
THE ATTRACTOR STATES OF THE FUNCTIONAL BRAIN CONNECTOME

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Abstract

Abstract:
todo

Keywords

Key Points:

- We propose a high-level computational model of "activity flow" across brain regions
- The model considers the functional brain connectome as an already-trained Hopfield neural network
- It defines an energy level for any arbitrary brain activation patterns
- and a trajectory towards one of the finite number of stable patterns (attractor states) that minimize this energy
- The model reproduces and explains the dynamic repertoire of the brain's spontaneous activity at rest
- It conceptualizes both task-induced and pathological changes in brain activity as a shift on the "attractor landscape"
- We validate our findings on healthy and clinical samples (~2000 participants)

1 Introduction

Brain function is characterized by the continuous activation and deactivation of anatomically distributed neuronal populations. While the focus of related research is often on the direct mapping between changes in the activity of a single brain area and a specific task or condition, in reality, regional activation never seems to occur in isolation (Bassett and Sporns [2017]). Regardless of the presence or absence of explicit stimuli, brain regions seem to work in concert, resulting in a rich and complex spatiotemporal fluctuation (Gutierrez-Barragan et al. [2019]). This fluctuation is neither random, nor stationary over time Liu and Duyn [2013]; Zalesky et al. [2014]. It shows quasi-periodic properties (Thompson et al. [2014]), with a limited number of recurring patterns known as "brain states" (Vidaurre et al. [2017]; Liu and Duyn [2013]; Richiardi et al. [2011]).

Whole-brain dynamics have previously been characterized with various descriptive techniques (Smith et al. [2012]; Vidaurre et al. [2017]; Liu and Duyn [2013]), providing accumulating evidence not only for the existence, but also for the high neurobiological and clinical significance, of such dynamics (Hutchison et al. [2013]; Barttfeld et al. [2015]; van der Meer et al. [2020]). However, due to the nature of such studies, the underlying driving forces remain elusive.

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Questions regarding the mechanisms that cause these remarkable dynamics can be addressed through computational models, which have the potential to shift our understanding from mere associations to causal explanations. Conventional computational approaches try to solve the puzzle by delving all the way down to the biophysical properties of single neurons and then aim to construct a model of larger neural populations, or even the entire brain ([Breakspear \[2017\]](#)). While such approaches have demonstrated numerous successful applications ([Kriegeskorte and Douglas \[2018\]](#); [Heinz et al. \[2018\]](#)), the estimation of all the free parameters in such models presents a grand challenge. This limitation hampers the ability of these techniques to effectively bridge the gap between explanations at the level of single neurons and the complexity of behavior ([Breakspear \[2017\]](#)).

An alternative approach, known as "neuroconnectivism" ([Doerig et al. \[2023\]](#)) shifts the emphasis from "biophysical fidelity" of models to "cognitive/behavioral fidelity" ([Kriegeskorte and Douglas \[2018\]](#)), by using artificial neural networks (ANNs) that were trained to perform various tasks, as brain models. While this novel approach has already significantly contributed to expanding our understanding of the general computational principles of the brain (see [Doerig et al. \[2023\]](#)), the requirement of training ANNs for specific tasks poses inherent limitations in their capacity to explain the spontaneous macro-scale dynamics of neural activity ([Richards et al. \[2019\]](#)).

In this work, we adopt a middle ground between traditional computational modeling and neuroconnectionism to investigate the phenomenon of brain dynamics. On one hand, similar to neuroconnectionism, our objective is not to achieve a comprehensive bottom-up understanding of neural mechanisms. Instead, we utilize an artificial neural network (ANN) as a high-level computational model of the brain (Figure 1A). On the other hand, we do not train our ANN for a specific task. Instead, we empirically set its weights based on data about the "activity flow" ([Cole et al. \[2016\]](#); [Ito et al. \[2017\]](#)) across regions within the functional brain connectome, as measured with functional magnetic resonance imaging (fMRI, Figure 1B). We employ a neurobiologically motivated ANN architecture, a continuous-space Hopfield network ([Hopfield \[1982\]](#); [Krotov \[2023\]](#)).

