Report on modelling key cognitive processes (D4.4.1 – SGA2)

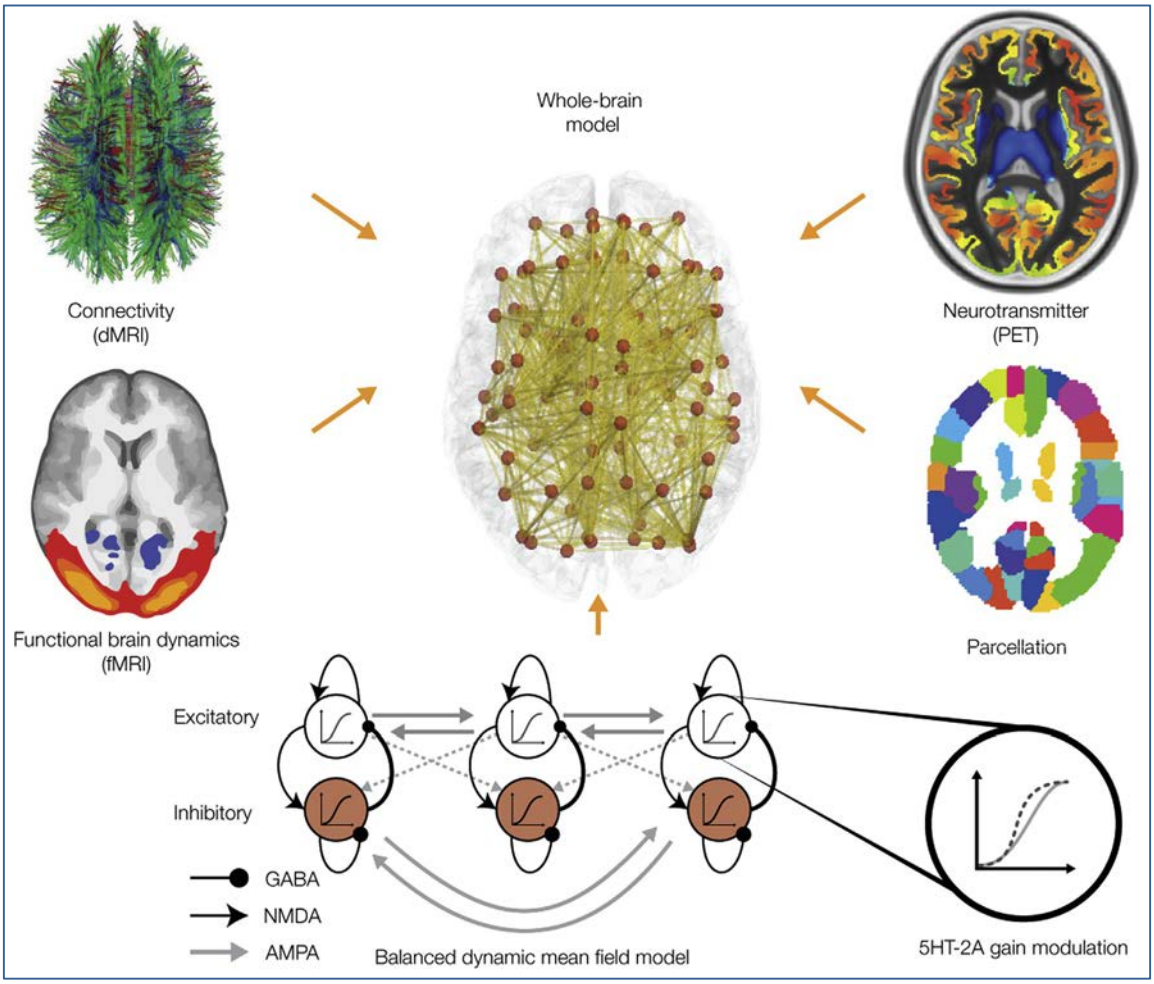

Figure 1: Adaptable modelling of whole-brain activity

Figure 1. Over the last decade modelling of whole-brain activity has focused on capturing the spatio-temporal features of resting-state, i.e. the activity of the brain while no particular task is being performed. So far, such models have assumed all brain regions to be identical but recent developments successfully included the regional differences of neurotransmitter densities, opening the door to investigate the pharmacological effects on the brain's dynamical behaviour via whole-brain modelling.

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Description in GA:	For consistent presentation of HBP results, SGA2 M24 Deliverables describing the accomplishments of an entire SP, WP or CDP have been prepared according to a standard template, which focuses on Key Results and the outputs that contribute to them. Project management elements such as Milestones and Risks will be covered, as per normal practice, in the SGA2 Project Periodic Report.
Abstract:	This report contains a description of the present status of the different models developed in WP4.4, as well as the associated publications and outputs.
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Target Users/Readers:	Neuroscientific community, Platform users, clinicians

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Table of Contents

1. Overview 4
2. Introduction 5
3. Key Result KR4.1 Develop models single-cell and population levels 6
3.1 Outputs 6
3.1.1 Overview of Outputs 6
3.1.2 Output 1: Models of motor control 6
3.1.1 Output 2: Models of sensory-motor integration 6
3.2 Validation and Impact 7
3.2.1 Actual and Potential Use of Output(s) 7
3.2.2 Publications 7
4. Key Result KR4.2 Plausible biological models of plasticity for large networks with non-trivial functionality. 7
4.1 Outputs 7
4.1.1 Overview of Outputs 7
4.1.2 Output 1: A neural-level model of spatial memory and imagery 8
4.1.3 Output 2: A computational model of visual recognition memory via grid cells 9
4.1.4 Output 3: Navigating with grid and place cells in cluttered environments 10
4.1.5 Output 4: Advantages and detection of phase coding in the absence of rhythmicity 11
4.1.6 Output 5: Reliability based arbitration of hippocampal and dorsal striatal decision making 12
4.1.7 Output 6: Coordinated HPC-mEC replay as structural inference. 13
4.1.8 Output 7: Development of novel computational approaches to spatial navigation. 13
4.2 Validation and Impact 14
4.2.1 Actual and Potential Use of Output(s) 14
4.2.2 Publications 14
5. Key Result KR4.3 Develop models of brain activity and function 15
5.1 Outputs 15
5.1.1 Overview of Outputs 15
5.1.2 Output 1: Models of spontaneous activity and sleep 15
5.1.3 Output 2: Whole-brain model for propagation of spontaneous activity 18
5.1.4 Output 3: Models of bottom-up and top-down visual processing 19
5.2 Validation and Impact 21
5.2.1 Actual and Potential Use of Output(s) 21
5.2.2 Publications 21
6. Conclusion and Outlook 22

Table of Figures

Figure 1: Adaptable modelling of whole-brain activity 1
Figure 2: Extension to episodic memory 8
Figure 3: Grid cells as a paradigm for visual recognition. 9
Figure 4: Spatial navigation in cluttered environments. 10
Figure 5: Grid cell firing patterns can encode multiplexed spatial information 11
Figure 6: Model of hippocampal and striatal contributions to spatial navigation 12
Figure 7: Interaction between place and grid cells for spatial localisation and learning 13
Figure 8: Modelling spontaneous cortical activity at cellular an population levels. 16
Figure 9: Overview of Integrating Multimodal Data Including Neuromodulation into a Whole-Brain Neuronal Model 17
Figure 10: Dynamic communicability expresses propagation of recurrent network activity 18
Figure 11: Understanding noise correlations in retinal visual processing. 19
Figure 12: Object recognition in movies requires integration of bottom-up and top-down processes. 20

1. Overview

The Human Brain Project is a great endeavour that will provide precious resources to advance the understanding and the simulation of the human brain in a few years. The theoretical and computational models developed in SP4 occupy a central position in the HBP. On the one hand, they are derived from experimental data produced in the HBP. On the other hand, models are implemented in the HBP Platforms, where they serve as "first users". These models also constitute the building blocks of work that will be continued in SGA3, such as bridging scales, network models, models of plasticity, models of cognitive processes and whole-brain models.

During the last century, a plethora of models have been proposed to reproduce different brain functions, but those have mainly targeted specific functions, e.g. the shift of attention from one object to another in the visual field, or the circuitry needed to produce eye-movements. Those models were born isolated from each other, very often ignoring the models written to reproduce other functions. Thus, the major challenge that theoretical and computational neuroscience faces in the following decades is that of putting those models together such that they work with each other to reproduce more complex brain functions. Work Package WP4.4 has made a large effort to bring selected models for different brain functions (rest, sleep, vision, motor control, memory and spatial navigation) to the frontline of research. While still isolated, these represent key models for the next level integration by filling important gaps into that common goal. This integrative process will take neuroscientists many years to accomplish, but, during SGA3, we will see the beginning of this path. The efforts done by WP4.4 so far will play a relevant role.

2. Introduction

During the last century a plethora of models have been proposed to reproduce different brain functions. So far researchers have targeted models for specific functions, e.g. the shift of attention from one object to another in the visual field, or the circuitry needed to produce eye-movements. Those models were born isolated from each other, very often ignoring the models written to reproduce other functions. A major challenge that theoretical and computational neuroscience faces in the near future is that of putting those models together such that they work with each other in order to reproduce more complex brain functions. The tools provided by the Human Brain Project (data, computation and simulation services) will certainly help confront this challenge. The science performed by the HBP also targets towards such integration of models. During SGA2, Work Package WP4.4 has made a large effort to bring models for selected brain functions (rest, sleep, vision, motor control, memory and spatial navigation) to the frontline of research. While still isolated, these models fill key missing gaps to facilitate the common goal of integrating several models in the future to study more complex behaviours.

This Deliverable presents the main results of WP4.4 during SGA2, organised around our contributions to three SP-level Key Results: KR4.1 (Develop models of single-cell and population levels), KR4.2 (Plausible biological models of plasticity for large networks with non-trivial functionality) and KR4.3 (Develop models of brain activity and function).

Towards KR4.1, Task T4.4.2 developed a model of the basal ganglia both at the neuronal level (80,000k spiking neurons; Lindhal *et al.*, 2017)) and at the population level using a rate-based description (Suryanarayana, *et al*, 2019; P1643). Both system-level models predicted that the inputs to striatum from the arkypallidal neurons in Globus Pallidus externa (GPe) could potentially play a role for motor control, e.g. in 'stop-signalling tasks'. Task T4.4.5, in cooperation with CDP4, corrected an existing model for saccade generation and reproduced its behaviour, replacing the regional dynamics by a recent mean-field model that models, exactly, the activity of a population of quadratic integrate-&-Fire neurons.

For KR4.2, both Tasks T4.4.4 and T4.4.6 have developed several models involving spatial memory and navigation, including goal-directed and planning of navigation in mazes and cluttered environments. The models were developed in collaboration with other HBP partners (SP3 / Episense and CDP7) towards their integration in both real and virtual robots. Additionally, it could be shown via modelling that different brain areas govern the learning of different rules, with the striatum learning ego-centric associations between sensory inputs and actions while the hippocampus learns an allo-centric representation of the environment based on place cells.

