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1 A model of a panoramic visual 2 representation in the dorsal visual 3 pathway: the case of spatial 4 reorientation and memory-based 5 search

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8 France.

10 **Abstract** Primates are primarily visual animals and understanding how visual information is
11 processed on its way to memory structures is crucial to the understanding of how memory-based
12 visuospatial behavior is generated. Recent imaging data demonstrate the existence of
13 scene-sensitive areas in the dorsal visual path that are likely to combine visual information from
14 successive egocentric views, while behavioral evidence indicates the memory of surrounding visual
15 space in extraretinal coordinates. The present work focuses on the computational nature of a
16 panoramic representation that is proposed to link visual and mnemonic functions during natural
17 behavior. In a spiking artificial neuron network model of the dorsal visual path it is shown how
18 time-integration of spatial views can give rise to such a representation and how it can subsequently
19 be used to perform memory-based spatial reorientation and visual search. More generally, the
20 model predicts a common role of view-based allocentric memory storage in spatial and not-spatial
21 mnemonic behaviors.

23 Introduction

24 Recent breathtaking advances in our understanding of rodent hippocampal memory system pave
25 the way for elucidating the organization of human spatial memory (*Burgess, 2014; Moser et al.,*
26 *2017*). One major difference between primates and rodents is the role of vision for behavior.
27 Primates are much more visual animals than rodents and understanding the link between primate
28 visual and medial temporal lobe (MTL) memory structures is an important and largely unexplored
29 open question (*Meister and Buffalo, 2016*). Experimental evidence indicates the existence of
30 functional and anatomical connections between these structures. Functional connections are
31 demonstrated by two principal lines of studies. First, visual behavior is informed by memory as
32 demonstrated by studies of novelty preference in both monkeys and humans (*Wilson and Goldman-*
33 *Rakic, 1994; Manns et al., 2000; Jutras and Buffalo, 2010a*). In the novelty preference paradigm,
34 the memory is assessed from looking time: well memorized stimuli are looked at less than novel
35 ones. The specific role of MTL structures in this phenomenon is derived from results showing
36 a decreased novelty preference after MTL lesions or in patients suffering from mild cognitive
37 impairment or Alzheimer's disease, often associated with MTL dysfunction (*McKee and Squire,*
38 *1993; Crutcher et al., 2009; Zola et al., 2013*). In monkeys, restricted lesions of hippocampal and/or

39 parahippocampal cortices also decreased novelty preference (*Zola et al., 2000; Pascalis et al., 2009;*
40 *Bachevalier et al., 2015*). Second, the link between visual and MTL structures is manifested in
41 coherent neural activities in the two structures. For example, activity of single MTL neurons is
42 modulated by visual saccades (*Sobotka et al., 1997*), the onset of visual stimuli strongly affects
43 hippocampal neural responses (*Jutras and Buffalo, 2010a*) and hippocampal theta oscillations are
44 reset by eye movements (*Jutras and Buffalo, 2010b; Hoffman et al., 2013*).

45 Anatomical connections between visual and memory structures have recently been charac-
46 terized in the novel framework of the occipital–parietal–MTL pathway of visuospatial processing
47 (*Kravitz et al., 2011*). There are three principal stages of information processing in this pathway
48 (*Figure 1A*). First, the occipito-parietal circuit processes visual information through visual areas
49 V1-V6 an egocentric (retinal) frame of reference. Successive information processing in these areas
50 is thought to extract visual features of increasing complexity, including motion and depth cues and
51 relay this information to the parietal cortex. Second, a complex network of interconnected parietal
52 structures relays highly-processed visual cues to support executive, motor and spatial-navigation
53 functions. These structures include the medial, ventral and lateral intraparietal areas (MIP, VIP,
54 LIP) strongly linked with eye movements processing; the middle temporal and medial superior
55 temporal (MT, MST) thought to extract high-level visual motion cues; and the caudal part of the
56 inferior parietal lobule (ciPL), the main relay stage on the way to the medial temporal lobe. The ciPL
57 sends direct projections to the CA1 of the hippocampus as well as to the nearby parahippocampal
58 cortex (PHC). In addition, it sends indirect projections to the same structures via the posterior
59 cingulate cortex (PCC) and the retrosplenial cortex (RSC). Within this complex network, neurons
60 at different neurobiological sites have been reported to code space in a world- or object-centred
61 reference frames (*Duhamel et al., 1997; Snyder et al., 1998; Chafee et al., 2007*). Moreover, both
62 PCC and RSC have been repeatedly linked to coordinate transformation between egocentric and al-
63 locentric frames of reference (*Vogt et al., 1992; Burgess, 2008; Epstein and Vass, 2014*). Importantly,
64 information processing in this pathway is strongly affected by directional information thought to
65 be provided by a network of head-direction cells residing in several brain areas, including RSC
66 (*Taube, 2007*). Finally, medial temporal lobe, and in particular the hippocampus, play a key role in
67 constructing an allocentric representation of space in primates (*Hori et al., 2003; Ekstrom et al.,*
68 *2003*).

69 Given functional and anatomical connections between visual and memory structures, the ques-
70 tion arises as to the nature of neuronal representations in the dorsal visual path. In addition to the
71 well-established role of parieto-retrosplenial networks in coordinate transformations (*Andersen*
72 *et al., 1993; Snyder et al., 1998; Salinas and Abbott, 2001; Pouget et al., 2002; Byrne et al., 2007*),
73 a largely unexplored question concerns the existence of an extra-retinal neural map of the remem-
74 bered visual space (*Hayhoe et al., 2003; Tatler and Land, 2011; Land, 2014*). That the task-related
75 visual retinotopic space is remembered has been suggested by studies showing that when asking
76 to recall a recent visual content, eye movements (on a blank screen) closely reflected spatial rela-
77 tions of remembered images (*Brandt and Stark, 1997; Johansson and Johansson, 2014*). Moreover,
78 preventing subjects from making eye movements decreased recall performance (*Johansson and*
79 *Johansson, 2014; Laeng et al., 2014*). That not only the retinal egocentric space is remembered
80 but also extra-retinal map of surrounding space is stored in memory is demonstrated in studies
81 showing that during natural behavior human subjects direct saccades toward extra-retinal locations,
82 suggesting that these locations are represented in memory, potentially in an allocentric frame
83 of reference (*Land et al., 1999; Hayhoe et al., 2003; Golomb et al., 2011; Melcher and Morrone,*
84 *2015; Robertson et al., 2016*). Even though suggested by the above studies, the nature of such an
85 extra-retinal map and neural mechanisms underlying its construction and storage are currently
86 unknown.

87 The present modeling study addresses the question of how such an allocentric representation of
88 surrounding visual space can be constructed and stored by the dorsal visual path – MTL networks.
89 We propose that the existence of such a representation relies on short-term memory linking

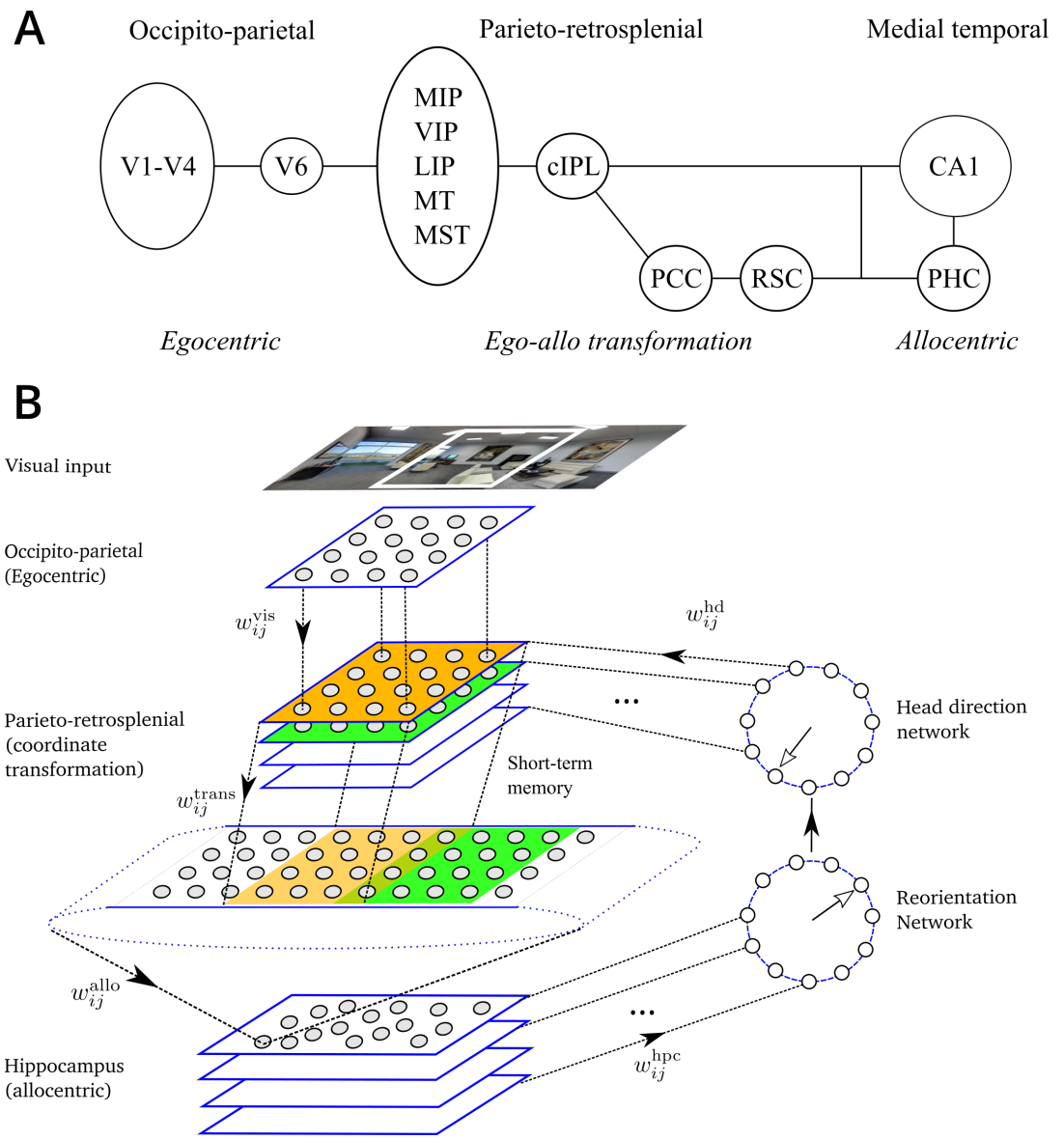


Figure 1. Model. A. Dorsal visual pathway of visuospatial information processing in primates (see text for details). B. Schematic representation of the model. Visual features present in the limited visual field constitute the model input. The model network is composed of 6 modules: (1) Occipito-parietal (egocentric); (2) Head-direction network; (3) Parieto-retrosplenial transformation network consists of the coordinate-transformation network and the output layer, which encodes visual features in an allocentric directional frame and spans 2π ; (4) Hippocampus; (5) Reorientation network. Projections from the occipito-parietal (visual) areas to the transformation network are topographic. Each head-direction cell activates the corresponding layer of the transformation network. Projections from the different layers of the transformation network to the parieto-retrosplenial output layer are also organized according to head direction: any two layers project topographically to overlapping portions of the output population shifted according to head direction. Synapses between the transformation network and the parietal output network are endowed with short-term memory. Different hippocampal subpopulations project to different neurons in the reorientation network, which in turn corrects head direction signal. Full arrows represent the flow of information in the network. Open arrows represent direction signals in the head direction and reorientation networks.

90 successive egocentric views and we study how the long-term memory of allocentric visual space can
 91 affect behavior in spatial and non-spatial experimental paradigms. In particular, our results suggest
 92 that allocentric memory effects during spatial reorientation and memory-based visual guidance

93 tasks can be explained by the existence of such a network.

