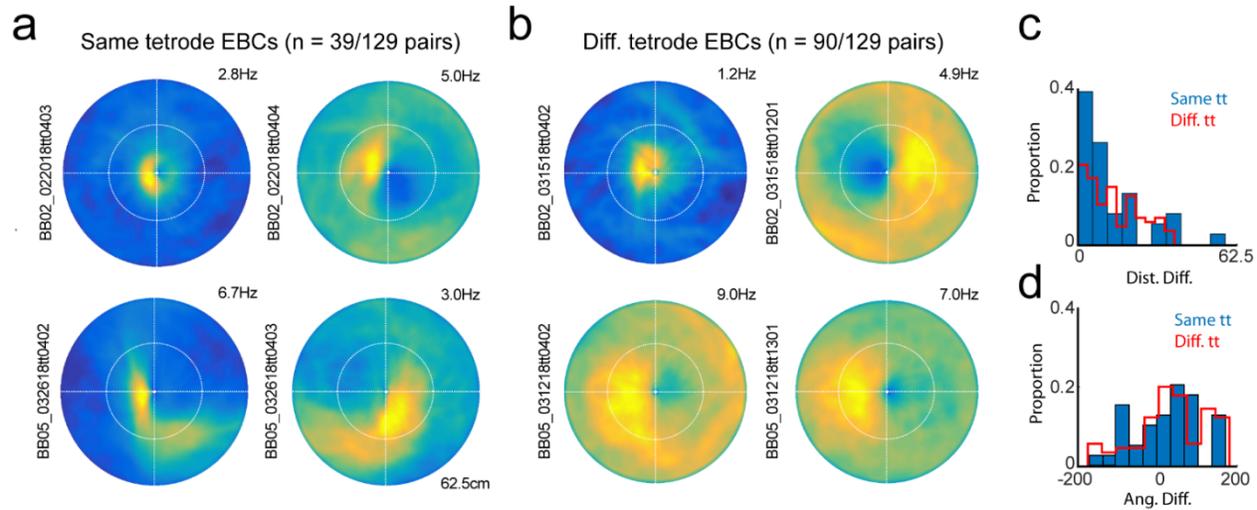
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1308 **Supplemental Figure 3. Simultaneously recorded egocentric boundary cells.** **a.** Each row  
1309 depicts egocentric boundary ratemaps for a pair of simultaneously recorded egocentric  
1310 boundary cells that were observed on the same recording tetrode. Top pair have similar EBC  
1311 receptive field locations while bottom pair have receptive fields on different sides of the animal.  
1312 **b.** Same as in **a**, but for simultaneously recorded neurons on different tetrodes. Top pair have  
1313 different receptive field locations while bottom pair have similar receptive fields. **c.** Histogram of  
1314 absolute difference in preferred distance for pairs of simultaneously recorded EBCs on the  
1315 same tetrode (in blue) and on different tetrodes (in red). **d.** Histogram of difference in preferred  
1316 orientation for pairs of simultaneously recorded EBCs on the same tetrode (in blue) and on  
1317 different tetrodes (in red).

