UCL NEUROSCIENCE

(Abstract) neural representations of spaces and concepts

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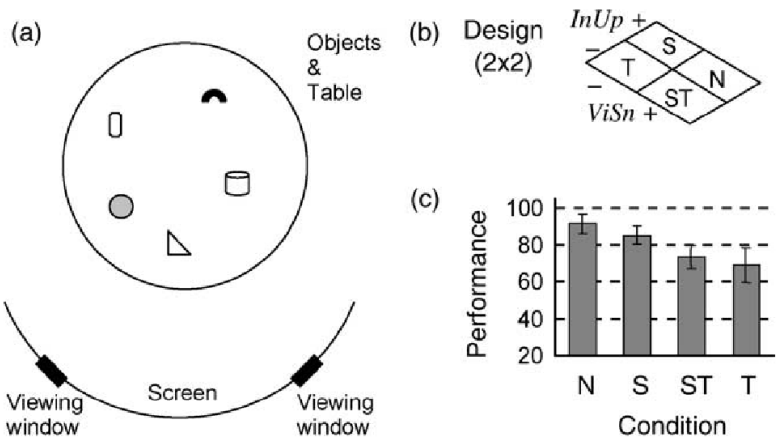
Abstract neural representations

1) *Frames of reference for spatial representation*
2) *Place cells & boundary vector cells*
3) *Neural level model of Spatial Memory and Imagery*
4) *Place and grid cells, environmental and self-motion inputs?*
5) *Grid cells as dynamic imagery?*
6) *Place and grid cells, representing states and transitions for planning?*

Multiple parallel representations in spatial memory.

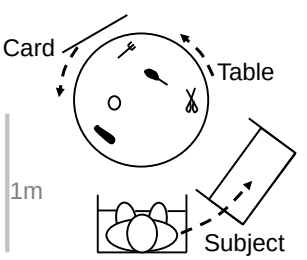
Effects of consistency with 'Visual Snapshots' & Internal 'Spatial Updating'

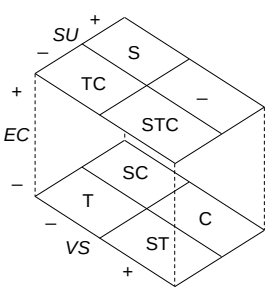
Wang & Simons 1999

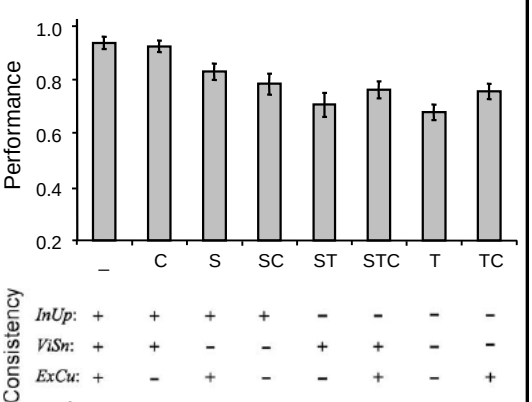


Multiple parallel representations in spatial memory.

Visual Snapshots (*egocentric*), Spatial Updating (*egocentric*) and External Cues (*allocentric*).







Burgess, Spiers, Paleologou, 2004

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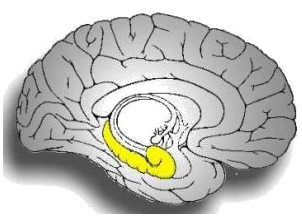
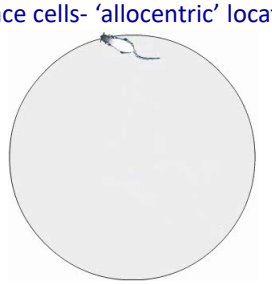
The hippocampus supports memory (e.g. HM), but how does it work?

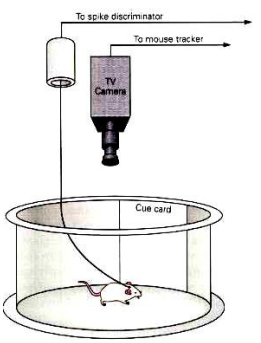


Spatial studies in rodents => likely neural representations.

Place cells- 'allocentric' location



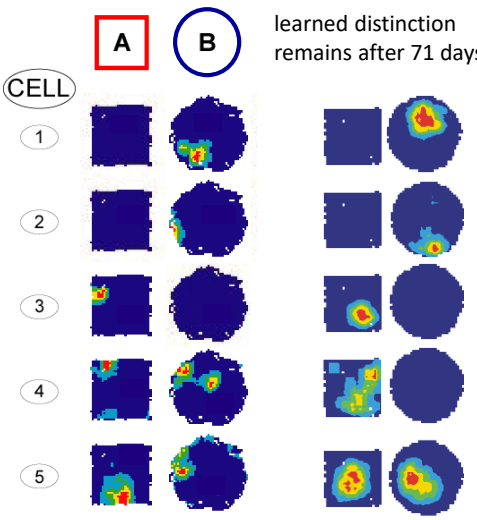
O'Keefe & Dostrovsky, 1971



Video by Julija Krupic

Place cells show long term memory and pattern completion

Place cell "remapping:" long-term memory for highly distinct environments.



learned distinction remains after 71 days..

Lever, Wills, Cacucci, Burgess, O'Keefe, 2002

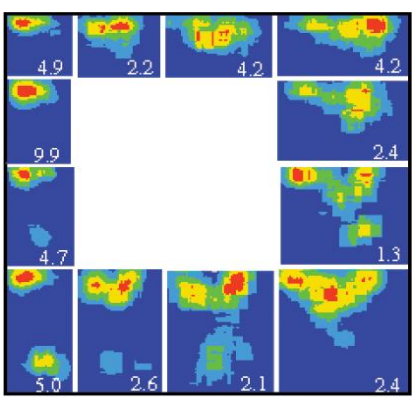
Place cell representation shows attractor dynamics

Wills, Lever, Cacucci, Burgess, O'Keefe, 2005

and 'pattern completion' depending on CA3 NMDA receptors

Nakazawa et al., 2002

Environmental boundaries particularly influence place cell firing



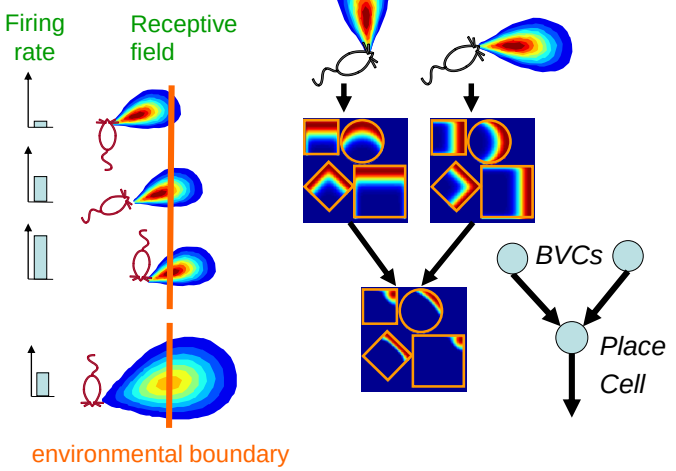
122cm

61cm

O'Keefe & Burgess (1996)

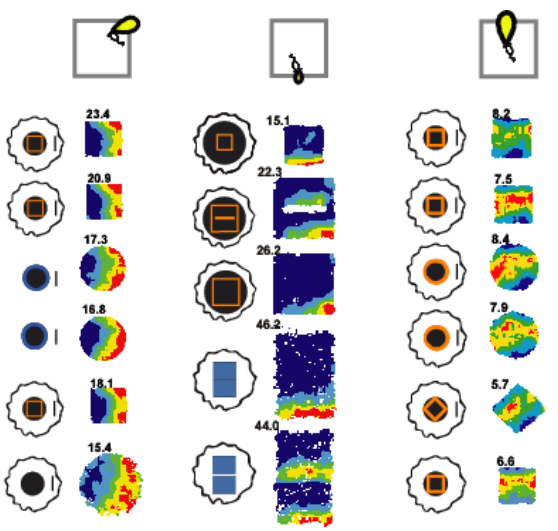
Place Cell firing as a thresholded sum of "Boundary Vector Cell" inputs

Boundary Vector Cells (BVCs) signal distance to boundary along an *allocentric* direction

