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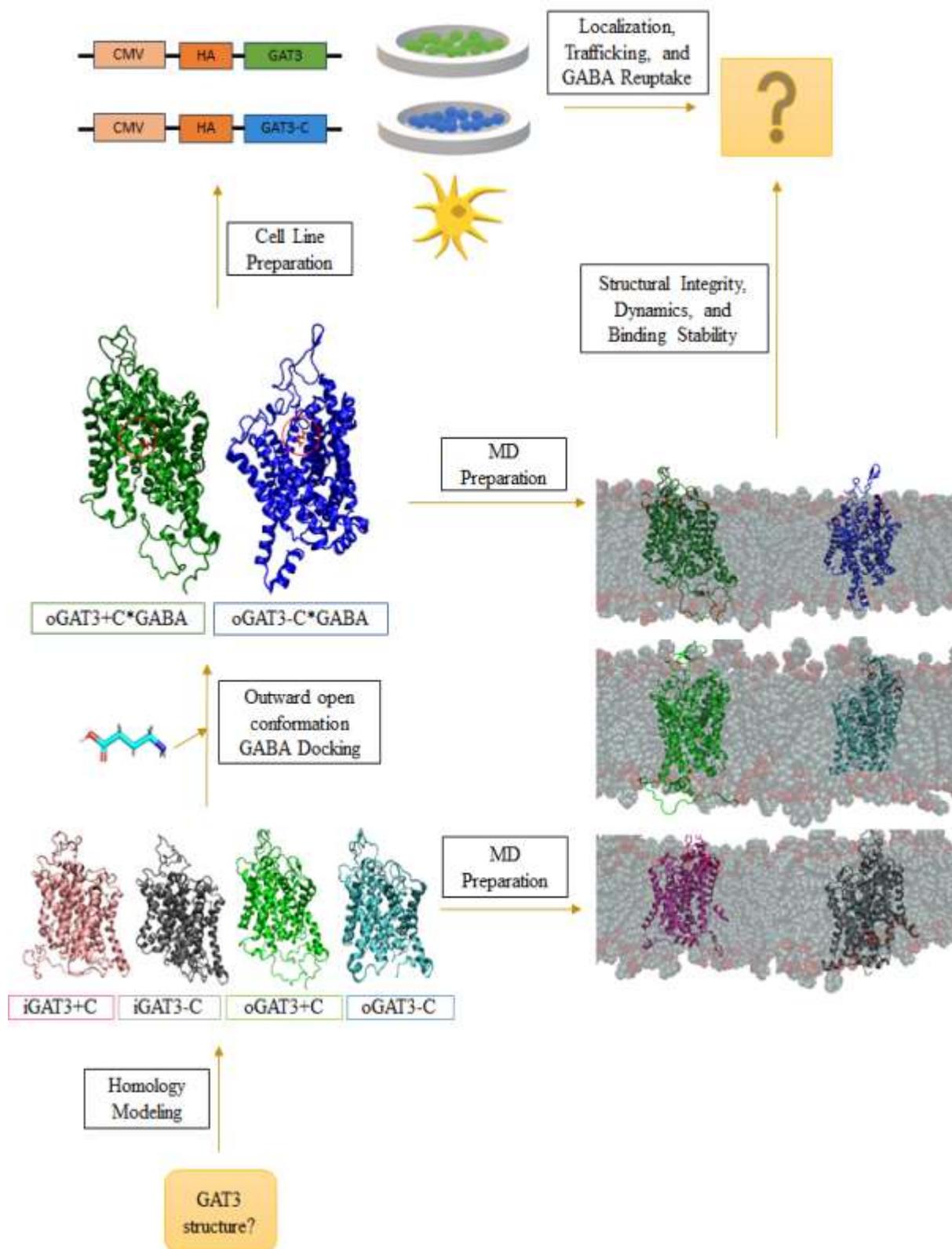Implementing arbitrary nonlinear low-dimensional dynamical systems in large neural networks

Structural and Functional Analysis of Astrocytic GABA Transporter GAT3 as a Therapeutic Target

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Abstract:

GABA transporter 3 (GAT3) is mainly located in the astrocytes in the brain, and it's responsible for regulating brain inhibitory neurotransmission through the reuptake of GABA molecules from the synapse. Alterations in GAT3 levels are related to multiple neurodegenerative and neurological diseases making it a promising therapeutic target. My research aims to analyze wild-type and C-terminal truncated GAT3 using computational and molecular biology tools to understand the effect of the C-terminal region on the protein's dynamic, localization, and trafficking. Due to the GAT3 structure being unknown homology modeling using Discover Studios 2016 was done to predict the outward (oGAT3) and inward (iGAT3) open confirmations for both the wild-type (GAT3+C) and the mutant (GAT3-C) structures. 100ns molecular dynamics (MD) was performed for an initial check of the structural stability, following that substrates docking was performed using AutoDock 1.5.7 to the outward open conformation resulting from MD for both targeted structures. The 100ns MD simulations show promising results of a possible impact of the C-terminal on GAT3 structural stability especially the inward open confirmation as the analysis suggests the C-terminal pushing a stronger closure of the extracellular gate and a bigger opening of the intracellular gate, but to fully understand the impact of the mutation a longer 1000ns simulation will be performed to the inward, outward, and docked outward conformations representing the wild-type and mutant GAT3. Cells will be transfected with pcDNA3.1(+) vector containing HA-tagged wild-type or mutant GAT3 and the localization and trafficking pattern of GAT3 will be analyzed.

CMV — HA — GAT3

CMV — HA — GAT3-C

Localization, Trafficking, and GABA Reuptake

?

Cell Line Preparation

Structural Integrity, Dynamics, and Binding Stability

oGAT3+C*GABA   oGAT3-C*GABA

MD Preparation

Outward open conformation GABA Docking

iGAT3+C   iGAT3-C   oGAT3+C   oGAT3-C

MD Preparation

Homology Modeling

GAT3 structure?

Entropic force or a homeostatic mechanism can maintain input-output relations of multilayer drifting assemblies

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Associative memories might be represented in the brain by groups of strongly interconnected neurons, called neuronal assemblies. Recent experimental findings suggest that such assemblies are not static but composed of different neurons at different times [1]. A theoretical model reproducing these findings is given by networks of drifting assemblies [2]: In a gradual process, assemblies exchange individual neurons between one another due to ever-present synaptic plasticity. So far, only single-layer networks of drifting assemblies have been considered. Biological neuronal assemblies are, however, thought to be distributed over several brain regions. How networks of drifting assemblies generalize to multiple layers is unknown.

Here we propose a model for multilayered networks of drifting assemblies. We introduce a novel form of homeostatic plasticity which we refer to as distributed homeostatic normalization. It promotes connections between neurons of different layers by separately normalizing intra- and interlayer weights. We show that distributed homeostatic normalization is capable of ensuring an even distribution of assemblies over two layers. In contrast to homeostatic plasticity mechanisms in previous models, distributed homeostatic normalization can act on biologically plausible timescales of a few hours [3] and still have the desired impact on the network structure. For large assemblies we find that a dedicated homeostatic mechanism is not necessary, as entropic force already leads to a sufficient distribution of the assemblies over multiple layers.

Our model demonstrates how continuous pathways from input neurons over multiple layers to output neurons can be established and maintained. The faithfulness of such input-output relations is essential for the conservation of memory and behavior. In having multiple layers, our networks resemble biological neural networks of the brain more closely than previous models did.

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Can simple models provide insights into how the cortico-cerebellar system represents and maintains time-varying activity?

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Neocortex and cerebellum, two major cortical structures in the brain, are interconnected via polysynaptic pathways forming the cortico-cerebellar system [1]. In motor regions this closed loop arrangement is thought to facilitate leaning and coordination of movements. Skilled motor tasks require the generation of precise sequences of motor command signals. To investigate how a recurrent neocortical circuit and a largely feedforward cerebellar circuit might contribute to learning precise temporal sequences we studied the properties of a simple recurrent neural network (RNN) and explored how coupling it to a feedforward perceptron influenced its performance in learning, representing and maintaining periodic signals of differing complexity. We first studied the properties of an RNN by adjusting the read-out weights of a single feedback loop to autonomously generate a cosine target signal with frequency w using least squares learning. The RNN's ability to maintain its output varied continuously with w and was optimal at frequency w_{opt}. In agreement with previous theoretical work [2], w_{opt} was predicted by the dimensionality of the RNN's population activity for a single frequency target signal. However, dimensionality was not a good predictor of learning performance for target signals with more than one frequency component. Rather we find that learning performance is related to the condition number (sensitivity of response to changes in the input) and the angles between the spanning vectors into which the RNN activity can be decomposed. These vectors represent the amplitudes and phases of the various frequency components present in the network. Surprisingly, when the RNN activity is perturbed by an additional external periodic signal of higher frequency (noise that could arise from harmonics generated by nonlinear neuronal thresholding), the output error is a discontinuous function of w, drastically increasing for frequencies much higher and lower than w_{opt}. Examination of the eigenvalues of the connectivity weights revealed outlier values with a real part >1, suggesting network instability underlies this failure to maintain the target signal. Interestingly, we find that learning performance can be qualitatively understood by the degree of alignment of the spanning vectors associated with the target signal and higher frequency noise in the RNN. Having gained some insight into the relationship between representations and learning in an RNN, we added a cerebellar granule cell layer-like feedforward perceptron to the RNN's feedback loop (P-RNN). Subjecting P-RNN to the same task as above, we find that, for a broad range of granule cell threshold values, it moderately outperforms the RNN. Our analysis reveals that this improvement arises from a trade-off of two opposing properties. The granule cell thresholds introduced additional frequency harmonics that generally deteriorate output stability of the system. However, this is counteracted by an increase in the spanning vector angles which improves learning

performance. Our results provide new insights into the relationship between the activity and learning in RNNs and suggest that the cerebellar granule cell layer could facilitate the maintenance of temporal signals by recasting neocortical representations into a form that separates signal from noise.

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Short and long thoughts: expressed by a cortex with regionally different time scales

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The Potts associative network, a neurally-informed generalisation of the Hopfield model [1], can serve as a simplified representation of global cortical dynamics. Considering memories to be sparsely distributed patterns of local cortical activity, we have studied latching dynamics – the largely random hopping through global attractor states driven by adaptation [2] – as a regime potentially underlying complex cognition such as language production and mind wandering [3]. In a recent study, we have differentiated a Potts associative network into two parts, representing frontal and posterior cortices, to crudely capture with distinct model parameters, including adaptation time scales, salient regional differences observed across mammals. We find that the frontal cortex leads latching in the posterior cortex, determining the sequence of memory states [4]. Here, we analyse the temporal structure of such dynamics.

