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Review

The brain that controls itself

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The brain is a complex adaptive system that is organized across broad spatiotemporal scales. This multiscale architecture poses unique computational challenges, as the brain must balance the segregation of specialized functions with their cooperative integration into broader cognitive processes, while also simultaneously remaining both stable yet flexible enough to robustly rapidly adapt to new challenges. Systems poised near critical points reflect this same trade-off, however they are typically coordinated by external control parameters. Here, we argue that diffuse projections from the subcortex act as intrinsic control parameters that allow the brain to control its own coherence and flexibility. We review biophysical computational models that demonstrate how diffuse projections enforce low-dimensional neural dynamics promoting system-wide coherence while maintaining a susceptibility to external changes. The findings suggest that these systems underlie the brain's capacity for complex, adaptive behavior, providing a foundation for exploring how diffuse projections influence higher-level cognitive processes and consciousness.

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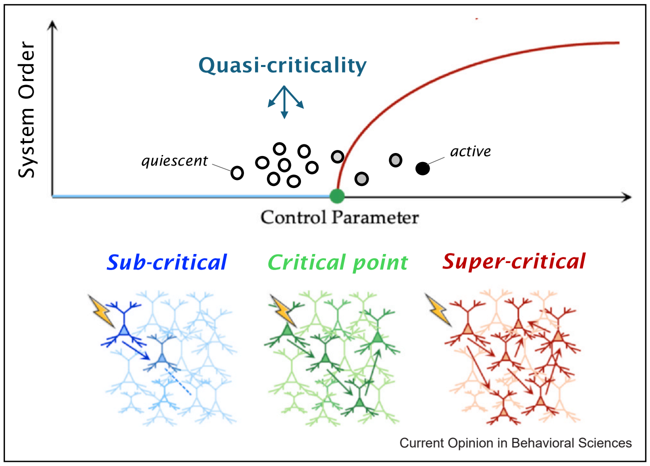
Introduction

The brain is a complex, adaptive system that is organised across broad spatial and temporal scales: from neurons to networks and from spikes to lifetimes [1–4]. This multiscale organisation necessitates the solution of a number of competing challenges, most notably regarding how the system balances specialised functions such as the execution of a motor skill with more global capacities such as a the differences between sleep and wake. To achieve this balance, neural systems must leverage anatomical segregation — to support specialist functional capacities within precise anatomical circuits — with integration — in which information from segregated and often anatomically distant subregions is recombined at larger spatiotemporal scales [5,6]. Second, the brain must retain sufficient sensitivity to fluctuations in evolving fitness landscapes [7] and also ensure that the host animal is flexible enough to make rapid changes when opportunities arise [8]. How the brain is arranged to achieve these distinct constraints and what physical mechanisms underpin them remain poorly understood.

A solution to this challenge may be found in details of the brain's neuroanatomical organisation. A number of circuits in the brain, such as the nonspecific, 'matrix' cells of the thalamus [9,10], the ascending neuromodulatory arousal systems [11,12], and the isodendritic core of the brainstem [13], project their axons in a relatively diffuse pattern that targets multiple neuroanatomically distinct regions. Importantly, these diffuse circuits are incompatible with the traditional notion of 'message passing' between individual neurons that are typically ascribed to targeted (i.e. region specific and spatially constricted), feed-forward projections between neurons [14]. Instead, by influencing the spiking activity of a distributed group of regions in the brain, often including sets of regions that cross-traditional functional boundaries, we argue that these diffusely projecting neurons perform a function that is equivalent to altering the temperature of a glass of water [15] (Figure 1). In much the same way that an external temperature source can increase the kinetic energy of water molecules, we argue that diffusely-projecting neurons act as a control parameter, modulating the gain of a range of diverse neurons, capable of shifting them between local, segregated dynamics and more globally integrated dynamics, which has flow-on effects for the types of computations that can be performed by the neurons.

Physical systems are often described with respect to phase transitions — wholesale shifts in the global order — that occur following small changes to a control parameter [16]. A well-known example of a control parameter is the effect that temperature has on water: namely, the ability to shift the state from solid to liquid to gas. Taking inspiration from physical systems that permit percolation events, the network connectivity of the brain has also been argued to represent a key order parameter for the system [16]. Specifically, the critical brain hypothesis [17] argues the brain is poised near the critical point of a phase transition between quiescence and runaway activity, which leads to numerous functional benefits from a diversity of

Figure 1



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Quasi-critical brain states. Top panel — In second-order phase transitions, the amount of order (e.g., oscillatory synchrony; y-axis) is nonlinearly related to small changes in a control parameter (e.g., neuronal excitability; x-axis). Below the critical point (denoted as a green dot), the system has low order (subcritical; blue), whereas above the critical point, the system has increasing order (supercritical; red). Bottom panel — In a hypothetical neuronal population, a subcritical regime is associated with an absorbing quiescent state that arises from ineffective interactions between neurons, leading to stimuli that effectively dissipate; near criticality, there is maximal percolation among the network, whereas in the supercritical regime, heightened interactions are such that the network is overexcited by external inputs leading to runaway activity. In a quasi-critical system (such as the brain), there is a diversity of individual states, such that the majority of the system can remain subcritical/quiescent, while an ever-changing subset transitions across the critical point to become supercritical. Figure and legend reproduced from Ref. [12].

