Abstract

A Neural Level Model of Spatial Memory and Imagery

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Bridging the gap between neurophysiological and behavioral descriptions of a cognitive agent requires an understanding of how higher cognitive functions relate to neuronal response properties. Spatial memory constitutes a rare case of cognition for which we can draw on a rich catalog of behavioral, neuropsychological and functional imaging findings on one side and a vast literature of electrophysiological research and modeling studies on the other. In this context the so-called Byrne, Becker and Burgess-model (henceforth BBB-model) of spatial memory and imagery (Byrne et al. 2008) has proposed a functional account of human spatial memory and imagery, with associated phenomena like hemispatial neglect, in terms of single neuron responses. The neural populations are modeled after cell types reported in rodent electrophysiology studies, including place cells (O'Keefe and Dostrovsky, 1971), head direction cells (Taube et al., 1990), and boundary vector cells (Lever et al. 2009). Using these cell types, the BBB-model shows how an egocentric representation of the local sensory environment (i.e. a specific point of view) can be transformed into a viewpoint-independent (allocentric) representation for memory (bottom-up mode of operation) (cf. Figure 1). The egocentric-allocentric transformation is assigned to a gain-field circuit in retrosplenial cortex. Running the transformation in reverse allows for the reconstruction of a specific point of view based on the underlying viewpoint-independent memory (i.e. imagery, top-down mode of operation). To move from a purely geometric representation of space (an agent's location relative to boundaries) to scenes (a space populated by objects) we present an extension of the BBB-framework (henceforth the BBBB-model). We include egocentric and allocentric representations of discrete objects and embed them in the spatial context of boundaries (cf. Figure 2). Object representations are encoded into spatial memory with the help of a rudimentary form of attention, and can populate the egocentric representation of the geometric context in imagery. Most importantly, the novel representations can be mapped onto electrophysiological findings similarly to place cells, head direction cells and boundary vector cells in the original model. Further extending the link to known single cell responses we show how mental navigation (imagined movement in familiar environments) and mental simulation (imagined movement in unfamiliar environments) might occur with the help of grid cells (Hafting et al. 2005). Driving the point of view in imagery with the help of grid cells also allows for a mechanistic interpretation of the phenomenon known as preplay (Olafsdottir et al. 2015). The BBBB-model thus proposes how the grid cell module is embedded in the wider systems level-function of the MTL. It provides a strong conceptual framework for how to think about hippocampal function and Papez circuit in the context of spatial cognition, in particular concerning scene-construction based on viewpoint-independent spatial memories, hemispatial neglect, mental navigation and mental simulation.

References

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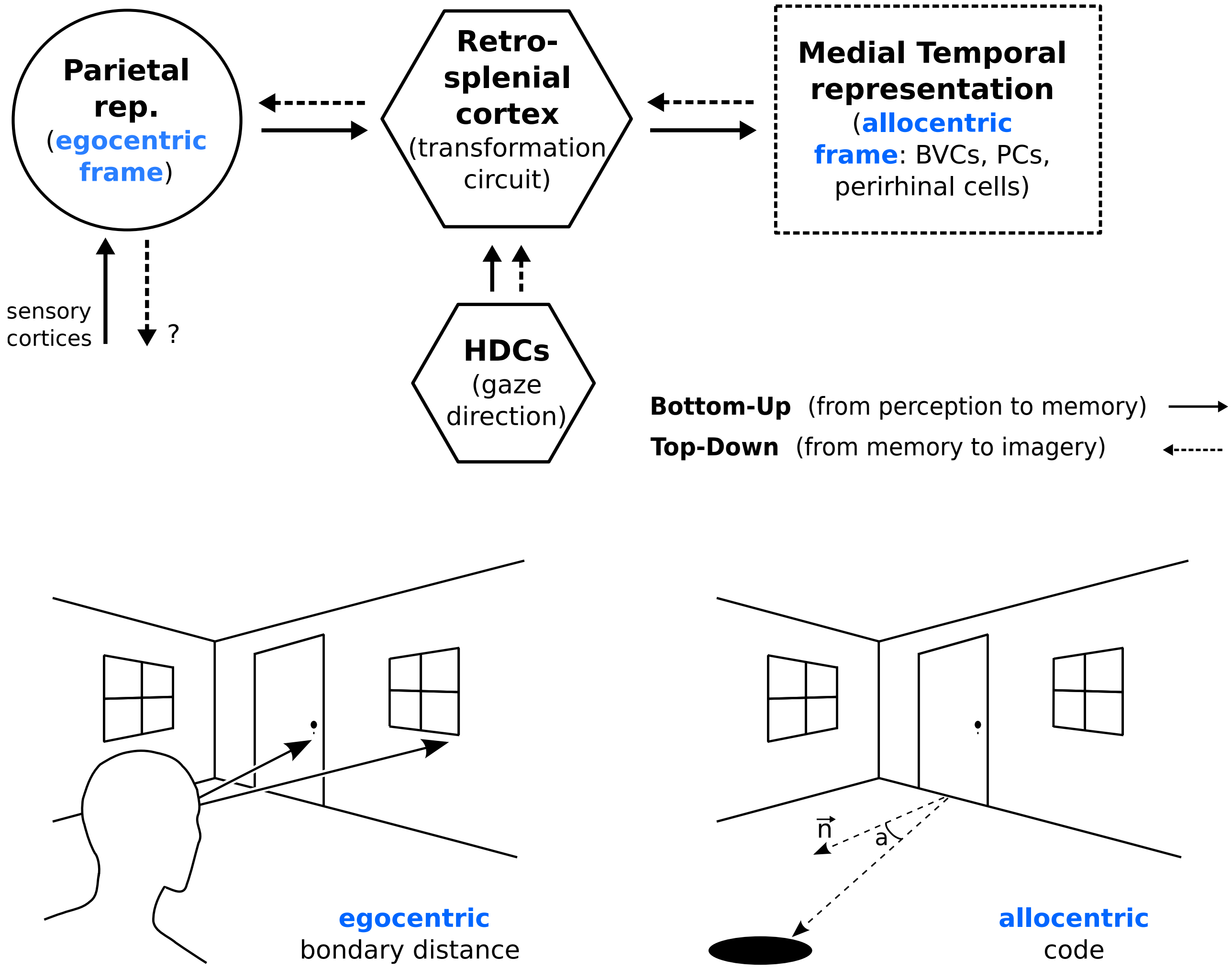