94 **Methods**

95 The model is a spiking neuron network constructed to reflect information processing steps thought
96 to be performed by successive stages of neuronal processing in the primate dorsal visual path
97 described above (**Figure 1A**). To reflect in a simplified way the main processing stages in the pathway,
98 our model of the dorsal pathway is composed of 5 main modules or subnetworks (**Figure 1B**). First,
99 the module representing information processing in the occipito-parietal circuit essentially applies
100 a set of Gabor-like orientation filters to the incoming visual images, a standard assumption for
101 basic V1 processing. We do not model eye movements, and assume that a retinotopic visual
102 representations obtained at the level of V1 has been remapped, by the time it arrives into the
103 parietal cortex, to a head-fixed representation by taking into account eye position information
104 (**Duhamel et al., 1997; Snyder et al., 1998; Pouget et al., 2002**). Even though gaze independent,
105 this head-fixed representation is egocentric, or view-dependent, in the sense it depends on the
106 position and orientation the modeled animal (i.e., its head) in space. Second, we model the
107 directional sense by a network of cells whose activity is approximately Gaussian around their
108 preferred orientations (**Taube, 2007**) and that is sending projections to the parietal cortex (**Brotchie**
109 **et al., 1995; Snyder et al., 1998**). Third, both the activities of the egocentric network and the head
110 direction signal converge onto the network modeling the role of the parieto-retrosplenial network in
111 coordinate transformation. This transformation network uses head direction to convert egocentric
112 visual representations into a head-orientation-independent, or world-fixed representation. This
113 coordinate transformation is done essentially by the same mechanism as the retinotopic-to-head-
114 fixed conversion mentioned above, but in contrast to previous models it does so using low-level
115 topographic visual information. The resulting orientation-independent visual representation is
116 often referred to as spatiotopic, or allocentric, since visual features are determined a world-fixed
117 directional reference frame. Fourth, the allocentric output of the parieto-retrosplenial network
118 arrives to the hippocampus, modeled by a network of cells that learn, by a competitive mechanism,
119 allocentric visual patterns provided by the parietal network. As will be clear from the following, in the
120 context of spatial navigation these cells can be considered as place cells, whereas in a non-spatial
121 context they can be considered as representing memorised visual stimuli. Finally, the reorientation
122 module associates allocentric memories with directional reference frame and feeds back to the
123 head direction cells. The activity of this network represents the correction signal for self-orientation.
124 When the memorized information corresponds to the newly arrived one, the correction signal is
125 zero, whereas in the case of disorientation or in response to specific manipulations of visual cues, it
126 can provide fast adjustment of the self-orientation signal. In the Results section we show that a
127 similar reorientation mechanism can be responsible for behavioral decisions in spatial, as well as
128 non-spatial tasks in primates.

129 **Occipito-parietal input circuit**

130 The occipito-parietal network is modeled by a single rectangular sheet of $N_x \times N_y$ visual neurons,
131 uniformly covering the visual field. In all simulations, except Simulation 6 below, the size of the
132 visual field was limited to $160 \times 100^\circ$, approximately representing that of a primate. The activities of
133 these visual neurons are computed in four steps. First, input images are convolved (using OpenCV
134 `filter2D()` function) with Gabor filters of 4 different orientations ($0, 90^\circ, 180^\circ, 270^\circ$) at 2 spatial
135 frequencies (0.5 cpd, 2.5 cpd), chosen so as to detect visual features in simulated experiments.
136 Second, the 8 convolution images are discretized with $N_x \times N_y$ grid, and the maximal response at
137 each position is chosen, producing an array of $N_x N_y$ filter responses. These operations are assumed
138 to roughly mimic retinotopic V1 processing (**Heeger, 1992**), transformed into a head-fixed reference
139 frame using eye-position information. Third, the vector of filter activities at time t is normalized to
140 have maximal value of unity. Fourth, a population of $N_{\text{vis}} = N_x N_y$ Poisson neurons is created with
141 mean rates given by the activity of the corresponding filters scaled by the constant maximal rate

142 A_{vis} (see **Table 1** for the values of all parameters in the model). For a Poisson neuron with rate r , the
143 probability of emitting a spike during a small period of time δt is equal to $r\delta t$ (**Gerstner et al., 2014**).

144 **Head direction**

145 The head direction network is composed of $N_{\text{hd}} = 36$ Poisson neurons organized in a circle, such
146 that neurons' preferred directions ϕ_k are uniformly distributed between 0 and 2π . The tuning curves
147 of the modeled head-direction neurons are Gaussian with maximum rate A_{hd} and width $\sigma_{\text{hd}} = 8^\circ$.
148 Thus, the rate of head-direction neuron k when the model animal's head is oriented in the direction
149 ϕ is given by

$$r_k^{\text{hd}} = A_{\text{hd}} \exp\left(-\frac{(\phi - \phi_k)^2}{\sigma_{\text{hd}}^2}\right) \quad (1)$$

150 Such a network generates a Gaussian activity profile centered around ϕ . Our model does not
151 explicitly implement a line attractor dynamics hypothesized to support head direction signal (**Zhang,**
152 **1996**), but it is consistent with it. Head direction cells have been found in several brain areas
153 in rodents and primates (see **Taube, 2007**, for review), and there is evidence that parietal cortex
154 receives head direction signals (**Brotchie et al., 1995**).

155 **Parietal transformation network**

156 The parietal transformation network is inspired by previous models (**Becker and Burgess, 2001;**
157 **Byrne et al., 2007**) but in contrast to them it operates directly on activities of the Gabor-like visual
158 cells. The transformation of coordinates between the head-fixed and world-fixed coordinates
159 is performed by multiple subpopulations of leaky integrate-and-fire (LIF) neurons organized as
160 two-dimensional layers of neurons (see **Figure 1**). Neurons in each layer of the transformation
161 network are in a one-to-one relationship with the visual population and so at each moment t each
162 transformation layer receives a copy of the egocentric (head-fixed) visual input. Therefore, the
163 number of neurons in each transformation layer is equal to N_{vis} . Apart from the visual input, the
164 transformation network also receives input from the population of head direction cells. There
165 is a topographic relationship between the sub-populations of the transformation network and
166 different head directions: each head-direction cell sends excitatory projections to neurons only in
167 one associated layer of the transformation network. Thus, input from head-direction cells strongly
168 activates only a small subset of transformation layers which transmit visual information to the
169 downstream population. More specifically, only the layers which are associated with head directions
170 close to the actual orientation of the head are active. The number of layers in the transformation
171 network is then equal to N_{hd} , giving the total number of neurons in the transformation network
172 $N_{\text{trans}} = N_{\text{vis}}N_{\text{hd}}$.

173 Thus, in a k -th layer of the transformation network, the membrane potential $v_i(t)$ of the LIF
174 neuron i in is governed by the following equation (omitting the layer index for clarity):

$$\tau_m \frac{dv_i}{dt} = V_{\text{rest}} - v_i + g_i^{\text{ex}}(t)(E_{\text{ex}} - v_i) + g_i^{\text{in}}(t)(E_{\text{in}} - v_i) + R_m I_{\text{ext}} \quad (2)$$

175 with the membrane time constant τ_m , resting potential V_{rest} , excitatory and inhibitory reversal
176 potentials E_{ex} and E_{in} , as well as the membrane resistance R_m . When the membrane potential
177 reaches threshold V_{th} , the neuron fires an action potential. At the same time, v_i is reset to V_{reset}
178 and the neuron enters the absolute refractory period Δ_{abs} during which it cannot emit spikes. A
179 constant external current I_{ext} is added to each neuron to simulate baseline activity induced by other
180 (unspecified) neurons from the network.

181 The excitatory conductance in these neurons depends only on the visual input (and thus is inde-
182 pendent from k). It is modeled as a combination of α -amino-3-hydroxy-5-methyl-4-isoxazolepropionic
183 acid (AMPA) and N-methyl-d-aspartate (NMDA) receptor activation $g_i^{\text{ex}} = (1 - \alpha)g_i^{\text{ampa}} + \alpha g_i^{\text{nmda}}$, that are

184 described by

$$\tau_{\text{ampa}} \frac{dg_i^{\text{ampa}}}{dt} = -g_i^{\text{ampa}} + \tau_{\text{ampa}} \sum_{j \in \{\text{vis}\}} w_{ij}^{\text{vis}} s_j(t) \quad (3)$$

$$\tau_{\text{nmda}} \frac{dg_i^{\text{nmda}}}{dt} = -g_i^{\text{nmda}} + g_i^{\text{ampa}} \quad (4)$$

185 where the index j runs over input (visual) neurons connected to it, w_{ij}^{vis} are the connection weights
 186 and $s_j(t) = 1$ if a presynaptic spike arrives at time t and $s_j(t) = 0$ otherwise. Constants τ_{ampa} and τ_{nmda}
 187 determine the time scales of receptor activation.

188 In contrast, the inhibitory conductance depends only on the head-direction cells and ensures
 189 that a small subset of transformation layers (i.e. those associated with nearby head directions) are
 190 active. To implement it, we employ a simple scheme in which all transformation layer neurons are
 191 self-inhibitory, and this inhibition is counteracted by the excitatory input from the head-direction
 192 cells. Thus, the inhibitory conductance of the i -th neuron in the k -th layer is given by

$$\tau_{\text{gaba}} \frac{dg_i^{\text{in}}}{dt} = -g_i^{\text{in}} + G_{\text{inh}} + \tau_{\text{gaba}} \sum_{k \in \{\text{hd}\}} w_{ik}^{\text{hd}} s_k(t) \quad (5)$$

193 where G_{inh} is the constant maximum amount of self-inhibition and w_{ik}^{hd} are the synaptic weights
 194 of connections from the head-direction cells. In the current implementation, there is one-to-one
 195 correspondence between the head-direction cells and the layers of the transformation network, so
 196 $w_{ik} = 1$ only for associated head-direction cell ϕ_k and $w_{ik} = 0$ otherwise.

197 All layers of the transformation network project to the parietal output population, which codes
 198 image features in an allocentric (world-fixed) directional frame. The parietal output population is
 199 represented by a two-dimensional neuronal sheet spanning $360 \times 100^\circ$, that is a full panoramic view.
 200 It is encoded by a grid of $N_x^{\text{allo}} \times N_y^{\text{allo}}$ neurons. Each layer of the transformation network projects
 201 to a portion of the population according to the head direction associated with it associated with
 202 this layer (see **Figure 1**). Since any two nearby layers of the transformation network are associated
 203 with head directions shifted relative to each other by $360^\circ / N_{\text{hd}} = 10^\circ$, the overlap between their
 204 projections on the parietal output layer is 140° .

205 Thus, at each moment in time, a spiking representation of the current visual stream (i.e. a spiking
 206 copy of the visual input, gated by the head direction cells) arrives to the allocentric neurons spatially
 207 shifted according to the current head direction. For example, if two egocentric views (each spanning
 208 160°) are observed at head directions -45° and 45° with respect to an arbitrary north direction,
 209 these two views arrive at the allocentric population spatially shifted relative to one another by 90° ,
 210 so that the activated neurons in the allocentric population span 230° . To ensure that subsequent
 211 snapshots are accumulated in time (e.g. during head rotation), the synapses between neurons in
 212 the transformation layers and the allocentric population are endowed with short-term memory,
 213 implemented by a prolonged activation of NMDA receptors (**Durstewitz et al., 2000**). Such synapses
 214 result in a sustained activity of allocentric output neurons during a period of time sufficient for
 215 downstream plasticity mechanism to store information from accumulated snapshots.