Within this architecture, the topology of the functional connectome naturally defines an energy level for any arbitrary activation patterns and a trajectory towards one of the finite number of stable patterns that minimize this energy, the so-called attractor states. Our model also offers a natural explanation for brain state dynamics. In the presence of weak noise, the system does not converge into an equilibrium state but undergoes "bifurcation", enabling it to traverse extensive regions of the state space, moving on a path restricted by the "gravitational pull" of different attractor states (Figure 1C).

In this simplistic yet powerful framework, both spontaneous and task-induced brain dynamics can be conceptualized as a high-dimensional path that meanders on the reconstructed energy landscape in a way that is restricted by the "gravitational pull" of the attractors states. The framework provides a generative model for both resting state and task-related brain dynamics, offering novel perspectives on the mechanistic origins of resting state brain states and task-based activation maps.

In the present work, we first explore the attractor states of the functional brain connectome and construct a low-dimensional representation of the energy landscape. Subsequently, we rigorously test the proposed model through a series of experiments conducted on data obtained from 7 studies encompassing a total of $n \approx 2000$ individuals.

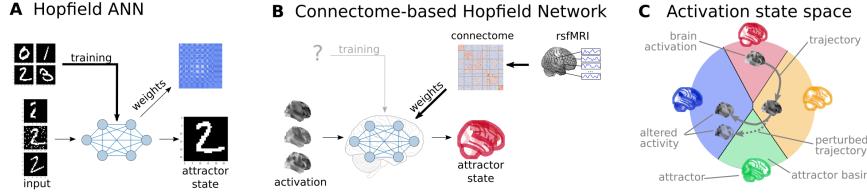
These analyses include evaluation of robustness and replicability, testing the model's ability to reconstruct various characteristics of resting state brain dynamics as well as its capacity to detect and explain changes induced by tasks or pathological conditions.

These experiments provide converging evidence for the validity of connectome-based Hopfield networks as models of brain dynamics and highlight their potential to provide a fresh perspective on a wide range of research questions in basic and translational neuroscience.

2 Results

2.1 Connectome-based Hopfield network as a model of brain dynamics

First, we explored the attractor states of the functional brain connectome in a sample of $n=41$ healthy young participants (study 1). We estimated interregional activity flow ([Cole et al. \[2016\]](#); [Ito et al. \[2017\]](#)) as the study-level average of regularized partial correlations among the resting state fMRI timeseries of $m = 122$ functionally defined brain regions (BASC brain atlas, see Methods for details). We then used the standardized functional connectome as the w_{ij} weights of a continuous-state Hopfield network ([Hopfield \[1982\]](#), [Koiran](#)



A) Hopfield artificial neural networks (ANNs) are a form of recurrent ANNs that serve as content-addressable ("associative") memory systems. Hopfield networks can be trained to store a finite number of patterns (e.g. via Hebbian learning). During the training procedure, the weights of the Hopfield ANN are trained so that the stored patterns become stable attractor states of the network. Thus, when the trained network is presented partial or noisy variations of the stored patterns, it can effectively reconstruct the original pattern via an iterative relaxation procedure that converges to the attractor states. **B)** Instead of training the Hopfield network to specific tasks, we use the topology of the functional brain connectome to define the weights of the Hopfield network. Following from the strong analogies between the relaxation rule of Hopfield networks and the activity flow principle that links activity to connectivity in brain networks, we propose the constructed connectome-based Hopfield network as a computational model for macro-scale brain dynamics. **C)** The proposed computational framework assigns an energy level, an attractor state and a position in a low-dimensional embedding to brain activation patterns. Additionally, it models how the whole state-space of viable activation patterns is restricted by the dynamics of the system how alterations in activity and/or connectivity modify these dynamics.