Towards KR4.3 a variety of models of brain activity and function have been carried out, each aimed at filling gaps within broader pipelines of the HBP. The work performed can be gathered into two streams. The work of T4.4.1 has conceived models of spontaneous activity in the cerebral cortex, both at the level of networks of spiking neurons and at the macroscopic level where each region of interest is characterised by a population or mean-field model. Task T4.4.2, on the other hand, has developed models of visual processing at the retina and of visual recognition merging bottom-up and top-down streams.

3. Key Result KR4.1 Develop models single-cell and population levels

3.1 Outputs

3.1.1 Overview of Outputs

3.1.1.1 List of Outputs contributing to those models

- Output 1: Models of motor control (C1025, C2390).
- Output 2: Models of sensory-motor integration (C1857, C1207, C1070).

3.1.1.2 How Outputs relate to each other and the models (link to the Key Results)

The two Outputs are independent from each other although both aim at bridging the gap between the neuronal and the population levels by modelling concrete circuitries. Output 1 targets the modelling of the basal ganglia and their interconnections using both neuronal and population models. The goal of Output 2 was to reproduce an existing model of saccade generation using population models that represent exact neuronal populations. During SGA3, the results of both Outputs will be further employed in WP3.

3.1.2 Output 1: Models of motor control

_(KTH) Two different models of the basal ganglia system have been investigated previously under this KR to test hypotheses on the role of basal ganglia in 'action selection', and to generate hypotheses on the underlying network mechanisms. One model used up to 80,000 spiking neurons (Lindahl *et al.*, 2017; doi: 10.1523/ENEURO.0156-16.2016; from SGA1) while the other model represented different neuron populations using a rate based description (Suryanarayana, et al, 2019; from SGA2; P1643). Both these system level models predicted that the inputs to striatum from the arkypallidal neurons in Globus Pallidus externa (GPe) could potentially play a role for motor control, e.g. in 'stop-signalling tasks'. However, the timing when the arkypallidal neurons needed to be activated to interrupt the activity in the striatal projection neurons (SPN) was difficult to reconcile with experimental data from the different basal ganglia nuclei, and when measured in behaving rodents. Therefore, we investigated the hypothesis that dendritic plateaus (i.e. NMDA spikes) in SPNs are involved when SPNs increase their firing rate during movement initiation. Our model predicted that arkypallidal 'stop responses' can suppress movement-related activity in the striatum by suppressing the dendritic plateau potentials. The results from this modelling study were presented during the 2019 Conference on Cognitive Computational Neuroscience in Berlin (https://ccneuro.org/2019/), see reference[1].

3.1.1 Output 2: Models of sensory-motor integration

In line with the CDP4 objectives, to unify individual models involved in the visuo-motor integration loop, we contributed to the refinement of a previous model for saccade generation of the eyes (Gancarz & Grossber, 1998). The model contained several biological and dynamical simplifications which have been tuned. Additionally, we attempted an extension of the model for further biological

[1] https://ccneuro.org/2019/Papers/ViewPapers.asp?PaperNum=1205

plausibility, by replacing the local dynamics of the regions by a recent neuronal population model. The work was performed in collaboration with a student from UM partner visiting UPF. See further details and results in the SGA2 CDP4 compound Deliverable D2.5.1 (D12.1 D61), KRc4.1.

3.2 Validation and Impact

3.2.1 Actual and Potential Use of Output(s)

The work produced for the models of motor control, which maps onto C1025, were developed during SGA1 and SGA2. Their evolution and improvement will continue during SGA3, contributing to WP3. The model for saccade generation in Output 2 is integrated into a broader pipeline within CDP4 for implementation in the Neurorobotics Platform. This work will continue to be developed during SGA3, as part of WP3.

3.2.2 Publications

N/A

4. Key Result KR4.2 Plausible biological models of plasticity for large networks with non-trivial functionality.

4.1 Outputs

4.1.1 Overview of Outputs

4.1.1.1 List of Outputs contributing to this KR

- Output 1: A neural-level model of spatial memory and imagery (C2409).
- Output 2: A computational model of visual recognition memory via grid cells (C2409).
- Output 3: Navigating with grid and place cells in cluttered environments (C2500).
- Output 4: Advantages and detection of phase coding in the absence of rhythmicity (C2408).
- Output 5: Reliability based arbitration of hippocampal and dorsal striatal decision making (C984).
- Output 6: Coordinated HPC-mEC replay as structural inference (C2408).
- Output 7: Development of novel computational approaches to spatial navigation

4.1.1.2 How Outputs relate to each other and the Key Result

All research outputs focus on the modelling aspects of hippocampal function and the adjacent, functionally connected regions. The models thus consider the same spatially related cell types (place, grid, boundary vector, head direction and object vector cells).

The models are largely standalone. Functionally, there is some dependence:

- Output 6 describes how stable ‘maps’ of the world might be learned.
- Outputs 1,2,3,5 utilise these maps for higher-level functions.

4.1.2 Output 1: A neural-level model of spatial memory and imagery

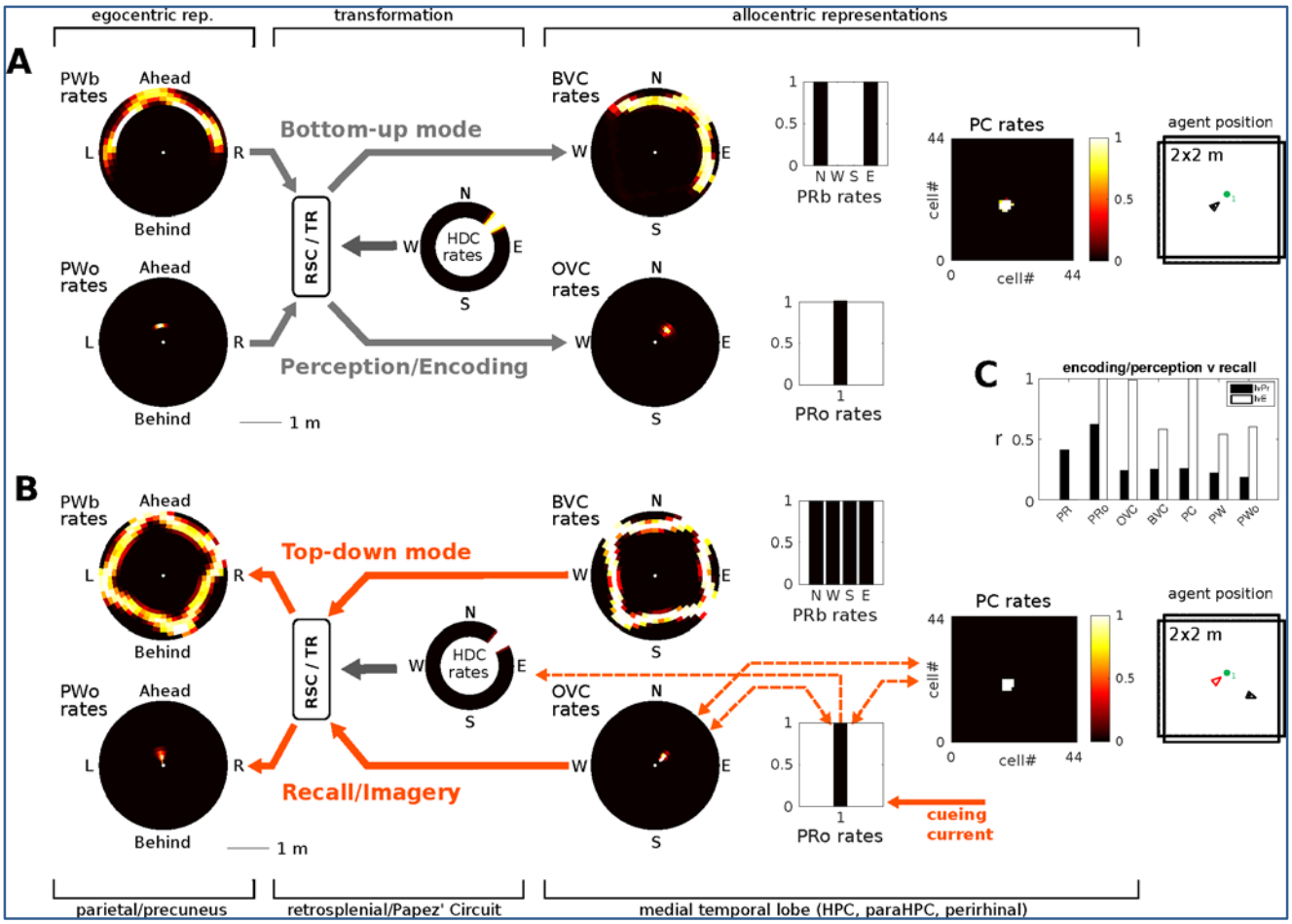

Figure 2: Extension to episodic memory

A) In the bottom-up mode of operation, sensory inputs drive the model and items can be encoded into memory, when the agent encounters them in an environment (right panel, agent is a triangle, the object a dot). Population snapshots of the model at the moment of encoding during an encounter with a single object in a familiar spatial context are shown. Left to right: PWb/o populations driven by sensory input form an egocentric representation of the environment. These populations project to a head-direction-modulated transformation circuit (RSC/TR, hypothesised to be in retrosplenial cortex, details omitted for clarity); The transformation circuit projects to BVCs and OVCs which, together with perirhinal identity neurons constitute the main drive to place cell (PCs; coding for the agents' location); perirhinal (PRb/o) neurons are driven externally, reflecting object recognition along the ventral visual stream. At the moment of encoding, reciprocal connections between PCs, OVCs, PRo neurons are learned. B) In the top-down mode of operation the model re-instates egocentric parietal representations (reflecting visuospatial imagery) reconstructed from memory. The agent has moved away from the object (current agent location: black triangle; right panel). Cueing the agent to remember the encounter with the object in (A), current is injected into the corresponding PRo neuron (right of panel). This drives firing of connected PCs (dashed orange connections, learned at encoding). PCs become the main drive to OVCs, BVCs and PRb neurons. BVC and OVC representations are transformed to their PW counterparts, thus reconstructing egocentric parietal representations (PWb/PWo) similar to those at the time of encoding (left of panel). Thus, the agent reconstructs the spatial scene of the encounter from the previous point of view (red triangle, in rightmost panel). Colour code: heat maps show population firing rates frozen in time. Black: zero firing rate, white: maximal firing rate.