216 The membrane potential of the i -th neuron in the allocentric output population is governed by
 217 **Equation 2** with the synaptic conductance terms determined as follows. First, the excitatory AMPA
 218 conductance is given by **Equation 3** but with the input provided by transformation network neurons
 219 via weights w_{ij}^{trans} . Second, the NMDA conductance is described by **Equation 4**, but with the synaptic
 220 time scale increased by a factor of 6. This is done to ensure sustained activation of the output
 221 neurons upon changes in the visual input. Third, inhibitory input is set to zero for these neurons.

222 Learning the weights in the transformation network

223 The connection weights w_{ij}^{vis} from the visual neurons to the parietal transformation cells and w_{ij}^{trans}
 224 from the parietal transformation cells to the parietal output neurons are assumed to be learned
 225 during development by a supervised mechanism, similar to the one proposed to occur during

226 sensory-motor transformation learning (*Zipser and Andersen, 1988; Salinas and Abbott, 1995*). In
 227 this models it is proposed that when an object is seen (i.e. its retinal position and an associated
 228 gaze direction are given), grasping the object by hand (that operates w.r.t. the body-fixed reference
 229 frame) provides a teaching signal to learn the coordinate transformation. A similar process is
 230 assumed to occur here, but instead of learning body-based coordinates using gaze direction, the
 231 model learns world-fixed coordinates using head direction.

232 More specifically, synaptic weights in the coordinate-transformation network were set by the
 233 following procedure. First, the network was presented with an edge-like stimulus at a random
 234 orientation and at a randomly chosen location in the visual field. Second, upon the stimulus
 235 presentation, the head direction was fixed at a randomly chosen angle ϕ . Third, neurons in the
 236 transformation layers associated with the chosen head direction were activated with the average
 237 firing rates equal to the rates of the corresponding visual neurons, while neurons in the parietal
 238 output layer were activated with the same average rates but shifted according to the chosen head
 239 direction (representing the teaching signal). Fourth, the synaptic weights in the network were set
 240 according to the Hebbian prescription:

$$w_{ij}^{\text{vis}} = r_i^{\text{trans}} r_j^{\text{vis}} \quad (6)$$

$$w_{ij}^{\text{trans}} = r_i^{\text{trans}} r_j^{\text{allo}} \quad (7)$$

241 where r_i^{vis} , r_i^{trans} and r_i^{allo} are the mean firing rates of the corresponding visual neurons, transformation
 242 network neurons and parietal output neurons, respectively. Fifth, the weight vector of each neuron
 243 was normalized to have the unity norm. This procedure has been performed for edge-like stimuli
 244 at 4 different orientations (corresponding to 4 Gabor filter orientations), placed in the locations
 245 spanning the whole visual field and at head directions spanning 360° . Synaptic weights (*Equation 6-7*)
 246 were fixed to the learned values prior to all the simulation presented here. No updates were
 247 performed on these weights during the simulations.

248 Hippocampal neurons

249 As a result of the upstream processing, neuronal input to the hippocampus represents visual
 250 features in an allocentric directional frame. Neurons in the parietal output population are connected
 251 in an all-to-all fashion to the population of modeled hippocampal cells and the connection weights
 252 that are updated during learning according to an spike-timing-dependent plasticity (STDP) rule
 253 below. In addition, lateral inhibition between hippocampal neurons ensures a soft winner-take-all
 254 dynamics, such that sufficiently different patterns in the visual input become associated with small
 255 distinct subpopulations of hippocampal neurons.

256 Thus, the membrane equation of the i -th hippocampal neurons is given by *Equation 2*. The
 257 excitatory conductances are given by *Equation 3-4*, but with the input provided by the parietal
 258 output neurons via weights w_{ij}^{allo} . Upon the initial entry to a novel environment these weights are
 259 initialized to small random values. During learning, the amount of synaptic modification induced by
 260 a single pair of pre- and post-synaptic spikes is given by

$$\frac{dw_{ij}^{\text{allo}}}{dt} = G_{\max} \left[a_j^{\text{pre}} s_i(t) - a_i^{\text{post}} s_j(t) \right] \quad (8)$$

261 where $s_i(t)$ and $s_j(t)$ detect pre- and post-synaptic spikes, respectively, and

$$\begin{aligned} \frac{da_j^{\text{pre}}}{dt} &= -\frac{a_j^{\text{pre}}}{\tau_{\text{pre}}} + A_+ s_j(t) \\ \frac{da_i^{\text{post}}}{dt} &= -\frac{a_i^{\text{post}}}{\tau_{\text{post}}} + A_- s_i(t) \end{aligned} \quad (9)$$

262 The inhibitory conductance of the hippocampal neuron is governed by the following equation:

$$\tau_{\text{gaba}} \frac{dg_i^{\text{in}}}{dt} = -g_i^{\text{in}} + \tau_{\text{gaba}} \sum_{j \in \{\text{hpc}\}} w_{ij}^{\text{inh}} s_j(t) \quad (10)$$

263 in which τ_{gaba} determines the time scale of synaptic inhibition as before, and the weights $w_{ij}^{\text{inh}} = W_{\text{inh}}$
264 are constant and ensure that each hippocampal neuron inhibits all other hippocampal neurons
265 proportionally to its activity.

266 The hippocampal circuit is complex and consists of several interconnected populations. In our
267 simple model of hippocampal activity we consider only the first stage of hippocampal processing of
268 visual information that is likely to be the CA1, which receives direct projections from the entorhinal
269 cortex, an input gateway to the hippocampus.

270 Reorientation network

271 During one continuous experimental trial (e.g. an exploration trial in novel environment or an
272 observation of a novel image on the screen), the reference frame for head direction is fixed and all
273 processing operations in the network are performed with respect to the origin of this reference
274 frame. In particular, an allocentric information stored by the hippocampus as a result of the trial
275 can be correctly used for future action only if the origin of the reference frame is stored with it.
276 Therefore, if in a subsequent trial, the actions to be performed require memory of the previous one,
277 the network should be able to recover the original directional reference (this of course can happen
278 only the visual information received at the start of the trial is considered familiar). Reorientation is
279 the process by which the origin of the stored reference frame is recovered.

280 Our model of this process rests on the assumption that it is automatic, fast, bottom-up, and
281 does not require costly object/landmark processing. The support for this assumption comes from
282 a large body of reorientation studies in many animal species including primates, showing that
283 object identities are ignored during reorientation (*Cheng and Newcombe, 2005*). The conditions in
284 which most of the reorientation studies were performed usually are such that there is no single
285 conspicuous point-like cue in the environment that can be reliably associated with a reference
286 direction. For example, in many studies the directional cues come from the geometric layout of the
287 experimental room. Lesion studies in rats suggest that reorientation in such conditions requires
288 an intact hippocampus (*McGregor et al., 2004*). Furthermore, we propose that this reorientation
289 network is active all the time, in contrast to being consciously “turned on” when the animal “feels
290 disoriented”. Therefore, we expect that its effects can be observed even when no specific disorien-
291 tation procedure was performed. In particular, we suggest in the Results that a manipulation of
292 objects on the screen can result in automatic corrections of directional sense that can be observed
293 during visual search.

294 The reorientation network in the model is organized similarly to the head-direction network and
295 consists of N_{re} neurons with preferred positions uniformly distributed on a circle. Therefore, the
296 difference between two nearby reorientation cells is $\Delta\phi = 2\pi/N_{\text{re}}$. The membrane potential of the
297 i -th reorientation neuron is described by the LIF equation (*Equation 2*). Excitatory conductances
298 are described by *Equation 3-4* with the input to the neuron provided by hippocampal place cells via
299 weights w_{ij}^{hpc} . There is no inhibition in the network, and so the inhibitory conductance is set to 0.
300 The ability of the network to perform reorientation is determined by afferent connection weights
301 from the hippocampal cells, which are determined as follows.

302 Since all allocentric information learned during a trial is linked to the same directional frame, all
303 hippocampal cells learned during the trial are connected to a single neuron of the reorientation
304 network, the one with the preferred direction 0° (*Figure 2*). The connection weights between the
305 hippocampal cells and the neuron are updated using STDP rule, *Equation 8-9* (this is not essential
306 for the model to work, so that setting the weights to a constant value will give similar results). Once
307 the training trial is finished, N_{re} copies of the learned hippocampal population are created, each
308 corresponding to a separate neuron in the reorientation network. In each copy, all cells have the
309 same input and output weights as the corresponding cells in the original population, but their
310 connection profile is different. In particular, the copy that corresponds to the reorientation neuron
311 with preferred direction $\Delta\phi$ is connected to pre-synaptic cells are shifted by the same angle in the
312 topographically-organized allocentric layer (*Figure 2*). In machine learning literature, this technique

313 is called “weight sharing” and it allows to achieve translation invariance for detection of objects in
314 images. Here, we apply a similar technique in order to detect familiar snapshots and head direction
315 associated with them.

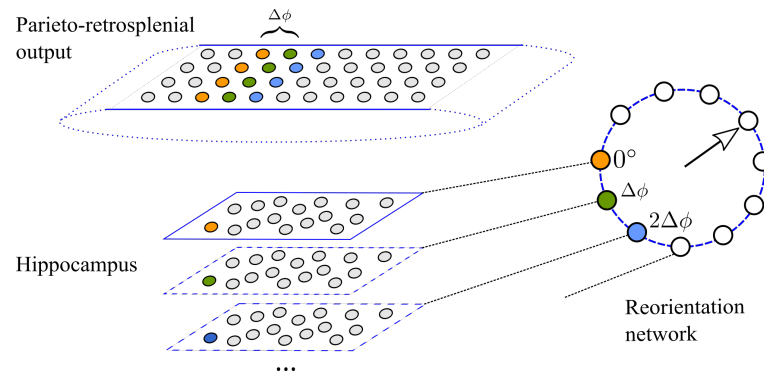


Figure 2. Implementation of the reorientation network. Top: the output population of the parieto-retrosplenial network. Bottom: hippocampal cells. The population outlined by full lines is the original population learned during training. As a result of learning, the hippocampal cell shown in orange is connected to the presynaptic cells of the same color (connection weights not shown). All cells in the original population are connected to a single cell (o°) in the reorientation network (Right). The hippocampal populations outlined by dashed lines are copies of the original population that implement weight sharing: the hippocampal cell shown in green (blue) has the same connection weights as the orange cell, but it is connected to pre- and post-synaptic cells shifted by $\Delta\phi$ ($2\Delta\phi$). The number of copies of the original hippocampal population is the same as the number of neurons in the reorientation network.

316 Suppose, for example, that as a result of learning during a trial, a hippocampal cell is associated
317 with 4 presynaptic cells in the output layer of the transformation network (cells shown in orange in
318 **Figure 2**). Suppose further that during an inter-trial interval the head direction network has drifted
319 (or was externally manipulated), so that at the start of the new trial the internal sense of direction
320 is off by $2\Delta\phi$. When the animal sees the same visual pattern again, it will be projected onto the
321 allocentric layer shifted by the same amount (blue cells in **Figure 2**). This will in turn cause the
322 hippocampal subpopulation that includes the blue cell to be most strongly active, such that the
323 activity peak of the reorientation network signals the orientation error. The reorientation is then
324 performed by readjusting the head direction network to minimize the reorientation error. In the
325 current implementation this is done algorithmically by subtracting the error signal from the actual
326 head direction, but it can also be implemented by attractor dynamics in the head direction layer.

327 Simulation details

328 The spiking artificial neural network model described above was implemented using Python 2.7
329 and Brian 2 spiking neural network simulator (*Stimberg et al., 2019*). The time step for neuronal
330 simulation was set to 1 ms, while the sampling rate of visual information was 10 Hz, according
331 to the proposals relating oscillatory brain rhythms in the range 6–10 Hz to information sampling
332 (*Hasselmo et al., 2002; Busch and VanRullen, 2010*). At the start of each simulation, the weights
333 w_{ij}^{allo} and w_{ij}^{hpc} were initialized to small random values (the other weights were trained as described
334 earlier and fixed for all simulations), see **Figure 1B**. Parameters of the model are listed in **Table 1**,
335 and the sections below provide additional details of all simulations.