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Figure 1: **Connectome-based Hopfield networks as models of macroscale brain dynamics.**

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[1994]) consisting of m neural units, each having an activity $a_i \in [-1, 1]$. Hopfield networks can be initialized by an arbitrary activation pattern (m activations) and iteratively updated, until convergence ("relaxation"), according to the following equation:

$$\dot{a}_i = S(\beta \sum_{j=1}^m w_{ij} a_j - b_i) \quad (1)$$

where \dot{a}_i is the activity of neural unit i in the next iteration and $S(a_j)$ is the sigmoidal activation function $S(a) = \tanh(a)$ and b_i is the bias of unit i and β is the so-called temperature parameter. For the sake of simplicity, we set $b_i = 0$ in all our experiments. Importantly, in our implementation, the relaxation of the Hopfield network can be conceptualized as the repeated application of the activity flow principle, simultaneously for all regions: $\dot{a}_i = \sum_{j=1}^m w_{ij} a_j$. The update rule also exhibits strong analogies with the inner workings of neural mass models (Breakspear [2017]) as applied e.g. in dynamic causal modelling (see Discussion for more details).

Hopfield networks assign an energy to every possible activity configurations (see Methods), which decreases during the relaxation procedure until reaching an equilibrium state with minimal energy (Figure 2A, top panel, Hopfield [1982]; Koiran [1994]). We used a large number of random initializations to obtain all possible attractor states of the connectome-based Hopfield network in study 1 (Figure 2A, bottom panel).

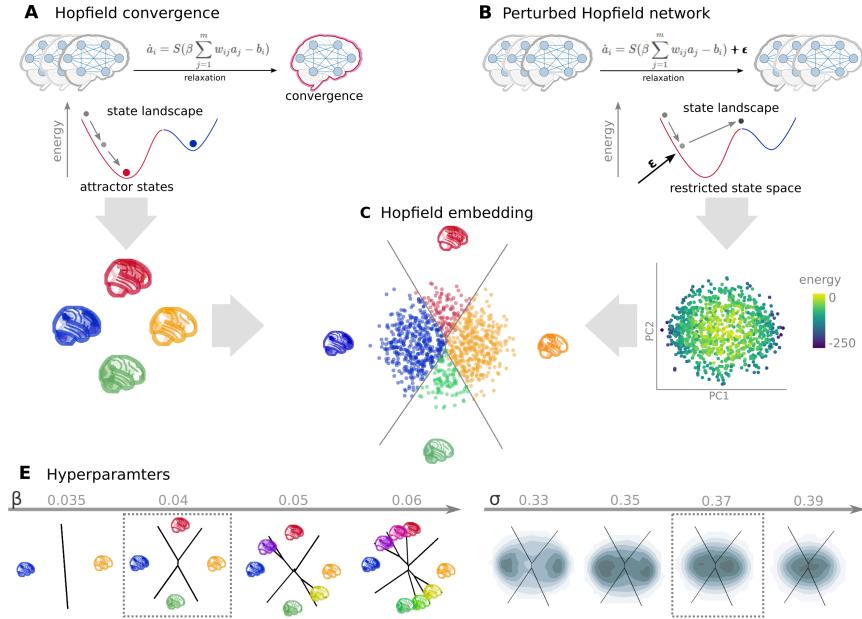


Figure 2: Empirical Hopfield-networks.

We observed that, in line with theory, increasing the temperature parameter β results in an increasing number of attractor states ((Figure 2E, left) appearing in symmetric pairs (i.e. $a_i = -a_j$). For the sake of simplicity, we set $\beta = 0.4$ for the rest of the paper, resulting in 4 distinct attractor states (2 symmetric pairs).

Without modifications, connectome-based Hopfield networks always converge to an equilibrium state. To account for stochastic fluctuations in neuronal activity (Robinson et al. [2005]), we add weak Gaussian noise to the connectome-based Hopfield network, to prevent the system reaching equilibrium. This approach, similarly to Stochastic DCM (Daunizeau et al. [2012])), induces a "stochastic walk" of the internal state (activity pattern) of the network that may traverse extensive regions of the state space, determined by the "gravity field" (basins) of multiple attractor states (Figure 2B).