In a homogeneous network, adaptation times set a unique timescale for latching. When they differ sufficiently between the two halves, instead, latching follows the slowly adapting frontal cortex. Interestingly, in the intermediate regime, when the characteristic adaptation times are closer to the ratio of 1:4, we find that latching duration varies within the same sequence, with short and long latches admixed (see Figure 1). When simple fronto-posterior pattern pairs are then replaced by more complex combinatorial memory structures, we observe that short posterior latches can be nested within long frontal ones, suggesting a mechanism for the spontaneous emergence of long short-term memory (LSTM) functionality at the cortical network level.
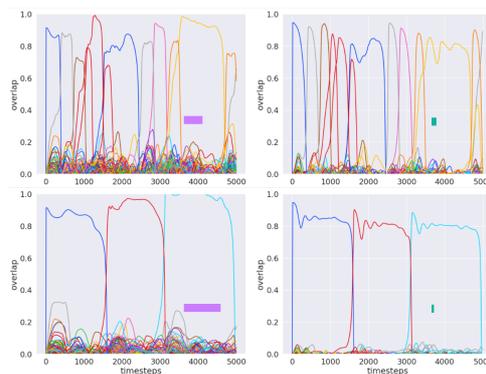

Figure 1: Hybrid Potts network with differentiated timescales

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Effects of Potassium and Calcium Currents in a Neuronal Network

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The human brain exhibits a wide range of different patterns, for instance synchronized oscillations during sleep and asynchronous behavior during the learning process [1]. However, neuronal synchronizaton may contribute to neurological disorders [2]. With regard to neuronal desynchronization,The flux through the neuronal membrane plays the crucial role in asynchronous activities [3]. In this work, we investigate how the flux of slow potassium and calcium ions can impact the dynamic behavior of one or more neurons. In our initial analysis, we find that, in a single neuron, slow potassium conductance can induce an adaptation in the firing rate. We verify that the high-threshold calcium and low-threshold calcium have no effect on the firing rate. Conversely, when examining the coefficient of variation, we observe that specific combinations of the slow potassium and calcium ion values can lead to a transition from asynchronous firing patterns to synchronous burst activities. Subsequently, we investigate the dynamical behavior of a neuronal network composed a thousand coupled neurons. Utilizing the Kuramoto order parameter, we explore how coupling intensity can directly influence the dynamic behavior of the neuronal network. We focus on the transition from asynchronous firing activities to synchronous bursts. Lastly, we delve into the role of slow potassium ions in the dynamical behavior transition of the neuronal network. We demonstrate that the presence of slow potassium conductance, by varying the value of coupling intensity, promotes a bistable regime in certain regions of the network, where asynchronous firing dynamics coexist with synchronous burst activities. Our results enhance the understanding of the intricate ionic interactions within a neuronal network and establish a direct connection with neurobiology, offering potential experimental interventions for empirical testing.

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A neural field approach for modeling flickering-induced visual illusions

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We present a framework for investigating the visual sensory processing underlying the perception of flickering-induced visual illusions in the primary visual cortex V1, focusing on flickering geometric stimuli used in psychophysical experiments such as MacKay [1] and Billock-Tsou [2]. We adapt the classical Wilson-Cowan/Amari-type neural field equation ([3, 4]) to model the evolution of the population of activated neurons in response to the flickering input. This differential equation is of the form:

$$\partial_t u = -u + \omega * f(u) + I, \tag{1}$$

where $*$ denotes the convolution in space, ω is a difference of Gaussians connectivity kernel , f a firing rate function, and I a time-periodic external input that captures the cortical response to the flickering visual stimulus. The linearity or non-linearity of (1) is determined by the firing rate function f, and the solution u corresponds to the perceived visual pattern in V1.

Firstly, we show that u exponentially decays to a time-periodic state as t goes to infinity. Secondly, under linear firing rate function, we characterize how flicker-periodicity can modulate neural activation and affect visual perception of resulting visual patterns such as the one obtained by MacKay's experiment. Finally, we perform numerical simulations to illustrate how the non-linearity of (1) intervenes in generating visual patterns consistent with experiments by Billock-Tsou. These results extend a previous study conducted in the static case [5] and offer insights into the mechanisms underlying visual illusions induced by flickering stimuli, highlighting the important role of non-linear dynamics in modeling visual perception.

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The power of memory: the decimation scheme for symmetric matrix factorization

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Factorizing a matrix with a rank comparable to its dimension into two matrix factors is a notoriously hard and unsolved problem in high-dimensional inference. Matrix factorization is encountered in several applications such as sparse coding, recommendation systems, image and video denoising and inpainting.

Given how much we rely on artificial intelligence algorithms, to which matrix factorization is crucial, it is of paramount importance to have a predictive theory for its accuracy. In the last decade this problem has eluded every attempt to compute its Bayes-optimal limits, i.e. the insurmountable bounds of performance provided by Information Theory.

In our work we propose an alternative procedure, that we called "decimation", that maps matrix factorization into a sequence of neural network models for associative memory, akin to the Hopfield model. Each of them depends on the ability to recall "memory patterns" of the preceding ones. Although sub-optimal in general, this novel scheme offers the advantage of completely analyzable performances. Finally, I will exhibit an "oracle" algorithm based on the ground-state search of a neural network, which shows performances that match the theoretical prediction,and beats other algorithms that were the state-of-the-art prior to our work.

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Amplification abounds, but not without a toll. The trade-off between stability and amplification in Dalean networks

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Cortical neurons exhibit rich, time-dependent patterns of activity that are often selective to specific stimuli [1,2]. From a dynamical systems perspective, such complex activity can be conceptualised as transient amplification [3,4]. It is, however, unclear if transient amplification is an artefact of a carefully tuned model, or a naturally occurring phenomenon. Moreover, minute changes in the connectivity of amplifying networks can cause catastrophic dynamic instabilities [5]. How biological circuits could settle into stable, yet amplifying connectivity manifolds in an ever-changing brain is unknown.

Here, we show that transient amplification is a ubiquitous network quality that can be achieved without fine-tuning. We use Schur decomposition to find--for each synapse--a set of constraints that allows us to sample Dalean and stable connectivity matrices (DS) in linear rate models. We find that within this space, the fraction of amplifying networks increases both with connectivity strength and network size, revealing a predominantly amplifying DS. We then demonstrate that there exists a trade-off between richness of dynamics and robustness to connectivity perturbations. For this, we consider a simpler system of one excitatory and one inhibitory unit. We find a set of constraints that each synapse must observe, and derive analytically the space of Dalean, stable, and amplifying matrices (DSA). We show that the most amplifying networks are the ones closest to the instability boundary. Interestingly, circuits can safely traverse DS (i.e. learn) without risking catastrophe by way of homeostatic constraints that prevents crossing the instability boundary. Our findings argue for the biological plausibility and ubiquity of transient amplification and show how stability and amplification constrain the nature of connectivity changes in neural systems.

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An efficient coding theory for cortical connectivity

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Cortical circuits transform sensory inputs into distributed neural firing patterns via the concerted interactions of excitatory and inhibitory cell types. However, the principles relating cortical connectivity to efficient sensory codes are poorly understood [1]. Two fundamental properties of cortical connectivity shape representations of sensory stimuli: 1) neurons with shared stimulus preferences connect more strongly and frequently than those with disparate preferences (stimulus-specific connectivity), and 2) excitatory and inhibitory synaptic inputs to each neuron are co-tuned and approximately equal (E-I balance). A substantial literature has investigated the functional properties of circuits endowed with these properties [2] and the learning rules that give rise to their formation [3], providing mechanistic explanations for various phenomena observed experimentally in visual cortex, such as contrast-invariant tuning curves and cross-orientation suppression. However, a normative, first principles explanation for cortical connectivity and the response properties it generates is currently lacking.

Here, we asked whether these properties could emerge from an efficient coding objective. We developed a method to adjust the recurrent weights of an E-I network to maximise the Fisher information of the response $\mathcal{I}_F(\theta_s)$ for a given ensemble of input stimuli $\{\theta_s\} \in \mathcal{S}$ (fig A). We found that networks optimised to encode stimulus orientation at varying contrasts exhibit stimulus-specific connectivity and co-tuned E/I synaptic currents (E-I balance) (fig B). Excitatory connectivity selectively amplifies input patterns, while recurrent inhibition maintains dynamical stability (inhibitory-stabilisation). Although the network was not directly incentivised to encode stimulus contrast, both E and I cells exhibited contrast-invariant tuning curves (fig C). Finally, although the network was optimised to encode a single stimulus orientation, the network exhibited cross-orientation suppression when two orientations were presented simultaneously. Taken together, we show that fundamental features of cortical circuit connectivity, dynamics and response properties can be accounted for by an efficient coding principle.
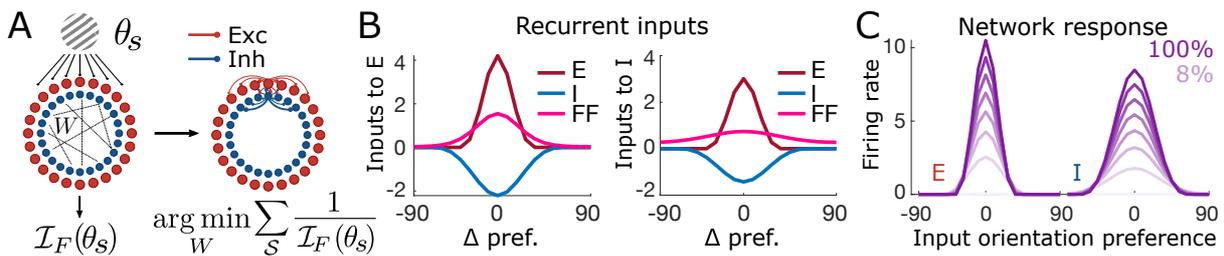
(A) We optimise the recurrent network connectivity W to maximise the total Fisher information of the excitatory network output $\mathcal{I}_F(\theta_s)$. (B) The optimised network is in a strongly recurrent regime, where the recurrent excitatory synaptic current (red) amplifies the feedforward input (pink) and is balanced by the inhibitory synaptic current (blue). (C) The emerging network exhibits contrast-invariant tuning curves.

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Neuromodulated recurrent neural networks

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Abstract: Neuromodulatory (NM) signals are powerful and prevalent influences on behavior, however, their specific role within neural circuits is poorly understood [1]. A common way to probe circuit dynamics is by analyzing task-optimized recurrent neural networks (RNNs), yet RNN models rarely incorporate NM effects. We propose the neuromodulated RNN (NM-RNN) (Fig. 1), which consists of two linked subnetworks corresponding to neuromodulation ($z(t)$, eqn. 1) and output generation ($x(t)$, eqn. 2). We model the output generation subnetwork as a low-rank RNN, and allow the output of the NM subnetwork ($s(z(t))$, eqn. 1) to scale the low-rank factors of the output generation weight matrix ($W_x(z(t))$, eqn. 2).

$$\tau_z \frac{dz(t)}{dt} = -z(t) + \mathbf{W}_z \phi\left(z(t)\right) + \mathbf{B}_z u(t), \quad s\left(z(t)\right) = \sigma\left(\mathbf{A}_z z(t) + b_z\right) \quad (1)$$

$$\tau_x \frac{dx(t)}{dt} = -x(t) + \mathbf{W}_x\left(z(t)\right)\phi\left(x(t)\right) + \mathbf{B}_x u(t), \quad \mathbf{W}_x\left(z(t)\right) = \sum_{i=1}^{K} s_i(t) m_i n_i^\top \quad (2)$$

One intuitive way to understand how neuromodulation impacts the output generation network is by considering the case where the output generation network is linear and symmetric with orthogonal m_i. In this case, we may reparameterize the system state in terms of $h(t) = \mathrm{M}^\top x(t)$, the component in the column space of $\{m_i\}$, and $h_\perp(t)$, the component lying outside of $\{m_i\}$. The dynamics of each component evolve according to the dynamics

$$\tau_x \frac{dh(t)}{dt} = -h(t) + \mathbf{S}(t)h(t), \qquad \tau_x \frac{dh_\perp(t)}{dt} = -h_\perp(t) \quad (3)$$

where $\mathbf{S}(t) = \mathrm{diag}\left(s(t)\right)$. In the absence of inputs, the solution to this system is

$$h_k(t) = h_k(0)\exp\left(-\int_0^t \frac{\left(1 - s_k(t')\right)}{\tau_x} dt'\right), \qquad h_{\perp_k}(t) = h_{\perp_k}(0)\exp\left(-\frac{t}{\tau_x}\right) \quad (4)$$

In words, $h(t)$ is controlled by the NM signal, while $h_\perp(t)$ decays according to τ_x. In our model we restrict $s(t)$ to lie within $[0, 1]$, so we see that when $s_k(t) > 0$, $h_{\perp_k}(t)$ decays more rapidly than $h_k(t)$. This means that in essence, the NM signal can control the time constants of the low-rank RNN.