336 Simulation 1: Egocentric-allocentric transformation

337 The first simulation was inspired by the study of *Snyder et al. (1998)*, in which monkeys observed
338 visual stimuli at identical retinal locations, but for different orientations of the head with respect
339 to the world, in order to assess whether parietal neurons were modulated by the allocentric head
340 direction. Thus, in this simulation, the head direction angle ϕ was varied from -50° to 50° in 100
341 sessions. For each trial of a session, the mean rates of the head-direction neurons were calculated

Parameter	Value	Description
Neuron numbers		
$N_x \times N_y$	80×50	Parieto-occipital network size
N_{hd}	36	Head direction network size
$N_x^{allo} \times N_y^{allo}$	180×50	Parietal output layer size
N_{re}	36	Reorientation network size
Mean amplitudes in the input populations		
A_{vis}	100	Spikes/s., Maximum rate of the parieto-occipital network
A_{hd}	100	Spikes/s., Maximum rate of the head-direction network
Parameters of the LIF model		
V_{rest}	-65	mV, Resting potential
V_{th}	-55	mV, Spiking threshold
V_{reset}	-65	mV, Reset potential
E_{ex}	0	mV, Excitatory reversal potential
E_{in}	-80	mV, Inhibitory reversal potential
E_{in}	250	m Ω , Membrane resistance
Δ_{abs}	$1^{a-c}, 2^d$	ms, Absolute refractory period
α	$0.9^{a,b}, 0.3^{c,d}$	Balance between AMPA and NMDA receptor
τ_{ampa}	5	ms, AMPA receptor time scale
τ_{nmda}	$100^{a,c,d}, 600^b$	ms, NMDA receptor time scale
τ_x	2.5	ms, NMDA receptor time scale
τ_m	$10^{a,c,d}, 20^b$	ms, Membrane time scale
τ_{gaba}	10	ms, GABA receptor time scale
I_{ext}	$20^{a-c}, 40^d$	mA, External input current
G_{inh}	2	Self-inhibitory conductance
STDP		
G_{max}	$0.05^c, 0.1^d$	Maximal weight change
A_+	0.005	Maximal potentiation amplitude
A_-	$A_+ \times 1.05$	Maximal depression amplitude
τ_{pre}	20	ms, Potentiation time scale
τ_{post}	$15^c, 17.5^d$	ms, Depression time scale
Other parameters		
σ_{hd}	8°	Tuning curve width of head direction cells
W_{inh}	1.0	Lateral inhibition weight in the hippocampal population

Table 1. Parameters of the model. a, Occipito-parietal circuit. b, Parieto-retrosplenial transformation network. c, Hippocampus. d, Reorientation network.

342 according to **Equation 1** and fixed for the rest of the trial. The stimulus (vertical black bar, width:
 343 10°) was shifted horizontally across the midline of the visual field ($160 \times 100^\circ$) from left to right in 1°
 344 steps, such that it remained at each position for 100ms. The neuronal spikes were recorded from
 345 the occipito-parietal network, the parieto-retrosplenial transformation network and its output layer,
 346 for each stimulus position across 10 trials per session. Mean firing rates were then calculated from
 347 these data.

348 **Simulation 2: Accumulation of successive views using short-term synaptic memory**
 349 The aim of the second simulation was to illustrate the synaptic mechanism for an integration of
 350 successive visual snapshots in time, instrumental for spatial coding. We model a monkey that
 351 remains in the same spatial location and turns its head from left to right. Thus, the model was
 352 presented with a set of 9 successive overlapping views ($160 \times 100^\circ$) taken from a panoramic ($360 \times 100^\circ$)
 353 image, 100ms per view. Initial head direction was arbitrarily set to 0° .

354 Simulation 3: Encoding of allocentric visual information during spatial exploration
355 In the third simulation we studied the role of temporal accumulation of visual information for
356 spatial coding. The model ran through a square 3D environment (area: 10×10 m, wall height 6 m) for
357 about 10 min so as to cover uniformly its area. The visual input was provided by a cylindrical camera
358 (160 × 100°) placed at the location of the model animal. At each spatial location 9 successive views of
359 the environment were taken in different directions (as in the Simulation 2). The vector of mean firing
360 rates of the occipito-parietal neurons at a single spatial location and orientation constituted the
361 egocentric population vector. The mean firing rates of the the parieto-retrosplenial output neurons
362 at each location constituted the allocentric population vector (this population vector is independent
363 from orientation as a result of coordinate transformation). To compare spatial information content
364 in the two populations, we first estimated intrinsic dimensionality of the two sets of population
365 vectors. This was performed using two recent state-of-the art methods: DANCo (*Ceruti et al., 2014*),
366 as implemented by the `intrinsicDimension` R package, and ID_fit (*Granata and Carnevale, 2016*).
367 For both methods, the principal parameter affecting dimensionality estimation is the number of
368 neighbors for each point in the set that is used to make local estimates of the manifold dimension.
369 Second, we used two different methods to visualize the structure of the low-dimensional manifold:
370 Isomap (*Tenenbaum et al., 2000*) and t-SNE (*van der Maaten and Hinton, 2008*). To extract principal
371 axes of the manifold, we used PCA on the data points projected on two principal dimensions
372 provided by the above methods. We chose the parameter values for which the visualized manifold
373 best approximates the original space. We then determined a set of points (i.e. population vectors)
374 that lie close to the principal axes of the manifold and visualized them in the original environment.
375 If the manifold structure corresponds well to the spatial structure of the underlying environment,
376 the principal axes of the manifold should lie close to the principal axes of the environment.

377 Simulation 4: Visual responses of hippocampal neurons in an image memorization task
378 This simulation was inspired by the study of *Jutras and Buffalo (2010a)* in which a large set of
379 novel visual stimuli was presented to monkeys on a computer screen. Neuronal activity in the
380 hippocampal formation in response to the visual stimuli was recorded. One of the results of
381 this study suggested that hippocampal neurons encode stimulus novelty in their firing rates. To
382 simulate this result, we presented to the model 100 novel stimuli randomly chosen from the dataset
383 retrieved from http://www.vision.caltech.edu/Image_Datasets/Caltech101. The stimuli (resized to
384 160 × 100 pixels) were shown to the model successively in one continuous session (500ms stimulus
385 presentation time + 1000ms inter-trial interval with no stimuli) and the activities of the hippocampal
386 neurons during learning were recorded.

387 Simulation 5: Spatial reorientation
388 In this simulation of the experiment of *Gouteux et al. (2001)*, the testing room was a rectangular
389 3D environment with area 20×10 m and wall height 6m. In the “No cues” task the only visual
390 features in the room were provided by the outlines of the walls. In the other 3 tasks, a square
391 visual cue was presented in the middle of one of the walls with the edge length equal to 1/6
392 (small cue), 1/3 (medium cue) or 1/2 (large cue) of the environment width. Each task consisted
393 of two phases, exploration and reorientation. During the exploration phase the modeled animal
394 uniformly explored the environment, as in Simulation 3. The reorientation phase composed multiple
395 trials. At the beginning of each trial, the model was placed at one of spatial locations covering
396 the environment in a uniform grid. At each of these locations, 9 successive views were taken.
397 Reorientation performance was assessed in two ways: (i) only the first view at each location was
398 used for reorientation; (ii) successive views accumulated over 60 successive positions were used for
399 reorientation.

400 Simulation 6: Memory-based visual search

401 In this simulation we used a dataset of visual images used in the study by *Fiehler et al. (2014)*. This
402 dataset consists of 18 image sets corresponding to 18 different arrangements of the same 6 objects
403 (mug, plate, egg, jam, butter, espresso cooker). Each set includes a control image (all objects on the
404 table in their initial positions) and images in which one of the objects is missing (target object) and
405 one or more other objects displaced to the left or to the right. In the simulation we used only a
406 subset of all images in a set that included either 1, 3 or 5 of the objects mentioned above displaced
407 either to the left or to the right (referred to as “local” condition in *Fiehler et al., 2014*), giving rise
408 to 6 experimental conditions. In each condition, there were 18 test images of displaced objects,
409 plus the associated control images. Taking into account the distance between the animal and the
410 screen as well as the size of the image (provided by *Fiehler et al. (2014)*), we calculated the size
411 of the image in degrees of visual field. We then determined a rectangular portion of the image
412 ($30 \times 15^\circ$) that included all objects in initial and displaced positions in all images. The contents of this
413 area served as an input to the model. Thus, in this simulation the spatial resolution of the visual
414 input was higher than in the previous simulations as the visual field of the model was smaller, but
415 the size of the input network was kept the same.

416 During each simulation trial, the image of objects in initial positions was first presented to the
417 network during 2000 ms and stored by the hippocampal cells. The image of displaced objects (in
418 one of the 6 conditions above) was subsequently presented to the network for the same amount of
419 time and the orientation error was read out from the mean firing rates of the reorientation network.

420 Results

421 We first show that properties of neuronal firing along the simulated neural pathway from the
422 visual cortex to the hippocampus reflect those of biological neurons along the pathway. We then
423 demonstrate how backward projections from the hippocampus to the head direction network, can
424 explain hippocampal influence on head direction during spatial reorientation and memory-based
425 visual search.

426 Visual and parietal model neurons encode sensory representations in distinct ref- 427 erence frames

428 We start with a characterization of modeled dorsal-visual path neurons in the case when a simulated
429 animal is assumed to sit in front of a screen and is free to rotate its head (*Duhamel et al., 1997*;
430 *Snyder et al., 1998*, for simplicity, we assume that rotation occurs only in the horizontal plane). The
431 firing rate of occipito-parietal (input) neurons and the output parietal neurons as a function of the
432 allocentric position of a visual stimulus (i.e. a vertical bar moving horizontally across the visual field)
433 was measured for two different head directions (*Figure 3A,B*). For a neuron in the input population,
434 a change in head direction induces the corresponding change of the receptive field of the neuron,
435 since its receptive field shifts together with the head along the allocentric position axis (*Figure 3C*).
436 In contrast, for a parietal output neuron, a change in head direction does not influence the position
437 of its receptive field, which remains fixed in an allocentric frame (*Figure 3D*). To show that this is
438 also true on the population level, we measured, for all visual input cells and all parietal output cells,
439 the amount of shift in its receptive field position as a function of head direction shift, while the
440 head was rotated from -50° to 50° . For cells in the occipito-parietal visual area, the average linear
441 slope of the dependence is close to 1, whereas in the allocentric parietal population the average
442 slope is close to 0 (*Figure 3E*), meaning that these two populations encode the visual stimulus
443 in the two different reference frames: head-fixed and world-fixed. These properties of model
444 neurons reproduce well-known monkey data showing that different sub-populations of parietal
445 cortex neurons encode visual features in the two reference frames (*Duhamel et al., 1997*; *Snyder*
446 *et al., 1998*).