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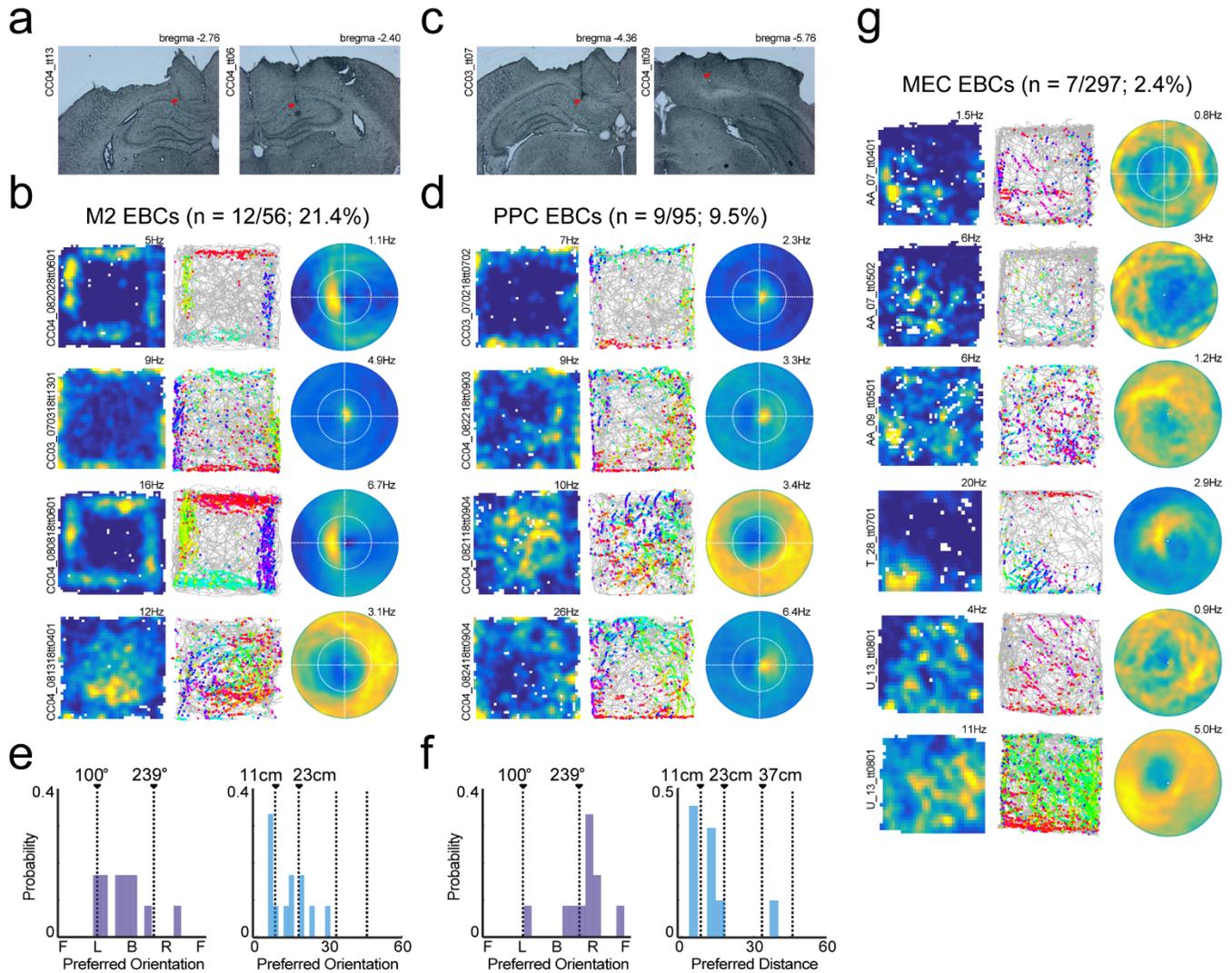
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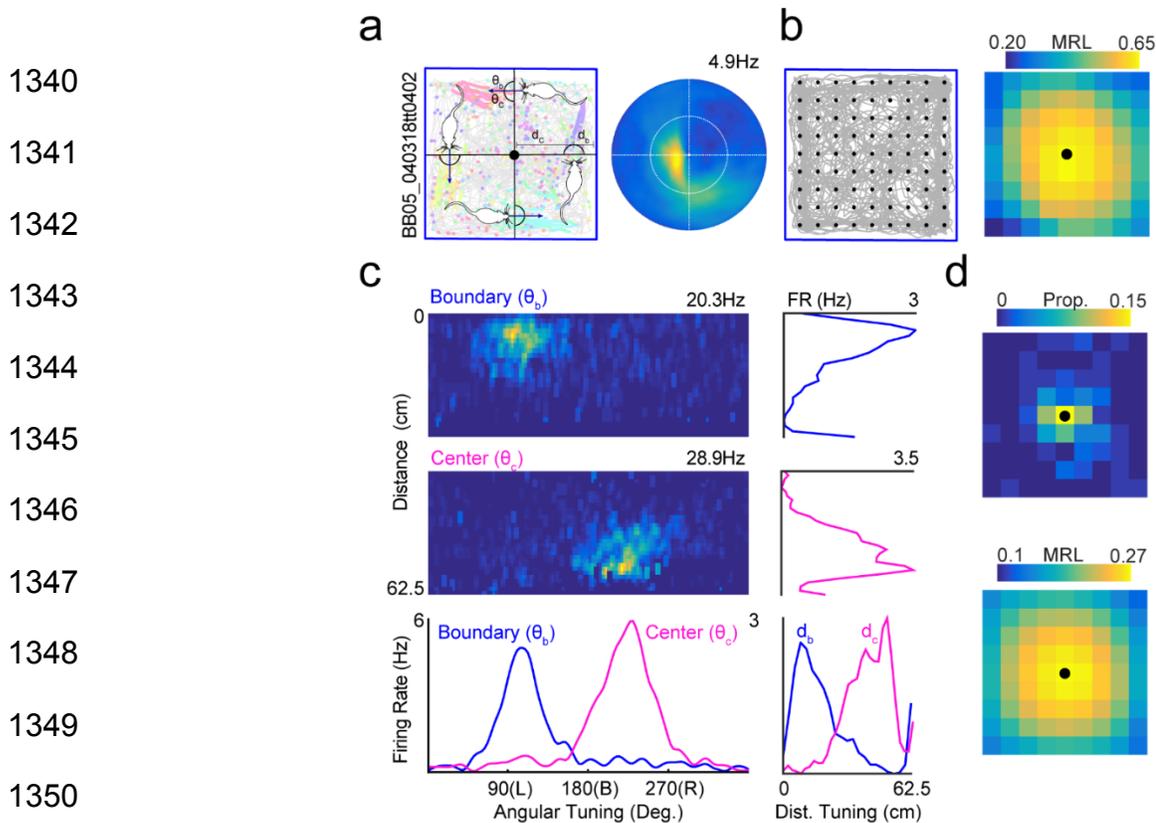
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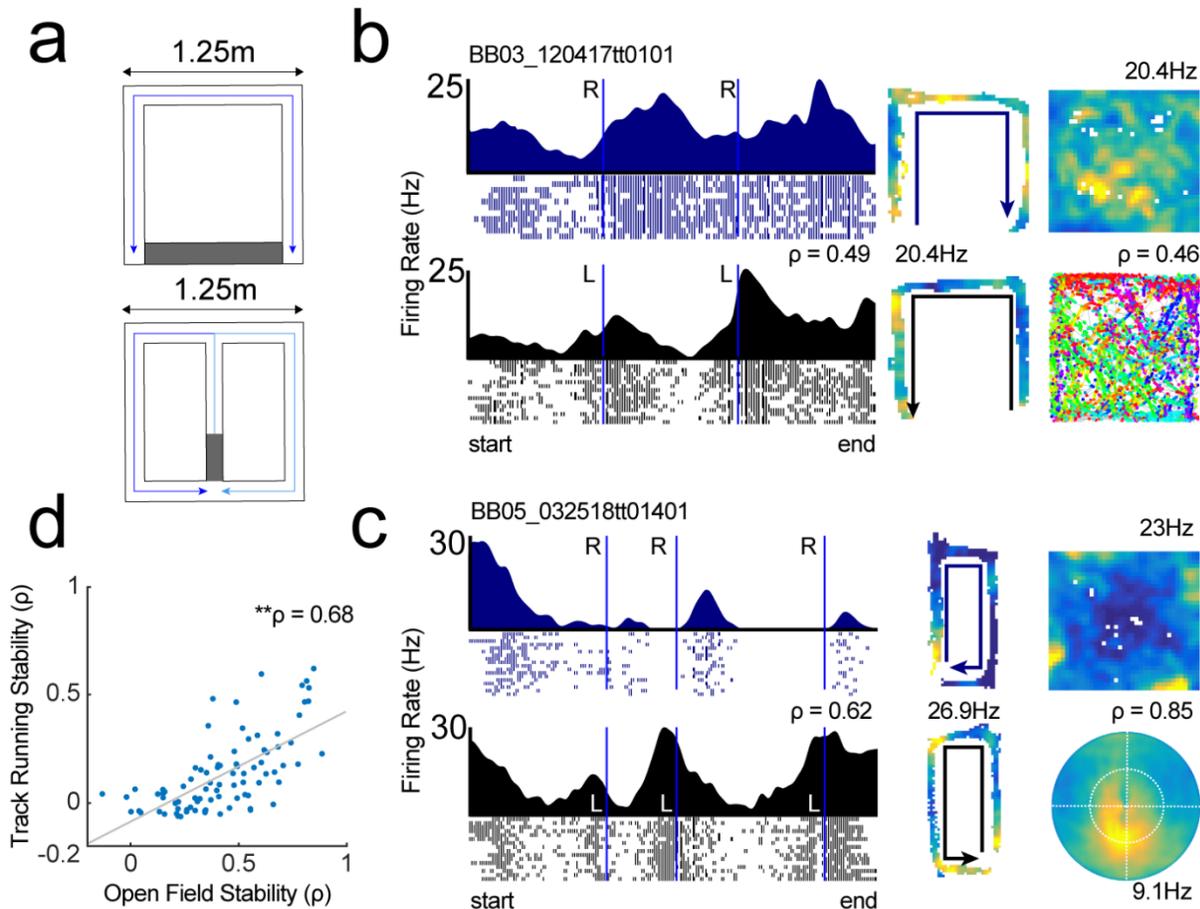
1329 **Supplemental Figure 4. Egocentric boundary cells in secondary motor cortex and**  
 1330 **posterior parietal cortex but not medial entorhinal cortex. a.** Example histology showing  
 1331 placement of recording tetrodes in secondary motor cortex (M2). **b.** 2D ratemaps, trajectory  
 1332 plots and egocentric boundary ratemaps (EBR) for 4 example M2 neurons with EBC sensitivity.  
 1333 **c.** Example histology showing placement of recording tetrodes in parietal cortex (V2/PPC). **d.**  
 1334 2D ratemaps, trajectory plots and egocentric boundary ratemaps (EBR) for 4 example V2/PPC  
 1335 neurons with EBC sensitivity. **e.** Preferred orientation and distance for M2 neurons identified as  
 1336 EBCs. **f.** Preferred orientation and distance for V2/PPC neurons identified as EBCs. **g.** All  
 1337 detected medial entorhinal cortex EBCs.