We hypothesise that the resulting dynamics reflect many important characteristics of spontaneous activity fluctuations in the brain and may serve as a useful generative computational model of large scale brain dynamics. To sample the resulting state space, we obtained 100.000 iterations (starting from a random seed

pattern) of the stochastic relaxation procedure with a Hopfield network initialized with the mean functional connectome in study 1 ($n=44$). Next, to increase interpretability, we obtained the first two components from a principal component analysis (PCA) on the resulting state space sample to construct a low-dimensional embedding. Largely independent on the free parameter σ (variance of the noise), the first two principal components (PCs) explained around 15% of the variance in the state space, with low energy states (attractor states) located at the extremes of the PCs (Figure 2B, bottom plot). The PCA embedding was found to be largely consistent across different values of β and σ (Figure 2E). For all further analyses, we fixed $\sigma = 0.37$, as a result of a coarse optimization procedure to reconstruct the bimodal distribution of empirical data on the same projection (Figure 2E, see Methods for details) On the low-dimensional embedding, which we refer to as the *Hopfield projection*, we observed a clear separation of the attractor states (Figure 2C), with the two symmetric pairs of attractor states located at the extremes of the first and second PC. To map the attractor basins onto the space spanned by the first two PCs (Figure 2C), we obtained the attractor state of each point visited during the stochastic relaxation and fit a multinomial logistic regression model to predict the attractor state from the first two PCs. The resulting model achieved a high prediction accuracy (out-of-sample accuracy 96.5%). Attractor bases were visualized based on the decision boundaries of this model (Figure 2C). We propose the Hopfield projection depicted on (Figure 2C) as a simplified representation of brain dynamics, as modelled by connectome-based Hopfield networks, and use it as a basis for all subsequent analyses in this work.

2.2 Reconstruction of resting state brain dynamics

The obtained attractor states resemble familiar, neurobiologically highly plausible patterns (Figure 3A). The first pair of attractors (mapped on PC1) resemble the two complementary “macro” systems described by Golland et al. [2008] and Cioli et al. [2014]: an “extrinsic” system that is more directly linked to the immediate sensory environment and an “intrinsic” system whose activity preferentially relates to changing higher-level, internal context (a.k.a the default mode network). The other attractor pair spans an orthogonal axis between regions commonly associated with active (motor) and passive inference (visual).

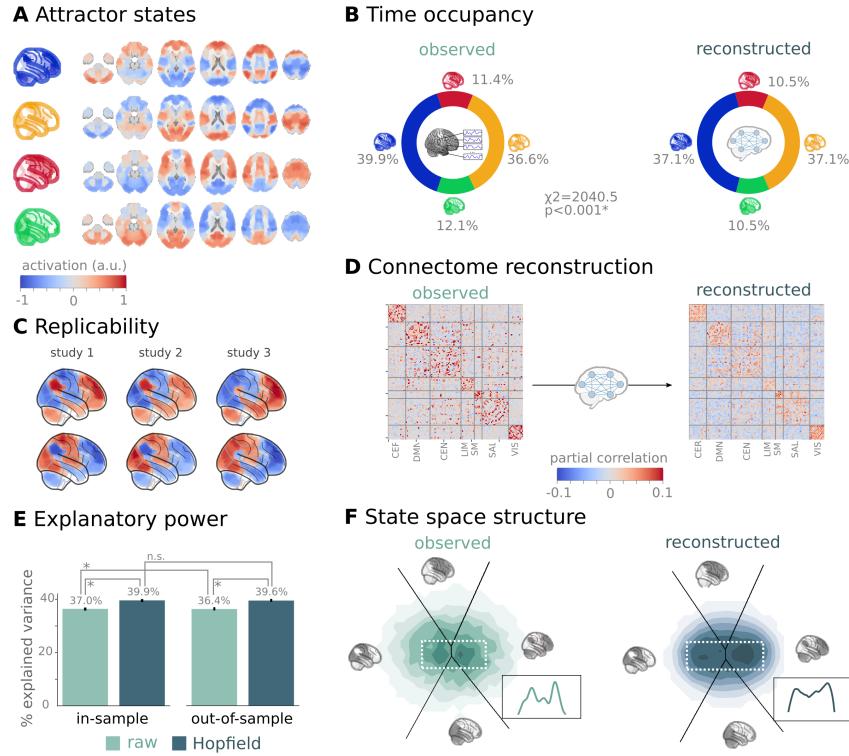


Figure 3: Empirical Hopfield-networks reconstruct real resting state brain activity.