We train NM-RNNs and low-rank RNNs on the measure-wait-go task, where the network must measure and reproduce interval times [2]. On both trained and unseen intervals, the NM-RNN has improved performance over the low-rank RNN. We found that the NM-RNN's NM signal has channels which are associated with distinct aspects of the task, and ablating these signals destroys performance. Our results show how the NM-RNN distributes task computation across low-rank factors. For future work, we plan to investigate how NM-RNNs may facilitate continual learning in the multi-task setup explored in Driscoll et al [3]. In general, the NM-RNN framework offers a novel method to investigate the effects of NM on neural dynamics.
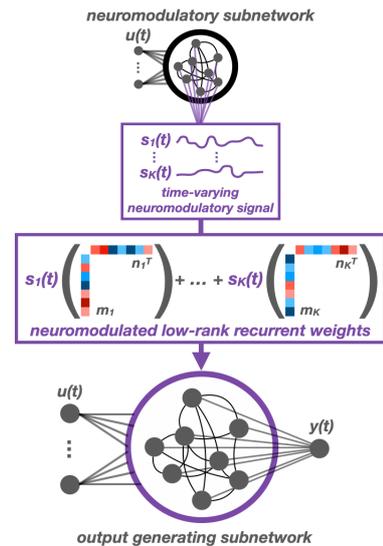

Fig 1. Model Overview

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Network Development in Silico: The Role of Inhibition in Activity-Dependent Neuronal Growth and Migration

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The timely maturation of inhibition in neuronal networks is considered crucial for stable activity dynamics that support normal brain function. Meanwhile, excitatory neuronal interactions are essential for network formation in early development. In the developing brain, there exists a gradual transition in GABAergic signaling: from depolarizing to hyperpolarizing, which impacts on the processs of network formation. Moreover, the level of inhibition depends on the fraction of inhibitory neurons as well as the mesoscale structural organization of the network that dictates its interconnectivity. Here, activity-dependent structural plasticity (ADSP) regulates neuronal connectivity and network activity in a homeostatic closed loop. However, the interplay between E-I interaction and ADSP in regulating the mesoscale structure, connectivity, and activity of developing networks remains poorly understood. To disentangle interactions among neuronal growth, migration, and inhibition, we utilized computational growth models that capture developmental aspects exhibited in cultured neuronal networks. Preliminary results suggest that asymmetric interactions between E/I neurons crucially impact on evolving network architectures. Increasing the fraction of INs prolonged neuronal growth and migration phase, which enhanced the size of neurite fields and clustering of neurons. Overall, this led to higher connectivity levels and lower network modularity in mature networks. Effectively, inhibition delayed down-regulation of neuronal growth and migration by prolonging the developmental time-course until network stability was attained. Our models can be used to explore various developmental scenarios and provide hypotheses that can be tested and constrained experimentally with in vitro networks from dissociated cortical cultures.
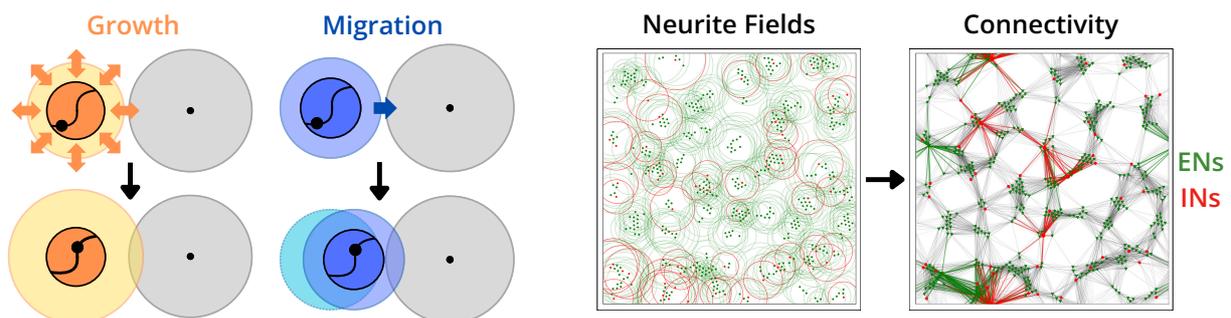
Figure 1: **Neuronal growth and migration.** To reach a homeostatic setpoint in activity, a neuron expands its neurite field or migrates towards other neurons to increase connectivity. Opposing influences from E-I interactions dictate the course of morphological, structural, and functional differentiation in the network. Neurite overlap defines connectivity among neurons.

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The insect compass system: from theory to circuitry

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Insects exhibit remarkable navigation abilities over long distances to find food or reach other places of interest before returning to their nests. This ability requires heading integration – maintaining an estimate of one's heading angle by integrating angular velocity signals over time. We seek to understand the neural and computational bases of insects' heading integration abilities by proposing a normative theory of heading integration based on simple requirements for biological plausibility and mathematical stability.

Previous work has shown that insects encode positions and directions as sinusoidal bumps of activity within a ring shaped population of neurons. It has been speculated that the sinusoidal activity profiles are useful because they allow the population of neurons to easily add vectors through phasor arithmetic [1], where the distance and direction of a vector are encoded as the amplitude and phase of a sinusoidal signal respectively.

Based on our theory, we prove that the phasor arithmetic explanation is only part of the story – there are a whole family of circuits with this property. We can characterise the possible heading integration circuits based on the Fourier spectra of their weights and activity profiles. From these, we show that the circuit with sinusoidal activity and weights has the maximal signal to noise ratio while requiring minimal neural activity. We then test this novel prediction of sinusoidal weights against experimental data. We use a network analysis approach, counting direct and indirect pathways between the neurons encoding heading, and find that the neural connectivity in both the locust [2] and fruit fly [3] closely match our sinusoidal prediction.

Additionally, we show that using Oja's rule (a variant of Hebbian learning) the circuit self-organises naturally to our predicted sinusoidal synaptic connectivity. This means the circuit could be developed naturally by this learning rule, and would be robust to synaptic perturbations. Furthermore, we postulate that a heading integration circuit with 8 neural columns, as is present in fruit flies, locusts, and other insect species [2], has the simplest possible genetic encoding of any functional circuit [4].

Our work establishes a principled mathematical theory for understanding neural circuits for heading integration in insects. We hope this novel insight can aid further investigations into how brains of different species perform robust navigation.

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Improving optimal control in systems with biologically realistic multiplicative and internal noise

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To act in the world, we integrate sensory information as we move our sensors and body through the external environment, creating perception-action loops. Movements alter sensory inputs, which are then compared with predictions and used in planning future movements to accomplish internal objectives. However, these mechanisms are challenged by different noise-sources, coming from the integration of sensory feedback and the motor output itself [1]. Furthermore, neural representations are subject to internal fluctuations, which affect estimation processes and, consequently, behaviour [1, 2]. Stochastic optimal control theory formalizes these concepts to explain behaviour through optimality principles at the algorithmic level [3]. In this context, having an optimal solution is crucial for assessing the rationality of the observed behavior. Our work is then particularly relevant in the context of inverse optimal control [5]. A control problem involves designing the optimal control law, or state-to-action policy, to minimize a cost-function of a system, determined by task goals and energetic costs [4]. Exact solutions to the control problem can only be derived under linear dynamics, additive Gaussian noise, and a quadratic cost function, exploiting the independence between estimation and control [4]. However, when considering a realistic noise-model of the sensory-motor system (including multiplicative noise at the feedback and motor output levels and internal noise in the estimation process), this independence breaks down, requiring additional assumptions and approximations to derive optimal control laws [4]. In this work, we introduce two algorithms that outperform, in terms of cost minimization, state-of-the-art solutions for stochastic control problems in the presence of internal noise. We provide both heuristic and mathematical explanations for this improved performance, offering a practical application for sensory-motor control. These developments will allow stochastic control theory to be applied a to broader range of problems in systems neuroscience.

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Synthesizing naturalistic visual textures with multiscale, nonlinear constraints using deep neural samplers

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The efficient coding principle states that a sensory system is tuned to the statistics of its natural input. In the same framework, the visual system is expected to be tuned to the statistics of natural visual scenes. Visual textures are "a family of visual patterns that share certain local regularities" [1] and they are useful in understanding how efficient coding applies not only to natural but also to artificial visual inputs. Three kinds of algorithms have been proposed for texture synthesis: parametric models computed on a set of statistical constraints [2]; methods in which local statistics are top-down, mathematically determined, but is limited to low order correlations that result in unnatural synthetic textures [3]; models representing textures as the correlations between the feature maps of a deep convolutional neural network resulting in nonlinear, multiscale and photorealistic representations [4].

We propose a novel approach for texture synthesis: a combination of a Variational Autoencoder (VAE [5]) for image generation and of a pre-trained convolutional neural network for defining the natural textures space (VGG-16 [6]). The goal is to characterize such space with nonlinear multi-scale representations, and to go beyond the limit of the low-order correlations developed by [3]. However, we want to use the same top-down approach from [3] to disentangle the information carried by the latent code of VAE.

VAE's Encoder reduces the input image to a vector, the latent code; the Decoder reconstructs the image from the latent code sampling from a Gaussian distribution. In this process VAE generates new images that show new, synthetic examples of the visual textures in the original images. The original and the generated texture images then are given to VGG-16 to represent the texture characteristics adapting the technique in [4]. More precisely, we compute the Gram Matrices of VGG-16's feature maps for each original-generated textures pair to discard spatial information. Consequently, we will manipulate the latent code of the VAE to affect some features of the generated textures. In particular we think that, for each dimension of the latent vector, there is a corresponding texture feature.

The model is trained with a combination of two losses: 1) one guides the learning of VAE minimizing the KL distance between the latent distribution and the Gaussian prior to sample for generating the output; 2) one defines the perceptual difference between original and generated texture by means of a weighted MSE between pairs of Gram Matrices. We are employing this technique on multiple datasets, including natural images taken from different environments exploiting their different visual characteristics.