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1351 **Supplemental Figure 5. Egocentric vector tuning to center of arena for generalized linear**  
1352 **models. a.** Left, schematic depiction of the angular and distance relationships between the  
1353 animal, the boundary, and the arena center when the animal is running parallel to arena walls.  
1354 Right, egocentric boundary rate map for an EBC with trajectory plot on left plot. **b.** To analyze  
1355 whether the egocentric bearing and distance to the arena center could function as a predictor in  
1356 generalized linear modelling we analyzed strength of egocentric bearing and distance tuning to  
1357 a 9x9 grid of locations that spanned the entirety of the environment (see Wang, Chen, et al.,  
1358 2018). Right plot depicts the strength (as measured by mean resultant length, MRL) of  
1359 egocentric vector tuning to all 9x9 grid locations for the neuron depicted in **a**. The heatmap  
1360 corresponds to magnitude of the MRL, and the black dot depicts the grid location with the  
1361 strongest egocentric tuning which, in this case, corresponds to the center of the arena. **c.** For  
1362 the same neuron we calculated egocentric bearing and distance tuning to the nearest point on  
1363 the boundary (top left EBC heatmap) and the grid location with maximum tuning (center of  
1364 arena, bottom left EBC heatmap), and compared their vector components by averaging across  
1365 angular and distance dimensions of each matrices. Plots to the right of each EBC heatmap  
1366 show average distance tuning to the nearest boundary (blue) and center (pink) with each  
1367 overlaid on the bottom right plot. Below the EBC heatmaps are overlaid averages of preferred  
1368 angular tuning for nearest boundary (blue) and arena center (pink). The tuning plots at the  
1369 bottom for both reference points show a clear relationship and so we utilized the egocentric  
1370 boundary and distance to the central location for GLM analyses. **d.** Top, 2D histogram showing  
1371 the proportion of RSC EBCs with maximum MRLs at each grid location. Greatest proportion is  
1372 at or near the center of the arena in baseline sessions when boundaries are excluded. Bottom,  
1373 mean MRL tuning for all grid locations across all RSC EBCs shows maximum egocentric vector  
1374 tuning to the arena center in baseline sessions when boundaries are excluded.