Figure 1: Simplified schematic of the BBB model. **A** processed inputs from sensory cortices (not shown) reach parietal areas. The parietial representation is egocentric in nature. I.e. it is coded in the reference frame of the sensory receptors or preprocessed into head/body-centered frame of reference. Egocentric distance to boundaries is assigned to the parietal representation and is a stand-in for the richer sensory experience of humans. Retrosplenial cortex, modulated by current head direction performs the transformation from egocentric to allocentric coding. The allocentric code corresponds to a set of active boundary vector cells and place cells. At a given location a specific set of boundary vector cells is co-active with the corresponding place cells. The identity or texture of a given boundary is coded for by perirhinal neurons. Black arrows indicate the flow of information during perception and memory encoding (bottom-up). Dotted arrows indicate the reverse flow of information, reconstructing the parietial representation from view-point invariant memory (imagery, top-down). **B** Sketches illustrating of the egocentric (left panel) and allocentric frame of reference (right panel), where the door is chosen as a reference landmark, and the vector n denotes the normal vector for the reference landmark. The angle a is coded for by head direction cells. A place cell which codes for the location indicated by the black ellipse is reciprocally connected to boundary vector cells coding for the configuration of boundaries experienced/remembered at the given location.

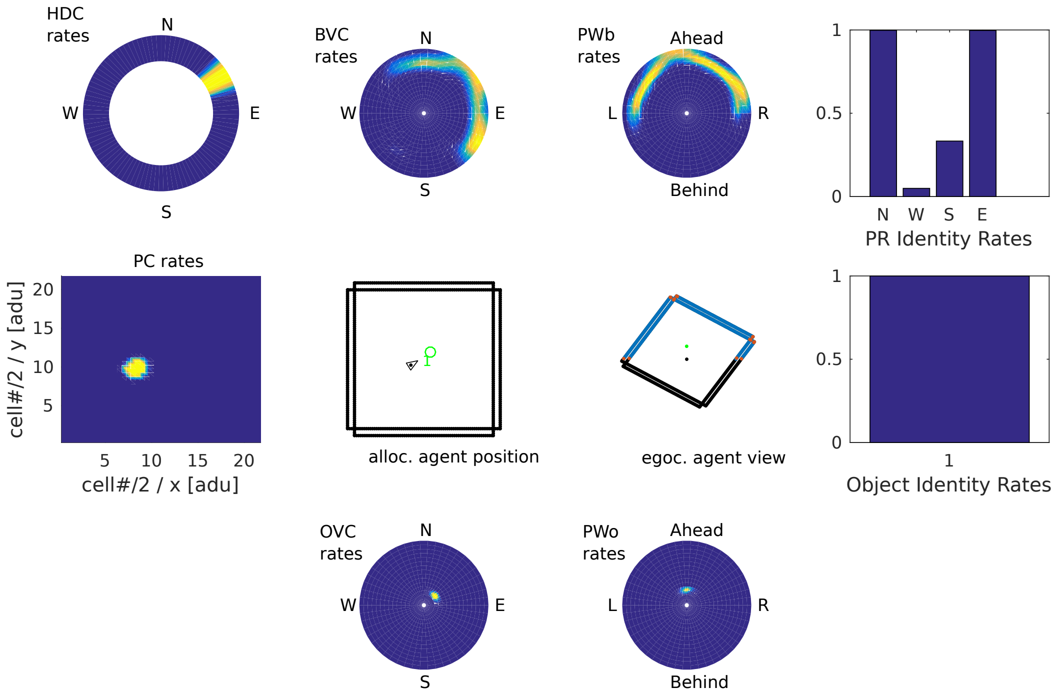

Figure 2: Example of population snaptshots of the BBBB-model. Bright colors indicate high firing rates. Snapshots show the neural activity patterns of all model constituents (except for retrosplenial cortex) during perception (bottom-up mode of operation). Sensory inputs to the parietal population (PWb/o) are determined and continuously updated by an agent model navigating a simple environment (central plots). To produce meaningful plots spatially selective cells are ordered according to the topology of their receptive fields in real space (e.g. note the outline of the environmental boundaries in the BVC plot). **Labels: HDC:** head direction cells, **BVCs:** boundary vector cells (allocentric frame of reference), **PWb:** boundary selective parietal neurons (egocentric frame of reference), **PR:** perirhinal neurons signaling boundary or object identity, **PC**: place cells, **OVC**: object vector cells (allocentric frame of reference), **PWo**: object location sensitive parietial neurons. Central plots show the allocentric agent position (black triangle, left) and its field of view (180 degrees, blue) in the arena.