timescales, increased susceptibility to external stimuli, and optimised information processing. While evidence of criticality (or near criticality) in the brain is growing [15,16,18–22], a new question has emerged of identifying the biophysical and anatomical features that control the brain's proximity to criticality. We argue that diffusely projecting neurons in the brain instantiate a quasi-critical brain state that strikes a dynamic balance between stability and flexibility, providing a necessary basis for complex, adaptive dynamics and the formation of the many varied brain states known to characterise our waking lives.

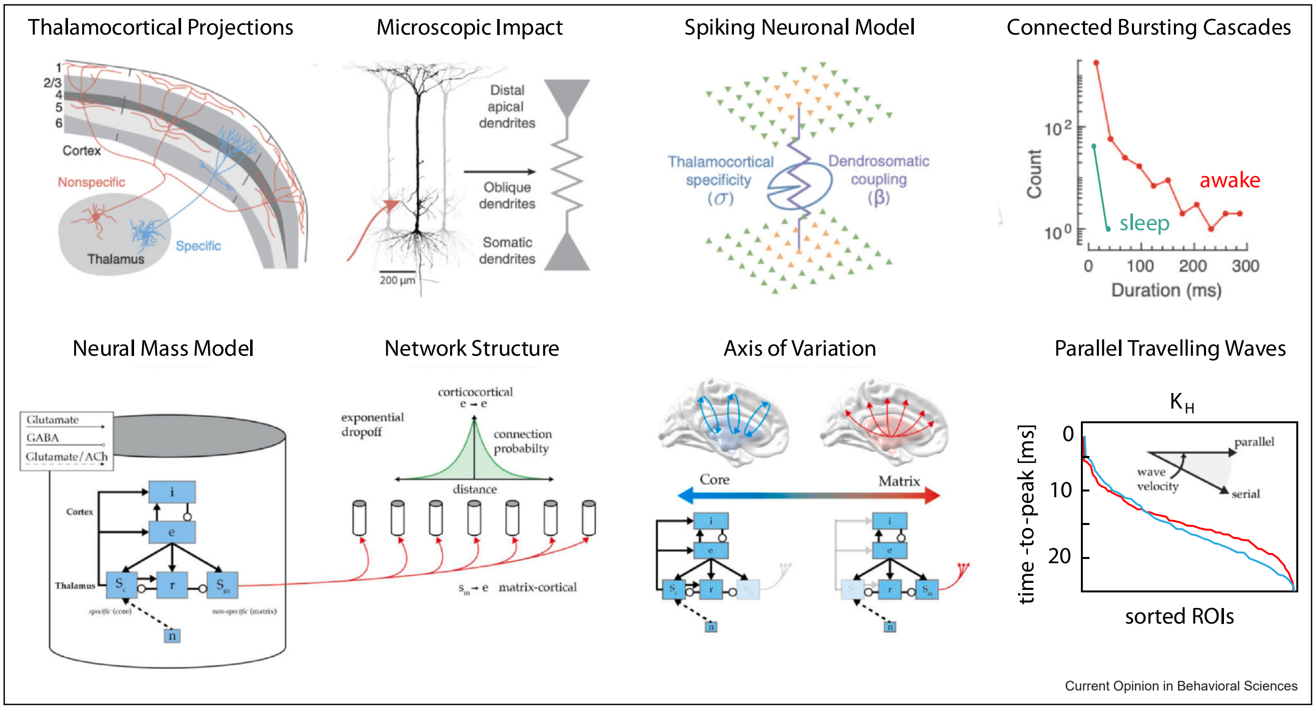
Demonstrating a causal control parameter of the brain, however, is quite challenging. Lesion evidence is unhelpful, as damage to diffusely projecting cells typically has devastating consequences for arousal and conscious awareness [10,11,23]. In addition, while we have access to tools for causally manipulating these cells in animal models, it is difficult to collect high-resolution neuroimaging data from sufficiently large portions of the brain to afford effective testing of the downstream system-level impacts of the cells' impact on whole brain dynamics. While there is a range of indirect evidence from a suite of recent experiments [24,25], we instead here focus on methods that allow for direct control over the putative mathematical relationships at the core of the interactions between diffusely projecting nuclei and the rest of the brain: namely, biophysical computational models. Among a wide variety of modelling approaches, here, we focus on two distinct strategies (Figure 2): cellular-level modelling, which focuses on spiking activity of neurons [26]; and mean-field modelling, which provides a zoomed-out view of average populations firing rates [27]. Both approaches afford distinct interpretations and in turn can be more easily fit to neuroimaging data collected at different spatial and temporal scales.