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1376 **Supplemental Figure 6. Comparison between RSC neurons recorded in free foraging and**  
1377 **during track running.** **a.** Schematic of two different tracks animals ran along. Gray zone

1378 indicates reward location. **b.** Linearized firing rate vectors split into left-turning and right-turning  
1379 routes with corresponding 2D ratemaps for two RSC neurons. Left column in blue, mean firing rate  
1380 for route with right turns and trial spike trains. Left column in black, mean firing rate for  
1381 route with left turns and trial spike trains. 2D ratemaps for track running depicted in middle  
1382 column. Right column, 2D ratemap and trajectory plot. **c.** Same as **b**, but right column depicts  
1383 2D ratemap and corresponding egocentric boundary ratemap. This neuron shows spatial  
1384 selectivity on track near turns and is an egocentric boundary neuron in the open field. Critically,  
1385 the EBC receptive field does not explain apparent counterclockwise (left) turning preference on  
1386 the track. **d.** Scatterplot depicting Spearman's  $\rho$  for open field stability versus track running  
1387 stability for all RSC neurons recorded in both conditions. Significant positive correlation  
1388 indicates that neurons that were stable in one condition were more likely to be stable in the  
1389 other.

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1393 **Methods**

1394 **Subjects.** Male Long-Evans rats (n = 7; Charles River Labs, Wilmington, MA) were housed  
1395 individually in plexiglass cages and kept on a 12-h light/dark cycle. Rats had continuous access  
1396 to food during a habituation period lasting approximately 1 week. After this period, animals were  
1397 food restricted until they reached 85-95% of their weight during free feeding. Water was  
1398 available continuously. All procedures were approved by the Institutional Animal Care and Use  
1399 Committee at Boston University.

1400 **Shaping/behavior.** Animals were acclimated to the primary testing room for approximately one  
1401 week. During acclimation, rats were handled by multiple researchers and trained to consume  
1402 both Froot Loops (General Mills, Battle Creek, MI) and 45mg chocolate pellets (Bio-Serv,  
1403 Flemington, NJ). After animals readily ate both food items they were exposed to one of two  
1404 familiar open fields used for baseline sessions for 20 to 45 minutes per day. The first open field  
1405 was 1.25m<sup>2</sup> with four black walls 30 cm in height. The second arena was 1.25m<sup>2</sup> with three black  
1406 walls and one white wall 30 cm in height. Both arenas were placed on a dark gray textured  
1407 rubber floor that was cleaned between sessions. Two animals (BB01 and BB03) performed a  
1408 goal directed navigation task in a different arena and testing room prior to being utilized for the  
1409 current study.

1410 **Surgical procedures.** Rats were surgically implanted with custom-fabricated hyperdrives in  
1411 aseptic conditions. Each hyperdrive was composed of 12 to 16 nickel chromium tetrodes (12µm,  
1412 Kanthal-Sandvik, Hallstahammar, Sweden) that could be independently moved in as small as  
1413 35µm increments. Guide cannulae for each tetrode were collectively configured in one of three  
1414 arrays: 1) filling a single hypodermic tube approximately 2mm<sup>2</sup> in diameter, 2) across two  
1415 conjoined hypodermic tubes that were ~1.5mm<sup>2</sup> in diameter spanning a total of ~3mm or, 3)  
1416 across four conjoined hypodermic tubes that were ~1.25mm<sup>2</sup> in diameter and spanned a total of  
1417 ~5mm. For the second and third configurations, the long axis of the electrode array was  
1418 positioned to target an extended region of the anterior-posterior axis of retrosplenial cortex.

1419 Animals were anesthetized using a combination of inhaled isoflurane (0.5% initial concentration)  
1420 and ketamine/xylazine administered via intraperitoneal injection (Ketamine: 12.92 mg/kg,  
1421 Acepromazine: 0.1mg/kg, Xylazine: 1.31 mg/kg). After the animal was determined to be under  
1422 anesthesia (as assessed via loss of the toe pinch reflex), the animal was positioned in a  
1423 stereotaxic apparatus, a 0.1mg/kg dose of atropine was administered subcutaneously, and the  
1424 head was shaved. Excess hair was removed via application of Nair (Church & Dwight Co.,  
1425 Ewing, NJ) and the scalp was cleaned with 70% ethanol and Betadine (Avrio Health L.P.,

1426 Stamford, CT). 0.9% sodium chloride was administered subcutaneously hourly throughout the  
1427 surgical procedure.

1428 Following a midline incision and subsequent clearing of connective tissue, a ground screw was  
1429 positioned above the cerebellum and 5-8 anchor screws were affixed in an array around the  
1430 perimeter of the exposed skull. A large craniotomy was centered above retrosplenial cortex  
1431 (relative to bregma: A/P: -2mm to -7mm; M/L  $\pm$ 0mm-1.75mm). The exact size and position of  
1432 the craniotomy was dependent upon the aforementioned configuration of the hyperdrive array.  
1433 Next, dura was resected and the hyperdrive was positioned such that guide cannula rested  
1434 gently against the dorsal surface of the brain. Excess exposed tissue within the craniotomy was  
1435 protected with Kwik-Sil (World Precision Instruments, Sarasota, FL), and the implant was  
1436 secured to anchor screws with dental cement. Tissue around the implant was cleaned with  
1437 saline, 70% ethanol, and hydrogen peroxide. Antibiotic ointment was applied into the wound,  
1438 sutured if necessary, and Neosporin was applied around the site. Prior to removal from  
1439 anesthesia tetrodes were lowered approximately 0.25mm D/V. Animals received post-operative  
1440 antibiotics (Baytril: 10mg/kg) and analgesics (Ketofen: 5.0mg/kg) for five days after surgery and  
1441 were freely fed. After one-week post-operation animals were handled and reacclimated to the  
1442 testing room and free foraging environments prior to the initiation of experiments.