Hopfield networks are known to exhibit remarkable robustness to noisy input (Hopfield [1982]) and even to corrupted weights (ref). We found that this property renders connectome-based Hopfield networks as

a strikingly robust tool (Supplementary Analysis X), showing a remarkable replicability (mean Pearson's correlation \mathbf{XX}) across the discovery datasets (study 1) and two independent replication datasets (study 2 and 3, Figure 3C).

Further analysis in study 1 demonstrated that connectome-based Hopfield models very accurately reconstruct several characteristics of true resting state data. First, the Hopfield projection explained a large amount of variance in the real resting state fMRI data in study 1 (mean $R^2 = 0.15$) and generalized well to study 2 (mean $R^2 = 0.13$) and study 3 (mean $R^2 = 0.12$) (Figure 3E). Explained variance significantly exceeded that of a PCA performed on the real resting state fMRI data itself (Figure 3E).

Second, during stochastic relaxation, the connectome-based Hopfield network spends three-quarter of the time on the basis of the first two attractor states (equally distributed across the two) and one-quarter on the basis of the second pair (again equally distributed). To test if this characteristic can also be found in real resting state data, we obtained normalized and cleaned mean timeseries in $m = 122$ regions from all participants in study 1 obtained the attractor state of each time-frame via the connectome-based Hopfield network. We observed highly similar temporal occupancies to those predicted by the model (χ^2 -test of equal occupancies: $p < 0.00001$, Figure 3B).

Third, during the stochastic relaxation procedure, connectome-based Hopfield models generate regional timeseries that retain the partial correlation structure of the real functional connectome the network was initialized with, indicating a high-level of construct validity (Figure 3D). To

Finally, our connectome-based Hopfield model also accurately reconstructs the bimodal distribution of the real resting state fMRI data on the Hopfield projection (Figure 3F).

The ability of the connectome-based Hopfield model to reconstruct such characteristics of remarkable, given that the model was neither trained to reconstruct nor informed about any spatial (bi-modal distribution, explanatory performance) or temporal patterns (temporal state occupancy) of the brain. The only information the model was provided with was the functional connectome, which was used to initialize the network and to constrain the dynamics of the network during stochastic relaxation. The fact that the model is able to reconstruct such characteristics of resting state brain dynamics, which are not explicitly encoded in the connectome, suggests that the connectome-based Hopfield model captures important relationships between the topology of brain connectome of the dynamics of the brain activation.

2.3 An explanatory framework for task-based brain activity

The proposed framework provides a natural account for how activation patterns in the brain dynamically emerge from the underlying functional connectivity. To illustrate this, we obtained task-based fMRI data from a study by [Woo et al. \[2015\]](#) (study 4, $n=33$, see Figure 3), investigating the neural correlates of pain, with focus on self-regulation. We found that time-frames from obtained from periods with pain stimulation (taking into account hemodynamics, see Methods for details) locate significantly differently on the Hopfield projection than time-frames obtained from periods without pain stimulation (permutation test, $p < 0.001$, Figure 4A, left). Energies, as defined by the Hopfield model, were also significantly different between the two conditions (permutation test, $p < 0.001$), with higher energies during pain stimulation. The Hopfield-projections thus provide an intuitive account for how the underlying functional connectivity of the brain can give rise to different activation patterns, depending on the current input. Change in input (i.e. task) does not switch to the brain into a distinct mode of operation but acts as a perturbation of the system's dynamics, resulting in mean activations changes that are only reliable measurable over an extended period of time, as done by conventional task-based fMRI analyses.