Based on previous work on human episodic memory (Byrne *et al*. 2008) we have built a model of how neural representations of egocentric spatial experiences in the parietal lobe interface with viewpoint-independent representations in medial temporal lobe to enable key aspects of spatial cognition. The model shows how populations of known types of spatial cells (place cells, head-direction cells, boundary- and object-vector cells, grid cells, and parietal gain-field neurons) map onto higher cognitive function in a modular way. The interactions between these populations across multiple brain regions provide a mechanistic account of spatial memory, scene construction, novelty-detection, and mental navigation. In particular, the model shows how so-called object vector cells (OVCs) may allow memory for items to be incorporated into a contextual representation based on

extended environmental boundaries (as expressed in the firing of boundary vector cells; or BVCs). The same cells provide the neural correlated of objects in context during recall/visuospatial imagery (Figure 2). Simulations have been implemented in MatLab (using rate coded neurons) and a manuscript has been published in ELife (Bicanski and Burgess, 2018, P1365) and was accompanied by press releases from UCL and the HBP.

Comparison to human episodic memory has been initiated in collaboration with SP3 Episense (Emrah DUZEL): looking at human hippocampal involvement in pattern completion using 7T fMRI (Grande *et al.*, 2017). Some aspects of the model are being shared with partners in SP3 Episense (Tony PRESCOTT, Martin PEARSON), who are developing a version of the spatial memory model for use on a robotic platform.

4.1.3 Output 2: A computational model of visual recognition memory via grid cells

We have built a model of visual recognition memory (Bicanski & Burgess 2019, Current Biology, P1849) that exploits parallels between spatial memory and vision. This model provides the first account of how grid cells may contribute to vision by guiding eye-movements from memory. These cells map the visual field of view in the same way that spatial grid cells map an environment an agent moves in. The model provides the first mechanistic theory to connect cells typically engaged in spatial cognition (grid cells) to visual computations. The model proposes that grid cells encode the spatial relationships between features of an object or a visual scene, and allow eye movements to be directed to the locations of other expected features based on hypothesised stimulus identity. That is, memory-guided eye-movements reflect perceptual hypotheses. We have made strong predictions at the behavioural and neurophysiological level and showcased how one shot learning of visual exemplars may occur with the help of grid cells.

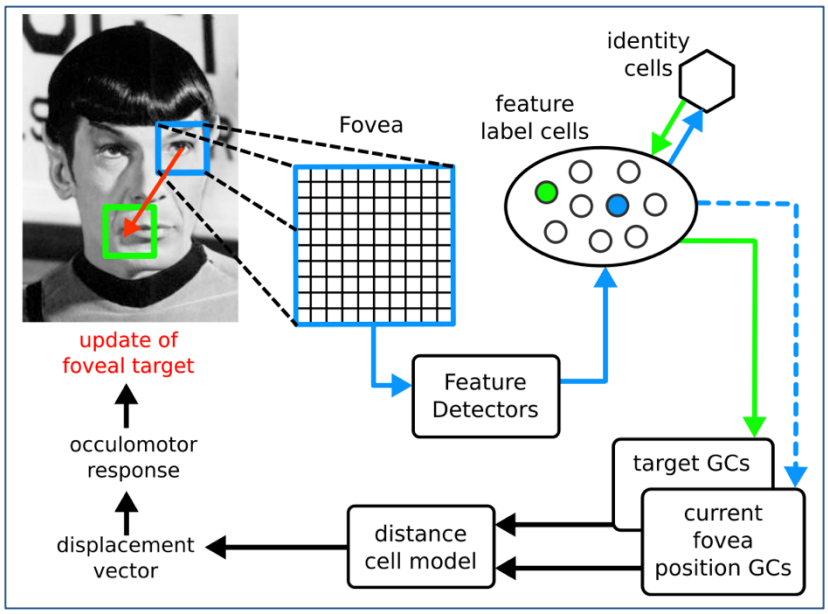

Figure 3: Grid cells as a paradigm for visual recognition.

Model schematic: Grayscale images are sampled by a square fovea (blue square). Feature detectors drive feature label cells, each coding for a particular salient feature. During training each feature label cell has been associated with a grid cell population vector (current position grid cells, blue cell and dashed arrows). All feature label cells of a given stimulus are bi-directionally connected to a single cell coding for the identity of the attended stimulus. Upon firing of an identity cell, the currently active feature label cell is inhibited and identity cells select the next feature label cell to be active (short green arrow and cell), which is associated with its own grid cell population vector (target grid cells). Current and target position grid cell representations yield the next saccade vector (red arrow on image). Note, the selection of the feature label cell corresponds to a prediction of the next sensory discrimination.

4.1.4 Output 3: Navigating with grid and place cells in cluttered environments

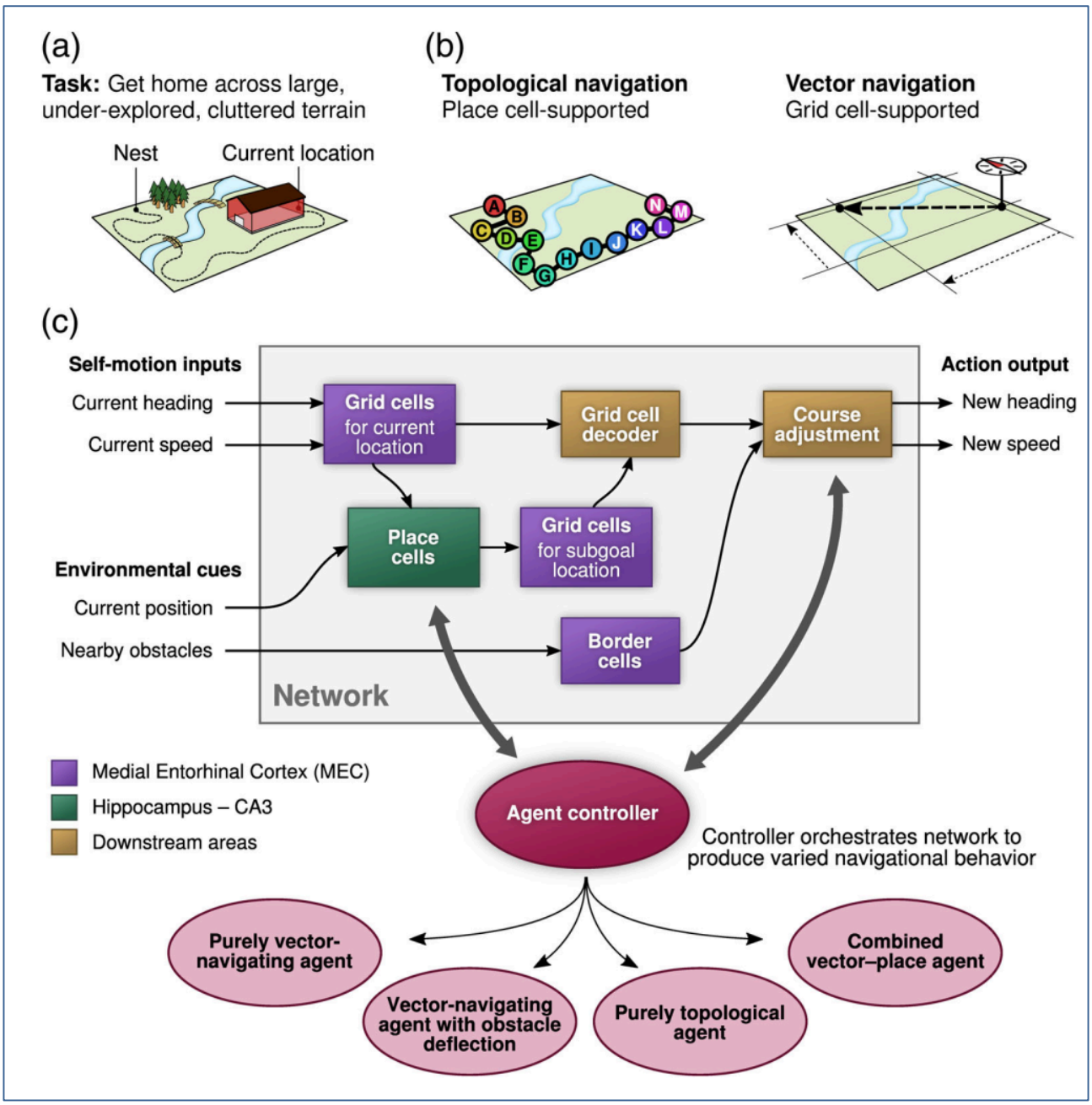

Figure 4: Spatial navigation in cluttered environments.

(a) Stereotypical navigation task. An agent has travelled across unknown terrain to a remote location and wishes to return to its nest, with limited knowledge of the environment. (b) Two major navigation paradigms supported by neurophysiological evidence. Place cells likely support topological navigation, where knowledge about locations' interconnectivity is used to reach the goal. Grid cells likely enable the calculation of distances and angles for straight-line trajectories between arbitrary pairs of previously visited locations (vector navigation). (c) Model overview. Network portion (grey box) remains fixed across all trials. An external agent controller orchestrates components in the network in order to produce a variety of navigational strategies, either primarily vector-based navigation, primarily topological navigation, or combined strategies utilising a mixture of information from grid cells, place cells, and border cells. A grid cell decoder performs vector navigation toward a subgoal provided by the place cells. Border cells provide local obstacle information to a course adjustment mechanism. Box colours indicate related areas in the hippocampal formation.

We have built a model of flexible navigation in cluttered environments by combining several types spatially selective cell types. Place cells have been associated with a topological strategy for navigation, while grid cells have been suggested to support metric vector navigation. Grid cell-based vector navigation can support novel shortcuts across unexplored territory by providing the direction

toward the goal. However, this strategy is insufficient in natural environments cluttered with obstacles. By integrating a grid cell-based vector navigation mechanism with local obstacle avoidance, mediated by border cells and place cells, whose interconnections form an experience-dependent topological graph of the environment, we were able to achieve good navigational performance in complex environments. When vector navigation and object avoidance fail (i.e. the agent gets stuck), place cell replay events set closer subgoals for vector navigation. This strategy is particularly useful where the environment is underexplored. The simulated agent was also able to successfully navigate experimental maze environments from the animal literature on to cognitive mapping.