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Pruning and generalization capacity of Restricted Boltzmann Machines for

… Junior Scientists Workshop on Recent Advances in Theoretical Neuroscience …

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A Restricted Boltzmann Machine (RBM) is a generative neural network consisting of one layer of visible neurons fully connected to a second layer of hidden neurons, with no connections within the same layer. They are commonly used for unsupervised learning, often serving as an initial or intermediate layer in deeper models. Our investigation focuses on RBMs to understand the impact of pruning on their generalization capacity—the ability of the model to generate realistic and diverse samples that capture the underlying patterns of the training data. Our study presents outcomes from extensive numerical simulations and preliminary analytical findings. The focus is on understanding how pruning influences the learning processes of RBMs and similar models, shedding light on optimizing their structure for improved efficiency maintaining robust generalization capabilities.

Shaping manifolds in equivariant recurrent neural networks

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Neural computations rely on the collective dynamics of populations of neurons, which exhibit rich structure in their coordinated activity [1]. An important source of structure are recurrent connections between neurons, which can generate continuous attractors, also known as activity manifolds, which have been used as models for the head direction system [2], grid cells [3] or orientation selectivity [4]. Although numerous particular cases have been studied, general principles linking network connectivity and the geometry of attractors remain to be uncovered. Here, we address this question by using group representation theory to formalize the general relationship between the symmetries in connectivity and in the resulting neural manifold.

We start by revisiting the classical ring model, a continuous attractor network generating a circular manifold [5,6], and extract the key underlying features: (i) the connectivity can be interpreted as a circular convolution [7];

(ii) this confers rotational symmetry to the set of attractors of the dynamics;

(iii) circular convolution can be expanded in Fourier basis, leading to a low-dimensional latent model [8];

(iv) the latent model retains the original rotational symmetry and determines the stability and dimensionality of the manifold.

Based on the principles of geometric deep learning, we generalize this framework to arbitrary symmetries, using the theory of group representations. Specifically, we introduce a new class of *low-rank equivariant recurrent neural networks*, where the connectivity is defined via a group convolution [9], which confers group symmetry to the attractors. Using the group Fourier transform, the network can then be reduced to a low-dimensional model, that preserves the original symmetries and determines the manifold's stability and dimensionality.

Our findings elucidate the relationship between the symmetry of the connectivity and the symmetry of the neural manifold, offering a new method to generate manifolds with a wide range of symmetries, such as tori and spheres.

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Rhythmically structured predictive coding enables invariant semantic recovery

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Our ability to perceive speech is resilient to variations in voice, rate, and temporal interruptions. While inference models addressed the first two [1], the computational principles by which speech understanding remains impervious to temporal restructuring are largely unexplored. Previous studies indicated intriguing recoveries in comprehension when speech interruptions were over 1 Hz [2] and temporally compressed speech was segmented with silences of specific durations [3, 4]. Here, we show that predictive coding, constrained by endogenous rhythms, accounts for these quizzical results and enables robust speech recovery.

We build upon the major hypotheses that the rhythmic structure of speech establishes temporal windows, allowing the brain circuits to effectively process auditory signals. Moreover, rhythmic activity is hierarchically structured in line with the structure of speech [5] and modulates predictive coding so that successful comprehension relies on actively minimizing contextual uncertainty and surprise [6]. These in turn modulate theta and delta rhythms, respectively [7]. Integrating this evidence, we propose a predictive coding framework (BRyBI), which implements a hierarchy of rhythms and actively minimizes both uncertainty and surprise. The theta rhythm in the BRyBI reduces uncertainty in the subsequent phoneme distribution. Theta rhythm entrainment by speech minimizes errors in the gamma code of phonemes. On the other hand, the delta rhythm enables temporally-structured semantic prediction error minimization, thereby implementing online word-context inference.

BRyBI allows for robust speech recognition under temporal perturbations such as compression, interruption, and segmentation. Furthermore, behaviors observed experimentally so far have escaped explanation, such as error-related potentials that emerge naturally in BRyBI; speech-rhythms coherence decreases for theta and grows for delta with increased uncertainty and surprise. In sum, we suggest that oscillation-constrained predictive coding generically explains the results of multiple experiments with temporal scale alterations and provides a new view of the speech recognition process in the brain.

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Perceptual decision making of nonequilibrium fluctuations

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A key function of the brain is to process noisy sensory data to make fast and accurate decisions in an ever-changing environment. However, how we adaptively process the exact stochastic fluctuations in stimuli remains largely unexplored. To bridge this gap, here we conducted behavioral experiments with human participants viewing movies of nonequilibrium Brownian dynamics simulations, characterized by a given drift velocity and diffusion coefficient. Participants judged the motion as leftward or rightward. The rate of stochastic entropy production that emerged from the stimulus trajectory enabled us to measure the noise in the system. Overall, the results uncovered fundamental performance limits, consistent with recently established thermodynamic trade-offs involving speed, accuracy, and dissipation. Specifically, decision times proved to be sensitive to entropy production rates. Moreover, for a given level of accuracy, we observed that participants behave suboptimally, i.e., they take more time on average to decide than that required for an optimal response as quantified by the sequential probability ratio test. In view of such suboptimality, we developed an alternative account based on evidence integration with a memory time constant. This revealed that humans tackle stimuli that are farther from equilibrium at a quicker rate at the expense of relying on larger memory about the stimuli's past outcomes. This adaptive integration time scale significantly improved trial-by-trial predictions on decision metrics. To conclude, this study demonstrates that perceptual psychophysics, using stimuli rooted in nonequilibrium physical processes, provides a robust platform for understanding how the brain makes decisions based on stochastic information.

Criticality in the Macaque Brain

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Experimental evidence has shown that a healthy brain might operate near Criticality [1]; an advantageous state in terms of information processing capacity as well as maximum dynamic range which is associated with interesting features such as, the well-known neuronal avalanches, long-range correlation, and scale-invariance in space and time domain. This evidence has been found in cell cultures, in vitro, and in anesthetized animals in vivo [2, 3]. However, some recent studies are challenging this hypothesis in behaving animals (awake cortex) [4]. The cortical activity shows a rich dynamical repertoire ranging from synchronous to the desynchronized states and this could be correlated with the degree of (or deviation from) criticality brain dynamics expresses.Following this hypothesis, the avalanche-like statistics of cortical activity can be used to characterize the state of the brain dynamics.

We look for hallmarks of criticality in several cortical regions of the macaque monkey during an Object-in-Place task [5], focusing on specific not-behaving epochs.

- White Screen Period: in which a white-screen is passively watched (for ~15 seconds)
- Resting State Epochs lasting for ~5-10 minutes

We use the local field-potential (LFP) recorded in premotor cortices and in the frontal pole to detect significant negative fluctuations [2]. We computed the critical exponents and the scaling relations between them [6, 8]. For being critical, the scaling relation between critical exponents is crucial so we use the deviation from this relation as a measure (Deviation from Criticality Coefficient, DCC). Furthermore, the Coefficient of Variation of the multi-unit activity signal is used to distinguish between different dynamical states. We contrasted these measures to check whether and at which level of the cortical activity the brain is approaching the critical point.

Preliminary results suggest that the activity during the resting state/white screen epoch is far from being critical, however the distance to the critical point is modulated through time in an area-specific manner. The goal is to investigate whether there is a correlation between the cortical state and deviation from criticality in different cortical regions.

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Learning with high dimensional chaotic systems

Chaotic dynamics can naturally arise in high-dimensional heterogeneous systems of interacting variables. The simplest examples are random recurrent neural networks. I will discuss how to study simplified models of this kind through dynamical mean field theory (DMFT) and show that the corresponding chaotic dynamics can be tuned and shaped by synaptic connections to perform a set of interesting tasks. I will show how DMFT can be used to explore and describe the space of synaptic connections leading to good performances of the corresponding trained dynamical systems. This is based on:

Fournier, Urbani, Statistical physics of learning in high-dimensional chaotic systems, JSTAT 2023
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The Role of Prefrontal Spatial Coding in Supporting Contextual Association

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Neurons in the medial prefrontal cortex (mPFC), a region critical for flexible behaviour and memory recall, have been shown to represent spatial information along with the hippocampus (HPC). However, the nature of spatial representations in the prefrontal cortex is disputed, with evidence for both specific and generalized representational forms. [1, 2, 3, 4] Previous work has found reactivation in the mPFC both during sleep and awake periods. During sleep, after the learning of a task, mPFC reactivation occurred simultaneously with hippocampal SWRs. [5] Furthermore, hippocampal and mPFC trajectory reactivation were also seen to occur independently during awake immobility, and the occurrence of mPFC trajectory reactivation positively correlated with rule-switching performance. [1]

Interactions between the HPC and mPFC are critical for learning, memory consolidation, and solving spatial tasks. Nonetheless, it is still unclear how behavioral demands drive the appearance of task-relevant spatial information in the mPFC, the nature of its generalization, and the role of spatial reactivations across areas over the course of learning.

We train rats to learn two cue-reward paired associations in parallel in a radial 8-arm maze and simultaneously record from the mPFC and HPC across multiple days of learning. Rats must flexibly adapt their behavior based on which cue is presented to find the context-specific reward. We observe individual differences in the strategies used by the rats to learn the task with a jump in performance after 6-7 days of training. Preliminary results suggest that spatial representations occur in the mPFC of naïve animals, which can generalize between the reward locations. This also suggests the presence of reactivation in the mPFC and ongoing analysis will permit the further understanding of its role in learning.

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Evolutionarily conserved fMRI network dynamics in the mouse, macaque, and human brain

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Abstract

Evolutionarily relevant networks have been previously described in several mammalian species using time-averaged analyses of fMRI time-series. However, fMRI network activity is highly dynamic and continually evolves over timescales of seconds. Whether the dynamic organization of resting-state fMRI network activity is conserved across mammalian species remains unclear. Using frame-wise clustering of fMRI time-series, we find that intrinsic fMRI network dynamics in awake macaques and humans is characterized by recurrent transitions between a set of 4 dominant, neuroanatomically homologous fMRI coactivation modes (C-modes), three of which are also plausibly represented in the rodent brain. Importantly, in all species C-modes exhibit species-invariant dynamic features, including preferred occurrence at specific phases of fMRI global signal fluctuations, and a state transition structure compatible with infraslow coupled oscillator dynamics. Moreover, dominant C-mode occurrence reconstitutes the static organization of the fMRI connectome in all species, and is predictive of ranking of corresponding fMRI connectivity gradients. These results reveal a set of species-invariant principles underlying the dynamic organization of fMRI networks in mammalian species, and offer novel opportunities to relate fMRI network findings across the phylogenetic tree.

Online cognitive maps through neuromodulated hebbian learning

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During navigation, animals dynamically create rich representations of the environment, forming personalized cognitive maps. The hippocampal area CA1 features spatial cells that adapt based on behavior and internal states. Computational models have usually obtained spatial tuning by training a deep recurrent network for solving path integration, over numerous epochs, using backpropagation [1, 2, 3]. However, such methods do not closely align with the real-time local learning used by animals. Additionally, the formed spatial maps are solely oriented towards solving a specific task, and fail to capture the full richness of non-spatial features that might be relevant for more complex behaviours. This study introduces a rate model that dynamically generates place cells as the agent navigates the environment. Online tuning is achieved through rapid Hebbian plasticity, lateral competition triggered by shortage of dopamine [4], and a supra-threshold theta oscillatory current that pushes cells to bind to new input patterns. This model successfully creates a representation of visited areas and consolidates recurrent connections among similarly tuned cells. Such connections are essential for active navigation; they make possible to generate plausible trajectories directly within the network manifold, and then select physical actions accordingly. Importantly, factors such as theta frequency and dopamine influence the density of the place cells, impacting the encoding of behaviorally relevant information [5, 6].