1443 **Electrophysiological recordings.** Neural signals were amplified at two headstages attached to  
1444 a 64 channel electrical interface board and acquired by a 64 channel Digital Lynx acquisition  
1445 system (Neuralynx, Bozeman, MT) Signals were digitized, filtered (0.3-6.0kHz), and amplified  
1446 (5,000-20,000X). Timestamps of individual action potentials were detected online when the  
1447 signal crossed an acquisition threshold on any individual electrode composing a tetrode. At the  
1448 conclusion of each experiment, spikes were manually sorted to individual single units using  
1449 Offline Sorter (Plexon Inc., Dallas, TX) and the following features: peak-valley, peak, and  
1450 principal components 1-3. Two diodes attached to the electrode implant delineated the location  
1451 of the animal which was tracked at 30Hz via a camera positioned above the recording arena.

1452 An experimental session began with an initial 15-30 minute recording while the animal free  
1453 explored and consumed either Froot Loops scattered by an experimenter, chocolate pellets  
1454 released at random intervals from a dispenser positioned above the arena, or both (Open Ephys  
1455 Pellet Dispenser designed by Maurer Lab, <https://github.com/jackpkenn/PelletDispenser>). After  
1456 adequate spatial coverage was achieved the animal was removed from the arena and placed  
1457 back in its home cage for a period of 1 hour minimally. During this period, the experimenter  
1458 completed clustering of action potentials into single neurons and examined two-dimensional

1459 spatial ratemaps (described below) to assess whether any of the cells from the baseline session  
1460 exhibited egocentric boundary vector sensitivity. If no EBCs were present, tetrodes were  
1461 typically lowered between 35 and 70 $\mu$ m. If EBCs were present, a second experimental session  
1462 was conducted in which the animal explored an open field in one or more of the following  
1463 configurations:

- 1464 1) Open field session: The same arena from the baseline session to assess the stability of  
1465 EBCs in familiar environments.
- 1466 2) Open field rotation: The same arena from the baseline session rotated 45° relative to the  
1467 testing room and all visible distal cues present therein.
- 1468 3) Circular open field: A familiar circular arena of 1.1m diameter.
- 1469 4) Open field expansion or contraction: If an expansion experiment was planned the initial  
1470 baseline session was conducted in a familiar 1.25m<sup>2</sup> arena that enabled reconfiguration  
1471 of walls. Following the baseline session, walls were uniformly moved outwards relative to  
1472 the center point of the baseline configuration to a size of 1.5m<sup>2</sup> or larger. In a small  
1473 number of recordings, walls were either: moved non-uniformly to increase the length of  
1474 the arena along a single axis of the environment or, contracted to decrease the size of  
1475 the environment. Across all possible wall movements, the arena was altered in size by  
1476 approximately 20% along each dimension.
- 1477 5) No wall open field: If a no wall arena experiment was planned the initial baseline session  
1478 was conducted in a familiar 1.25m<sup>2</sup> environment that was placed approximately 20cm  
1479 above the floor. Following this session, the walls were removed from this arena creating  
1480 a platform with no walls that the rat explored for a second time. In a small number of  
1481 sessions, the animal explored the familiar 1.25m<sup>2</sup> that was situated on the testing room  
1482 floor, then in a second session, explored a different familiar arena lacking walls placed  
1483 approximately 8" above the floor.

1484 All arenas were positioned such that the animal could easily see the broader recording room  
1485 and an array of stable distal cues. In some cases, the manipulation session was followed by a  
1486 return session to the familiar baseline arena.

1487 **Histology.** Animals were anesthetized with 0.5% isoflurane and small electrical lesions were  
1488 made at the end of tetrodes that had preliminarily been identified as having EBCs. After one  
1489 week, animals were deeply anesthetized with isoflurane, injected with sodium pentobarbital, and  
1490 transcardially-perfused with 0.9% saline followed by 10% formalin. The brain was extracted from  
1491 the skull and post-fixed overnight with 10% formalin, then stored in 0.1M phosphate buffer until

1492 two days before slicing when it was transferred to a 0.1M phosphate buffer/30% sucrose  
1493 solution. The brain was snap frozen using 2-methylbutane and sliced into 40-50um coronal  
1494 sections using a cryostat (Leica CM3050S, Leica Biosystems, Buffalo Grove, IL). Slices were  
1495 mounted on gelatin covered microscope slides and allowed to dry, then photographed (Nikon  
1496 DXM1200 camera mounted on Olympus BX51 light microscope). Tetrode lesions and tracts  
1497 were clearly visible in all animals. Coordinates of tetrode locations and final tetrode depths were  
1498 registered with respect to pre-implant photographs of guide cannulae array configurations and  
1499 tetrode turning logs, respectively.