4.1.5 Output 4: Advantages and detection of phase coding in the absence of rhythmicity

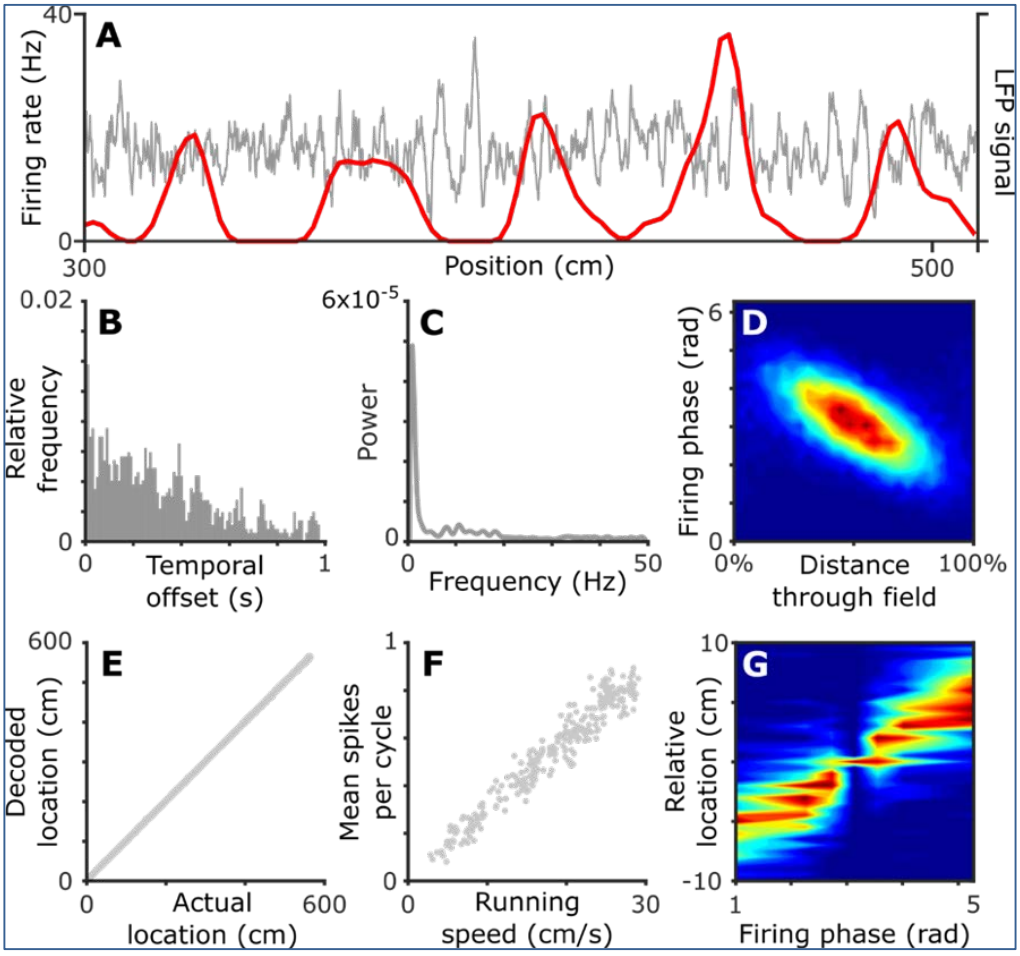

Figure 5: Grid cell firing patterns can encode multiplexed spatial information

A) Grid cell firing rate along a 1D track (red line) generated using a baseline oscillation with highly variable frequency (grey line) recorded from depth electrodes in human hippocampus. B, C) Grid cell spike train auto-correlogram and power spectrum, which exhibit no clear rhythmicity. D) Grid cell firing phase relative to the baseline oscillation, which becomes progressively earlier as each firing field is traversed. E-G) Accurate decoding of multiplexed spatial information from grid cell population activity in each oscillatory cycle. Location on the track can be recovered from population firing rates (E); running speed from the number of spikes in each cycle (F); and movement direction from population firing phase (G).

We have developed a phenomenological model of grid cell firing, in order to assay the specific contribution made by the phase (i.e. temporal) coding of spatial variables to localisation and navigation. In the rodent brain, both place and grid cells exhibit “theta phase precession”, with theta firing phase becoming progressively earlier in each oscillatory cycle as the spatial receptive field is traversed. Coordinated phase precession across the active place cell population generates "theta sweeps" of activity in each oscillatory cycle, such that locations behind the animal (along its

current movement trajectory) are represented early in each oscillatory cycle and locations ahead of the animal are represented late in the oscillatory cycle.

Our simulations demonstrate that this allows place / grid cells to encode movement direction in their firing phase, in addition to running speed and location being encoded in population firing rates. Hence, within a single oscillatory cycle, grid / place cell population activity encodes the agent's entire movement trajectory. Moreover, the phase code for location reduces ambiguity in the grid cell firing rate code for location, which can be particularly problematic when peak firing rates vary across fields (as observed empirically). Finally, we demonstrate that this result does not depend on prominent oscillatory activity with a relatively fixed frequency, consistent with intracranial EEG recordings from the human brain.

4.1.6 Output 5: Reliability based arbitration of hippocampal and dorsal striatal decision making

We have implemented a simulation of hippocampal and striatal contributions to spatial navigation, following the identification of the relevant cognitive architecture (Chersi and Burgess, 2015; Figure 6). The model consists of a network of rate-coded neurons, with different learning rules governing the different brain areas. Specifically, the striatum learns ego-centric associations between sensory inputs and actions through a temporal difference algorithm relying on reward prediction errors. For example, it can learn the association between seeing a cue and turning right. The model hippocampus, by contrast, learns an allo-centric representation of the environment based on place cells. To test our model, we used it to solve an adaptation to the classic Morris Water Maze task (Pearce et al. 1998), where the goal is to find a hidden platform submerged under opaque water.

An example result of these simulations is shown in Figure 6. Both the striatal model and the hippocampal model can learn relatively short paths to the goal. However, because the striatal learning is dependent on reward prediction errors, it shows 'blocking': it does not learn to respond to a second cue when a preceding cue is already fully predictive of reward. This model provides a framework for application to a series of spatial and non-spatial cognitive tasks. All simulations were run using Python.

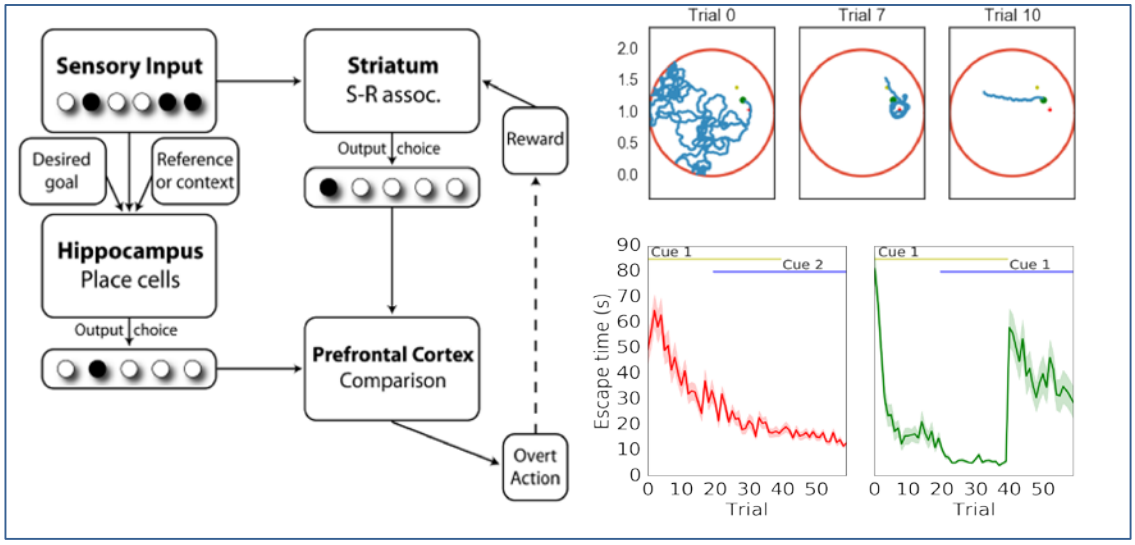

Figure 6: Model of hippocampal and striatal contributions to spatial navigation

Left panel: model architecture. Separate navigational strategies are computed in the hippocampus and striatum, and the prefrontal cortex compares the respective outputs. Right upper panel: example trajectories showing learning in the Morris Water Maze over trials. Right lower panel: performance on the maze as measured by the time needed to find the platform. Red and green horizontal lines indicate the presence of two spatial cues. Agents using a hippocampal learning strategy (red line) show learning of the platform location over trials, unaffected by changes in the landmark. Those using a striatal learning strategy (green line) exhibit 'blocking' of learning from a second cue, as evidenced by the drop in performance upon the disappearance of Cue 1.

4.1.7 Output 6: Coordinated HPC-mEC replay as structural inference.

Evans and Burgess (NeurIPS, 2019) proposed a model of the interaction between place and grid cells for spatial localisation and learning. This model was the first model to propose a function for experimental observations showing coordinated 'offline' reactivation of the hippocampus and entorhinal cortex during 'replay' of waking experience. The model proposes that the entorhinal cortex is able to compute a metric embedding of distinct associative experiences stored in the dense recurrent dynamics of CA3, which is achieved by a process of probabilistic message passing.

The model also poses a biophysically detailed implementation of message passing between CA3 and mEC, predicting the existence of synchronised traveling waves of activity.

Evans and Burgess (submitted)[2] extended this work, modelling the responses of grid cells during gain manipulations in virtual reality (Chen *et al*. 2019 –P1816; SP3).

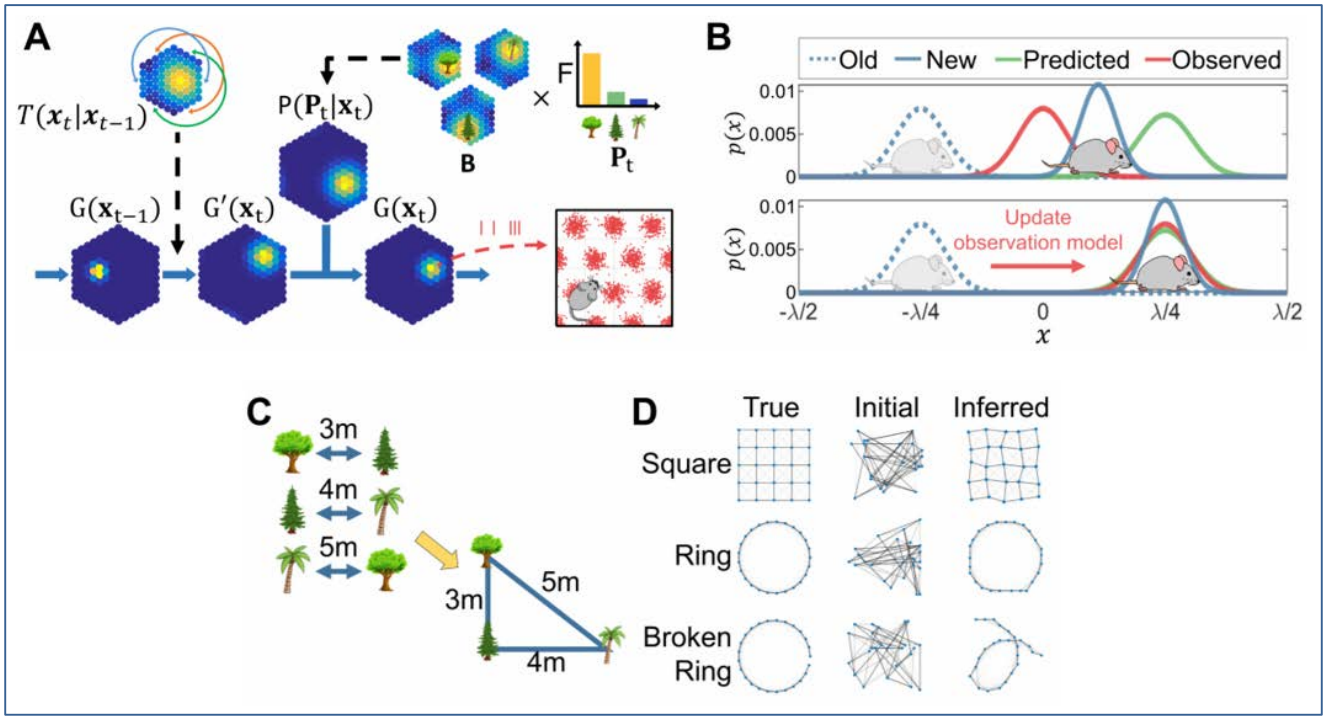

Figure 7: Interaction between place and grid cells for spatial localisation and learning

A Grid cell firing rates at time *t* are updated by path integration before correction by weighted input from PC firing. Each hexagon defines a single grid module with NG GCs. Plotting spikes from a single GC against the position of the animal generates the GC firing pattern. B Learning corrects the observation model towards the predicted estimate. C Inferred distances are used to recover the absolute structure of the world. D Structural inference on static structures with noisy initial priors ("Initial"). Inferred structure is sensitive to the topology of the environment ("Broken Ring").