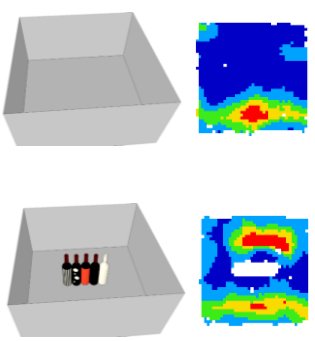


O'Keefe & Burgess, 1996; Hartley et al 2000

BVCs found in subiculum & entorhinal cortex



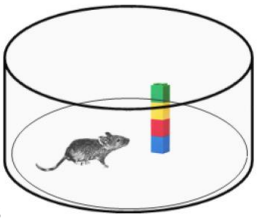
Including those firing at a distance



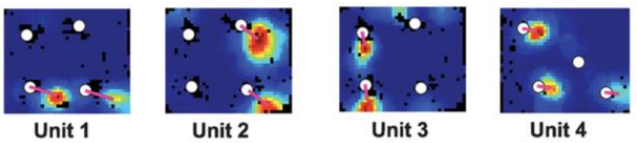
Steve Poulter & Colin Lever

Lever, Burton, Jeewajee, O'Keefe, Burgess, 2009
See also Barry et al, 2006; Solstad et al, 2008

Object Vector Cells

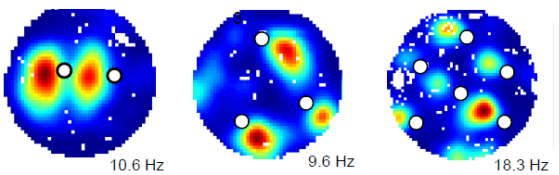


Recently found, in hippocampus



Desmukh & Knierim, 2013

and medial entorhinal cortex



Hoydal..Moser 2019

Reviewed in Bicanski & Burgess, 2020

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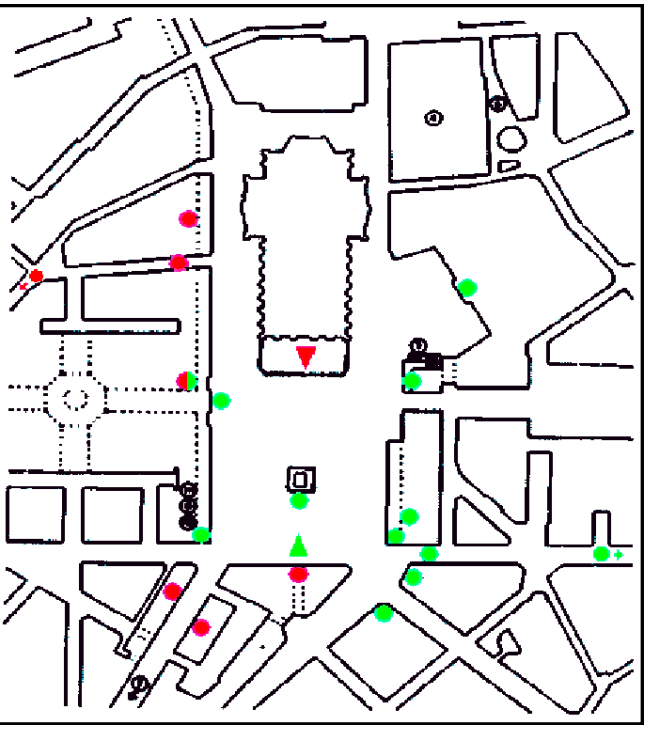
Hemispatial neglect in memory of Milan square following right parietal damage.

⇒ formation of an egocentric representation in parietal cortex from a stored allocentric representation in medial temporal lobe?



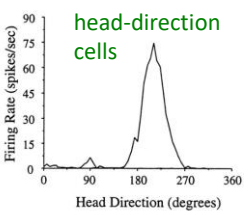
Bisiach & Luzzatti(1978)

Several identified neural representations support spatial cognition

Hippocampal formation (allocentric)

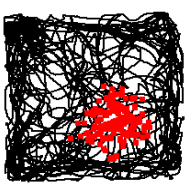
Sensory, **Parietal**, Motor cortices (egocentric)

head-direction cells



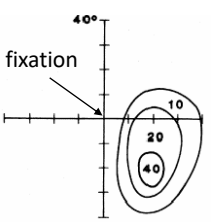
Ranck et al, 1984;
Taube et al, 1990

place cells

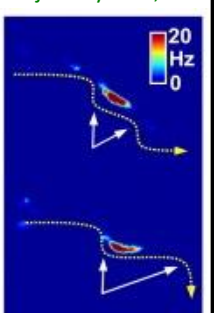


O'Keefe & Dostrovsky, 1971

retinal receptive fields

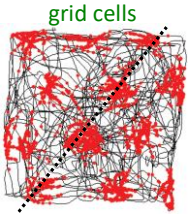


trajectory cells,



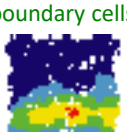
Nitz 2009

grid cells



Hafting et al., 2005

boundary cells

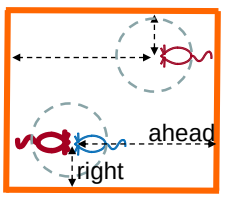


Lever et al, 2009
Solstad et al, 2008

Frames of reference for neural coding

'egocentric'

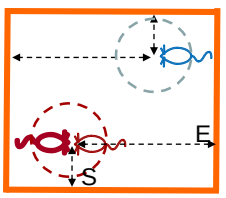
Body-centred location of objects



Perception
Action/Imagery

'allocentric'

World-centred location of agent



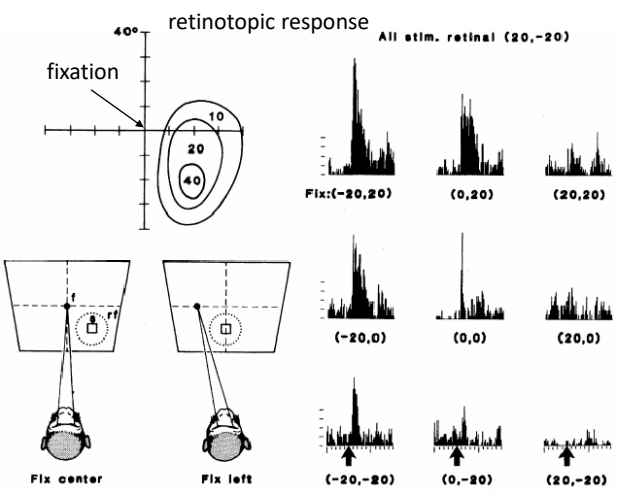
Place cells
Head-direction cells

Burgess et al 2001

'Gain field' responses in posterior parietal cortex

i.e. conjunctive responses to (retinotopic) *visual input x gaze direction*

Size of retinotopic visual response is modulated by direction of gaze:



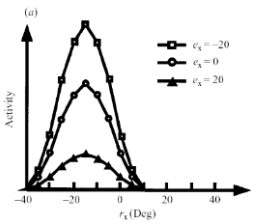
Andersen et al 1985

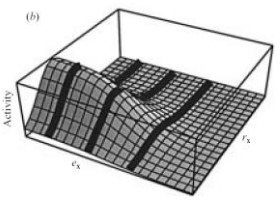
or by *direction of the head (Snyder et al 1998).*
Similar responses seen in parieto-occipital ctx (Galletti et al., 1995)

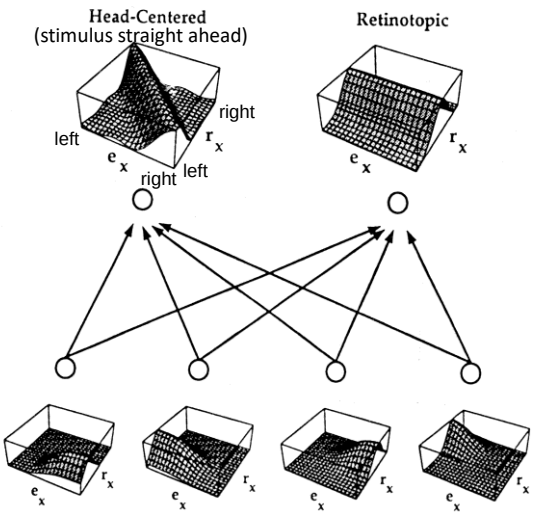
Gain field neurons can produce 'head-centred' or retinotopic representations.