## 1500 **Data Analysis**

1501 *Two-dimensional (2D) spatial ratemaps and spatial stability.* Animal positional occupancy within  
1502 an open field was discretized into 3x3cm spatial bins. For each neuron, the raw firing rate for  
1503 each spatial bin was calculated by dividing the number of spikes that occurred in a given bin by  
1504 the amount of time the animal occupied that bin. Raw firing rate maps were smoothed with a 2D  
1505 Gaussian kernel spanning 3cm to generate final rate maps for visualization. Individual raw firing  
1506 rate maps were also computed after dividing the session into halves. To assess spatial stability  
1507 of an individual RSC neuron, the similarity of the two raw firing rate maps from non-overlapping  
1508 halves of the recording session was calculated using the non-parametric Spearman's rank  
1509 correlation coefficient. To determine whether a given spatial stability value was greater than  
1510 expected by chance we next conducted randomization tests wherein the spike train for each  
1511 RSC neuron was circularly shifted relative to spatial position 100 times, and individual firing rate  
1512 maps were constructed for non-overlapping halves that were then correlated. The spatial  
1513 stability correlation values following randomizations were collapsed into a single distribution for  
1514 all neurons and randomizations and the 99<sup>th</sup> percentile of all values was calculated. RSC  
1515 neurons with real spatial stability correlations greater than this threshold were determined to  
1516 have robust two-dimensional spatial stability.

1517 *Construction of egocentric boundary ratemaps.* Egocentric boundary ratemaps (EBR) were  
1518 computed in a similar manner as 2D spatial ratemaps but referenced relative to the animal  
1519 rather than the spatial environment. The position of the boundaries relative to the animal was  
1520 calculated for each position sample (i.e. frame). For each frame, we found the distance, in  
1521 2.5cm bins, between arena boundaries and angles radiating from 0° to 360° in 3° bins relative to  
1522 the rat's position. Critically, angular bins were referenced to the current movement direction of  
1523 the animal such that 0°/360° was always directly in front of the animal, 90° to its left, 180°  
1524 directly behind it, and 270° to its right. Intersections between each angle and environmental

1525 boundaries were only considered if the distance to intersection was less than or equal to  $\frac{1}{2}$  the  
1526 length of the most distant possible boundary (in most cases this threshold was set at 62.5cm or  
1527 half the width of the arena). In any frame the animal occupied a specific distance and angle  
1528 relative to multiple locations along the arena boundaries, and accordingly, for each frame, the  
1529 presence of multiple boundary locations were added to multiple  $3^\circ \times 2.5\text{cm}$  bins in the  
1530 egocentric boundary occupancy map. The same process was completed with the locations of  
1531 individual spikes from each neuron, and an EBR was constructed by dividing the number of  
1532 spikes in each  $3^\circ \times 2.5\text{cm}$  bin by the amount of time that bin was occupied in seconds.  
1533 Smoothed EBRs were calculated by convolving each raw EBR with a 2D Gaussian kernel (5 bin  
1534 width, 5 bin standard deviation).

1535 For EBR construction and other analyses in the current work, movement direction was defined  
1536 as the instantaneous derivative of the position signal whereas head direction was the  
1537 instantaneous angle calculated from the location of two position tracking diodes. Movement  
1538 direction was utilized as the primary directional variable in EBR construction but a comparison  
1539 to head direction determined the latter to be a less robust signal for egocentric boundary vector  
1540 tuning.

1541 *Head direction cell identification.* For each neuron, the mean resultant length of the firing rate as  
1542 a function of head direction was calculated as

1543 
$$R_m = \frac{\cos(\bar{\theta}) \sum_{i=1}^n F_i \cos(\theta_i) + \sin(\bar{\theta}) \sum_{i=1}^n F_i \sin(\theta_i)}{\sum_{i=1}^n F_i}$$

1544 where  $\bar{\theta}$  was the head direction of firing and  $F_i$  and  $\theta_i$  were the firing rate and head direction for  
1545 bin  $i$ . Head direction cells (HD) were identified as those cells with  $R_m$  greater than 0.20. HD cells  
1546 ( $n = 27/555$ ; 4.9% of all RSC neurons) were removed from the possible pool of RSC EBCs.

1547 *Identification of neurons with egocentric boundary vector tuning.* To identify neurons with  
1548 significant egocentric boundary vector sensitivity we began by calculating the mean resultant  
1549 (MR) of the cell's egocentric boundary directional firing collapsed across distance to the  
1550 boundary. The mean resultant was calculated as

1551 
$$MR = \left( \sum_{\theta=1}^n \sum_{D=1}^m F_{\theta,D} * e^{i*\theta} \right) / (n * m)$$

1552 where  $\theta$  is the orientation relative to the rat,  $D$  is the distance from the rat,  $F_{\theta,D}$  is the firing rate in  
1553 a given orientation-by-distance bin,  $n$  is the number of orientation bins,  $m$  is the number of

1554 distance bins,  $e$  is the Euler constant and  $i$  is the imaginary constant. The MRL is defined as the  
1555 absolute value of the mean resultant and characterized the strength of egocentric bearing tuning  
1556 to environment boundaries. We next computed the preferred orientation of the egocentric  
1557 boundary ratemap as the mean resultant angle (MRA)

1558 
$$MRA = \arctan2\left(\frac{\text{imag}(MR)}{\text{real}(MR)}\right)$$

1559 We estimated the preferred distance by fitting a Weibull distribution to the firing rate vector  
1560 corresponding to the MRA and finding the distance bin with the maximum firing rate. The MRL,  
1561 MRA, and preferred distance were calculated for each neuron for the two halves of the  
1562 experimental session independently. Next, the MRL was computed for each neuron following 100  
1563 random, unrestricted, circular shifts of the spike train relative to position. The 99<sup>th</sup> percentile of the  
1564 MRL distribution across all neurons was determined.