4.1.8 Output 7: Development of novel computational approaches to spatial navigation.

The research activities focused on the development of novel computational approaches to characterise goal-directed spatial navigation and planning in the hippocampus - ventral striatum circuit (C3037, T4.3.4); novel computational methods for the data analysis of neural data in the hippocampus and medial temporal lobe during spatial navigation and planning tasks (C3036, T4.5.4); and a novel robotic implementation of goal-directed navigation and planning within the Neurorobotics Platform (C3035, T4.4.6). All this work is carried out under CDP7; the relevant

[2] Evans and Burgess N. (submitted) Online and offline inference in the hippocampal-entorhinal system.

information is provided in the CDP7 SGA2 Deliverable D4.4.2 (D24.2 D122) section "Key Result KRc7.3 Hierarchical navigational planning – computational modelling "

4.2 Validation and Impact

4.2.1 Actual and Potential Use of Output(s)

The spatial memory model (Output 1) has had considerable impact since its publication, garnering 44 citations within 19 months since publication. Similarly, the visual recognition memory model (Output 2) has achieved 10 citations within 10 months since publication. Its code has been downloaded multiple times, with researchers reaching out to Dr Andrej BICANSKI after the download. A key theme of Outputs (1-3) is that different aspects of grid cell function are showcased by each model, which may particularly inform future large-scale models capable of multiple behaviours concurrently across domains.

Output 4 describes empirical methods that can be used to reveal phase coding in the absence of prominent EEG rhythmicity. These methods can be applied to a variety of existing or novel data sets, obtained from any mammalian species, to probe the existence and function of phase coding across a variety of cognitive domains. Results have been presented at the iNav symposium in Bad Gastein, Austria (June 2016); HBP hippocampal meeting in Paris, France (May 2017); Cosyne conference in Breckenridge, USA (March 2018); BCCN-UCL Navigation Retreat in Munich, Germany (July 2019); and seminars at the Psychology department in the University of Bangor, UK (December 2019), UCL Wellcome Trust Centre for Human Neuroimaging, UK (February 2020), and Donders Institute in Nijmegen, Netherlands (April 2020).

A key component of Output 5 is its applicability to both spatial and non-spatial tasks. It thus provides a crucial bridge to studying broader aspects of behaviour. Work has been presented at COSYNE (2020) conference.

Output 6 makes strong and detailed predictions about the nature of hippocampal place cell dynamics and learning. The HBP has developed a detailed model of the hippocampus, in which these predictions could be tested. Work has been presented at COSYNE (2018) and NeurIPS (2019) conferences.

4.2.2 Publications

Output 1: A neural-level model of spatial memory and imagery

Bicanski A, Burgess N. *A neural-level model of spatial memory and imagery*. Elife. 2018 Sep 4; 7:e33752. P1365

Output 2: A computational model of visual recognition memory via grid cells

Bicanski A, Burgess N. *A computational model of visual recognition memory via grid cells*. Current Biology. 2019 Mar 18;29(6):979-90. P1849

Output 3: Navigating with grid and place cells in cluttered environments

Edvardsen V, Bicanski A, Burgess N. *Navigating with grid and place cells in cluttered environments*. Hippocampus. 2019 Aug 13. P1930

Output 4: Advantages and detection of phase coding in the absence of rhythmicity

Bush, D, Burgess, N. *Advantages and detection of phase coding in the absence of rhythmicity*. Hippocampus. 2020; 1– 18. P2444

Output 6: Coordinated HPC-mEC replay as structural inference.

Evans and Burgess N. (2019) *Coordinated hippocampal-entorhinal replay as structural inference*. Advances in Neural Information Processing Systems. P2215

5. Key Result KR4.3 Develop models of brain activity and function

5.1 Outputs

5.1.1 Overview of Outputs

5.1.1.1 List of Outputs contributing to this KR

- Output 1: Models of spontaneous activity and sleep (C1858, C999).
- Output 2: Whole-brain network model for the propagation of spontaneous activity (C1859).
- Output 3: Models of bottom-up and top-down visual processing (C2296, C980).

5.1.1.2 How Outputs relate to each other and the Key Result

This KR was intended to embrace a variety of models of brain activity and function, each aimed at filling gaps within broader pipelines of the HBP. The work performed can be gathered into two streams. One relates to the modelling of spontaneous activity and whole-brain activity (Outputs 1 and 2). These models have served as inspiration for the design of WP1 in SGA3, where the technical requirements to carry out their simulations within EBRAINS will be resolved. For example, a collab was created (https://collab.humanbrainproject.eu/#/collab/34586/nav/239746) in order to identify the missing technical gaps for running whole-brain simulations on the platforms: from loading atlas data to running the simulations and analysing their results. On the other hand, (Output 3) gathers models of visual perception and attention, bottom-up and top-down. These models have been developed with integration into the Neurorobotics Platform in mind for integrated pipelines of visual recognition.

5.1.2 Output 1: Models of spontaneous activity and sleep

During SGA2, the CNRS partner has conceived several models of spontaneous activity in cerebral cortex, using networks of spiking neurons modelled by the AdEx model. First, the spiking activity of excitatory and inhibitory neurons was quantified from experimental data, from human and monkey micro-electrode recordings (Peyrache & Destexhe, 2019 – P2042; Susin & Destexhe, 2020 – P2360). The constraints obtained from these analyses, in particular about inhibition, were used in the network models. The workflow to integrate unit recordings into models, up to brain scales was summarised recently (Goldman *et al.*, 2019 – P2222, see Figure 8). For modelling sleep, experimental data were used from different animals, comparing slow-wave sleep (SWS) and anaesthetised states, and it was discovered that there are two types of slow waves, distinguishing SWS from anaesthesia (Nghiem *et al.*, 2020 – P1509). The transitions between the two types of slow-waves could be realised *in vitro*, in collaboration with an experimental group, thanks to the work of an EITN postdoc. CNRS also participated to a modelling study of functional connectivity (Hahn *et al.*, 2019 – P2368), which was initiated during an extended visit at the EITN by a postdoc from the group of Gustavo DECO. Finally, HBP models were also used to investigate the genesis of propagating waves of activity in V1 of awake monkey, and the role of these waves in vision (Chemla *et al.*, 2019 – P1510).

Note that all models described here are compatible with neuromorphic systems and their implementation is in progress.

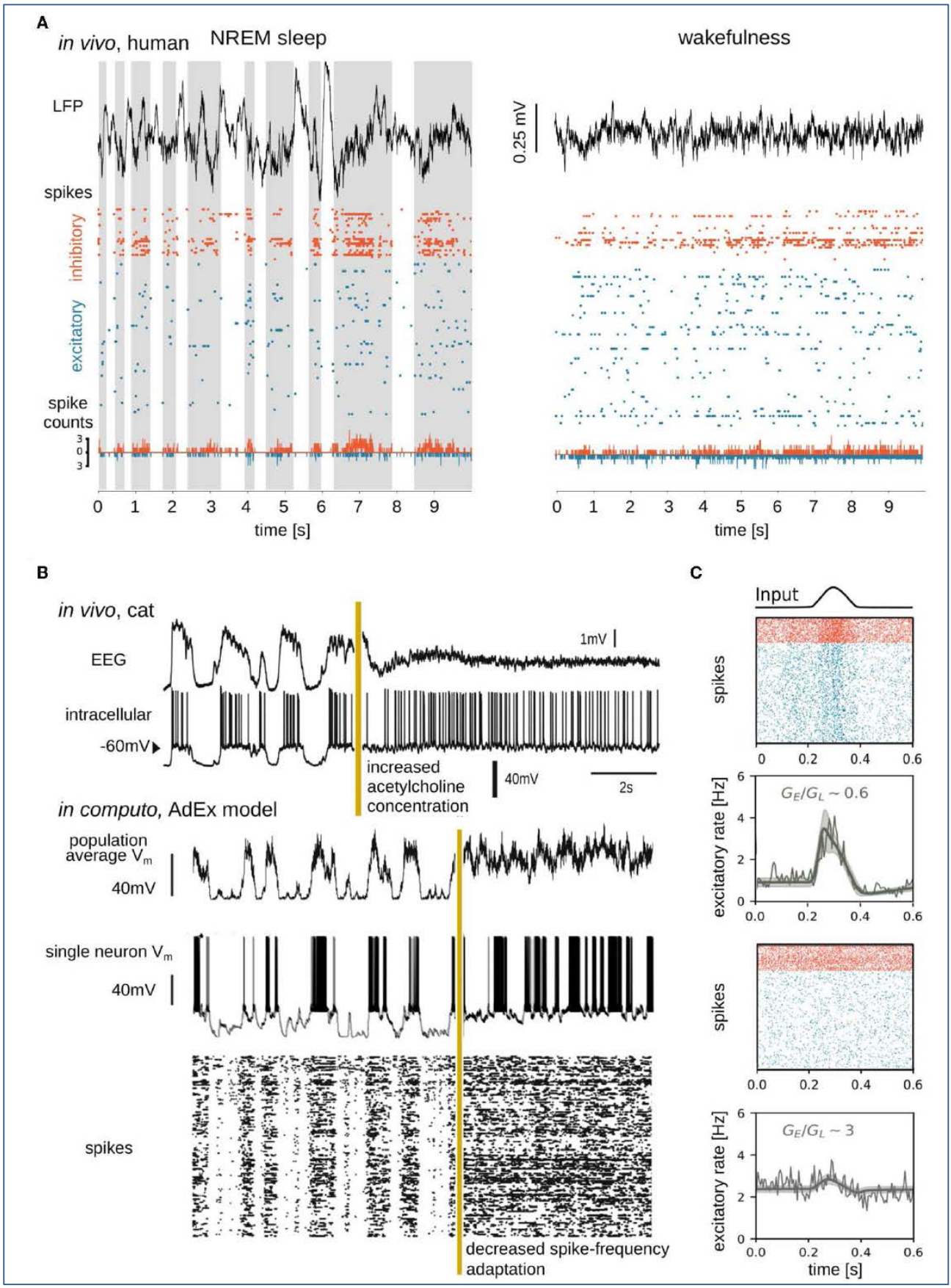

Figure 8: Modelling spontaneous cortical activity at cellular an population levels.