Participants were instructed to up- or down-regulate their pain sensation (resulting in increased and decreased pain reports and differential brain activity in the nucleus accumbens, NAc, see [Woo et al. \[2015\]](#) details), which resulted in further changes of the location of momentary brain states on the Hopfield-projection (permutation test, $p < 0.001$, Figure 4A, right). Interestingly, self-regulation did not manifest in significant energy changes (permutation test, $p = 0.36$). This suggest that visualizing data on the Hopfield projection can also capture changes in brain activity that originate from intrinsic modulation, rather than from changes in external input.

The proposed framework offers much more than visualization and inference of resting state and task based data on the Hopfield projection. It can provide a generative model for observed activity changes that can be used to predict brain activity under different conditions. To illustrate this, we used the Hopfield model to simulate brain activity during pain stimulation and self-regulation. First we registered the frame-to-frame transitions in the real fMRI data (all four conditions: rest, pain without self-regulation, downregulation,

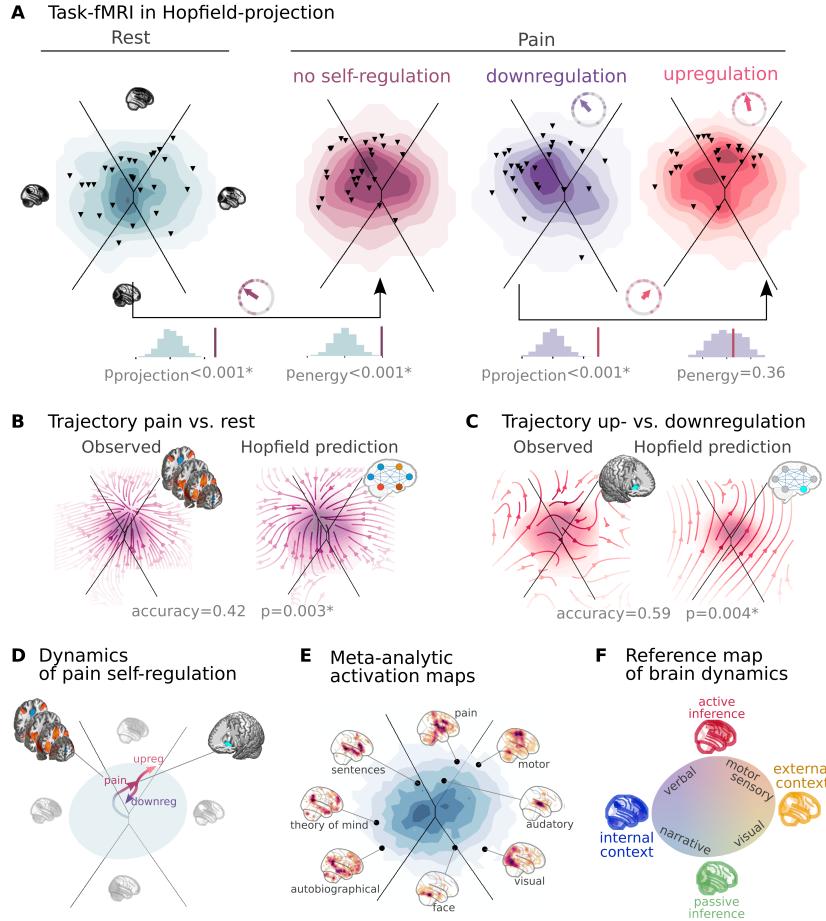


Figure 4: Empirical Hopfield-networks reconstruct real task-based brain activity.

upregulation) and converted those into the Hopfield embedding (resulting in a 2-dimensional vector on the Hopfield projection for each transition). Then, we assessed the mean direction in various segments of the projection (on a 6x6 grid). Next we took the difference of these mean directions between rest and pain (no regulation) (Figure 4B, left side), as well as between down- and upregulation (Figure 4C, left side). This analysis revealed remarkable non-linear trajectory patterns, showing the most likely direction the brain proceeds towards from a given state (activity pattern) in a given condition (pain without self-regulation or upregulation), as compared to the reference state (rest and downregulation, respectively). In case of pain vs. rest, brain activity is pulled toward a "ghost attractor" located in the proximity of the Hopfield projection typical pain activation map, as observed via conventional task-based fMRI analyses. In terms of attractor states, this belongs to the basin of attractor corresponding to sensory and motor processes (active inference). In case of up vs. downregulation, brain activity is pulled generally towards a similar direction, although with non-linear local perturbations and the lack of a clear ghost attractor.