447 The receptive fields of the intermediate neurons of the coordinate transformation network

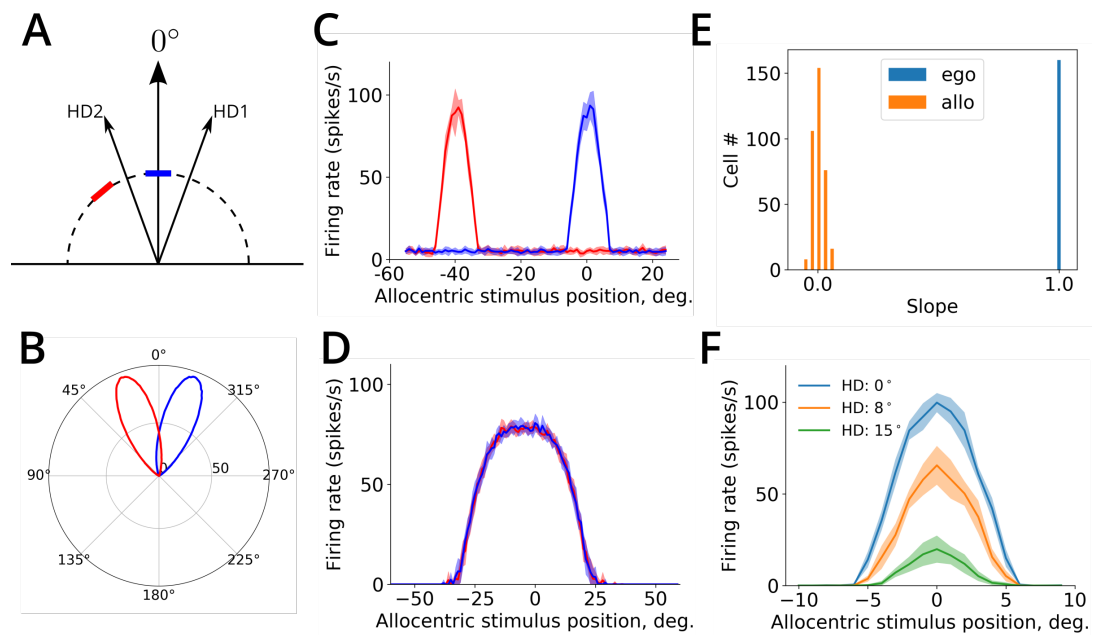


Figure 3. Properties of neurons in the coordinate-transformation network. A. A schematic representation of the receptive field of one input visual input neuron at two head directions (HD1 and HD2). The position of the receptive field of the neuron is shown by the blue and red bar for HD1 and HD2, respectively. B. The population activity of head direction cells in the model at 20° (HD1) and -20° (HD2). C. Tuning curves of an input visual neuron (\pm SD) for the two head directions represented in B. D. Tuning curves of an allocentric output neuron for the same head directions. E. Histograms show the distributions of the linear dependence slopes between the shift in the receptive field position and the shift in head direction, for egocentric (in blue) and allocentric (in orange) neuronal populations. F. Transformation network neurons are gain-modulated by head direction. Stimulus tuning curves of the same neuron for three different head directions are shown.

448 exhibit gain modulation by head direction (**Figure 3F**), as do monkey parietal neurons (**Snyder et al.,**
 449 **1998**). The hypothesis of reference-frame conversion via gain modulation has been extensively
 450 studied in both experimental and theoretical work, in the context of sensory-motor coordination
 451 during vision-guided reaching (**Avillac et al., 2005; Pouget and Sejnowski, 1997; Salinas and Abbott,**
 452 **2001**). While coordinate-transformation processes involved in the two cases are conceptually
 453 similar, the underlying neuronal computations can differ substantially, because the former requires
 454 simultaneous remapping for the whole visual field, while the latter is limited to the computation of
 455 coordinates for a single target location (i.e. a representation of the point-like reaching target). This
 456 difference limits the use of noise-reducing attractor-like dynamics that is an essential component
 457 in point-based sensory-motor transformation models (**Pouget et al., 2002**), because in full-field
 458 transformation the information and noise are mixed together in a single visual input stream.

459 **Spatial coding using temporal accumulation of successive views**

460 Because of a limited view field, at each moment in time the simulated animal can directly observe
 461 only a restricted portion of visual environment (i.e. a visual snapshot, see **Figure 4A,B**). That these
 462 snapshot-like representations are represented in memory, has been demonstrated in a number of
 463 studies showing viewpoint-dependent memory representations (**Diwadkar and McNamara, 1997;**
 464 **Christou and Bühlhoff, 1999; Gaunet et al., 2001**). Moreover, experimental evidence suggests that
 465 visual information can be accumulated from successive snapshots during e.g. head rotation, giving
 466 rise to a panoramic-like representation of the surrounding environment that can inform future
 467 goal-oriented behavior (**Tatler et al., 2003; Oliva et al., 2004; Golomb et al., 2011; Robertson et al.,**
 468 **2016**). A candidate neural mechanism for implementing such integration is short-term memory, i.e.
 469 the ability of a neuron to sustain stimulus-related activity for a short period of time (**Goldman-Rakic,**

470 1995). In our model, this is implemented by sustained firing via prolonged NMDA receptor activation
471 (Figure 4C). Combined with STDP learning rule in the connections between the parietal output
472 neurons and the hippocampus, this mechanism ensures that a time-integrated sequence of visual
473 snapshots is stored in the synapses to hippocampal neurons. In particular, head rotation results in
474 a temporarily activated panoramic representation in the population of output parietal neurons that
475 project to CA1. STDP in these synapses ensures that these panoramic representations are stored in
476 the synapses to downstream CA1 neurons (Figure 4D).

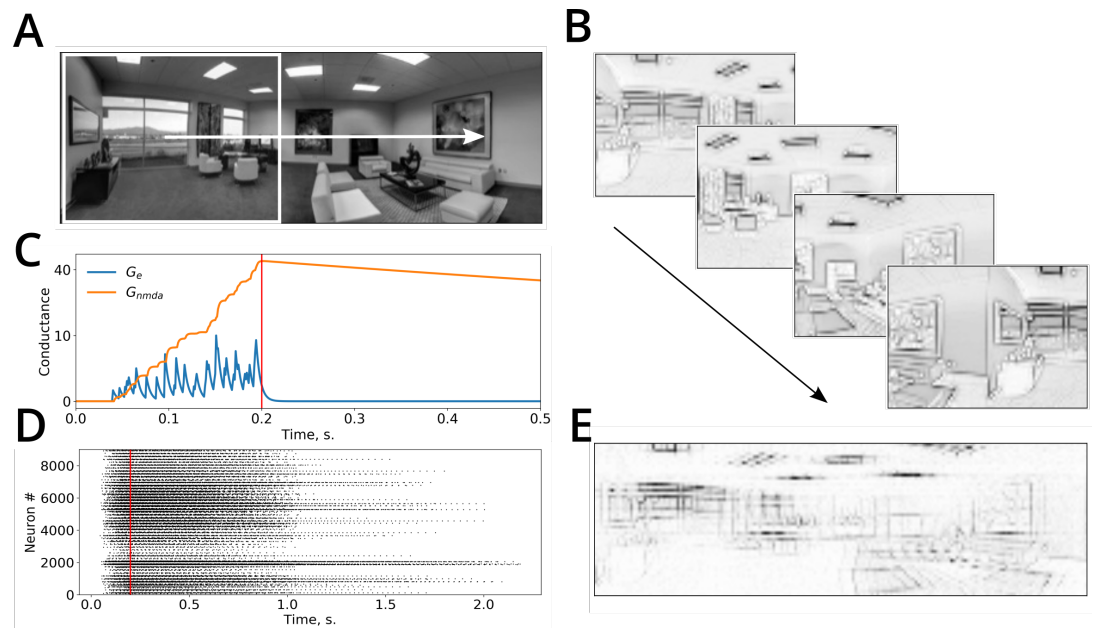


Figure 4. Temporal accumulation of successive visual snapshots in the model. A. A panoramic image of an environment superimposed with the visual field of the simulated animal (white rectangle). The white arrow shows the direction of visual scan path. B. Several successive visual snapshots along the scan path shown in A are represented by mean firing rates of the occipito-parietal (egocentric) network. C. An example of the evolution of AMPA and NMDA receptor conductances of parieto-retrosplenial output neurons as a function of time. Stimulus onset: $t = 0$, stimulus offset: $t = 200\text{ms}$ (red line). D. Raster plot of spiking activities of the output neurons showing short-term memory in this network. An input is presented at time 0 and is switched off at the time shown by the red vertical line. The neurons remain active after stimulus offset due to NMDA-receptor mediated short-term memory. E. Synaptic weight matrix of a single hippocampal neuron after learning stores the activity of the parieto-retrosplenial output layer accumulated over several successive snapshots shown in B.

477 A large amount of experimental evidence suggests that many animal species encode a geometric
478 layout of the surrounding space (Cheng and Newcombe, 2005; O'Keefe and Burgess, 1996; Gouteux
479 et al., 2001; Krupic et al., 2015; Keinath et al., 2017; Bécu et al., 2019). Computational models of
480 spatial representation in rodents link this sensitivity to geometry with a postulated ability of the
481 animal to estimate distances to surrounding walls (Hartley et al., 2000) or to observe panoramic
482 visual snapshots of surrounding space (Cheung et al., 2008; Sheynikhovich et al., 2009), and rely on
483 a wide rodent visual field (320°). That the width of visual field plays a role in geometric processing
484 in humans was demonstrated in the study by Sturz et al. (2013), in which limiting visual field to
485 50° impaired performance in a geometry-dependent navigation task, compared to a control group.
486 We thus studied whether activities of egocentric and allocentric neurons in the model encode
487 information about the geometry of the environment and whether snapshot accumulation over time
488 plays a role in this process.

489 To do this, we run the model to uniformly explore a square environment and we stored popula-
490 tion rate vectors of the egocentric-visual and allocentric-parietal populations at successive time
491 points during exploration. More specifically, for the egocentric population, each population vector