Microelectrode recordings in humans (A) were used to constrain models, both at the cellular (B) and mean-field levels (C). The transition from different states could be achieved by simulating the action of acetylcholine (From Goldman et al., 2019).

Whole-brain network models are built upon two main ingredients. First, a structural connectivity network constraining which brain regions communicate via direct axonal fibres and usually derived from tractography. Second, a mean-field or population model characterising the dynamical behaviour of each individual region of interest (ROI). Over the last two decades such models have greatly helped elucidating the complex dynamical behaviour of the brain at rest. So far, the models assumed for simplicity that the local dynamics of the ROIs were all set at the same working point, implying a nearly identical distribution of parameters along the brain. However, it is well known that even for cortical regions their cytoarchitecture, receptor densities and other characteristics differ. Therefore, we developed a whole-brain network model accounting for the heterogeneous distribution of Serotonin receptor densities across cortical areas based on empirical measures. ROIs were simulated using the dynamic mean-field model (Deco *et al.*, 2014) with the gain controlling the neuronal response function was tuned individually for each ROI proportional to their known Serotonin receptor densities. The resulting model could reproduce the resting-state whole-brain dynamics of healthy volunteers after intake of LSD, proving that accounting for regional heterogeneities is crucial for the accurate modelling of non-linear dynamical influences of a variety of factors towards realistic and medical applications, such as the influence of drugs on brain's activity.

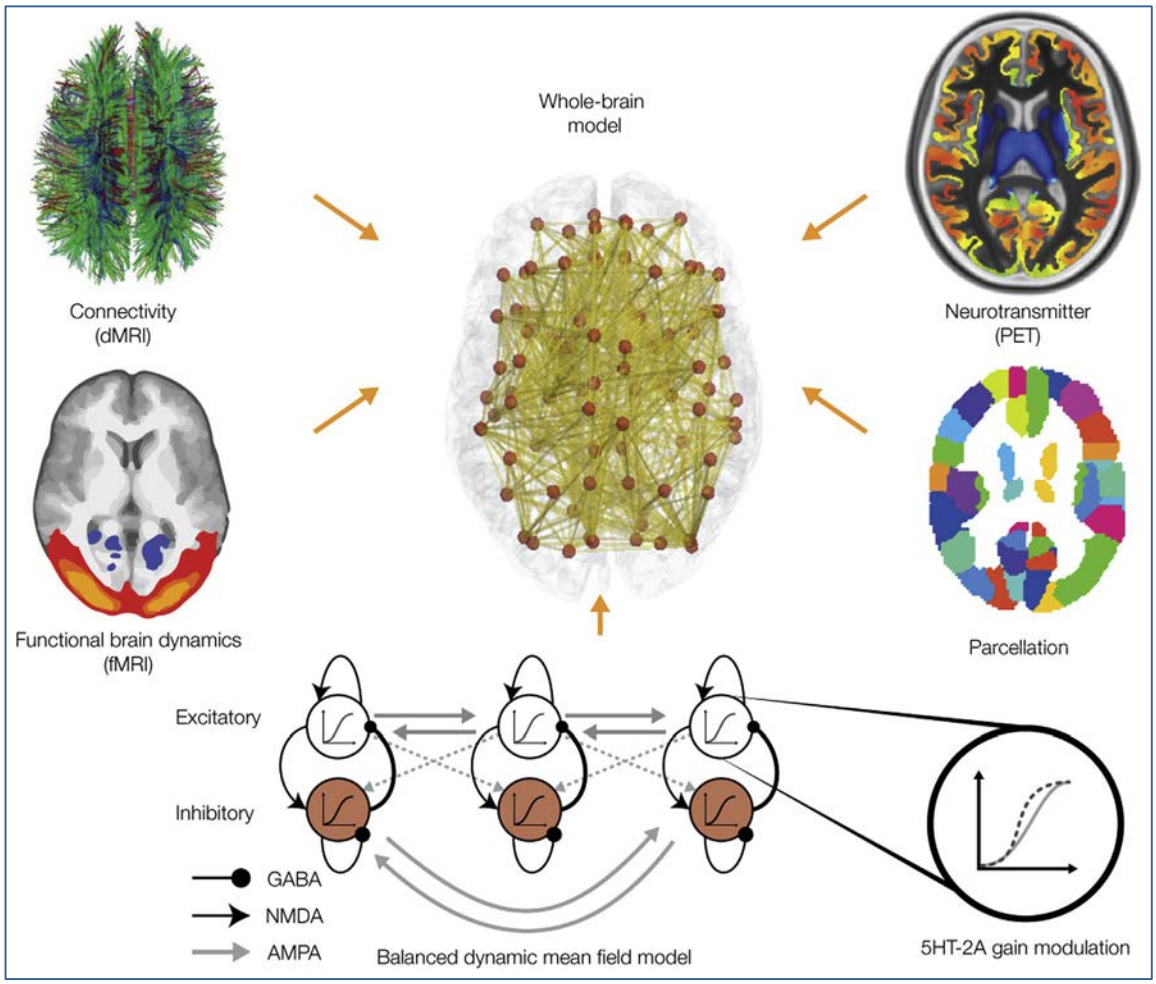

Figure 9: Overview of Integrating Multimodal Data Including Neuromodulation into a Whole-Brain Neuronal Model

We show the basic ingredients for the integration of multimodal neuroimaging data from structural (dMRI, top left), functional (fMRI, bottom left), and neurotransmission (PET, top right) using the same parcellation for each neuroimaging modality (bottom right) for generating a whole-brain computational model (middle). Each node of the model is using a realistic underlying biophysical neuronal model including AMPA, GABA, and NMDA synapses as well as neurotransmitter gain modulation (bottom row) of these.

5.1.3 Output 2: Whole-brain model for propagation of spontaneous activity

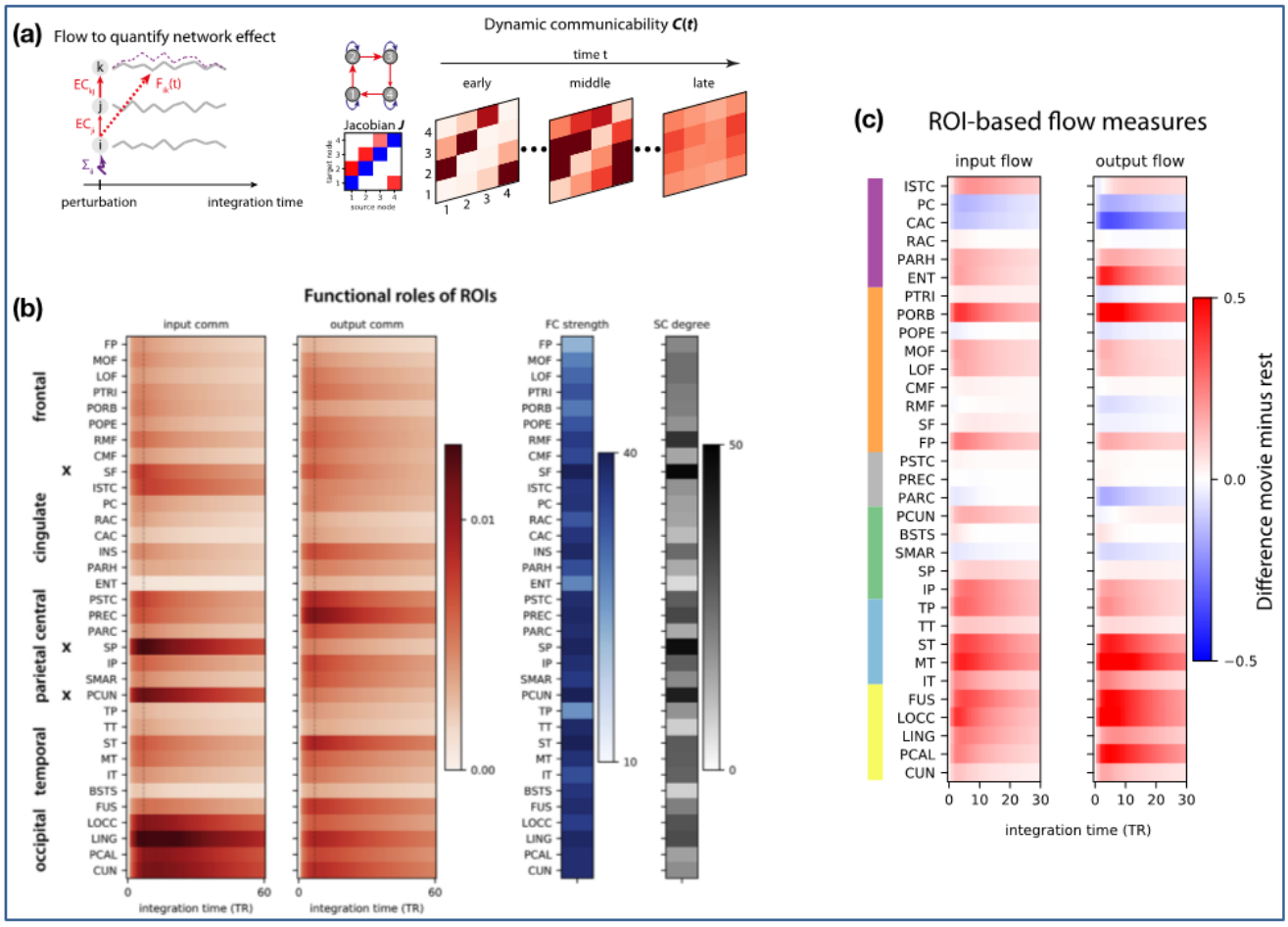

Figure 10: Dynamic communicability expresses propagation of recurrent network activity

(a) A perturbation applied to nodes generates a collection of states across the network. At early times it resembles the underlying connectivity, but over time the local effects of the perturbation homogenise. Dynamic communicability allows to study the temporal role of each ROI on the propagation of the perturbation. (b) In the resting-state ROIs typically classified as hubs display differentiated integrating or broadcasting properties. (c) In task data (here movie watching) flow differences reveal activation or inhibition of individual ROIs in respect to rest.