retinal position of stimulus = r_x

eye gaze angle = e_x



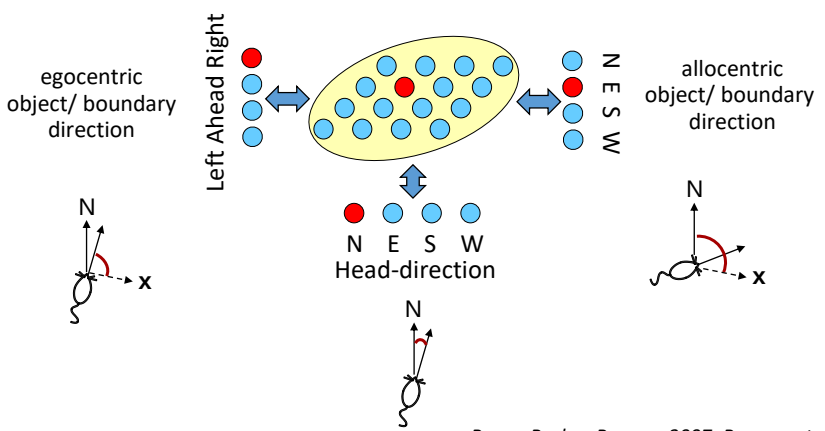




Pouget & Sejnowski, 1997

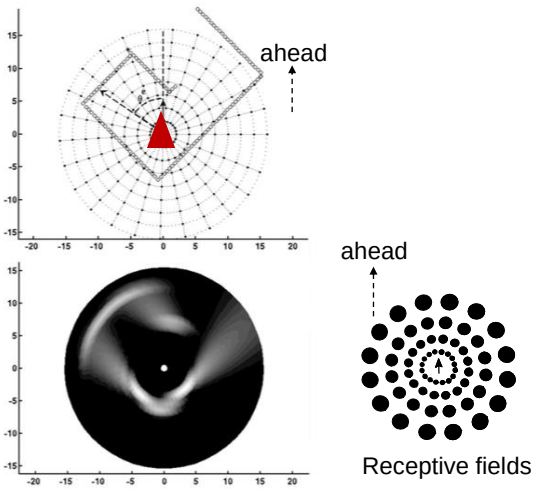
Model of memory & imagery for scenes

Egocentric-allocentric translation by 'gain-field' neurons
(i.e. conjunctive representations of egocentric sensory input x head direction)



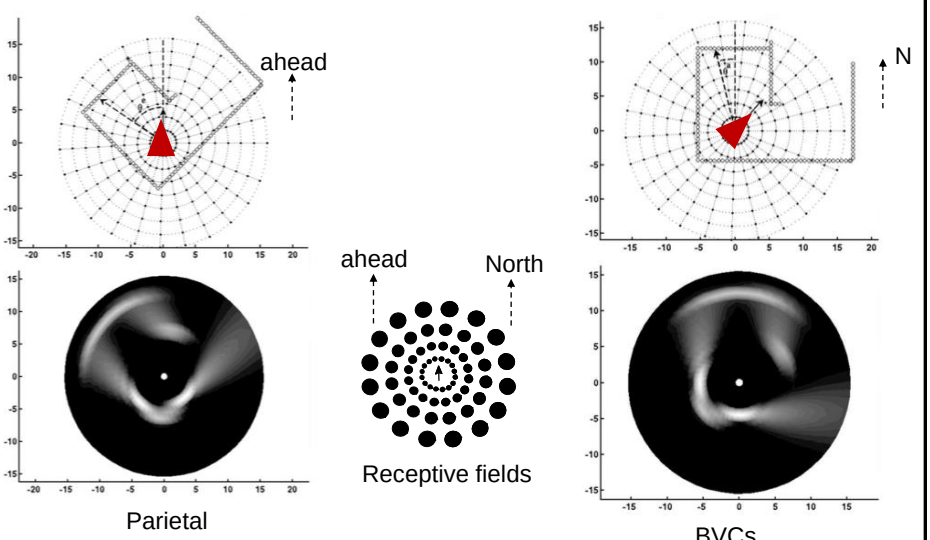
Byrne, Becker, Burgess 2007; Burgess et al., 2001;
See Pouget & Sejnowski, 1997; Deneve et al., 2001.

Scene representation by populations of egocentric or allocentric BVCs



egocentric representation (e.g. visual)

Scene representation by populations of egocentric or allocentric BVCs



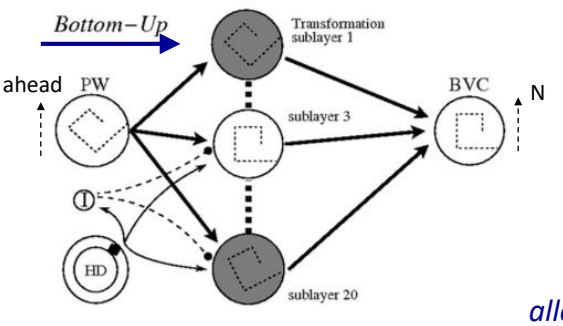
egocentric representation (e.g. visual)

allocentric representation

Becker & Burgess 2001; Burgess et al., 2001; Byrne, Becker, Burgess 2007

Ego-allo scene translation
(retrospenial cortex?)

'gain field' representation of
scene elements x head direction



perception

LTM

egocentric

allocentric

Byrne, Becker, Burgess 2007
Burgess et al., 2001
see also Pouget & Sejnowski 1997

Ego-allo scene translation
(retrospenial cortex?)

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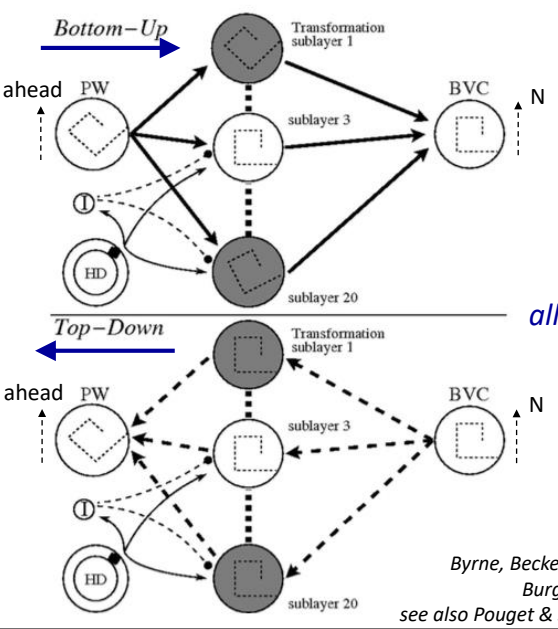


perception

LTM

egocentric

allocentric

imagery
(& action)

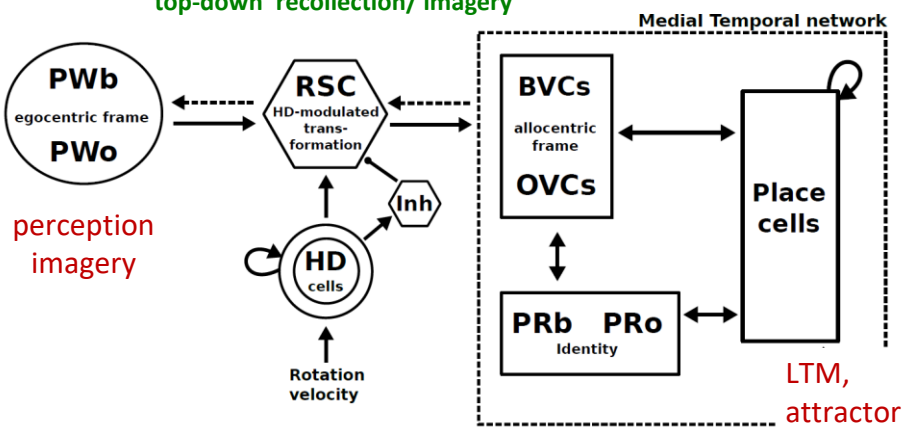
LTM

Byrne, Becker, Burgess 2007
Burgess et al., 2001
see also Pouget & Sejnowski 1997