Finally, we conducted a quantitative analysis of the representation capacity and shape while a simulated agent navigated a closed room. We observed that the formed place representation has a Shannon information content comparable to that of a network with hard-coded place fields. Furthermore, it can capture the topological structure of the environment and, in normal conditions, the geometry of the neural manifold is approximately Euclidean. However, in the occurence of salient events, the place cells become more clustered, resulting in a locally curved space [7] as measured by the metric tensor.

This model provides a biologically plausible framework for the generation of cognitive maps refecting what is relevant for the agent. The current step is to apply it to a goal-directed reinforcement learning task, and evolve through genetic algorithms an optimal policy for manipulating the neural geometry.

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Functional ultrasound mapping of large-scale connectivity networks in the mouse brain

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These authors contributed equaly

Whole-brain imaging methods such as functional Magnetic Resonance Imaging (fMRI) are widely used to examine intrinsic and task-evoked patterns of coordinated brain activity in humans. However, the application of task-based fMRI in preclinical species is complicated by the need to constrain animals within the scanner small bore. Recently, functional ultrasound imaging (fUS) has emerged as a promising technology to fill this gap, enabling neuroimaging investigations of the entire brain in behaving animals. To explore the potential of fUS, and demonstrate its validity against well-established techniques, we investigated its capability to map previously described resting-state functional networks in lightly sedated mice. For this purpose, we carried out multislice fUS acquisitions in lightly sedated mice using various anaesthetic mixtures. A preprocessing pipeline, reflecting the primary steps employed in fMRI timeseries analysis, has been designed for robustness and portability. The results obtained have been compared with the underlying structural connectome. We found that large-scale functional brain networks can be reliably mapped at the group level with fUS. The networks mapped include also a default mode network, which we found to be anticorrelated with a latero-cortical system. While overall network topography appears to be consistent across different sedation protocols, we show that a novel combination of anesthetics provides optimal fUS network detection without the need to use complex animal preparation procedures. Our results show that fUS can be effectively used to detect distributed resting-state networks in anaesthetized rodents comparable to well-established imaging modalities, such as fMRI.

Competition between memories for reactivation as a mechanism for long-delay credit assignment

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Animals learn to associate an event with its outcome, as in conditioned taste aversion when they gain aversion to a conditioned stimulus (CS, recently experienced taste) if sickness is later induced [2]. If there is another intervening taste (interfering stimulus, IS), the IS gains some credit for the causality of the outcome, reducing aversion to the CS. The known short-term correlational plasticity mechanisms do not wholly explain how networks of neurons achieve long-delay credit assignment[3]. We hypothesize that reactivation of prior events at the time of outcome causes specific associative learning between those events and the outcome. We explore the credit assignment using a spiking neural network model storing memories–through time-decaying synaptic strengthenings–of two events that inherently compete to be the cause. As one cause becomes more likely, the other becomes less likely to be the cause of the outcome. We explore how the time delay between the two events–via differences in intra-cluster synaptic strengths– and other network properties influence the degree of competition between the two memories for reactivation. We show how a later memory can be reactivated more often and reduce the reactivation of a prior memory. By reactivating the memories in a probabilistic way, neural networks could perform Bayesian inference to assign the credit in a biologically plausible way. Our results could explain the findings in the gustatory cortex about long-delay learning in conditioned taste aversion and overshadowing by an interfering stimulus [1].
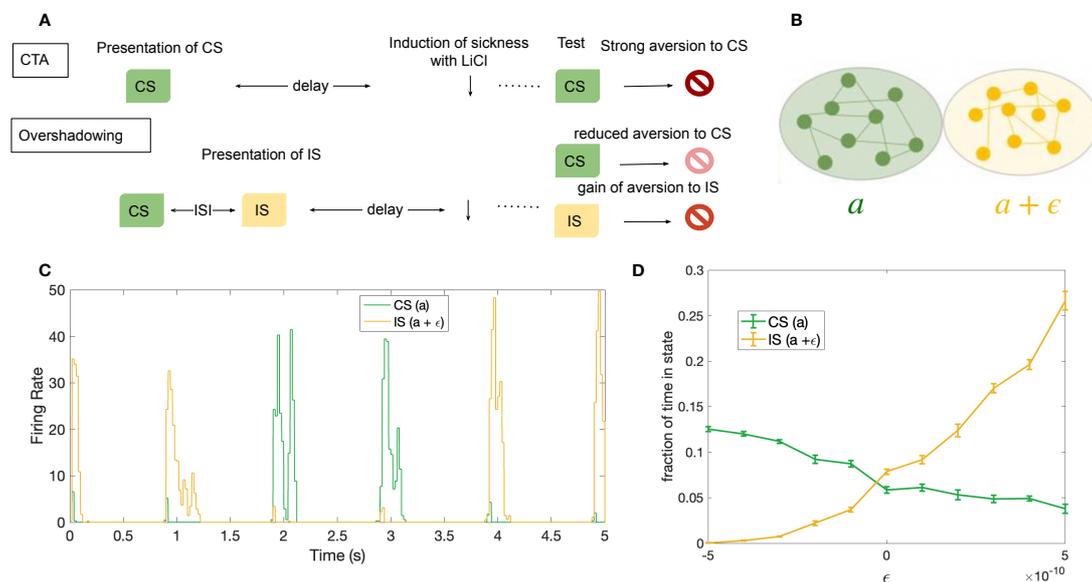

Figure 1: A. The sequence of events during CTA, and overshadowing. B. Connectivity of the network model. C. Reactivation of the CS and the IS ensembles. D. Fraction of time the network spends in the CS and the IS states as a function of the time difference between them via differences in intra-cluster synaptic strengths(ϵ).

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Eigenmode analysis of brain activity in a convoluted cortex via neural field theory

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Neural field theory (NFT) of the corticothalamic system has successfully explained a wide variety of phenomena, from EEG spectra and evoked potentials, to nonlinear phenomena such as seizures and Parkinsonian oscillations. Representing brain activity in terms of eigenmode expansion helps us understand brain dynamics in terms of its natural spatial modes (analogous to the natural modes of a vibrating string). NFT has also been used to understand brain connectivity, and its eigenmodes have been employed to solve the inverse problem of determining brain structure from functional connectivity. Most recently, the eigenmodes of a single brain hemisphere have been shown to be close analogs of spherical harmonics. They are also the building blocks for unihemsipheric modes, whose structure and symmetry properties explain many features of resting state and task-related activity.

Here, the evoked response potential (ERP) is modeled as an impulse response and is calculated numerically and analytically on both the convoluted and spherical cortex using NFT. The ERPs are expanded in terms of numerically calculated eigenmodes of a convoluted cortex and the results are compared to the spherical cortex. The effects of the complex folding in the convoluted cortex is explored and as well as how many modes contribute significantly to representing the ERP.

The main results are that numerically calculated eigenfunctions and corresponding eigenvalues are similar for multiple eigenmodes in the spherical cortex, but in the convoluted cortex, eigenvalues are individual for each eigenmodes due to the complex folding. We found that just a few handful modes are responsible for the basic features of ERPs in a convoluted cortex. The ERP peak decreases monotonically with increasing distance from the stimulus point. Due to complex folding in the convoluted cortex, ERPs are different between locations at the same distance from the stimulus point. ERP activity is strong near the stimulus locations, and spread through the whole cortex, decaying over time. At longer periods, the global mode is dominant. In conclusion of Robinson and Mukta [1,2] cortical folding has an effect on eigenmodes, which dominate the ERP activity with few modes. In future, this analysis of complex convoluted cortex will enable more realistic modeling and analysis of experimental brain signals.

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Although different architectures of quantum perceptrons have been recently put forward, the capabilities of such quantum devices versus their classical counterparts remain debated. Here, we consider random patterns and targets independently distributed with biased probabilities and investigate the storage capacity of a continuous quantum perceptron model that admits a classical limit, thus facilitating the comparison of performances. Such a more general context extends a previous study of the quantum storage capacity where using statistical mechanics techniques in the limit of a large number of inputs, it was proved that no quantum advantages are to be expected concerning the storage properties. This outcome is due to the fuzziness inevitably introduced by the intrinsic stochasticity of quantum devices. We strengthen such an indication by showing that the possibility of indefinitely enhancing the storage capacity for highly correlated patterns, as it occurs in a classical setting, is instead prevented at the quantum level.

Neural manifold discovery via dynamical systems

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Summary. Recent studies have proposed that neural circuits have a *task manifold*: i.e., a subset of the neural state-space to which neural activity is confined as an animal performs a task [1]. Thus, discovering and characterising these manifolds and their associated dynamics from experimental data can shed light on the neural computations unfolding within the brain during various cognitive tasks. Yet, common manifold discovery methods often do not take into account that neural data is generated by an underlying dynamical system. To address this, we first derive a general class of manifolds that neural dynamics can implement. Building on these results, we introduce a dynamical systems-based dimensionality reduction method for neural population data: *Manifold Discovery Through Dynamics* (MDTD). We illustrate its usefulness by applying it to recordings of the macaque motor and premotor cortex during a reach task [2], where we show that MDTD uncovers a manifold with behaviourally-relevant geometry. Overall, our framework offers a link between the geometric and dynamical perspectives on population activity, and provides a generative model to uncover task manifolds from neural data.

Background. Consider a collection of vector fields $X_i : \mathbb{R}^n \to \mathbb{R}^n$ for $i = 1, ..., m$ on the neural state space $\mathbb{R}^n$. Key results from differential geometry provide sufficient and necessary conditions under which these vector fields *define* an m-dimensional manifold with tangent space span $\{X_i\}$. MDTD allows *navigating* along the vector fields through the dynamics $\dot{\mathbf{y}}(t) = \sum_{i=1}^{m} c_i(t) X_i(\mathbf{y}(t))$, which generates trajectories on the manifold (Fig. **a**). We *fit* MDTD (i.e. find the optimal X_i's and c_i's) to neural data trajectories to uncover the latent manifold they lie on (Fig. **b**).