Neuroimaging techniques (fMRI) have been widely used to explore the associations between brain areas. Structural connectivity (SC) captures the anatomical pathways across the brain and functional connectivity (FC) measures the correlation between the activity of brain regions. However, the application of network theory is only a "static" representation despite the dynamic nature of time series obtained from fMRI. Here, we tune a multivariate Ornstein-Uhlenbeck (MOU) process

$$\dot{x}_i = -\frac{1}{\tau}x_i + \sum_{i=1}^{N} A_{ij}x_j + \xi_i$$

to reproduce the statistics of the whole-brain resting-state fMRI signals. Then, the dynamic communicability is defined as the Green function of the MOU on the network. That is, it describes the elementary and transient network response to an external impulse applied to all nodes (Figure 10a). Formally, dynamic communicability is defined as

$$\mathscr{C}(t) = |J^o| \left(e^{Jt} - e^{J^o t}\right)$$

where J is the Jaccobian of the networked MOU and J^0 is the Jaccobian of the intrinsic leakage. In contrast to classical graph theory, our model-based framework stresses the importance of taking the temporal aspect of fMRI signals into account, which allows us to identify a separation of time-scales and of individual roles of brain regions. Application of the model to interpret empirical data has led

to two published manuscripts[3][4] (P2464). In the case of resting-state activity the model shows that the input and output flow of brain regions typically classified as hubs may differ, separating the hubs between ROIs more prone to act as integrators and others to act as broadcasters (Figure 10b). When applied to study task data, e.g. subjects watching a movie, dynamic communicability allows to identify the change in flow of individual ROIs in respect to the resting-state, implying that some ROIs become more central during movie viewing while the flow through others is inhibited (Figure 10c).

5.1.4 Output 3: Models of bottom-up and top-down visual processing

We developed models of the retina that can accurately predict how the retinal network will respond to complex stimuli, and ultimately natural scenes. It is important to predict accurately the response that the retina will send to the brain during visuomotor tasks, like the ones explored in SP10, and one of our aims is to provide SP10 with a realistic retinal input. Our purpose is to build on the single-cell model developed in SGA1 and model how the entire population of ganglion cells respond to complex stimuli.

We have access to data where hundreds of neurons are recorded simultaneously showing that cells of the same type show specific fast noise correlation that are probably due to gap junction coupling. These correlations change the way the stimulus is encoded and must be taken into account in the model.

We have developed a novel statistical model based on copulas (a statistical tool), to parametrise these noise correlations. Thanks to our modelling strategy, we were able to predict the noise correlations even when the stimulus statistics were changed. Our model was thus able to generalise many sets of stimuli.

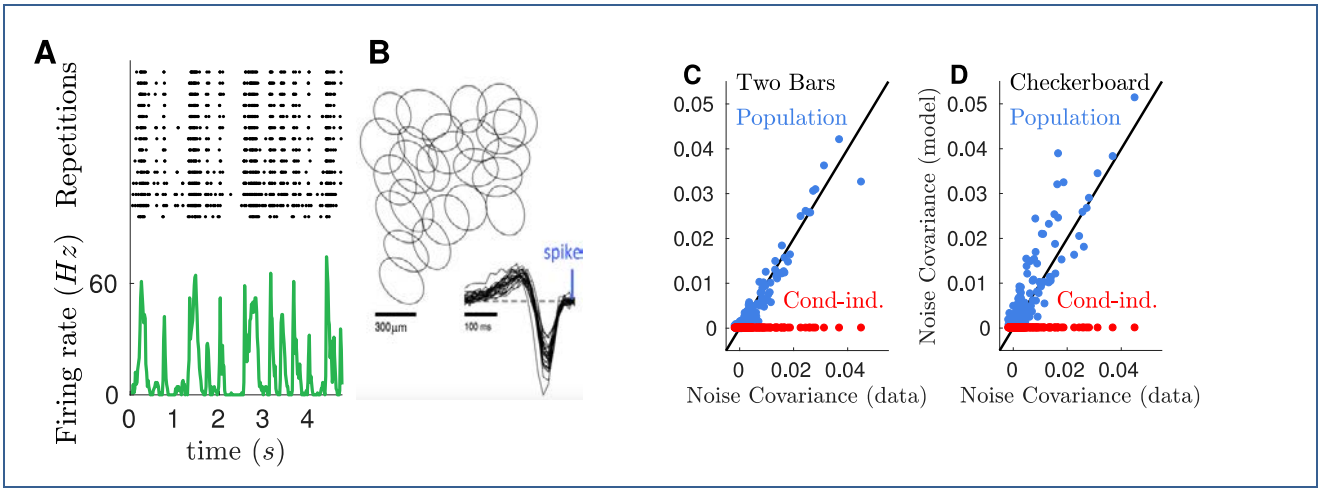

Figure 11: Understanding noise correlations in retinal visual processing.

(A) Top: activity of one ganglion cell over repeated presentations of the same stimulus. Bottom: firing rate of the cell across time. (B) Receptive field mosaic of the isolated OFF ganglion cells. (C) Our model predicts empirical noise covariances when applied on a testing set (blue points). Conditionally-independent model predicts zero noise covariances (red). (D) Same as (C), but when the couplings are inferred from response to a different type of stimulation.

We have then shown that, with only a few parameters, our model allowed predicting noise correlations even across different recordings, simply from the physical location of the recorded cells. This is a major advance since it allows generalising across experiments. We have taken advantage of

[3] Gilson M, Kouvaris, NE, Deco G, Mangin J-F, Poupon C, Lefranc S, Rivière D & Zamora-López G (2019) Network analysis of whole-brain fMRI dynamics: A new framework based on dynamic communicability NeuroImage 201, 116007.

[4] Gilson M, Zamora-López G, Pallarés V, Adhikari MH, Senden M, Tauste-Campo A, Mantini D, Corbetta M, Deco G & Insabato A (2020) Model-based whole-brain effective connectivity to study distributed cognition in health and disease. Network Neuroscience 4(2).

this to develop an approach to stitch together recordings performed at different times, on different retinas. This allows us to simulate the responses of extremely large populations of ganglion cells to complex stimuli. We have shown how this method allows estimating how synchrony scales with the number of neurons. This strategy allows to provide a realistic input to large-scale models of the thalamo-cortical system.

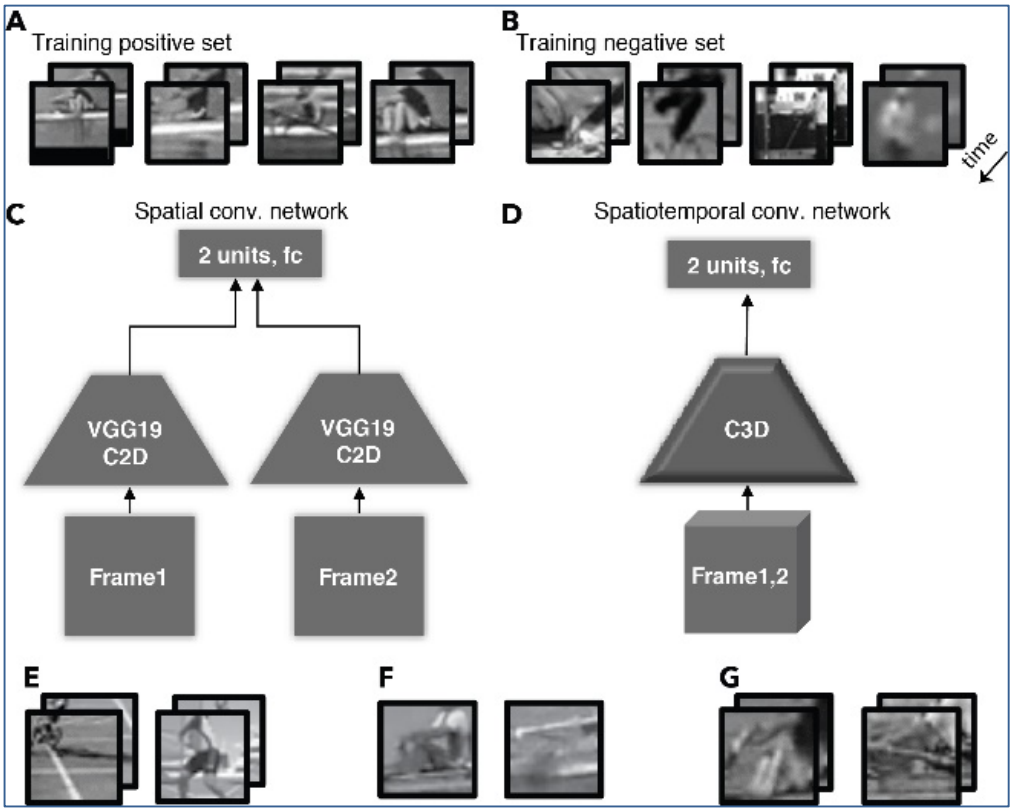

Figure 12: Object recognition in movies requires integration of bottom-up and top-down processes.

A, B binary classifier was trained to separate a positive set of similar minimal videos ("rowing"), from a negative set. C, D Human results were compared with deep-net models of video recognition. E, F, G different types of minimal images that computational models fail to recognise.

The goal of component 'Model for high-level contributions to low-level vision' was to develop functional and circuit models of integrating bottom-up with top-down processing in vision, with applications to Neurorobotics in SP10 for *in silico* models of behaviour, cognition and motor control. Our goal in the current work was to identify contributions of activations proceeding from high-level visual areas, in particular IT areas, to lower-level areas, in particular V1, which allow the visual system to perform reliable disambiguation and categorisation of image features that cannot be reliably recognised without the top-down contribution. In our last report we described a model for the full interpretation of minimal images, which shows that the visual task of categorising so-called 'minimal images' combines bottom-up processing with contribution from higher-level visual areas. In the current period, we extended our study, using a combination of a large-scale psychophysical study and computational modelling, from the domain of static images to spatio-temporal patterns. We developed a novel set of stimuli termed 'minimal videos', which are composed of a set of sequential frames (i.e. a video clip), in which humans can recognise an object and an action, but where further small reductions in either the spatial dimension or in the time dimension make the video clips unrecognisable. Using comparisons with deep-net models (Figure 12), we showed that minimal videos that are well-recognised by human observers are not recognised by current deep-network models of visual recognition from videos. We propose, based on the psychophysical testing and computational simulations, that (i) the human systems uses spatio-temporal features that are not used in current models, and (ii) similar to static minimal images studies in the past, the

recognition and interpretation of minimal videos requires a model that combines bottom-up with top-down processing. One paper is in preparation[5].