Model of memory & imagery for scenes

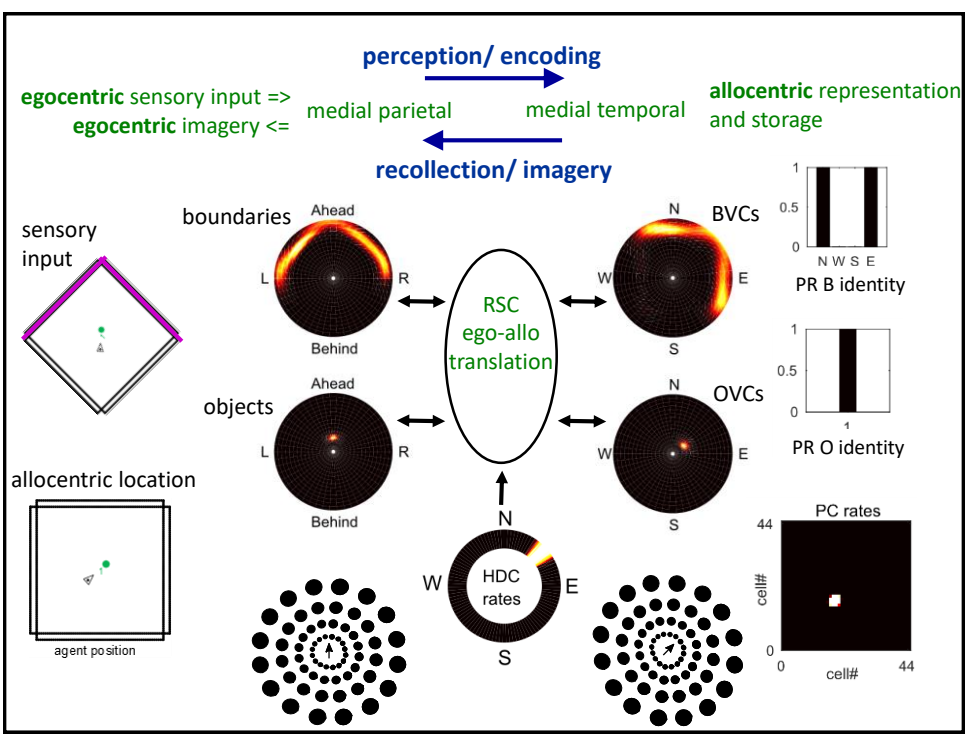

'bottom-up' encoding/ perception

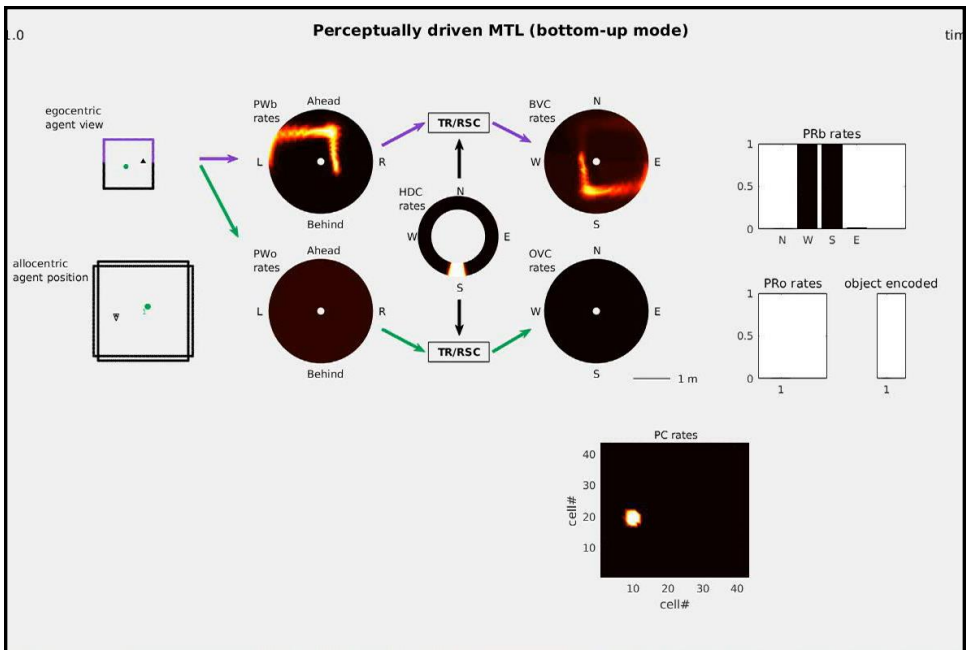
'top-down' recollection/ imagery



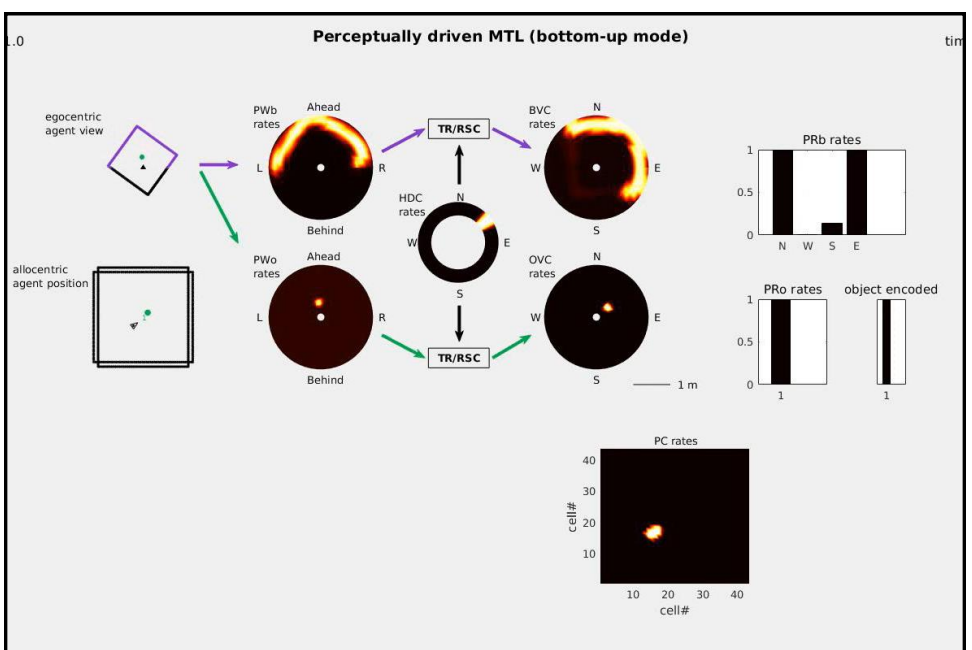
In a familiar environment, MTL connections generate a coherent scene consistent with a single viewpoint (place cells) and direction (HDCs)

Bicanski & Burgess, 2018; Byrne, Becker, Burgess 2007; Burgess Becker et al, 2001