Results. We applied MDTD to recordings from the motor and premotor cortex [2] (Fig. **c**). We found that the neural trajectories intrinsic to the inferred manifold directly correlated to the movement of the animal (Fig. **d**). To validate that it was the dynamical aspect of MDTD that enabled this, we applied classic dimensionality reduction methods including PCA and Isomap and found that they captured the task condition but not the geometry of the behaviour. Overall, we illustrate how MDTD can uncover behaviourally relevant geometry and dynamics from neural data.
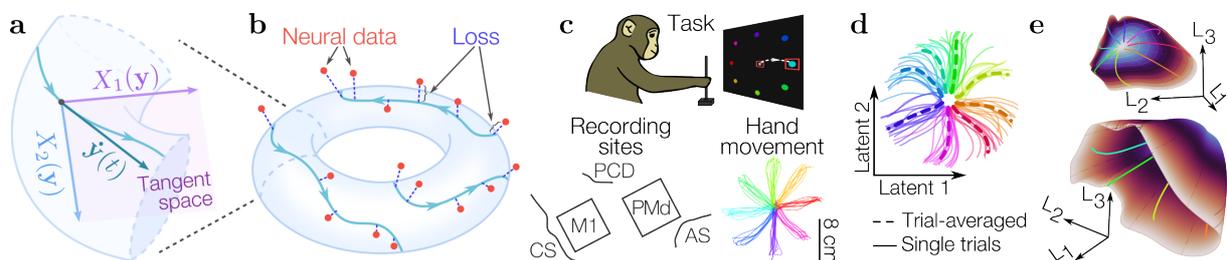
a. MDTD defines a manifold through dynamics on it. **b**. The manifold is inferred by fitting trajectories on it to data. **c**. Description of the neural data from [2]. **d**. Trajectories on the inferred manifold. MDTD recovers the geometry of the behaviour solely from the neural data. **e**. Two views of a low-dimensional embedding of the inferred manifold.

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Identifying learning algorithms using Brain Computer Interfaces

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By causally mapping neural activity to behavior [1], Brain Computer Interface (BCI) experiments offer an approach to studying the dynamics of sensorimotor learning and identifying the underlying learning algorithms [2]. Here, we used computational modeling and data analysis to study how monkeys performing a center-out task adapt to a changed output mapping. Learning this mapping from neural space (ca. 100D) to the 2D cursor position is a credit assignment problem [3] that is underconstrained, because changes along a large number of output-null directions do not influence the behavioral output. We hypothesized that different, but equally performing learning algorithms can be distinguished by the changes they generate in output-null dimensions. We study this idea in networks for three different learning rules (gradient descent, model-based feedback alignment and reinforcement learning) and three different network architectures that reflect distinct learning strategies (re-aiming [4], remodeling [5], recurrent dynamics). We find that various combinations of rules and architectures lead to changes in different low-dimensional subspaces of neural activity. Comparing these subspaces with available data from BCI experiments [6, 7, 8] suggests that monkeys learn in a subspace that is more similar to model-based learning and reinforcement learning than to gradient descent. For trained recurrent networks, the explored subspace also depends on the temporal structure of the input given to the network, highlighting the role of recurrent dynamics. Overall, our study suggests monkeys employ a combination of distinct strategies to learn BCI tasks.

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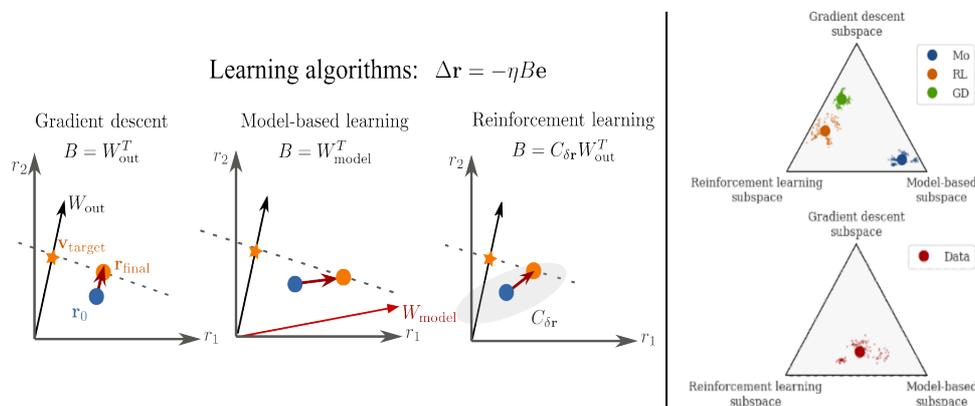[8] J. Hennig et al. eLife **7**, e36774 (2018).

Figure 1: (left) Potential learning algorithms underlying the BCI task, all changes depend on the cursor position error e and an algorithm-dependent term B; (right) low-D subspaces explored in simulations of the algorithms and BCI data [6, 7, 8]

How Noise Sources Shape Cortical Inter-areal Communication

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Hierarchical visual processing relies on the directional propagation of signals across brain areas to subserve computational goals. Recent work [1] leveraged simultaneous multi-area recordings to investigate the strength and directionality of inter-areal signaling, revealing that V1-V2 communication shifts from feedforward-dominated following stimulus onset to feedback-dominated during spontaneous activity. Importantly, this shift does not simply reflect a change in the directionality of the mean drive but rather results from trial-to-trial activity fluctuations predominantly traveling in different directions during evoked and spontaneous periods. What hierarchical circuit architectures support the observed directional flow of activity fluctuations? And what are the network mechanisms involved in the stimulus-dependent shift in the directionality of interactions?

Here, we investigated these questions by using two-area recurrent neural networks (RNNs). We first investigated the conditions that lead to a directional flow of activity fluctuations, as observed in neural data, in linearized circuit models. Through mathematical analysis and simulations [2,3] we concluded that, for arbitrary network connectivity, communication directionality is strongly determined by the difference in noise variance injected in the two areas. Based on this finding, we designed a model for noise sources in V1 and V2 that causes a shift in communication directionality, and is also consistent with biology. This includes a feedforward source associated with variability in the stimulus, and a persistent feedback source linked to slow global signals arising in higher-order areas [4,5]. To evaluate this mechanism in a larger and functional network, we focused on a predictive coding network [6], an established normative model of V1-V2 dynamics. We found that simulated activity could qualitatively recapitulate the main features of inter-areal communication observed in the data. Our approach allowed us to gain insight into possible network mechanisms underlying bi-directional and selective signaling as well as to constrain the space of models of inter-areal communication that are consistent with experimental observations.

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Priority Map Emerges in Performance-optimized Neural Network Models of Visual Search

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Visual search, the process of locating a specific item among a multitude of visually presented objects, is one of the most crucial behaviors in high-level animals and constitutes key experimental paradigms widely used in the studies of visual attention. Numerous computational models of this behavior have previously been developed, among which priority-map-based models are currently the most widely used [1-3]. A priority map is a conceptual representation of the priority assigned by the brain to different locations within the visual space, integrating both the bottom-up (saliency) and top-down (task-relevance) information across locations of the visual space, controlling the allocation of covert attention in covert search and guiding saccade sequence in overt search [4]. Priority-map-based models propose that the brain solves the visual search task by building a priority map of the visual space and applying a winner-take-all mechanism to select the target location. Lateral Interparietal Cortex (LIP), Frontal Eye Fields (FEF), and Superior Colliculus (SC), collectively known as the fronto-parietal attentional control network, have been identified as candidate areas for instantiating the priority map in the primate brain [4-8]. However, we still lack a complete understanding of how the distributed activity across these areas gives rise to the priority map representation and visual search behavior. To address this question, we modeled the neural computations underlying visual search by training a biologically-matched neural network architecture on this task. Our model consisted of three components: 1) a model of retina that matches the position-dependent sampling density in the primate retina; 2) a convolutional network model (CNN) mimicking the neural computations along the ventral visual pathway and; 3) a recurrent neural network (RNN) model of the fronto-parietal network. We found that after training: 1) RNN units exhibited cue-dependent response patterns similar to those observed in the primate fronto-parietal attention network during visual search; 2) Cue-similarity (a key indicator of priority) was linearly decodable from the RNN units, indicating that these units have developed a distributed representation of the priority map; 3) Decodability of cue-similarity exponentially decreased with increasing spatial distance, suggesting that the priority map is continuously represented within the RNN latent space. Altogether, we presented a neurally-plausible, image-computable model of visual search in which brain-like priority map representations emerged. The general-purpose architecture of the model makes it a viable candidate for being extended to modeling other visual attention tasks, providing means of simulating, and elucidating the underlying neural computations of visual attention.

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Computational model of Astrocyte-Neuron Networks

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Until recent times, glial cells, which constitute more than half of the mammal brain cells, have been neglected in the study of signal transmission and information processing in the nervous systems. This has been due to a long-lasting neuron-centric view of the brain functioning [1]. Nowadays, it is generally accepted that glial cells, particularly astrocytes, play diverse roles in brain function, including synaptic modulation, memory formation, and synchronization of neural population activities, in addition to providing structural support. This consolidated knowledge has induced theoretical neuroscientists to include astrocytes in their mathematical models of the brain [2, 3, 4].

The first part of this work focuses on optimizing and extending a recently published model [3], built with the neural simulator Brian 2 [5], one of the most flexible simulators for neuron-astrocyte networks. The model consists of a recurrent network of excitatory and inhibitory leaky-integrate-and-fire neural models endowed with astrocytes, activated by synaptic transmission and modulating it. We implement essential changes to the model, concerning neurons' spatial distribution in the network, neuron-neuron, and neuron-astrocyte connectivities. In particular, we introduce scale-free connectivity alongside commonly used random connectivity in the neuron network. Additionally, we explore astrocytic calcium dynamics, which plays a fundamental role in the mechanisms underpinning gliotransmitter release, and its effects on neuron activity. By tweaking some model parameters, we obtain both periodic behavior and larger and slower calcium oscillation that better reproduce what is experimentally observed [6]. Subsequently, we run simulations and analyses of the model in steady-state conditions, to outline the principal differences in the whole network spiking activity emerging when the astrocytes are included in the network or silenced, evaluating also the effects on activity for random/scale-free-like connectivities.

Finally, we compare the total average number of spikes emitted and the Inter-Spike Interval (ISI) distributions in the four cases under examination. Our analysis reveals that astrocytes reduce the number of spikes emitted by the network, indicating a global inhibitory effect on neurons. Furthermore, longer ISIs are more likely when astrocytes interact with neurons, consistent with the inhibitory action of astrocytes on neuron synapses. Interestingly, ISI distributions exhibit distinct trends depending on the type of connectivity, regardless of the presence of astrocytes. Specifically, probability density functions are approximately exponentially distributed for random networks, while they show power-law tails for scale-free-like networks.

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The Effects of Learning on the Hippocampal Representational Hierarchy

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Learning goal-oriented behaviours can induce changes in the hippocampal representation of space on a time scale of minutes. At longer time scales, it is less clear if changes in hippocampal representations are related to further learning, especially for non-spatial variables. Therefore, we monitored the evolution of these neural representations over multiple days to study their link to behaviour. We recorded the activity of the dorsal CA1 area of the hippocampus of rats using *in vivo* electrophysiology while animals learned a spatial association task. Animals had to remember the location of a reward given a set of contextual cues (visual and tactile) and then dig for food in those locations only. Their best performance was achieved after 3-5 days.

To assess the representation of different task variables such as position, reward, movement direction or context in the population activity, we used linear decoders and principal component analysis. We observed that, over days, the hippocampal code underwent a reorganisation of population activity in principal component (PC) space. Despite position explaining the highest variance of the pyramidal cell population at all times, we found that decoding of context from high-variance PCs improved with learning; this happened specifically at positions where it mattered for task performance and resulted in fewer dimensions being necessary for decoding. Also, the dimensions encoding context were different at different positions, which meant that context could be better decoded conditional on position. We confirm this hierarchy between position and context by hierarchical clustering of populations vectors, which shows that the main clusters of population activity are defined by animal position; within those clusters, sub-clusters referring to different contexts can be found and are better separated at task-relevant positions. When we contrasted these results with that of variables less relevant for task performance (e.g, movement direction), the encoding dimensions were also position-specific; nevertheless, we did not observe increased decoding accuracy at specific positions nor a reduction of dimensionality with learning.