1565 A neuron was characterized as having egocentric boundary vector tuning (i.e. an EBC) if it  
1566 reached the following criteria: 1) the MRL for both halves of the baseline session were greater  
1567 than the 99<sup>th</sup> percentile of the randomized distribution, 2) the absolute circular distance in  
1568 preferred angle between the 1<sup>st</sup> and 2<sup>nd</sup> halves of the baseline session was less than 45°, and 3)  
1569 the absolute difference in preferred distance between the 1<sup>st</sup> and 2<sup>nd</sup> halves of the baseline  
1570 session was less than 75% of the preferred distance for the entire session.

1571 To refine our estimate of the preferred orientation and preferred distance of each neuron we  
1572 calculated the center of mass (COM) of the receptive field defined after thresholding the entire  
1573 EBR at 75% of the peak firing and finding the largest continuous contour ('contour' in Matlab).  
1574 We repeated the same process for the inverse EBR for all cells to identify both an excitatory and  
1575 inhibitory receptive field and corresponding preferred orientation and distance for each neuron.

1576 *Clustering of EBC receptive field sub-types.* In an effort to identify trends in receptive field sub-  
1577 types including those exhibiting inverse receptive fields, we next clustered the EBC sub-  
1578 population using k-means ('kmeans' in MATLAB) and the following feature space: distance from  
1579 the origin to the global minimum of the EBR, distance from the origin to the global maximum of  
1580 the EBR, the stepwise percentage of the EBR that was greater than 20% to 90% of the  
1581 maximum firing rate in 10% bounds, and the dispersion of the EBR and inverse EBR. All  
1582 features were z-score normalized across the population of EBCs prior to clustering. K-means  
1583 was run on these features for up to 10 clusters and the total within-cluster sums of point-to-  
1584 centroid distances (SUMD) were examined to assess which K was appropriate for the current

1585 data. Repeated iterations of k-means clustering and qualitative inspection of the K vs SUMD  
1586 plot revealed a consistent elbow at  $K = 4$  clusters. Principal components analysis ('pca', in  
1587 MATLAB) was run on the same features to visualize whether k-means was partitioning distinct  
1588 clusters or a continuum.

1589 *Ratemap coherence, dispersion, and receptive field size.* For either egocentric boundary  
1590 ratemaps or 2D spatial ratemaps, coherence was defined as the Spearman's correlation  
1591 between each spatial bin and the mean firing rate of all adjacent bins. Dispersion was calculated  
1592 as the mean within rate map distance of the top 10% of firing rate bins. Receptive field size was  
1593 only calculated for egocentric boundary ratemaps (described below), and was defined by the  
1594 area (percentage of all egocentric boundary ratemap degree x cm bins) of the largest single  
1595 contour detected after selecting for bins with firing rates greater than 75% of the maximum firing  
1596 rate.

1597 *Self-motion rate maps and assessment of self-motion sensitivity.* Angular displacement ( $\theta$ ) was  
1598 calculated by determining the circular difference in movement direction between two position  
1599 samples (frames) separated by a 100ms temporal window. The total distance ( $d$ ) traveled  
1600 between these two frames was also calculated. The process was repeated for the full recording  
1601 by sliding a 100ms temporal window across all position frames and calculating these values.  
1602 Angular displacement and distance traveled were converted to Cartesian coordinates to  
1603 generate x- and y-displacement values in centimeters, which corresponded to lateral and  
1604 longitudinal displacements for each frame across the full recording.

1605 Two-dimensional displacements were binned (1cm) and convolved with a two-dimensional  
1606 Gaussian spanning 3cm. For each neuron, the same process was repeated for displacement  
1607 values that co-occurred with spike times to generate a spike occupancy map as a function of  
1608 displacement. Self-motion rate maps were constructed by dividing the spike occupancy map for  
1609 each neuron by the total time in each displacement bin. Bins occupied for less than 267ms were  
1610 removed from analyses as they typically were observed at extreme displacement values. Self-  
1611 motion ratemaps for each neuron were additionally constructed independently from interleaved,  
1612 non-overlapping, 1 second periods throughout the entire session to assess stability of self-  
1613 motion tuning. For quantification of self-motion tuning relative to a randomized distribution, all  
1614 aforementioned ratemaps were generated for each neuron 100 times after randomly shifting the  
1615 spike train relative to position.

1616 Self-motion ratemaps were quantified for their stability, left- versus right-turning preference, and  
1617 speed modulation. First, stability of self-motion tuning was quantified by correlating self-motion  
1618 ratemaps generated from non-overlapping periods for each neuron (**Figure 2c**). Next, turning  
1619 biases for clockwise versus counterclockwise movements (LvR FR ratio, **Figure 2d**) were  
1620 quantified by computing the ratio of summated firing for all displacement bins on the right side  
1621 and left side of the zero vertical line, respectively. Finally, speed modulation was assessed by  
1622 finding the mean firing rate as a function of longitudinal displacement (i.e. averaging over  
1623 columns of self-motion ratemaps) and correlating with the y-displacement value (**Figure 2e**). All  
1624 self-motion ratemap quantification was repeated for all randomized self-motion ratemaps as  
1625 mentioned above. Stability and turn-bias quantification were computed from displacement bins  
1626 that were occupied in both self-motion ratemaps or both halves of an individual self-motion  
1627 ratemap. All quantification was completed on non-smoothed self-motion ratemaps.