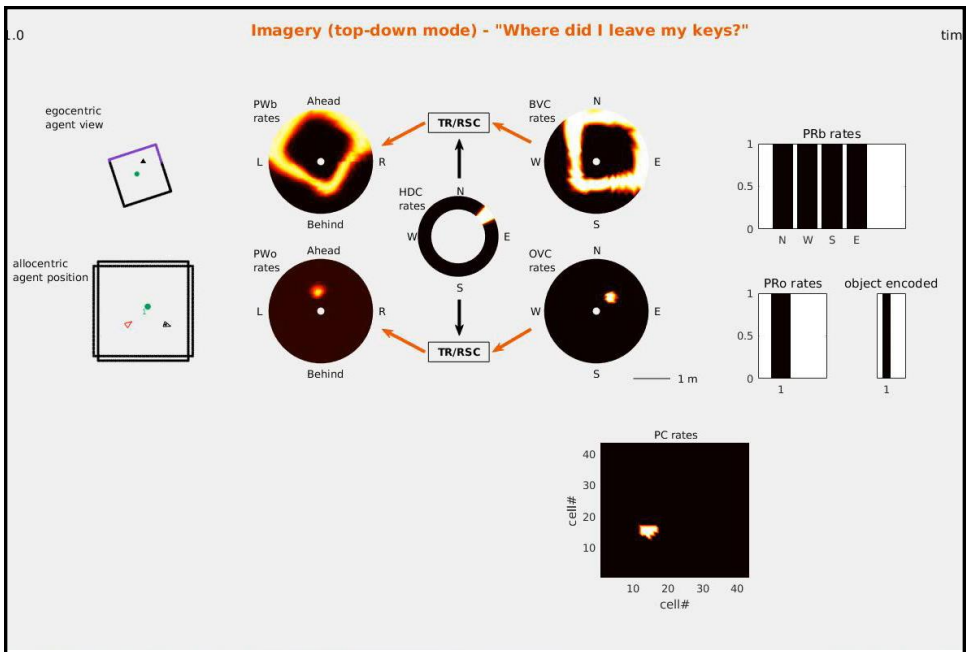




Encountering an object in a familiar environment

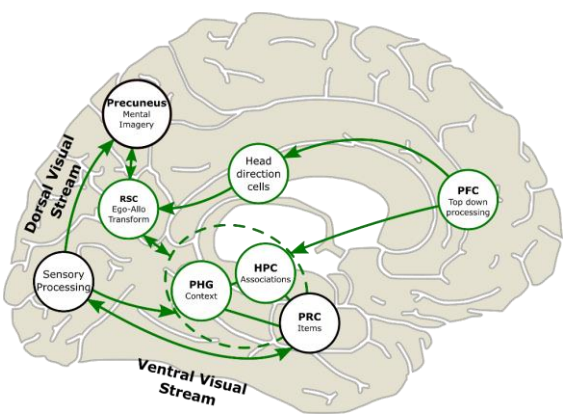


Recollection of encountering the object



Memory enhanced 'perception' of a familiar environment

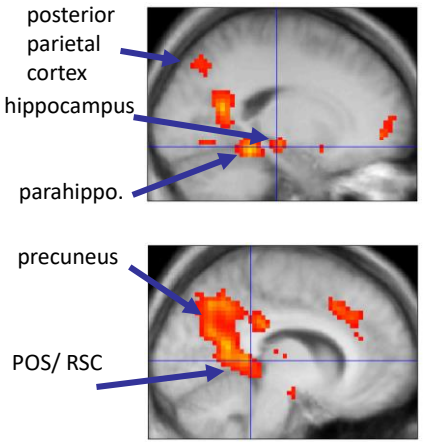
Model allows interpretation of fMRI patterns during recollection/ imagery



In a familiar environment, MTL connections ensure generation of a coherent scene, consistent with a single viewpoint (place cells) and direction (HDCs)

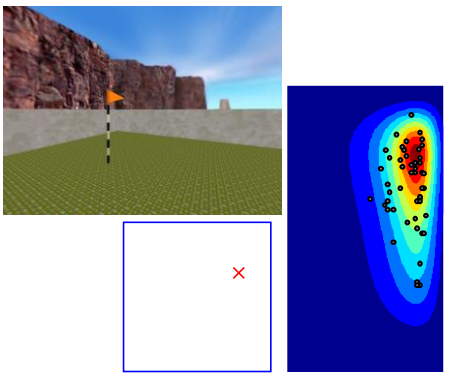
RSC supports egocentric-allocentric translation, required to associate (allocentric) internal representations with (egocentric) sensory representations
(Egocentric BVCs and OVCs have now been found, Hasselmo & Derdikman labs)

Model allows interpretation of fMRI patterns during recollection/ imagery



Burgess et al, 2001

& prediction of human search patterns



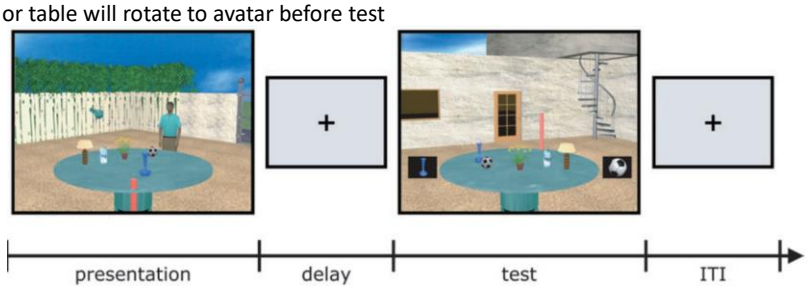
Hartley et al, 2004

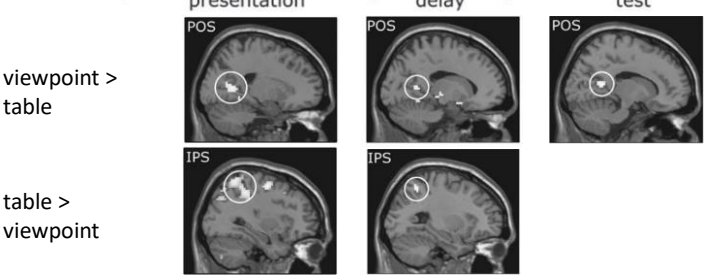
The network performs coherent spatial imagery, i.e. related to planning, 'episodic future thinking' and 'scene construction'

Addis and Schacter, 2007; Hassabis and Maguire, 2007

POS/ RSC activity and change of viewpoint in memory

Viewpoint or table will rotate to avatar before test





viewpoint > table

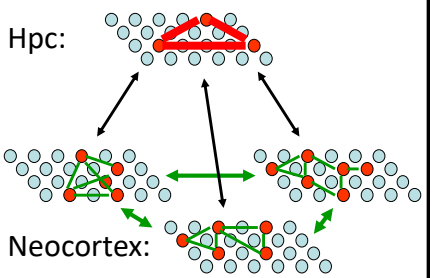
table > viewpoint

Lambrey et al 2013

RSC associates internal (allocentric) representations to (egocentric) sensory inputs
- strong associations form to stable sensory features *(e.g. Auger et al., 2012)*

Relation to pattern completion and models of Episodic Memory

- Pattern completion is seen in reconstruction of location-object-identity in scene.
- Consistent with Marr's model of hippocampus & Tulving's idea of holistic episodic recollection/ re-experience.
- Consistent with measures of pattern completion in Episodic memory
  see Horner et al (2015).



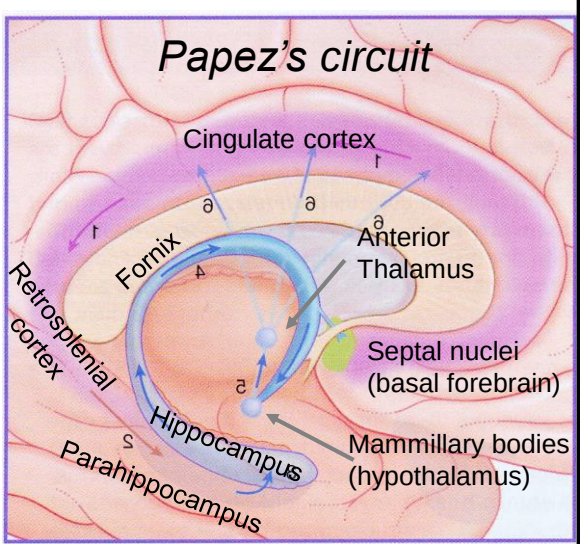
***Marr, 1971**; Gardner-Medwin, McNaughton, Alvarez, Squire, McClelland, O'Reilly, Treves, Rolls, Teyler & DiScenna; Damasio;*

Functional roles for Papez's circuit?

Hippocampus (place cells):
imposing a common viewpoint on retrieval/ imagery.

Fornix:
Head-direction cells: imposing a viewing direction
Theta cells/VCOs: grid cells, path integration, moving viewpoint in imagery.
ACh/novelty/learning

Diencephalic amnesia
(Aggleton & Brown, 1999; Gaffan; Delay & Brion 1969). E.g., patient NA *(Squire & Slater, 1978),* Korsakoff's syndrome.



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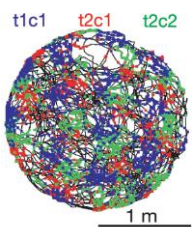
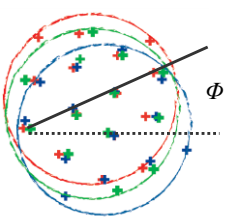
Grid cells – thought to represent location by integrating self-motion.