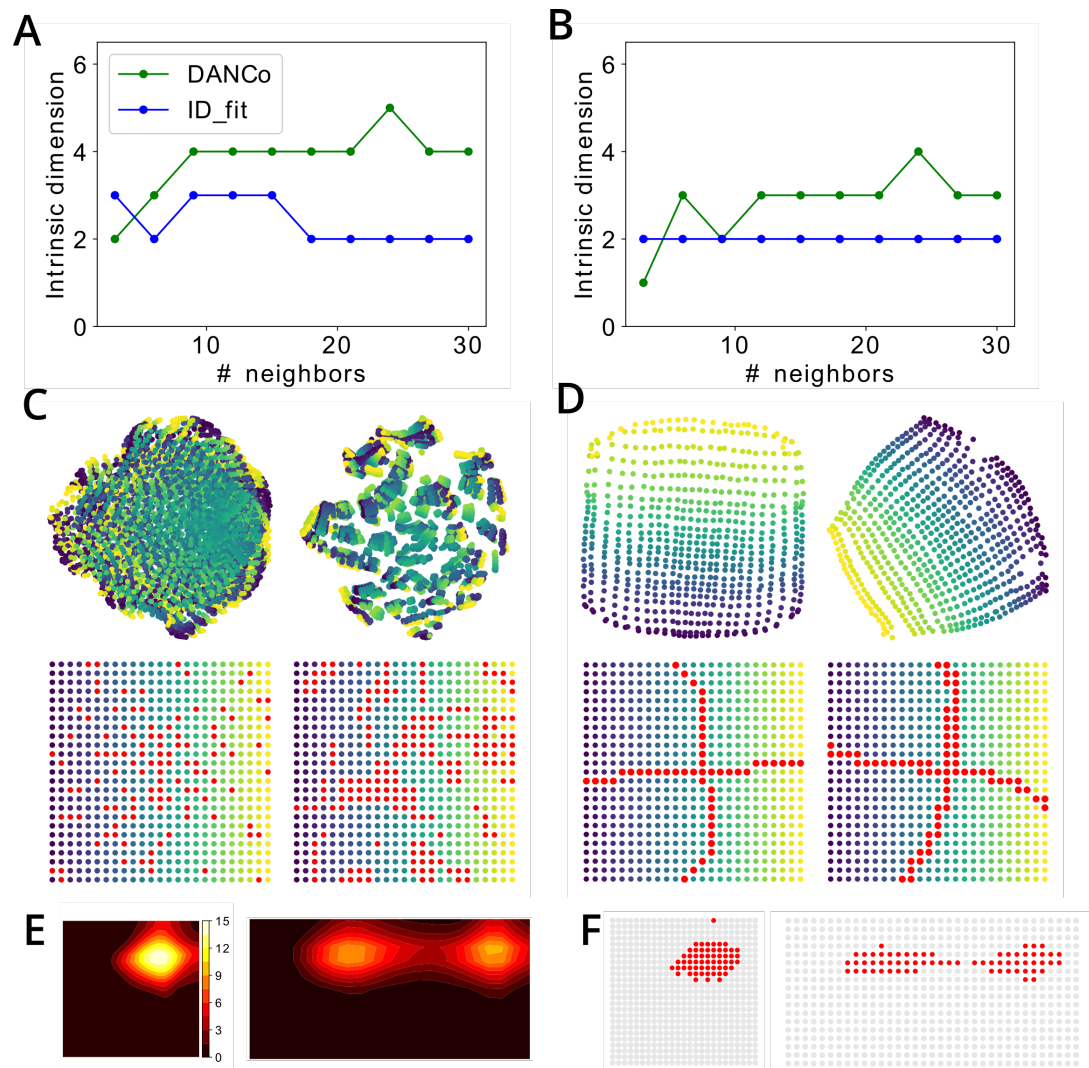


Figure 5. Representation of spatial relations by egocentric (occipito-parietal) and allocentric (parieto-retrosplenial) visual neurons. A,B. Estimation of intrinsic dimensionality of the set of population vectors in the egocentric (A) and allocentric (B) populations by two different state-of-the-art methods (DANCo and ID_fit). C,D. Top: Projection of the population vector manifolds onto a two-dimensional plane using Isomap (left) and t-SNE (right) algorithms. Color gradient from yellow to blue corresponds to the position at which the corresponding population vector was observed, as shown in the Bottom row. Red dots show population vectors that lie close to the principal axes of the 2D manifold of the principal space. C and D show population vectors of the egocentric and allocentric neuronal populations, respectively. E. An example of the receptive field of one hippocampal neuron after learning the environment before (left) and after (right) extension of the environment along its horizontal axis. F. For the same neuron as in E, red dots show locations in the environment where this neuron is winner in the WTA learning scheme.

492 corresponded to population activities evoked by the presentation of a single visual snapshot. In con-
 493 trast, for the allocentric population, each population vector corresponded to a panoramic snapshot
 494 obtained by accumulating several successive snapshots during head rotations (see Methods). The
 495 visual information content was identical in two sets of population vectors as they were collected
 496 during the same exploration trial. Population vectors in each set can be considered as data points in
 497 a high-dimensional space of corresponding neural activities. These points are expected to belong to
 498 a two-dimensional manifold in this space, since during exploration the model animal moves in a 2D
 499 spatial plane. The analysis of the intrinsic dimensionality of both sets indeed shows that it is about
 500 2 (Figure 5A,B). We then applied two different manifold visualisation techniques to see whether the

501 shape of manifold reflects the environment shape (see Methods). We found that when applied to
502 population vectors of the egocentric population, the structure of the manifold did not reflect the
503 layout of the environment (**Figure 5C**). In contrast, allocentric population activities reliably preserved
504 geometric information in the spatial organization of the manifold (**Figure 5D**). Moreover principal
505 axes of the manifold corresponded to the principal axes of the underlying environment only for
506 the population vectors of the allocentric population (bottom row of **Figure 5C,D**). The extraction of
507 principal axes of an experimental space has been proposed to underlie spatial decision making in
508 several experimental paradigms, including data from humans (**Gallistel, 1990; Cheng and Gallistel,**
509 **2005; Sturz et al., 2011**).

510 STDP in the connections between the parietal and hippocampal neurons ensures that allocentric
511 spatial views are stored in memory, while lateral inhibition in the hippocampal layer implements a
512 competition such that different hippocampal cells become selective to different localized regions of
513 the visuospatial manifold, which, by virtue of the coherent mapping on the real space, correspond
514 to spatial receptive fields (**Figure 5E**). When the geometry of the environment is modified, but
515 the memorised allocentric representation remains the same, modeled hippocampal cells express
516 corresponding modifications of their receptive fields (**Figure 5E,F**), potentially providing a purely
517 sensory basis for the effects of geometric manipulations observed in rats (**O'Keefe and Burgess,**
518 **1996**) and humans (**Hartley et al., 2004**). These simulations show how the egocentric-allocentric
519 conversion and short-term memory along the modeled dorsal visual pathway can be instrumental
520 in structuring the hippocampal input according to the geometric properties of the surrounding
521 space that were repeatedly shown to affect human navigation (**Hermer and Spelke, 1994; Bécu**
522 **et al., 2019**).

523 **Visual responses of hippocampal neurons reflect learning of visual stimuli**

524 The hippocampal memory network is thought to support a large spectrum of memory-based
525 behaviors, and therefore its basic properties should manifest themselves in situations other than
526 navigation. In particular, plasticity and competition, which are proposed to mediate fast hippocampal
527 learning of visual information in our model, occur not only during navigation but also in a
528 passive image viewing paradigm. In the next simulation inspired by the experiment of **Jutras and**
529 **Buffalo (2010a)** we used the stationary model to learn a set of 100 novel images presented in
530 a quick succession (see Methods) and recorded activities of modeled hippocampal neurons. In
531 response to the presented stimuli, some neurons increased their firing rates as a result of STDP
532 (winning neurons), while the rest of the neurons were inhibited (**Figure 6A**). Even though only a
533 few neurons won the competition for each particular stimulus, some neurons were selective to
534 a larger number of stimuli than others (**Figure 6C,D**). Therefore, stimulus-averaged firing rates of
535 different neurons expressed either a decrease in the average firing rate (for neurons that were
536 never winners), no change in the average rate (for neurons that were winners for a relatively small
537 number of stimuli), or an increase in the average rate (for neurons that were winners for a relatively
538 high number of stimuli, **Figure 6B**). There was a larger number of neurons expressed decreased
539 firing rates or no change, than those that increased their average rate (**Figure 6D**).

540 Under the assumption that a novelty-detection mechanism (assumed to reside in the hippocampus
541 or elsewhere, but not modeled here) prevents hippocampal firing in response to a repeated
542 stimuli, these results are in accord with the data from a number of studies showing that different
543 subsets of recorded hippocampal neurons either decreased, showed no changes, or increased their
544 activity in response to the presentation of a novel stimulus (**Jutras and Buffalo, 2010a; Rutishauser**
545 **et al., 2006; Viskontas et al., 2006**). In these studies of the role of novelty in hippocampal process-
546 ing, stimulus-averaged elevation of neural activity was considered as an indication of an abstract
547 (i.e. independent of stimulus identity) novelty processing in the hippocampus (**Jutras and Buffalo,**
548 **2010a; Rutishauser et al., 2006**). It is unclear how such an abstract representation of novelty can
549 be reconciled with the role of the hippocampus in navigation. In contrast, our simulation results
550 suggest that elevation or depression of stimulus-averaged firing rate in a neuron may be related to

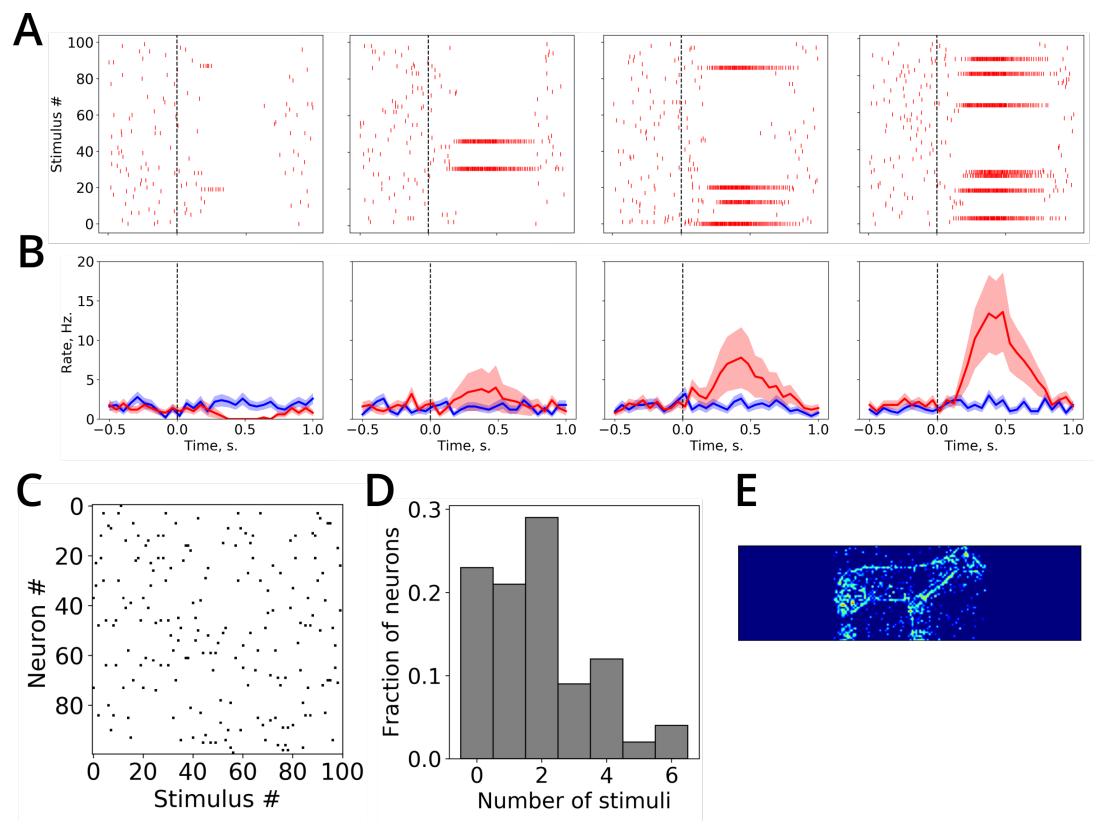


Figure 6. Visual responses of modeled hippocampal neurons. A. Spike raster plots for four example neurons in response to presented visual stimuli. B. Stimulus-averaged firing rates of neurons in A (mean \pm SEM shown in red), compared to baseline firing rates (shown in blue). The dashed vertical line represents the stimulus onset. C. Black dots correspond to winner neurons among all other neurons (vertical axis) for each of the presented stimuli (horizontal axis). D. The histogram shows the distribution of neurons with respect to the number of stimuli for which they are winners. E. An example of the weight matrix of a hippocampal neuron after learning.

551 the number of stimuli for which this neuron is winner.

552 **Top-down hippocampal input in spatial reorientation and memory-based search**

553 The population of the hippocampal neurons in the model represents the neural storage of (po-
554 tentially highly processed) visual information aligned with an allocentric directional frame by the
555 coordinate transformation network. In this section we show how this neural storage can affect two
556 types of behavior: (i) determination of position and orientation when a disoriented monkey is placed
557 into a familiar environment (*Gouteux et al., 2001*); and (ii) memory-guided visual target search
558 in an image viewing paradigm (*Fiehler et al., 2014*). While these two tasks may seem unrelated,
559 we propose that the same neural process, namely a reorientation of the head-direction network
560 based on the comparison between the newly obtained visual information and the contents of the
561 hippocampal allocentric storage, underlies behavioral decisions in these tasks.

562 **Spatial reorientation**

563 In a series of reorientation experiments with monkeys, *Gouteux et al. (2001)* have shown that
564 these animals relied on both the geometric information (given by the three-dimensional layout
565 of the rectangular experimental space) and non-geometric cues (e.g., landmark objects placed
566 near the walls or corners of the recording chamber). The authors paid specific attention to the
567 influence of landmark size on reorientation behavior. When small objects were placed near one of
568 the walls or in the corners of the room, the monkeys did not use these cues to reorient, and their
569 search pattern was determined based only on the geometric information. Importantly, this was

570 not because the monkeys did not notice the landmarks, since they performed exploratory actions
 571 towards them (looked at or touched them). Once the landmark size was increased however, the
 572 monkeys successfully used them for reorientation independently of their location and number.