Next, we aimed to assess, how much these non-linear dynamics can be reconstructed by the proposed framework. To simulate how brain dynamics alter during pain stimulation, we obtained a meta-analytic pain activation map (Zunhammer et al. [2021]) and introduced it with as additional signal on top of the Gaussian noise during the stochastic relaxation procedure. Note that, while adding such signal naturally results in a slight, linear shift on the Hopfield projection for each state generated during the stochastic relaxation procedure, that alone could only very weakly account for the observed nonlinear dynamics in the real data (Supplementary material X). After optimizing across 5 different signal-to-noise (SNR) values (logarithmically spaced between 0.001 and 0.1) we found that, with a very low amount of signal added (SNR=0.01) the connectome-based Hopfield model is able to provide a highly accurate reconstruction of the

observed non-linear differences in brain dynamics between the pain and rest conditions, including the "ghost attractor" of pain (Spearman's $\rho = 0.42$, $p=0.003$, Figure 4B, right side).

Interestingly, the same model was also able to reconstruct the observed non-linear differences in brain dynamics between the up- and downregulation conditions (Spearman's $\rho = 0.59$, $p=0.004$) with a very simple change; the addition (downregulation) or subtraction (upregulation) of activation in the NAc (the region in which Woo et al. [2015] observed significant changes between up- and downregulation). Importantly, in this analysis, we did not have to optimize any parameters of the model, we simply used the same low SNR for the NAC that we already found optimal in the previous analysis (SNR=0.01, Figure 4C, right side).

These results provide a fresh perspective on the neural mechanisms beyond pain and its self-regulation and provides a mechanistic account for the role of both "traditional" pain-related regions and the NAc in pain regulation (Figure 4D). These results also highlight, that the conceptual distinction between resting and task states might be - to a large degree - a false dichotomy. Rather, the brain is in a constant state of flux, which is only slightly perturbed by task states (even by so salient stimuli as pain) and the Hopfield projection can be used to visualize and quantify these dynamics.

To provide a comprehensive picture on how other tasks map onto the Hopfield projection, we obtained various task-based meta-analytic activation maps from Neurosynth (see Supplementary material X for details) and plotted them on the Hopfield projection (Figure 4E). This analysis revealed that the Hopfield projection can be used to visualize and quantify the dynamics of a wide range of cognitive processes, including sensory, motor, cognitive and social processes and reveals that the two principal axes of the projection map well to internal vs. external context and active inference vs. passive perception, respectively. In this coordinate system, visual processing is labeled "external-passive", sensory-motor processes "external-active", language, verbal cognition and working memory is labelled "internal-active" and long-term memory and autobiographic narratives fall into the "internal-passive" regime. This analysis also revealed that the Hopfield projection can be used to visualize and quantify the dynamics of a wide range of cognitive processes, including sensory, motor, cognitive and social processes and reveals that the two principal axes of the projection map well to internal vs. external context and active inference vs. passive perception, respectively.

These results highlight a very powerful feature of the proposed generative framework, namely that it can be used to simulate and predict brain activity under different conditions. Predicting the effect of lower or higher level of activity in certain regions, or lower or higher connectivity among them, on global brain dynamics and responses to various tasks provides unprecedented opportunities for forecasting the effect of interventions, such as pharmacological or non-invasive brain stimulation, on brain function.

2.4 Clinical relevance

Here I refer to Figure 3.