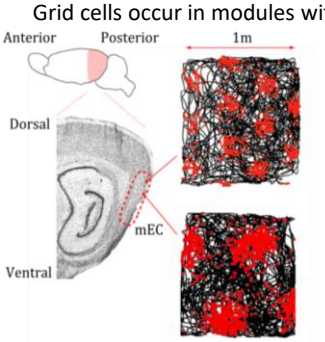
The grids of nearby cells share orientation & scale

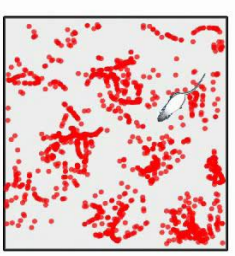


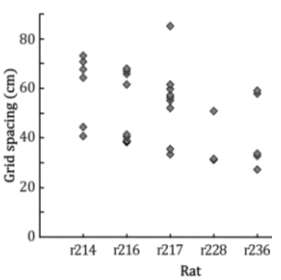


Hafting et al., 2005

Grid cells occur in modules with discrete scales







Barry et al, 2007;
see also Stensola et al., 2012

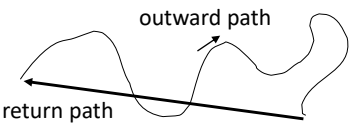
Video by Julija Krupic

Two ways to know where you are:

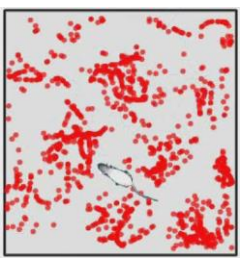
1. Environmental information

(Environmental boundaries particularly influence place cells)

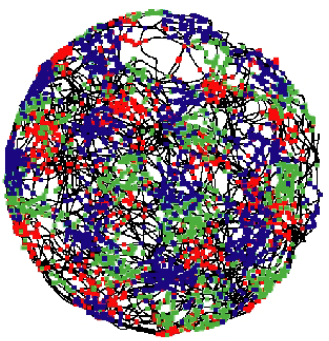
2. Path integration



Grid cells



Hafting et al., 2005



Video by Julija Krupic

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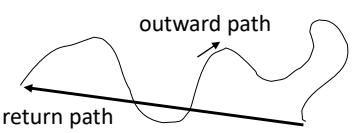
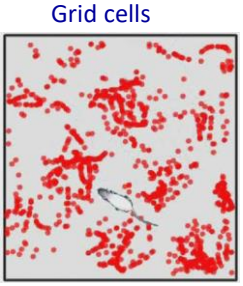
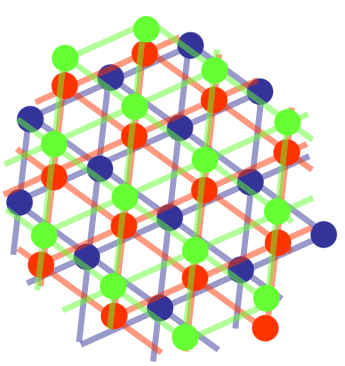


Grid cells



Hafting et al., 2005



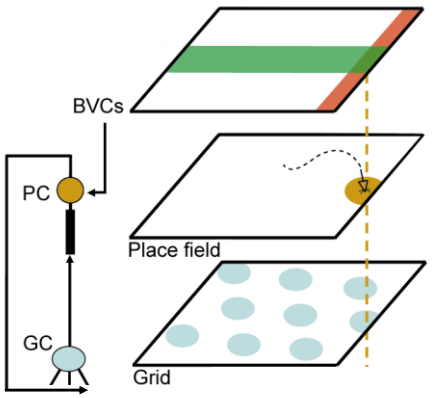
Video by Julija Krupic

Interactions between place cells and grid cells

Estimating self-location combines environmental & self-motion information

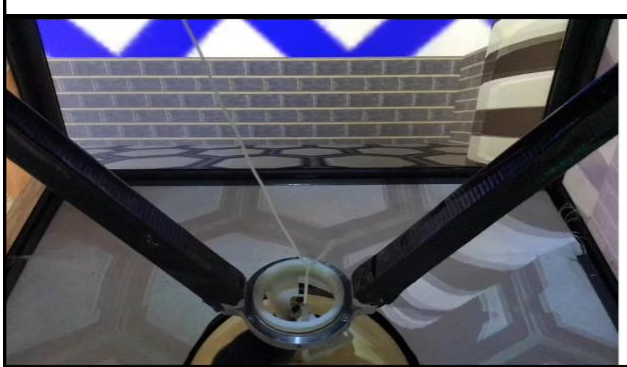
Environmental information
(⇔ Boundary Vector Cells)

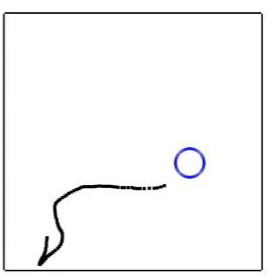
Self- motion

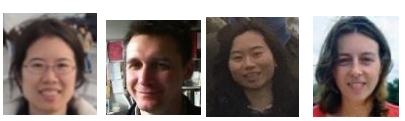


Burgess et al, 2007

2D VR for mice (invisible reward task)

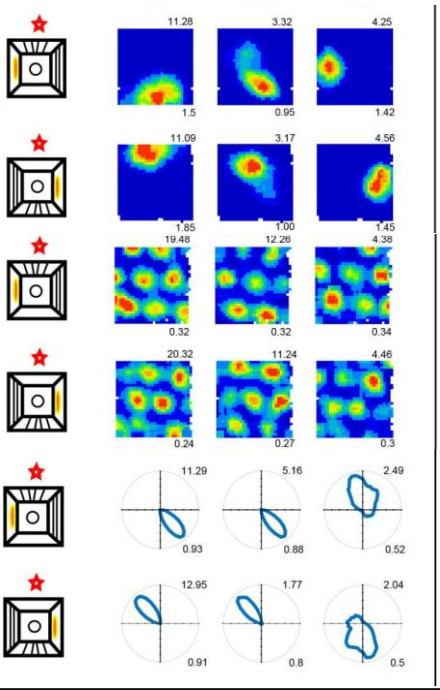




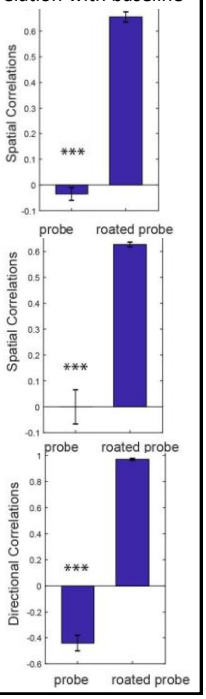


Guifen Chen, John King, Yi Lu, Francesca Cacucci, Neil Burgess, eLife 2018

2d VR allows expression of normal place, grid & head-direction firing patterns, controlled by virtual cues (e.g. 180º rotation of VR and entry point)