1628 *Generalized linear models.* In order to more directly test to what degree these neurons  
1629 represented egocentric compared to allocentric variables, we adopted a generalized linear  
1630 model framework. The probability of spiking in a given behavioral frame (33Hz) is described by  
1631 an inhomogeneous Poisson process, where the probability of spiking in a given frame is  
1632 described by the time varying variable  $\lambda$ :

1633 
$$P(\text{Spike} | t) = e^{-\lambda(t)}$$

1634 
$$\lambda(t) = \lambda_{FR} * \lambda(t)_{SelfMovement} * \lambda(t)_{Egocentric}$$

1635 Where:

1636 
$$\lambda_{FR} = \beta_0$$

1637 
$$\lambda_{SelfMovement}(t) = v_1 S + v_2 A$$

1638 
$$\lambda_{Allocentric}(t) = \rho_1 x + \rho_2 y + \rho_3 x^2 + \rho_4 y^2 + \rho_3 xy + \rho_6 \cos(\varphi) + \rho_7 \sin(\varphi)$$

1639 
$$\lambda_{Egocentric}(t) = \varepsilon_1 d + \varepsilon_2 d^2 + \varepsilon_3 \sin(\theta) + \varepsilon_4 \cos(\theta) + \varepsilon_5 d * \sin(\theta) + \varepsilon_6 d * \cos(\theta)$$

1640 Where  $\beta_0$  defines the baseline firing rate of the neuron. All subscripted variables are fit  
1641 coefficients weighting the other (time-varying) variables. S is the running speed of the animal  
1642 and A is the angular displacement of the animal, as described above. X and y are  
1643 measurements of the animal's position in the environment in pixels, and  $\varphi$  is the movement  
1644 direction. Finally, d is the animal's distance from the center of the environment, and  $\theta$  is the  
1645 egocentric angle to the center of the environment.

1646 Coefficients were determined by fitting to maximize log-likelihood (MATLAB function `'glmfit'`) of  
1647 the experimental spike train given the behavioral variables. For statistical tests, some number of  
1648 the coefficients were set to zero, giving a log-likelihood for the reduced model. The difference in  
1649 likelihood for the full versus reduced model was compared to a Chi-Square distribution (degrees  
1650 of freedom equal to the number of coefficients set to zero) to generate an analytic p-value.  
1651 While theoretically the change in log-likelihood should follow a Chi-Square distribution, this is  
1652 only the case when the spike train has been fit very well (eg: including all neuron-neuron  
1653 coupling terms). In line with previous approaches, we therefore also compared the change in  
1654 log-likelihood in two additional manners. First, we compared the change in log-likelihood to that  
1655 from 1000 randomly shuffled spike train, giving an empirical null-distribution. Secondly, when  
1656 comparing the relative effects of two variables (that is, comparing two reduced models to each  
1657 other), we can derive the difference in Akaike Information Criteria (dAIC) for each of the reduced  
1658 models, and compare their magnitudes. Example spike trains for each model were generated by  
1659 evaluating lambda for each behavioral time point (`'glmeval'`) and using this as the input to a  
1660 random Poisson Generator (`'poissrnd'`).

1661 *Assessment of theta-phase modulation.* For each experimental session an LFP channel was  
1662 identified that was qualitatively noise free. The LFP signal was filtered in the theta frequency  
1663 range (6-10Hz) and the phase for each spike from each neuron was estimated as the  
1664 instantaneous phase angle of the corresponding Hilbert transform (`'hilbert'` in Matlab). For each  
1665 neuron, the MRL and MRA were calculated on the full spike phase distribution using the circular  
1666 statistics toolbox (Berens et al., 2009; MRL, `'circ_r'`; MRA, `'circ_mean'`). We next randomly  
1667 shifted the spike train relative to theta phase 100 times for each neuron to generate a null  
1668 distribution of MRL values. RSC neurons with MRLs greater than the 95<sup>th</sup> percentile of the full  
1669 distribution of randomized MRL values were determined to be theta-phase locked.

1670 *Assessment of theta rhythmic spiking.* Spike train autocorrelograms were estimated by  
1671 generating a histogram of temporal lags between spikes in a 400ms temporal window  
1672 discretized into 20ms bins. For each neuron, the power spectrum of the autocorrelogram was  
1673 computed using the Fourier transform (`'fft'` in Matlab) and the peak in the theta frequency range  
1674 was identified (if it existed). If the mean power within 1Hz of this theta peak was 50% greater  
1675 than the mean power for the full power spectrum, the neuron was determined to exhibit intrinsic  
1676 theta spiking.

1677 *Gaussian Mixture Models.* Preferred orientation and preferred distance estimates were modeled  
1678 as mixtures of Gaussian distributions using orders from 1 to 10 (`'fitgmist'` in Matlab). Optimal

1679 models were identified as those that minimized the Akaike information criterion (AIC). The mean  
1680 of each Gaussian component is reported and a probability distribution function of the optimal  
1681 model was generated to visualize mixture model fit ('pdf' in Matlab).

1682 *Statistics.* Unless otherwise stated, non-parametric tests with a p-value threshold at 0.05 were  
1683 utilized for all statistical comparisons. Median and interquartile range are provided for all  
1684 distributions in which comparisons were made.

1685 *Data and code availability.* The toolbox used for alignment of behavioral and spike data, along  
1686 with basic analysis is available at <https://github.com/hasselmonians/CMBHOME>. The toolbox  
1687 used for egocentric boundary rate map generation and related analyses is available at  
1688 <https://github.com/hasselmonians/rscOpenFieldTuning> (to be made public before journal  
1689 acceptance). The toolbox used for GLM fits, evaluation, and spike-train generation is available  
1690 at <https://github.com/wchapman/pippin> (to be made public before journal acceptance).