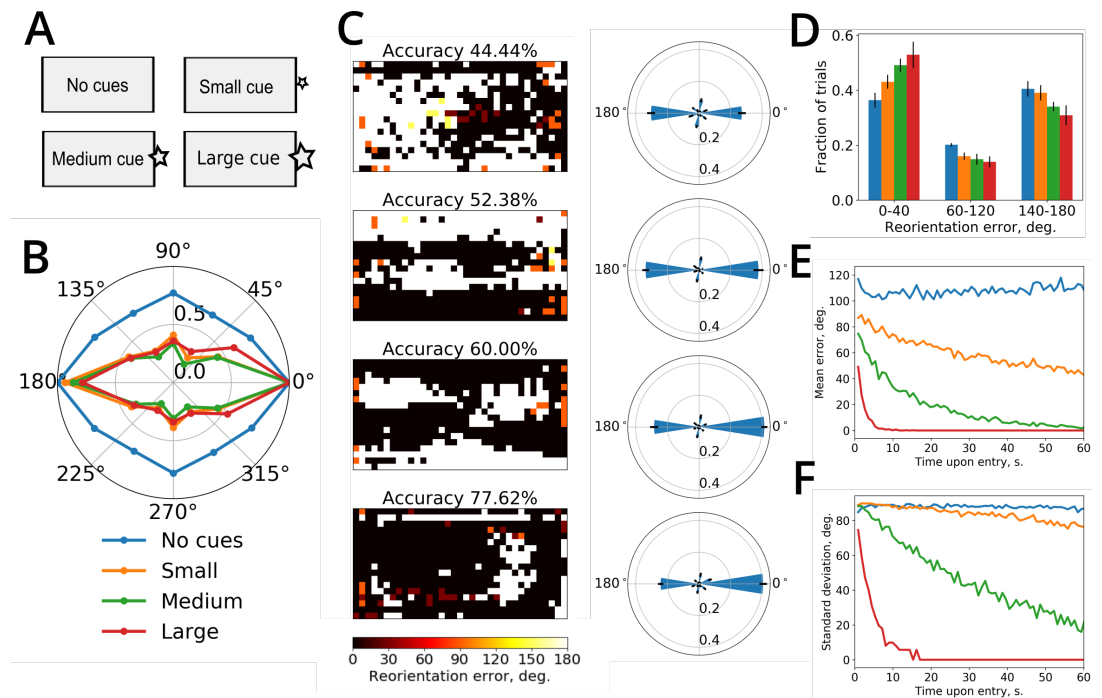


Figure 7. Simulation of the reorientation experiment. A. The experimental environment was a rectangular room (represented by the gray rectangle). The same reorientation simulation was run in four conditions: no visual cues apart from walls of the room, or 1 visual cue at three different sizes (small, medium, large). B. Polar plot of the mean activity of the reorientation network when the simulated animal was placed in various locations in the room. Dots mark the preferred locations of the reorientation N_{re} neurons. Colors from blue to red represent 4 experimental conditions. C. Rows from top to bottom correspond to experimental conditions as in A. Left: Reorientation maps show, for each location in the room, the reorientation error committed by the model after seeing only the first visual snapshot from that location (at a randomly chosen head orientation). The pixel color from black to white codes for the absolute value of the reorientation error from 0 to π . Right: polar histograms of reorientation errors (\pm SD), averaged over 9 random orientations at each location. D. Bar plot shows the distribution of the absolute reorientation errors (\pm SD) among the approximately correct orientation (0-40°), rotational error (140-180°) and other directions. E, F. Reorientation error mean (E) and its standard deviation (D) when progressively more snapshots were used for reorientation. Color code for D, E, F as shown in B.

573 To simulate these data, we tested the model in four reorientation tasks in a virtual three-
 574 dimensional rectangular room. In these tasks, either no landmark cues were present in the
 575 room, or one visual landmark of three different sizes was placed in the middle of one of the
 576 walls (**Figure 7A**). Each task comprised an exploration phase, during which the model randomly
 577 explored the environment, and a reorientation phase. In the reorientation phase the model was
 578 initialized with a random heading direction and placed back into the environment learned during
 579 the exploration phase at a random location. The performance of the model was assessed from the
 580 accuracy of reorientation: we assume that the animal will navigate to the correct corner if it has
 581 correctly estimated its initial heading, whereas it will make a navigation error if the reorientation
 582 error is high.

583 Once the information from the initial view reached the hippocampus upon the reentry to the
 584 environment, the activity of the reorientation network signalled the orientation error (**Figure 7B**).
 585 This error represented the discrepancy between the initial heading direction and the heading
 586 direction most consistent with the allocentric information stored in the projections from the place

587 cells to the reorientation network. The asymmetric shape of the polar plot reflects the influence of
588 the environment's geometric layout on reorientation: for the no-cue condition, the network activity
589 peaked at the correct (0°) and its rotationally opposite (180°) orientations with an identical average
590 amplitude. When the visual cue was present, its size determined the difference between the activity
591 peaks. Therefore, when reorientation was performed from different locations in the environment
592 (based only on the first view taken), the accuracy, measured as the percentage of locations with a
593 correctly determined orientation, was about 50% in the no-cue condition and raised to about 77%
594 in the large-cue condition (**Figure 7C**, left column). Reorientation maps (**Figure 7C**, right column)
595 suggest that depending on the position of the orienting cue in the room, some locations in the
596 environment provide better visual information for reorientation than others (shown by white areas
597 in the maps). The histograms of orientation errors (**Figure 7C**, right column, and **Figure 7D**) show
598 that, on average, a larger visual landmark provides a much better reorienting cue than a small one,
599 for which a similar number of correct decisions and rotational errors was observed (**Figure 7D**). This
600 is due to the fact that orientation is determined essentially by comparing the egocentric view from
601 the initial position with allocentric views stored in synaptic memory, without any explicit landmark
602 identification process. Therefore, influence of small visual cues becomes negligible with respect to
603 gross visual features of the surrounding space (corners, shapes of the walls, etc.). These results
604 are consistent with the hypothesis that reorientation is a fast, bottom-up process based on low-
605 level visual information (*Sheynikhovich et al., 2009*). Learning landmark identities and their spatial
606 relation to goals can be added by subsequent learning, but may not be taken into account unless
607 their are sufficiently salient compared to other (e.g. geometric) cues present in the environment
608 (*Cheng, 1986*).

609 So far the reorientation performance was assessed based only on the first view taken. The
610 reorientation performance is likely to increase if the animal is allowed to accumulated visual
611 information from successive views taken in the same location at different orientations or at different
612 locations, e.g. during initial movements through the environment. This is what happens in the
613 model, since increasing the number of snapshots that are used for reorientation improved its
614 accuracy (**Figure 7E,F**). In this case we placed the simulated animal at 60 successive positions, while
615 at each position the animal rotated its head to obtain a corresponding panoramic view. The activity
616 of the reorientation network was calculated as a sum of its activities after each successive view.
617 When a large cue was present, the simulated animal obtained an accurate orientation estimate
618 after visiting about 10 successive locations. In contrast, the mean error and standard deviation of
619 reorientation were decreasing much slower for smaller sized landmarks. Thus, our model describes
620 a neural mechanism for spatial reorientation which relies on an allocentric visual information stored
621 in the hippocampal network. This allocentric information feeds into a head-direction-like network,
622 assumed to reside in the retrosplenial cortex, that signals reorientation error and affect the sense of
623 direction via its input to the head-direction system of the brain (*Taube, 2007*). In addition to providing
624 a mechanistic basis for the reorientation process, which is a necessary part of navigational behavior
625 and whose existence is assumed (either implicitly or explicitly) in a number of computational models
626 of navigation, this model proposes how reorientation can be performed continuously, i.e. during
627 ongoing spatial behavior.

628 Memory-based visual search

629 To illustrate a potential role of the stored hippocampal representation in memory-based visual
630 tasks, we simulated the study of *Fiehler et al. (2014)*. In this study, head-fixed human subjects
631 remembered a visual scene with 6 objects on a table, presented on a computer screen (**Figure 8A**,
632 top). This encoding phase was followed by 2-s. delay (uniform gray image), and then the subjects
633 were presented with a modified scene in which one of the objects was missing (the target object)
634 and either 1, 3 or 5 other objects displaced horizontally (**Figure 8A**, bottom). The subjects were
635 required to point to the remembered location of the missing object. If the subjects had used
636 only an egocentric information (i.e. remembered object position with respect to the head), then

637 their performance would have been independent from the displaced objects. The results of this
638 experiment demonstrated in contrast that pointing performance was influenced by the non-target
639 objects, such that shifting a higher number of them induced a larger pointing error. Even though the
640 pointing error was always made in the direction of the object displacement in the image, the size of
641 the error only partially accounted for the veridical displacement of the objects. These data suggest
642 that human subjects combine allocentric (i.e. based on the information from the environment, in
643 this case represented by the visual features associates with displaced objects) and egocentric (i.e.
644 based on the memory of an egocentric location of the target object) information during memory-
645 based search (Fiehler *et al.*, 2014). The neural mechanism of this allocentric correction of the
646 egocentric memory is unknown.

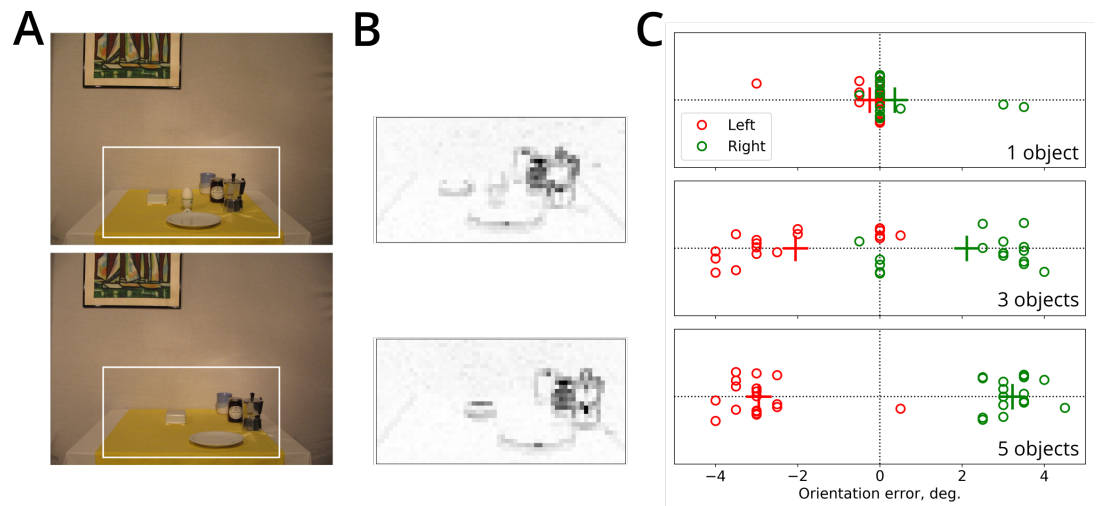


Figure 8. A. An example of the remembered (top) and test (bottom) images. In this example, the target object is the egg and 5 non-target objects were shifted to the right in the test image, compared to the encoded image. The white rectangle denotes the part of the image that was provided as input to the network. It corresponds to the part of the image most fixated by the subjects in the experiment. B. Mean firing rates of the egocentric neurons in the model for the encoded and test images shown in A. C. Orientation errors induced in the model by the presentation of the test images with 1 (top), 3 (middle) and 5 (bottom) displaced objects. Horizontal position of each dot corresponds to the maximal activity peak of the reorientation network. Different dots represent different sets of objects in the image dataset. Leftward and rightward displacements are shown in red and green, respectively. Crosses mark the mean displacement value per group. Random jitter along the vertical axis is added for clarity.