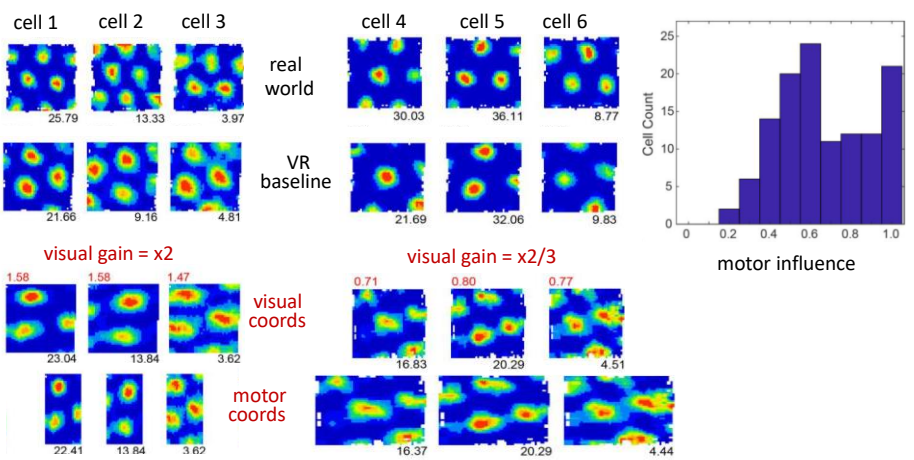


Correlation with baseline



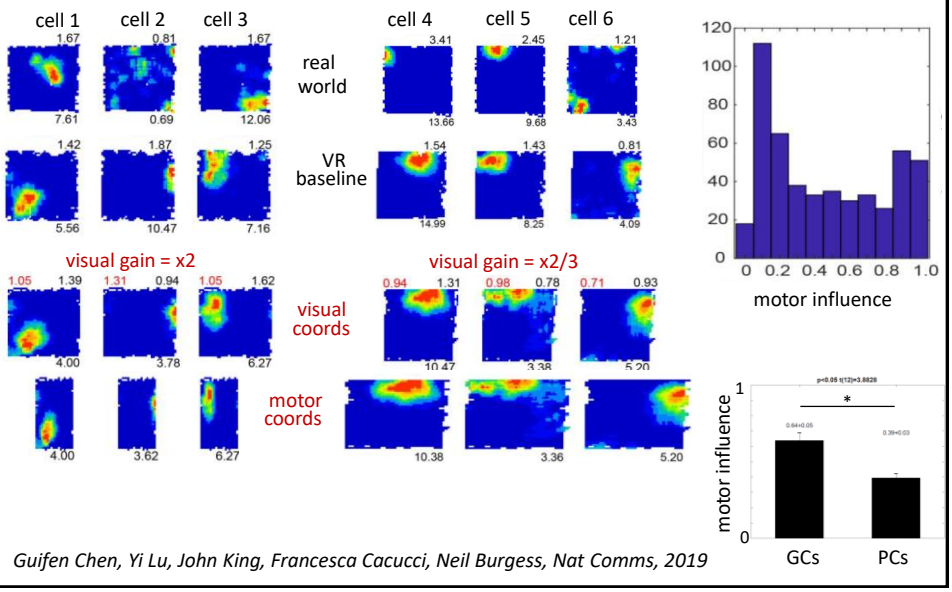
Chen et al, eLife 2018

Grid cell firing patterns reflect self-motion more than vision



Guifen Chen, Yi Lu, John King, Francesca Cacucci, Neil Burgess, Nat Comms, 2019

Place cell firing patterns reflect vision more than self-motion



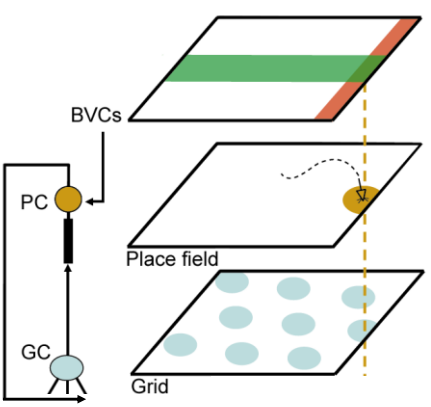
Guifen Chen, Yi Lu, John King, Francesca Cacucci, Neil Burgess, Nat Comms, 2019

Interactions between place cells and grid cells

Estimating self-location combines environmental & self-motion information.

Environmental information
(⇔ Boundary Vector Cells)

Self- motion

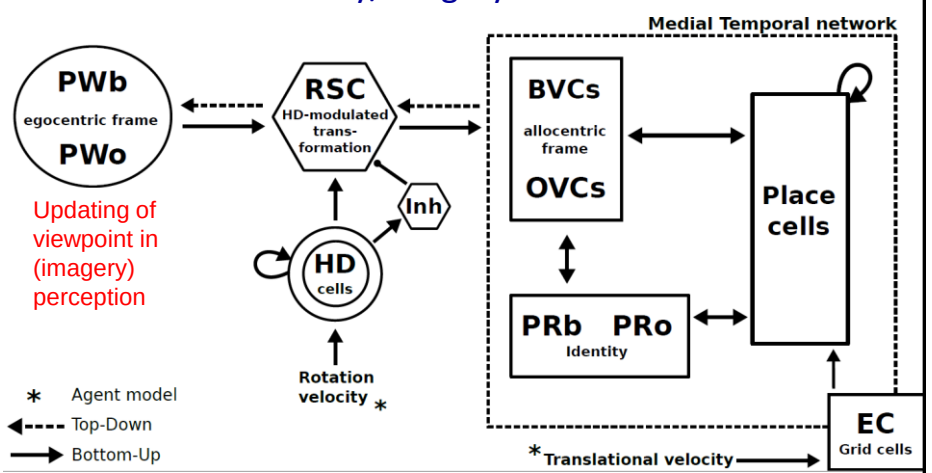


Burgess et al, 2007

Abstract neural representations

1) *Frames of reference for spatial representation*
2) *Place cells & boundary vector cells*
3) *Neural level model of Spatial Memory and Imagery*
4) *Place and grid cells, environmental and self-motion inputs?*
5) ***Grid cells as dynamic imagery?***
6) *Place and grid cells, representing states and transitions for planning?*

Grid cells and memory/imagery



Updating of viewpoint in (imagery) perception

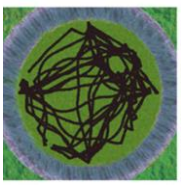
Allocentric updating of (imagined) location

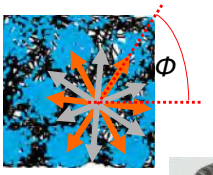
Bicanski & Burgess, eLife, 2018

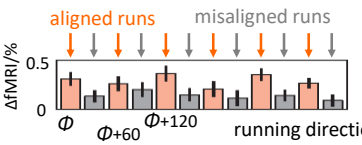
Grid cells in the human autobiographical memory system?

Doeller, Barry, Burgess, 2010

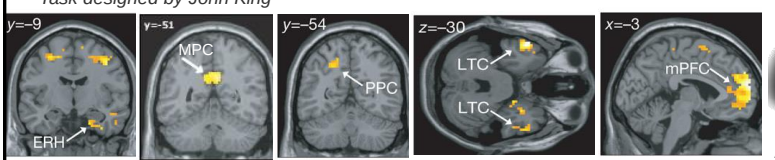
populations of *aligned* grids (modules) => changes in fMRI signal with virtual running direction







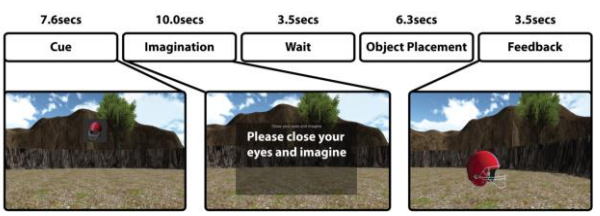
Task designed by John King

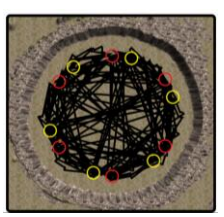


Autobiographical memory system

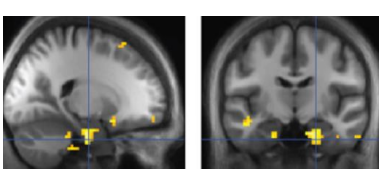
=> Grid cells allow path integration, and movement of viewpoint in imagery?

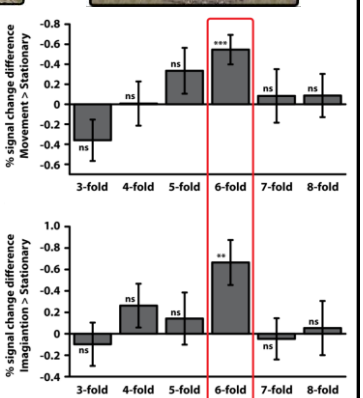
Grid-like processing of movement of viewpoint in imagery





60º symmetry in fMRI signal with *imagined* running direction in Entorhinal cortex (aligned with that in virtual movement)





Horner et al., 2016

Abstract neural representations

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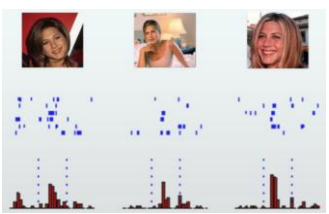
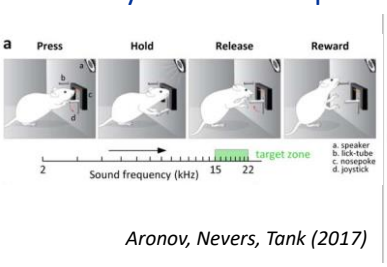
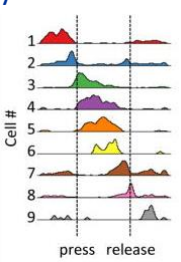
Hippocampal cells can represent abstract concepts, such as 'place' but also, e.g., personal identity or sound frequency?



Quiroga et al., (2005)

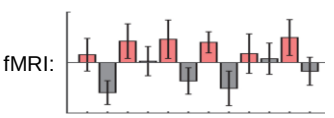


Aronov, Nevers, Tank (2017)

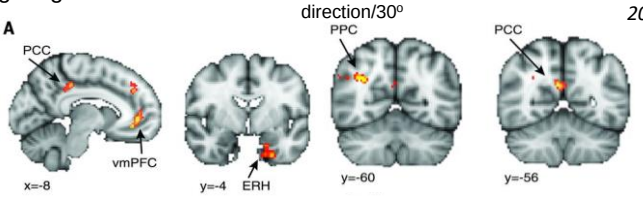


Grid cell firing patterns reflect the transition structure of learned conceptual spaces?