Altogether, our results show that non-spatial variables unequally contribute to the variance in hippocampal activity. This supports the idea that these representations are hierarchical, as suggested in previous studies [1,2]. In addition, we show that the contribution of each variable depends on position and adapts to behavioural demands during associative learning. Downstream from the hippocampus, this enables better decoding of environmental features learned to be relevant for behaviour. This suggests that hippocampal representations may play a role supporting behaviour not only over minutes or hours, but also over many days of learning.

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Intra-ripple Frequency Accommodation in an Inhibitory Network Model for Hippocampal Ripple Oscillations

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Hippocampal ripple oscillations have been implicated in important cognitive functions such as memory consolidation and planning [1]. Multiple computational models have been proposed to explain the emergence of ripple oscillations, relying either on excitation or inhibition as the main pacemaker. Nevertheless, the generating mechanism of ripples remains unclear. An interesting dynamical feature of experimentally measured ripples, which may advance model selection, is intra-ripple frequency accommodation (IFA): a decay of the instantaneous ripple frequency over the course of a ripple event [2]. So far, only a feedback-based inhibition-first model [3], which relies on delayed inhibitory synaptic coupling, has been shown to reproduce IFA [4]. Here we use an analytical mean-field approach and numerical simulations of a leaky integrate-and-fire spiking network to explain the mechanism of IFA [5]. We develop a drift-based approximation for the oscillation dynamics of the population rate and the mean membrane potential of interneurons under strong excitatory drive and strong inhibitory coupling. For IFA, the speed at which the excitatory drive changes is critical. We demonstrate that IFA arises due to a speed-dependent hysteresis effect in the dynamics of the mean membrane potential, when the interneurons receive transient, sharp wave-associated excitation. We thus predict that the IFA asymmetry vanishes in the limit of slowly changing drive, but is otherwise a robust feature of the feedback-based inhibition-first ripple model. Finally, we demonstrate that other ripple models (e.g. [6]) make different, testable predictions regarding IFA, which makes IFA a good marker for model selection that can advance the search for the generation mechanism of hippocampal ripples.

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Learning Dynamics for Non-Linear Perceptrons

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The ability of a brain or a neural network to efficiently learn depends crucially on both the task structure and the learning rule. Previous works have analyzed the dynamical equations describing learning in the relatively simplified context of the perceptron under assumptions of a student-teacher framework or a linearized output [1, 2, 3, 4, 5]. However, in addition to being an impediment to biological interpretations, these assumptions have precluded a detailed understanding of the roles of the nonlinearity and input-data distribution in determining the learning dynamics. Here, we use a stochastic-process approach to derive flow equations describing learning, which we can do order-by-order in the learning rate. We than apply this framework to the case of a nonlinear finite-dimensional perceptron with a sigmoidal activation function, performing binary classification on inputs drawn from anisotropic Gaussian distributions.

We characterize the effects of the learning rule (supervised or reinforcement learning, SL/RL) and input-data distribution on the perceptron's learning curve, the fixed point to which learning converges, and the forgetting curve as subsequent tasks are learned. In particular, we quantify how the input-data noise differently affects the learning speed under SL vs. RL, as well as determines how quickly learning of a task is overwritten by subsequent learning. More generally, this approach points a way toward analyzing learning dynamics for more-complex circuit architectures.
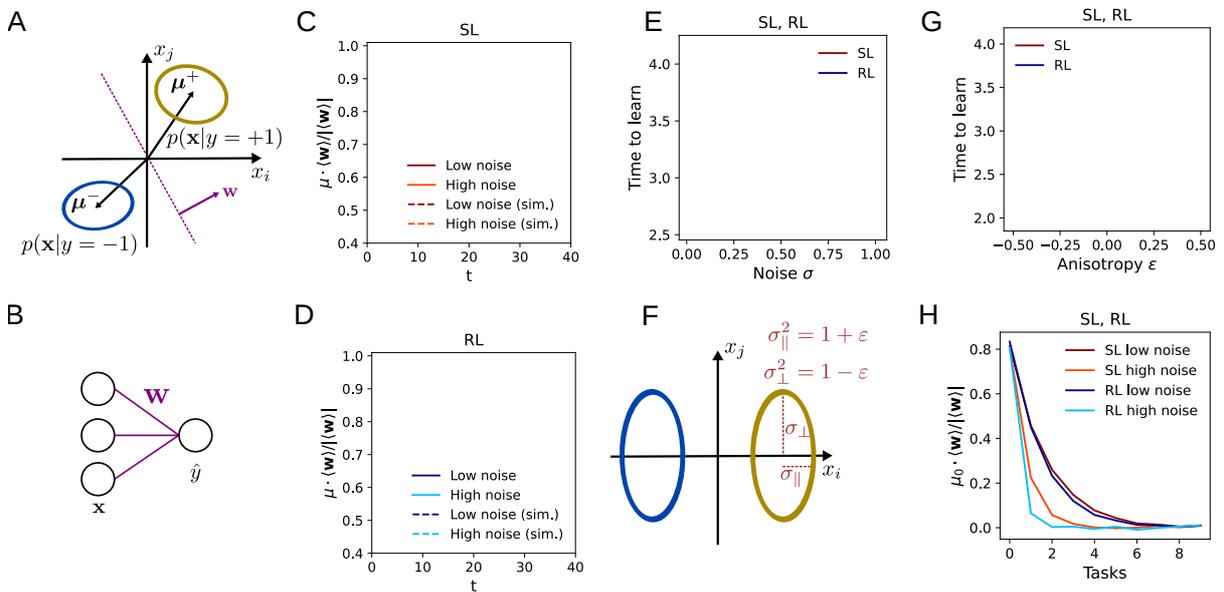
A, B: The perceptron classifies inputs from two multinormal distributions. The weight vector **w** is orthogonal to the classification boundary. **C, D**: The learning curves for the simulated perceptron follow the analytical results. **E**: Surprisingly,for isotropic inputs, time to learn the task increases with total noise for SL. **F, G**: For anisotropic inputs, the noise component in the decoding direction slows down learning. **H**: For continual learning, increased noise leads to faster forgetting.

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Characterization of the spatial properties of effective chromatic receptive fields based on chromatic induction

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Chromatic induction is the phenomenon by which the perceived color of a stimulus changes depending on the chromaticity of its surround. This change is repulsive, meaning it increases the contrast between the stimulus and its surround.

In this study, we developed a theoretical description of chromatic induction based on a linear formalism that includes a receptive field $\mathbf{G}(\mathbf{x}, \mathbf{x}')$, with a characteristic size σ associated with anatomical and physiological properties of the underlying neural networks. Therefore, a physical chromatic stimulus $\mathbf{r}(\mathbf{x})$ is processed by this receptive field, producing the percept $\mathbf{r}'(\mathbf{x})$, defined as

$$\tilde{\mathbf{r}}(\mathbf{x}) = \int d\mathbf{x}' \, \mathbf{G}(\mathbf{x}, \mathbf{x}')\mathbf{r}(\mathbf{x}'). \tag{1}$$

The percept $\mathbf{r}'$ and its associated physical stimulus $\mathbf{r}$ are described in their *perceptual coordinates*, elucidated in [1]. These coordinates allow us to exploit the symmetries of the color space to compute quantities of interest. The theory predicts that the ability to discriminate colors is optimal when the spatial frequency of the stimulus is $1/\sigma$.

We designed and conducted perceptual experiments that allowed us to access parameters of the receptive field by determining discrimination thresholds. Seven trichromatic volunteers participated in experiments where spatially structured chromatic stimuli were presented with modulation along three different directions in color space: $\mathbf{S}$, $\mathbf{L}$ - $\mathbf{M}$, and $\mathbf{L}$ + $\mathbf{M}$, the first two directions related to chromatic properties of the stimulus and the third related to its luminosity.

For each subject, and each direction in colour space, the spatial frequency yielding minimal detection threshold was determined. In line with the linear theory, we associated the inverse of the optimal frequency with the size σ of the receptive field. We found that the value of σ is smaller when the stimulus is modulated along the $\mathbf{L}$ + $\mathbf{M}$ direction compared to the other two directions, with a size of approximately $0.8°$ in the luminance direction and $2°$ in the chromatic directions for all volunteers.

In addition, the normalized detection threshold was smaller in the $\mathbf{L}$ + $\mathbf{M}$ direction. In conclusion, the luminance channel is more precise than the chromatic channels, both due to smaller thresholds and higher spatial resolution. The difference in optimal frequency between the luminance channel and the chromatic channels challenges the hypothesis of a linear model valid for the entire color space. The data indicate two parallel processing channels with different characteristic sizes. If we interpret receptive fields as an effective measure of lateral connections in the visual field, this work suggests that connections processing luminance information have a smaller lateral extent than those processing chromatic information.

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Theta phase precession and procession emerge depending upon upstream excitability in a CA1 place cell simulation study

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Hippocampal place cells offer a window into spatial navigation, building an internal, cognitive map of our external, physical environment. Place cells are excited in a spatially dependent manner, forming place fields that encode an animal's position in space. Firing within individual place fields is correlated with the extracellularly recorded theta rhythm, with place cell spike times progressively advancing to earlier and earlier phases of theta in a phenomenon known as theta phase precession (O'Keefe and Recce, 1993). The exact neurophysiological mechanisms that drive this phenomenon are still debated, and exploring these mechanisms relies heavily on computational models (Drieu and Zugaro, 2019; Sloin et al., 2024). Precession models most commonly draw on two seminal theories: (1) dual oscillator theory, wherein one theta pacemaker outpaces another to entrain spikes to a specific rhythm, or (2), asymmetric excitation theory, where directionally weighted networks propagate excitability across overlapping place fields. The latter requires a local assumption of dense recurrent connections, which is not applicable to all sub-regions of the hippocampus (e.g., CA1 contains sparsely interconnected neurons). The dual oscillatory theory is more robust with regards to observed experimental data but neglects upstream circuit-level interactions, which may be inherited and nonlinearly modulated within place fields. Recent modeling work has demonstrated that conductance changes in single place cells can influence extracellular theta via a resonant effect (Sinha and Narayanan, 2022). It has also been suggested that competition between firing rate adaptation in single cells and localized timing of external inputs can provoke either phase precession, or the lesser studied phase procession, where spike timing with respect to theta phase is reversed across theta cycles (Chu et al., 2024). Precession and procession are broadly theorized to represent retrospective and prospective encoding of an animal's location, and understanding the conditions under which one may dominate over the other can yield insights into how animals map virtual paths of the environment (Wang et al., 2020). To contribute to this effort, we present a conductance-based computational model of a place cell subjected to oscillatory inputs carrying spatial information and theta rhythmicity. External theta received at the cell dendrite is required in the model to promote phase precession, competing with somatic hyperpolarization to entrain somatic spike times. Progressively decreased theta input frequency resulted in a switch from precession to procession. Delayed onset of theta input induced longer periods of place cell excitability, increasing somatic firing early in the place field, which was exacerbated by delayed shunting inhibition. Finally, remodeling oscillatory inputs to the cell with a neural mass equation allowed for examination of the effects of upstream changes in excitability on firing rate and phase. Hyperexcitability of the upstream model resulted in phase procession, while hypoexcitability blocked both precession and procession.