647 We hypothesized that the influence of allocentric image information observed in this experiment
648 arises as a result of a slight misorientation of the head direction network due to the apparent shift
649 of visual features caused by the object displacement in the attended area of the image. In order
650 to demonstrate this effect, we first presented to the model an image of a control scene with all 6
651 objects (see **Figure 8A**, top, for an example). We used, with permission, the same image data set that
652 was used in the experimental study. As input to the network we only used the part of the image near
653 the objects, because in the experiment it was fixated most of the time and because of the evidence
654 that displacement of objects outside of this area had no influence on reaching performance (Fiehler
655 *et al.*, 2014). The network converted the visual input of the egocentric layer (**Figure 8B**) to an
656 allocentric representation according to the actual head direction (set to 0°), which was stored in the
657 synapses between the parieto-retrosplenial output cells and hippocampal cells as before. In this
658 simulation we ignored competition effects, since it was not required to remember multiple images.
659 Second, after the first scene was learned, an image of the scene with one object missing and either
660 1, 3 or 5 objects displaced (see **Figure 8B**, bottom) was presented to the model. The orientation error
661 caused by the object displacement can then be read directly from the activity of the reorientation
662 network (**Figure 8C**). As in the experiment, the number of displaced objects affected the amount of

663 allocentric correction. Since in the test images the displaced objects correspond only to a subset of
664 all visual features, the mean correction only partially account for the object displacement. Thus,
665 as in the case of spatial reorientation, the influence of the allocentric information (in this case
666 represented by low-level features of the presented image) is caused by the comparison between
667 the stored allocentric and incoming allocentric views, and the resulting activity of the reorientation
668 network that calibrates the head direction signal.

669 Discussion

670 The presented model focuses on the dorsal visual pathway for information processing, generally
671 thought to provide contextual or “where” information to memory structures in the MTL, by con-
672 trast to the ventral pathway mediating the processing of object/item representations or “what”
673 information (*Goodale and Milner, 1992; Kravitz et al., 2011*). The two pathways converge to the
674 hippocampus where both types of information are combined to form the episodic memories. Out-
675 puts of hippocampal processing go back to neocortical areas from which the input was originated.
676 In both spatial (e.g. spontaneous novelty exploration) and non-spatial (recollection/familiarity)
677 experimental paradigms the dorsal pathway has been implicated in the recollection of contextual
678 information (e.g. the scene or location where an item was observed) and not in remembering the
679 object identity (see *Eichenbaum et al., 2007*, for review). These proposals go in line with general
680 properties of neural activities along the dorsal pathway such as PHC and RCS. In particular, fMRI
681 studies that both RSC and PHC are activated by scene processing, with a part of PHC responding
682 equally strongly to images of spatial layouts with or without objects (*Epstein and Kanwisher, 1998;*
683 *Epstein, 2008*). RSC was shown to be more strongly implicated in recollection than familiarity (*Ep-*
684 *stein, 2008*) and is proposed to play a specific role in encoding spatial and directional characteristic
685 of landmarks and their stability *independent of their identity* (*Mitchell et al., 2018*).

686 In the present work, the selectivity to scenes and spatial layouts, as opposed to objects, during
687 spatial navigation is modeled simply as sensitivity to views (i.e. the total contents of the animal’s
688 visual field at one moment in time, usually acquired across multiple fixations, potentially associated
689 with accompanying head movements in natural conditions). Indeed, spatial layout information
690 is often available from a low-frequency representation of a view (*Kauffmann et al., 2015*, but see
691 *Rajimehr et al., 2011*), whereas object representations take up a much smaller portion of a view
692 and usually require high-spatial frequency analysis at a localized part of the image during visual
693 fixation. In our simple model, we represented the contents of a view by a retinotopic-like grid of
694 orientation-sensitive filter responses at just a few spatial frequencies, but a much more complex
695 visual processing can be “inserted” between our input visual layer and the parietal transformation
696 circuit (involving e.g., extraction of salience maps, depth processing, contour extraction, etc). The
697 coordinate-transformation circuit and the rest of the model are agnostic about the nature of features
698 provided to them as input, as long as these features are given in a retinotopic-like head-fixed frame
699 and take up the whole visual field. This last requirement excludes object processing, assumed
700 to be done in parallel in the ventral stream, since object representations are view-independent
701 and assume translation invariance over the visual field (*Serre et al., 2005*). The relative (i.e. size
702 dependent) sensitivity to objects in our model (see “Spatial reorientation”) arises from the fact that
703 large, distal and stable objects (or landmarks) that make up a large portion of a view are considered
704 as part of the layout, and not as identified objects/landmarks. In contrast, relatively small objects,
705 landmarks, or a high-frequency contents of other small localized portions of a view exert contribute
706 only weakly to the overall visual representation. Indeed, they are often overshadowed by gross
707 visual features present in views, such as corners, walls, and other large-scale visual structures
708 during comparison of new and remembered view-based representations (*Bécu et al., 2019*).

709 Our model can thus be considered as a model of encoding of contextual information, as opposed
710 to object-related one, and the notion of context is well defined: it is the visual information present
711 in the set of topographically-organized features present in a set of views (that could comprise only
712 one element) and stored in memory after the acquisition phase of a task. This notion of context can

713 be extended to a non-spatial setting (see “Memory-based visual search”): topographically-organized
714 image features present in attended part of the screen and stored in memory provide contextual
715 information with respect to any object-related information stored from the scene (such as the
716 identities of the objects in this experiment). In the absence of reliable object-related information
717 (such as the missing target object), contextual information can be used to drive behavior. The
718 important piece of information that is present in topographic representation of a scene, but is absent
719 in object-related memory, is spatial location. Indeed, one can assign position information within the
720 topographic representation of a view (with respect to an allocentric directional frame, or with respect
721 to the other features in the view). Therefore, (allocentric) view-based contextual representations
722 can serve as a basis for remembering spatial and directional characteristics of objects or landmarks
723 independent of their identity. Spatial locations in such a contextual representation can serve as
724 “place holders” for specific object/landmark information extracted and stored in the ventral visual
725 stream, or as “pointers” to this information. Such a notion of contextual information is well in line
726 with proposed role of the PHC and RSC in landmark processing (*Epstein, 2008; Mitchell et al., 2018*).

727 While the existence of view-based representations in human spatial memory is well established
728 (*Shelton and McNamara, 1997; Diwadkar and McNamara, 1997; Christou and Bühlhoff, 1999; Gar-*
729 *soffky et al., 2002; Burgess, 2006*), the existence of a spatiotopic representation of the surrounding
730 visual space is more controversial. Some proposals reject the existence of such a representation
731 (*O’Regan, 1992*), some suggest that only a limited number attended features survive beyond one
732 fixation (*Rensink, 2000*), and some suggest that a feature-rich representation is constructed by
733 accumulating information over time (see *Tatler and Land, 2011*, for review). For example, some
734 experimental evidence in favor of the latter view comes from studies showing that visual search
735 can be directed to remembered locations in a panoramic scenes and that visual saccades can be
736 programmed to reach previously observed targets outside of the current viewfield (*Land et al.,*
737 *1999; Oliva et al., 2004*). These and similar data suggest the existence of a quasi-panoramic repre-
738 sentation of surrounding visual cues, accessible for the planning of eye movements, i.e. most likely
739 topographic with respect to the visual space (*Golomb et al., 2011; Park et al., 2007; Melcher and*
740 *Morrone, 2015; Robertson et al., 2016*). While both egocentric and allocentric representations are
741 stored in memory, they are converted to an egocentric frame whenever possible (*Chen et al., 2011*).
742 By linking such a panoramic representation with its potential utility for spatial memory and the well
743 known role of the MTL in the storage of allocentric memories, we postulated the existence of an
744 allocentric, visually topographic representation of the surrounding space in the parieto-retrosplenial
745 circuit.

746 Whereas the allocentric representation in our model is purely visual, the possibility that it could
747 be multisensory can not be excluded (*Newell et al., 2005*). *Loomis et al., 2013* defined a similar
748 representation of surrounding 3D space as a “spatial image” with the following properties: (i) it can
749 be updated during movement with the eye closed; (ii) it exists in all directions; (iii) the information
750 from all sensory modalities converge onto a common, “amodal”, spatial image. While our model
751 is directly consistent with the second property, the third one can be implemented by converting
752 spatial locations of egocentric sensory signals at different modalities (e.g. haptic or auditory) into
753 the common allocentric framework. These locations (or placeholders) can then be linked to the
754 detailed representations of sensory experience in sensory-specific areas of the cortex, similarly
755 to the putative links between landmark locations and their high-frequency contents discussed
756 above. The first property can be assured by backward projections from the hippocampus to the
757 allocentric layer (not included in the model), by a mechanism previously proposed to support
758 spatial imagery (*Byrne et al., 2007*). One obvious candidate for the potential biological locus of
759 the panoramic visual representation is the PPC, since spatiotopic neuronal receptive fields were
760 observed in this area (*Snyder et al., 1998; Fairhall et al., 2017*). The parahippocampal place area, a
761 scene-selective subdivision of the PHC, while not sensitive to the images of the same scene from
762 different viewpoints (*Epstein, 2008*), can integrate visual information across saccades to form a
763 representation of a larger scene (*Golomb et al., 2011*). Finally, RSC and occipital place area were

764 recently shown to mediate the memory of panoramic visual representations (*Robertson et al.*,
765 **2016**).

766 There are two key differences between our model and a previous influential model of spatial
767 memory and imagery (*Becker and Burgess, 2001; Byrne et al., 2007*, see also *Bicanski and Burgess,*
768 **2016**). First, our model postulates the existence of a quasi-panoramic representation of surrounding
769 visual space, in topographic visual coordinates, as emerging experimental evidence suggests
770 (*Melcher and Morrone, 2015; Robertson et al., 2016*). We propose that such a representation (*i*)
771 accumulated from successive views using short-term memory; (*ii*) can be used for planning of eye
772 movements during natural behavior; (*iii*) serves for the storage of object/landmark position and
773 orientation information. In our model, the reference frame for this panoramic representation is
774 allocentric, and only a portion of it, corresponding to the current view field, is explicitly converted
775 to an egocentric visual representation (equivalent to the “parietal window” of *Byrne et al., 2007*).
776 Second, our model proposes a mechanism of fast bottom-up view-based reorientation of the
777 head direction system that was either absent (*Byrne et al., 2007*) or relied on the presence of
778 conspicuous landmarks linked directly to head direction cells (*Bicanski and Burgess, 2016*). A
779 number of reorientation studies mentioned earlier suggest that this neural process is independent
780 from landmark identities and can be performed in the absence of point-like landmarks. The
781 mechanism we use relies on weight sharing and as such is not, at its present implementation,
782 biologically realistic. The concept of weight sharing has been critical for recent successes of
783 brain-inspired neural networks and is widely used in models of biological networks of visual
784 processing (e.g. *Serre et al., 2005; Masquelier and Thorpe, 2007; Bartunov et al., 2018*). One
785 possible implementation of our proposed reorientation mechanism would require mental rotation
786 of the stored allocentric representations, while freezing the actual egocentric view in the input layer.
787 Such an implementation would make the model significantly more complex, without changing the
788 underlying computation.

789 To summarize, the model presented in this work explored the nature of visual representa-
790 tions in the parietal-medial temporal pathway for visuospatial processing and contributed to the
791 open question of the link between visual and memory structures in primates. It proposes that
792 a single, potentially multisensory, representation of surrounding environment is constructed by
793 time-integrated sensory snapshots. This putative representation provides a 3D coordinate space
794 within which positions of localized sensory events can be encoded and which can serve as basis for
795 eye-movement generation in natural conditions. This model thus provides a conceptual framework
796 for linking oculomotor behavior, visual and spatial memory.

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