5.2 Validation and Impact

5.2.1 Actual and Potential Use of Output(s)

Output 1

The whole-brain network model accounting for regional Serotonin receptor densities is the first of its kind, advancing the modelling to come in the next years. While whole-brain network models of the past have helped to understand the collective dynamics of the brain's activity at the mesoscopic scale, their success to reproduce empirical data has been limited. Addition of more detailed biological information to tune the individual regional activity is going to become the major challenge in the next years, as a useful compromise between simplicity and biological details to help, e.g. understand the alteration of brain's collective dynamics due to drug intake for medical applications.

Output 2

The model-based framework developed to define dynamic communicability and flow is intended to provide a general and comprehensive characterisation of brain connectivity, which uses the network's recurrent activity to describe its properties. In this framework, the connection strength became a built-in aspect of the network analysis, thus overcoming the difficulties of the classical approach based on graph theory to deal with weighted networks. In order to facilitate the use of the framework by the community or for future integration in the HBP Platforms a Python Package has been released (https://github.com/mb-BCA/NetDynFlow), which also includes a tutorial.

Output 3

The developed model of retinal processing not only helps understanding the role of the retina as the starting point where visual information is processed (rather than simply acquire visual information), the model can be implemented into the Neurorobotics Platform. Along SGA2 we studied the possibility of including the model into CDP4, where models comprising different stages of the visual stream have been integrated to simulate the object recognition and saccadic eye movements of a virtual robot. The retinal model could serve as the first layer of the model, providing the necessary information for the module identifying the saliency maps. While finally this integration did not happen during SGA2 for time constrains, the plausibility of such integration was positively assessed and thus it could be done in the future. On the other hand, the model developed by the WEIZMANN partner will help to understand the role of top-down inputs to area V1. It will improve recognition of local image regions in artificial vision systems and is thus suitable for integration in the Neurorobotics Platform as a module of broader models for visual recognition.

5.2.2 Publications

Output 1: Models of spontaneous activity and sleep

Deco G, Cruzat J, Cabral J, et al. (2018) Whole-brain multimodal neuroimaging model using Serotonin receptor maps explains non-linear functional effects of LDS. Current Biology 28, 3065 - 3074. P1569

Chemla, S., Reynaud, A., diVolo, M., Zerlaut, Y., Perrinet, K., Destexhe, A. and Chavane, F. Suppressive traveling waves shape representations of illusory motion in primary visual cortex of awake primate. J. Neurosci. 39: 4282-4298, 2019. P1510

[5] Sorochynskyi O., Deny S., Marre O. & Ferrari U. (preprint) From serial to parallel: predicting synchronous firing of large neural populations from sequential recordings. bioRxiv:1101.560656.

Goldman, J.S., Tort-Colet, N., di Volo, M., Susin, E., Boute, J., Carlu, M., Nghiem, T-A., Gorski, T. and Destexhe, A. Bridging single neuron dynamics to global brain states. Frontiers in Systems Neuroscience 13: 75, 2019. P2222

Hahn, G., Skeide, M.A., Mantini, D., Ganzetti, M., Destexhe, A., Friederici, A.D. and Deco, G. A new computational approach to estimate whole-brain effective connectivity from functional and structural MRI, applied to language development. Scientific Reports 9: 8479, 2019. P2368

Nghiem, T-A., Tort-Colet, N., Gorski, T., Ferrari, U., Moghimyfiroozabad, S., Goldman, J.S., Telenczuk, B., Capone, C., Bal, T., di Volo, M. and Destexhe, A. Cholinergic switch between two different types of slow waves in cerebral cortex. Cerebral Cortex, in press, 2020. arXiv preprint: https://arxiv.org/abs/1810.00816 P1509

Peyrache, A. and Destexhe, A. Electrophysiological monitoring of inhibition in mammalian species, from rodents to humans. Neurobiology of Disease 130: 104500, 2019. Open-access preprint: https://hal.archives-ouvertes.fr/hal-02157942 P2042

Susin, E. and Destexhe, A. Cellular correlates of wakefulness and slow-wave sleep: evidence for a key role of inhibition. Current Opinion Physiol. 15: 68-73, 2020. HAL preprint: https://hal.archives-ouvertes.fr/hal-02424374 P2360

Output 2: Whole-brain model for propagation of spontaneous activity

N/A

Output 3: Models of bottom-up and top-down visual processing

Ullman S. (2019) Using neuroscience to develop artificial intelligence. Science, 363 (6428), 692-693. P2517 (*in validation process*)

Ben-Yosef G., Kreiman G., Ullman S. (2020) Minimal videos: Trade-off between spatial and temporal information in human and machine vision. Cognition (Accepted). P2518 (*in validation process*)

6. Conclusion and Outlook

The goal of Work-Package WP4.4 has been to generate a variety of models of brain function and activity which, although not necessarily interrelated with each other, serve diverse purposes within the broader scopes of the Human Brain Project. This is in line with the objectives of SP4 (Theoretical Neuroscience) to play a central role in the workflows of the HBP by deriving models based on experimental data produced in the HBP and which are implementable in the HBP Platforms, thus constituting the building blocks for more complex, integrated pipelines that will be finalised during SGA3.

During SGA2, partner KTH (T4.4.2; KR4.1) has developed a model of the basal ganglia to understand the mechanisms behind 'action selection' in motor control, using rate-based population descriptions for the ganglia. This model represents an attempt to simplify, by crossing scales, of a model of the same system produced during SGA1. Both models predicted that the inputs to striatum from the arkypallidal neurons in Globus Pallidus externa (GPe) could potentially play a role for motor control, e.g. in 'stop-signalling tasks'. However, an issue identified was that the timing when the arkypallidal neurons needed to be activated to interrupt the activity in the striatal projection neurons (SPN) was difficult to reconcile with experimental data from the different basal ganglia nuclei, and when measured in behaving rodents. Therefore, the hypothesis was positively tested that dendritic plateaus (i.e. NMDA spikes) in SPNs are involved when SPNs increase their firing rate during movement initiation. Integration of these models into broader pipelines on EBRAINS will be finalised during SGA3, as part of the workflows in WP3.

Partner UPF (T4.4.5; KR4.1) attempted, in collaboration with UM (SP2) the reproduction of a previous model of saccade generation during eye-movement (Gancarz & Grossberger, 1998). First, several inaccuracies were identified in the original model description (at the network and at the dynamical level) which were corrected. Second, a replica of the model was created replacing the local regional dynamics by a recently developed mean-field population model (Montbrió *et al*, Phys. Rev. X, 2015). Unfortunately, results would undershoot the expected saccadic trajectories and eye-movements

would not reach target. Reasons for this behaviour are either (i) the adequate working-point for the ROI dynamics was not correctly assessed or (ii) that the network parameters of the original model need to be returned. To solve this, a systematic parametric search was designed but could not be accomplished on time, manpower was allocated in other activities of CDP4 of higher priority. Thus, for now the original model by Gancarz & Rossberger was maintained in CDP4, with the improvements that were implemented by the team.

Models have been developed by partner UCL (T4.4.4; KR4.2) aiming to bridge scales between populations of rate coded neurons to the behaviour of the animal, within the context of spatial cognition and memory. The simulations of striatal versus hippocampal memory systems allowed to examine the behavioural effects of different learning rules and compare them to the (pre-existing) experimental data in the Morris Water Maze. The episodic memory model extension to aspects of human episodic memory, enabling simulation of recollection of the spatial scene in which an object was encountered, and comparison with (pre-existing) experimental data. It was also examined how self-motion and environmental information are integrated in forming these neural representations of location, and have contributed the design of experiments to investigate this (collaboration with SP3 Episense). This work also modelled experiments that were conducted by this collaboration. We learned important lessons regarding how the brain performs simultaneous localisation and mapping: separately representing adjustable 'transition' and 'observation' models in grid and place cells respectively.

These models are being shared with investigators in SP3 (PEARSON, PRESCOTT) to aid their implementations of memory on robotic platforms. This transfer, and other valuable discussions, were facilitated by a joint three-day workshop which we organised in March 2019. In addition to core HBP collaborators, there were some participants external to the HBP, who were experts in their field. The event was therefore a valuable exercise in distributing the results of the HBP collaborations. Spiking neuron models were used as dictated by the investigated question, e.g. when modelling phase coding, and they will pave the way for implementation on SpiNNaker. In general, these models are amenable to implementation in both physical and virtual robots on the Neurorobotics Platform.

During SGA2, the CNRS partner (T.4.4.1; KR4.3) has conceived several models of spontaneous activity in cerebral cortex, integrating unit recordings into models, up to brain scales. For modelling sleep, experimental data (partly collected by SP3) were used from different animals, comparing slow-wave sleep (SWS) and anaesthetised states. The transitions between the two types of slow-waves could be realised *in vitro*. HBP models were also used to investigate the genesis of propagating waves of activity in V1 of awake monkeys, and the role of these waves in vision. All these models will be employed in WP1 and WP3 of SGA3, to aid both whole-brain modelling and modelling consciousness, integrated in pipelines running on EBRAINS.

Partner UPF (Task T4.4.1; KR4.3) achieved the goal to provide a whole-brain model for the propagation of external stimuli in the brain at rest. The originally intended model simplified to employ linear, noisy local dynamics instead of a nonlinear population model. The advantage of this approach is that analytical estimations could be derived for the expected propagation of external stimuli along the network (the flow), such as to characterise the properties of weighted connectivity networks, which has remained a major challenge until now. On the other hand, the whole-brain network model accounting for regional Serotonin receptor densities is the first of its kind, advancing the modelling to come in the next years, e.g., to characterise the alteration of the brain's collective dynamics after drug intake for pharmacological exploration. These models, have been a major motivation for the design of WP1 in SGA3. In order to understand the technical challenges to integrate complete modelling pipelines on EBRAINS (e.g. accessing data stored in EBRAINS to constrain parameters, preparing and launching the simulations, and analysing the results online), a Collab was created in collaboration with SP2 (MANGIN) and SP5 (DICKSCHEID) within the framework of CDP3 (https://collab.humanbrainproject.eu/#/collab/34586/nav/239746). The difficulties identified served to define workflows in WP1 of SGA3.

Finally, partners UPMC and WEIZMANN successfully delivered the planned models along the visual stream. UPMC improved the model for the retina which helps understanding the retina as an active part of the visual processing rather than a passive layer transducing visual information into electrical codes. Along SGA2 inclusion of this model into CDP4 was studied, to simulate within the Neurorobotics Platform a robot with object recognition and saccadic eye movements capabilities.

Although this integration could not be implemented during SGA2 due to temporal constrains, the feasibility of including the retinal model into the Neurorobotics Platform was positively assessed. On the other hand, the model developed by the WEIZMANN partner will help to understand the role of top-down inputs to area V1. It will improve recognition of local image regions in artificial vision systems and is thus suitable for integration in the Neurorobotics Platform as well, as a module for broader workflows simulating visual recognition.