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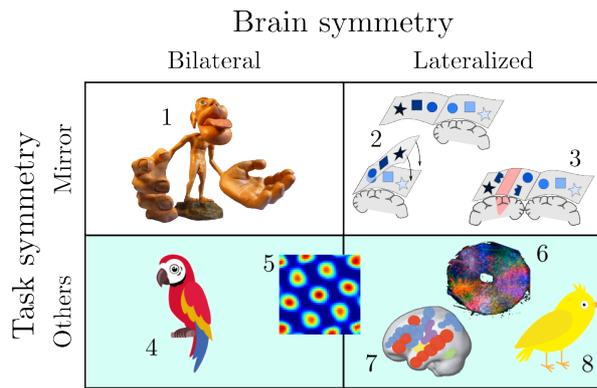
Figure 1: **Interplay between brain symmetry (or its breaking) and the symmetry (or lack thereof) of cognitive phenotypes.** Examples 1-4, 7, and 8 are mentioned in the text. 5 represents grid cells for navigation (symmetric in mice, lateralized in humans). 6 is the navigation system of the fly, which brings a toroidal geometry into play. Figure extracted from [1].

Symmetry and symmetry breaking in neural systems

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Most brains appear mirror symmetric but, upon close inspection, a series of asymmetries are revealed—notably so in the well-studied human brain. There are morphological differences (e.g. foldings or fissures more marked in one side) and lateralized function (e.g. human language is mostly left-hemispheric). Symmetry is a key concept that captivates mathematicians and physicists and invites the application of elegant theories to study associated phenomena. What is its role in neural systems? The brain's mirror symmetry comes from the bilaterian plan, thus is perfectly suited for body control (Fig. 1, top left). What happens when a task demands this symmetry but the brain loses it—as after hemispherectomy or stroke (Fig. 1, top right)? What becomes of bilaterality when a computational task does not need it (Fig. 1, bottom)? Is it retained, as parrots do to generate their speech (4 in Fig. 1)? Or does brain activity become lateralized, as it happens for human language (7) or in singing birds (8)?

My recent work aims at shedding some light upon these questions. In its most theoretical side, we tackled the long-standing hypothesis (traced back to Paul Broca) that increased cognitive complexity results in brain symmetry breaking. This popular conjecture lacks strong empirical support given the difficulty of measuring both complexity and asymmetry. Until recently, a rigorous mathematical framework to pose and resolve the issue was missing too. My recent paper [1] provides this framework, offers very strong mathematical support, and reveals regimes (depending on error rates, contributed fitness, and metabolic costs of neural circuits) in which either symmetry or lateralization become preferred as complexity increases. Another thread of my research has more clinical relevance, as it studies how brains are reorganized after hemispherectomy [2] or stroke [3]. These works suggest mathematical constraints to long-distance neural plasticity and illuminate seemingly contradictory findings about window periods to recover lost function after injury [2]. They also make connections between brain reorganization, phase transitions, and criticality; at the time exploring neurorehabilitation strategies quantitatively [3]. Understanding the interplay between internal and external symmetries and symmetry breaking offers great opportunity both for theoretical and empirical studies.

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Heterogeneity and response sharpening in balanced ring models

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Ring models are widely used in neuroscience to understand fundamental mechanisms of response sharpening and working memory. Ring models build of spiking neurons in the balanced state [1, 2], can robustly reproduce irregular activity, as observed in vivo, and exhibit various intriguing phenomena, such as response sharpening by short range inhibition [3] and feature tuning emerging in random networks [4]. In principle, balanced ring networks can be analyzed using a powerful mean-field theory that can capture even emergent response heterogeneity [5]. However, this approach - so far examined only for binary neuron networks [5] - appeared technically extremely involved. Here we present and analyze a class of analytically highly tractable spiking balanced ring models that enable to dissect circuit mechanisms of response tuning comprehensively and rigorously. We present results for ring models with both cosine-tuned and von mises-tuned connectivity and inputs. For the von mises case, the mean population activity profile is analytically obtained as infinite series of Bessel functions. In this case the activity profile is obtained directly from the balanced equation demonstrating that the profile is independent of the single neuron model and intrinsic heterogeneity. For the cosine-tuned network, a limiting case of von mises-tuning, the balance equation alone is insufficient to determine the population profile. Instead, the population profile is found to depend on a set of self-consistency equations for moments of the firing rate distribution across the network that we obtain in closed form. We present highly accurate approximate solutions to these self-consistency equations and show how they can be extended to determine the entire distribution of heterogeneous tuning curves in the network. Our results reveal strong indications that the population response profile is universal with respect to many biophysical parameters of synaptic interactions and detailed properties of the single neuron model used.

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Emergence of spiral waves in CA1 hippocampus network

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Traveling waves are remarkable spatial patterns which emerge in the cortex and hippocampus. These waves have been shown to contain precise information about an animal's spatial location [1]. Traveling waves play a crucial role in the human brain due to their ability to coordinate phase coding throughout the hippocampus [2] and are involved in synaptic plasticity. Rotating or spiral waves, characterized by the presence of a phase singularity (PS) at their center, are another pattern of brain waves. Spiral waves are important in cognitive processing and its properties are related to distinct cognitive tasks [3]. There have been several studies about the emergence of wave patterns, their relationship with network properties and how to detect them. Therefore, computational analysis are necessary to deepen our understanding of the spiral wave emergence. We investigate a novel method for detecting and studying the emergence of spiral waves as well as synchronization in a network that models the distribution of hippocampal pyramidal cells [4]. Inspired by the lack of simple methods for detecting spiral waves, we develop a novel and reliable method based on synchronization measurement tools to accurately identify and analyze spiral waves. Moreover, we propose a method for locate phase singularities (PS) in spiral waves. Our findings show that for different coupling strengths and connectivity radius, spiral and synchronization waves appear. In this work, we show that spiral waves are strongly dependent of the connectivity radius of each neuron due to the spatial properties which spiral waves possess. Notably, in some range of radius connection bistable regions are observed, highlighting the sensitivity of some wave patterns to initial conditions. Our results provide valuable insights into the mechanisms underlying spiral wave emergence.

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Abstract for Junior Scientists Workshop on Recent Advances in Theoretical Neuroscience

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For the olfactory associative learning to be specific, stimulus representation in the Kenyon cell (KC) population should be accurate with minimal activity overlap between different stimuli, which is achieved by the sparse and highly odor-specific KC response patterns. While a multitude of cellular and network mechanisms substantially increase the KC population sparsity, the proportion of KCs responding unreliably to a given odor over multiple trials is roughly three times larger than that of reliable responders [1, 3], leading to substantial response correlations between different odors. Considering dopamine signaling in the mushroom body lobes is unspecific with volume transmission, population sparseness alone is not sufficient to ensure specificity in associative learning. It has been recently shown, that additional axo-axonic interactions with muscarinic type-B receptors (mAChR-B) between KCs enhance the specificity in associative learning by suppressing both odor mediated Ca^{2+} signals and dopaminergic neuron driven cAMP signals [2], increasing learning specificity by inhibiting KCs responding unreliably to a given odor.

In this project, we theoretically investigate the functions and significance of lateral inhibition in learning specificity by comparing variants of KC population rate models with and without lateral inhibition. In line with the experimental observations, the naive model without lateral inhibition shows a lower degree of learning specificity when compared to the full model. Finally, we address possible mAChR-B related molecular mechanisms, such as activity-dependent gating of lateral inhibition, which leads to an overall enhancement in learning performance. Ultimately, we aim to propose an extended model for local mushroom body bouton computation, highlighting the importance of lateral interactions between KCs in learning and memory [4].

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Abstract template for Junior Scientists Workshop on Recent Advances in Theoretical Neuroscience

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In neuroscience, correlations between neurons have a significant impact on the encoding and decoding of information in neural population codes.

Correlations might play a role in generating codes across different timescales and in aiding the transmission and interpretation of information by downstream brain areas, thus influencing behavior. A unified conceptual picture of how local and biological plausible learning rules determine these so-called *noise correlations* is, however, currently missing.

Moreover, we still lack a theoretical framework to describe how population codes balance the constraints imposed by correlations. Noise correlations are known to be information limiting, but appear also to enhance signal propagation and thus have an effect beyond limiting the encoding of sensory information. Nonetheless, correlations may vary across the brain, ranging from weak correlations in sensory cortices, possibly beneficial to maximize information encoding with short timescales for dynamic stimuli, to stronger correlations in associative areas, optimal for stronger signal propagation and longer timescales[4].

Here we propose to study population codes by studying the learning dynamics of recurrent neural networks with ongoing Hebbian plasticity. A previous study of a network model in which neurons and synapses are mutually coupled dynamic variables analyzed the dynamical regimes that emerge from spontaneous activity [5] . We study the ability of this coupled dynamical system to learn, from the statistics of inputs, how to shape particular low-connectivity structures, which are known to be essential for implementing computations [3, 6]. Additionally, introducing Hebbian plasticity while presenting the network with a fixed stimulus has shown to introduce a variability in the neural responses, even if the network is in a non-chaotic regime. Thus, this plasticity-induced variability allows us to investigate correlations across-trials, which is a first step to develop a theoretical model of noise-correlations emerging from recurrent connections and to study their role in the encoding of information by downstream brain areas. Finally, we investigate if the representations learnt from local learning rules have a distributional simplicity bias, as observed in neural networks trained using stochastic gradient descent [7], and whether this bias can be relevant to build different time scales across the network.

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Implementing arbitrary nonlinear low-dimensional dynamical systems in large neural networks

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An increasing amount of findings highlight the significance of low-dimensional neural dynamics in the motor system, sensory pathways, and cognitive task representations. Recent studies have linked structure to low-dimensional activities by considering low-rank corrections to random synaptic efficacy matrices. However, these studies focused on Gaussian statistics, restricting the networks' dynamic repertoire. To understand how neural circuits implement diverse computations, we need a theory that deals with complex structures and accounts for arbitrary nonlinear low-dimensional dynamics.

In this work, we go beyond the current paradigm and consider low-rank matrices with higher-order statistics. For tractability, we use synaptic weights sampled from discrete statistics. We derive a dynamic mean-field theory for the low-dimensional activity generated by the low-rank weights. First, we show that i.i.d. weights with second-order statistics can produce only linear effective dynamics. Next, we show that appropriately choosing higher-order correlations can yield non-trivial collective dynamics. As an example, we generate a low-dimensional chaotic attractor. The low-dimensional chaos is different from chaos generated by large random networks and is characterized by higher correlations. Finally, we prove a universality theorem stating that a large low-rank nonlinear network can implement any smooth dynamical system. Importantly, we calculate the error bound for approximating arbitrary dynamical nonlinear dynamical systems and show it falls exponentially as the rank increases. Our work provides an essential missing link between structure and neural dynamics; it provides a prescription for constructing neural networks that implement non-linear dynamical systems using low-rank structures and a framework for analyzing trained networks.