Navigation in space of bird neck & leg length



Constantinescu, O'Reilly, Behrens 2016



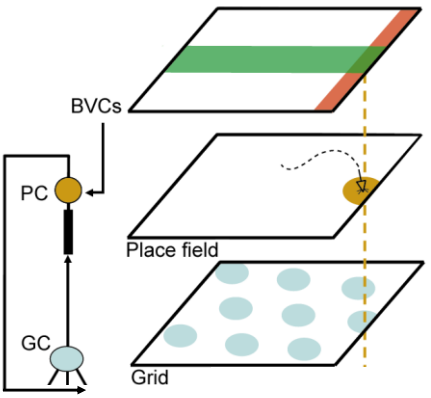
Interactions between place cells and grid cells

Representing bodies of conceptual knowledge (states) and transitions between them?

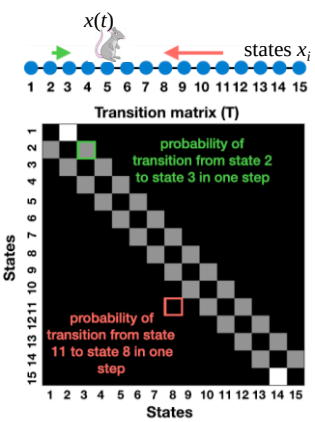
State information (place)

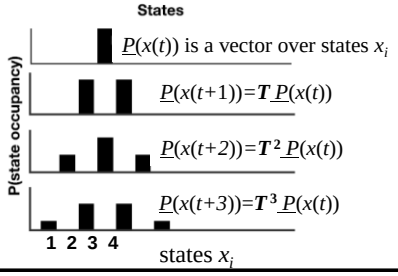
(⇔ Feature Vector Cells?)

Transition structure (self- motion)



'Intuitive Planning..'

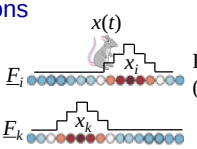




..with neural populations

PC_i firing profile is $\underline{F}_i$

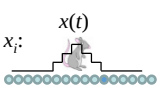
firing rate is $f_i(x(t))$:



$\underline{P}(x(t))$ is a vector over states x_i:

$\underline{P}(x(t)) \sim \Sigma_j\, f_j(x(t))\,\underline{F}_j$

$\underline{P}(x(t+1)) \sim \Sigma_j\, f_j(x(t))\boldsymbol{T}\underline{F}_j$



GC_i firing profile is $\underline{G}_i$

firing rate = $g_i(x(t))$:

$\underline{P}(x(t)) \sim \Sigma_j\, g_j(x(t))\underline{G}_j$

$\underline{P}(x(t+1)) \sim \Sigma_j\, g_j(x(t))\boldsymbol{T}\underline{G}_j$

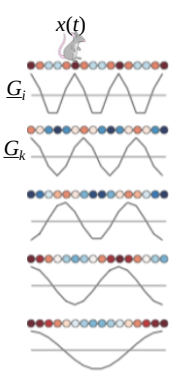
If $\boldsymbol{T}\underline{G}_j(x) = \lambda_j \underline{G}_j(x)$

$\underline{P}(x(t+1)) \sim \Sigma_j\, \lambda_j g_j(x(t))\underline{G}_j$

$\underline{P}(x(\tau \geq t) \mid x(t))$

$\sim \Sigma_j\, (\gamma\lambda_j + \gamma^2\lambda_j^2 + ..) g_j(x(t))\underline{G}_j$

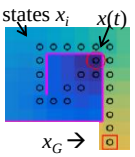
$\sim \Sigma_j\, g_j(x(t))\, \underline{G}_j\, /(1-\gamma\lambda_j)$



Stachenfeld, Botvinick, Gershman, Gerstner, Baram.. Behrens

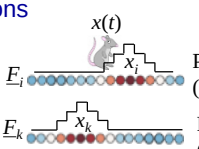
$P(x(\tau \geq t) = x_G \mid x(t))$
$\sim \Sigma_j g_j(x(t)) G_j(x_G)/(1-\gamma\lambda_j)$

the discounted future prob. of reaching x_G from $x(t)$, a.k.a the 'successor representation' $\boldsymbol{M}(x(t), x_G)$



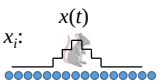
..with neural populations

PC$_i$ firing profile is $\underline{F}_i$
firing rate is $f_i(x(t))$:



PC$_i$ (peak at x_i)
PC$_k$ (peak at x_k)

$\underline{P}(x(t))$ is a vector over states x_i:



PC population

$\underline{P}(x(t)) \sim \Sigma_j f_j(x(t)) \underline{F}_j$
$\underline{P}(x(t+1)) \sim \Sigma_j f_j(x(t)) \boldsymbol{T}\underline{F}_j$

E.g. place cell read-out of GCs

PC$_i$ firing rate $f_i(x(t))$, driven by GCs, could approx. current or future occupancy of state x_i

$P(x(t) = x_i) \sim f_i(x(t)) = \Sigma_j w_{ij} g_j(x(t))$

[e.g. Hebbian $w_{ij} \sim \underline{F}_i . \underline{G}_j$]. Then

$P(x(t+1) = x_i) \sim \Sigma_j \lambda_j w_{ij} g_j(x(t))$

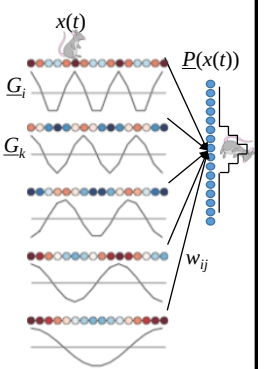
$P(x(\tau \geq t)=x_i) \sim \Sigma_j w_{ij} g_j(x(t)) /(1-\gamma\lambda_j)$

GC$_i$ firing profile is $\underline{G}_i$
firing rate = $g_i(x(t))$:

$\underline{P}(x(t)) \sim \Sigma_j g_j(x(t)) \underline{G}_j$
$\underline{P}(x(t+1)) \sim \Sigma_j g_j(x(t)) \boldsymbol{T}\underline{G}_j$

If $\boldsymbol{T}\underline{G}_j(x) = \lambda_j \underline{G}_j(x)$
$\underline{P}(x(t+1)) \sim \Sigma_j \lambda_j g_j(x(t)) \underline{G}_j$

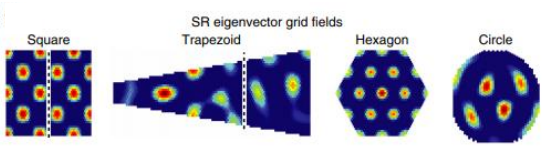
$\underline{P}(x(\tau \geq t) \mid x(t))$
$\sim \Sigma_j (\gamma\lambda_j + \gamma^2\lambda_j^2 + ..) g_j(x(t)) \underline{G}_j$
$\sim \Sigma_j g_j(x(t)) \underline{G}_j /(1-\gamma\lambda_j)$



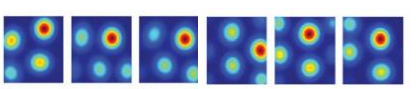
Stachenfeld, Botvinick, Gershman, Gerstner, Baram.. Behrens

Using Eigenvectors of the task Transition Matrix as basis vectors to represent state occupancy makes prediction easy..

.. and Grid firing profiles might be Eigenvectors of a *diffusive* transition matrix $\boldsymbol{T}$ (i.e. $\boldsymbol{T}\,\underline{G}_i(x) = \lambda_i \underline{G}_i(x)$), or of the *covariance* matrix of PC firing (e.g. learned via Oja's rule)



(*Stachenfeld et al., 2017*)



(*Dordek et al., 2015*)

Implications

- Place cell read-out shifts from current to future locations by re-weighting Grid cell inputs, and can give 'Successor Representation' i.e. $P(x(\tau \geq t)=x_i) \mid x(t))$
- Successor Representation allows navigation to any other state (via gradient ascent)
- *Common transition structure across tasks captured by GCs*, while PCs reflect specific sensory input & 'remap', allows generalisation by separating structure from content, (*Whittington et al Cell, 2020*)

Conclusions

- Considerable progress has been made in understanding how environmental and self-motion information combine in neural representations of location and orientation in rodents.
- We can use this to create a neural-level understanding of spatial memory, learning and imagination in humans, and begin to apply it to conceptual knowledge?

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