3 Discussion

3.1 Neurobiological validity

The activity flow principle has been shown to successfully predict held out brain activations by combining the activations and connection weights to the target region [1]. The proposed empirical Hopfield network builds on the knowledge derived from this framework, combining the architecture of a Hopfield network with the connectome as its pre-trained weights. Given an input activation for every region, the network will iterate upon this input state until a mathematical minimum is reached, producing an attractor state. An attractor state represents a configuration of activations in every region and is considered a recalled memory of the network. The network topology is multistable, producing different stable attractor states based on the temperature of the network and the initial activation pattern, which stimulates the network.

- significance

A further scenario rests on the role of ghost attractors [109](<https://www.nature.com/articles/nn.4497#ref-CR109>) "Deco, G. & Jirsa, V.K. Ongoing cortical activity at rest: criticality, multistability, and ghost attractors. J. Neurosci. 32, 3366–3375 (2012).", a dynamic landscape of remnant attractors each of which has an incomplete basin, hence allowing the system to 'wander' through large swathes of the phase space under the influence of weak noise 110.

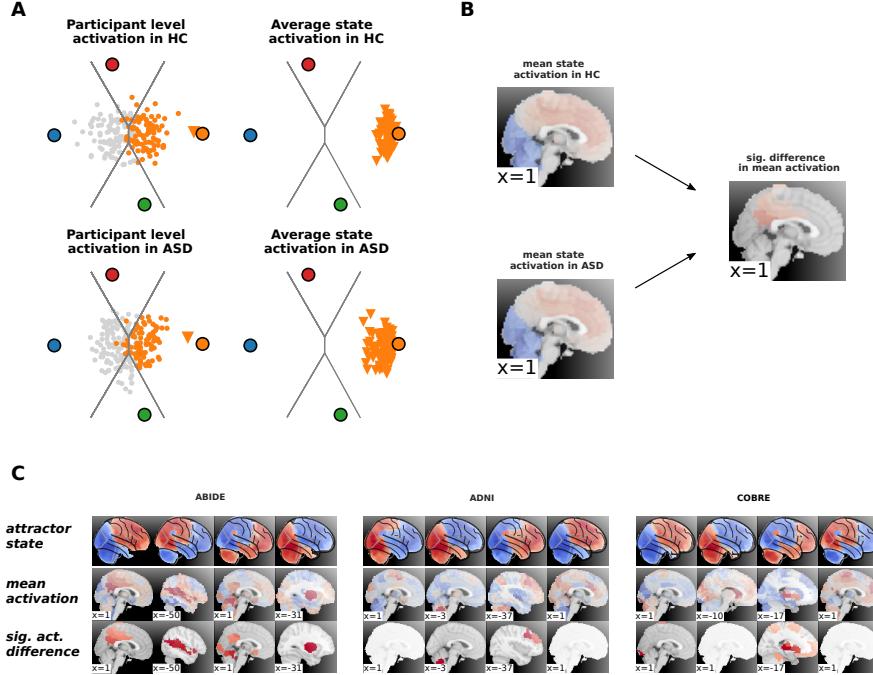


Figure 5: Outlook: Empirical Hopfield-networks' clinical validity.

4 Methods

4.1 Hopfield network

The weights w_{ij} have to be symmetric and the diagonal elements are set to zero.

Todo

Todo

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study	modality	analysis	n	age (mean±sd)	%female	references
study 1	resting state	discovery	41	26.1±3.9	37%	Spisak et al. [2020]
study 2	resting state	replication	48	24.9±3.5	54%	Spisak et al. [2020]
study 3	resting state	replication	29	24.8±3.1	53%	Spisak et al. [2020]
study 4	task-based	pain self-regulation	33		todo	Woo et al. [2015]
study 5 (Neurosynth)	task-based	coordinate-based meta-analyses	14371 studies in total	•	•	D. [2011]
study 6 (ABIDE)	resting state	Autism Spectrum Disorder	ASD: 98, NC: 74	todo	todo	todo
study 7 (ADNI)	resting state	Alzheimer's Disease vs. Mild Cognitive Impairment	AD:, MCI: , Mild Cognitive Impairment	todo	todo	todo
study 8 (CO-BRE)	resting state	Schizophrenia	SCH: , HC:	todo	todo	todo

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