Diffuse projections support coherence and integration

In a system in which there is a large number of interacting elements, the collective behaviour of the individual elements necessarily strikes a trade-off between their individual expression and the coherence of the whole system. While collective behaviour does not always require a global control signal (consider a murmuration of starlings or schools of fish: both systems produce coherent order out of locally implemented rules; [30,31]), the process of coherent behaviour benefits from the presence of a coordinated signal that it passed to the whole group [15,32] — an orchestra will find it easier stay in synch on a challenging piece if there is a conductor keeping time. By its very nature, a coordinating signal is inherently low-dimensional — for example, a set of cells that sends diffuse projections to the rest of the brain is of much lower dimensionality than the much larger system to which it projects, simply due to the fact that there are orders of magnitude less afferent cells [13,24,33,34]. This suggests that the impact of a diffusely projecting system should coincide with robust modulation in the dimensionality of simulated signals from models of diffusely projecting neural systems.

The dimensionality-augmenting nature of an effective control parameter is clearly exemplified in a neural mass model designed to mimic the diffuse projections of both the brainstem and matrix thalamus [15]. In this model, a set of corticothalamic masses was constructed with weak, local connectivity and then a diffuse, coupling term was swept — transitioning the network of corticothalamic masses through distinct cooperative regimes: at low levels, there was small spatially localised coordination; in the middle zone, there was substantial hierarchical coordination and reconfiguration across the network; and at high levels, there was global coordination, but erratic behaviour (due to local instabilities driving high oscillatory firing rates). The proportion of variance explained by the first principal component of the systems dynamics peaked in the intermediate regime: namely, when the influence of the low-dimensional constraint had the maximal impact on the systems dynamics (Figure 2). In this intermediate

Figure 2



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Microscale versus macroscale biophysical modelling approaches. Top row — features of the microscale neuroanatomy (such as different classes of thalamocortical projections) can be translated into the microscale impacts (gating burst firing in layer 5B pyramidal neurons) that are then built into reduced spiking models that then explore the impact of these neuroanatomical features on population-level activity patterns — distinct regimes of this model (fit to sleep [teal] and awake [red] electrophysiology) show different scaling relationships (i.e., the slope of the line). Bottom row — at the macroscale, neural mass models can be built that mimic connectivity principles between distinct neuroanatomical populations, with emergent activity patterns then examined as a function of network structure or global parameter adjustments, such as the balance between similar topographic principles identified in the top left diagram — stimulating a cortical region with rich connections to matrix thalamus caused travelling waves to evolve in parallel (red) versus serial (blue).
Figures taken from Refs. [28,29]

regime, we found diffuse control can exploit neurobiological heterogeneity by pushing the system as a whole towards a critical boundary — where extensions of spatial and temporal correlations are observed — but importantly preferentially impacting subsets determined but this heterogeneity. That is, it supports novel coalition formation whilst maintaining global stability — a process known as quasi-criticality (Figure 1).

At the micro- to meso-scale, similar observations have been made in spiking neuronal models [22,28,35]. Inspired by work detailing a specific class of pyramidal neuron in the cerebral cortex [36], we built a dual-compartment spiking model that simulated the impact of diffuse projections (again, reflecting either the brainstem or matrix thalamus) onto the burst firing dynamics of these cells [28]. These diffuse projections target precise sites within the dendritic tree of thick-tufted pyramidal neurons, wherein they can mediate the release of calcium transients that transition the cells from a regular spiking regime into a burst firing mode that has been linked to conscious perception [37] and arousal [38] albeit with different cell-specific impacts imposed by the expression of distinct classes of neuromodulatory receptors [11,12]. By sweeping the spatial extent of this intercompartmental-coupling signal, we observed a similar signature to the neural mass model: namely, increasing the spatial extent of the coupling induced a low-dimensional constraint, increasing signatures of integration and information processing in the emergent spiking dynamics.

The low-dimensional unity that is brought about by diffusely projecting systems of the brain has been linked separately to numerous cognitive benefits [39]. For instance, a large number of functional neuroimaging studies have demonstrated that distinct cognitive capacities are associated with the expression of distributed, yet relatively low-dimensional, spatiotemporal patterns of blood flow [40] or local field potentials [41,42], which are both consistent with the capacity of diffusely projecting systems. These clear links have quite intuitive connections: cognitive tasks typically (though not always) involve the coordination of multiple different specialist systems in the brain [43]. The extent to which you can bring these specialist systems to work together is a crucial factor in the effective completion of the task at hand, so long as you do not integrate the system to the extent that the specific capacity of each subsystem is lost [44]. With this in mind, we turn our attention to this other constraint: the need to retain specificity.

Diffuse projections promote susceptibility and flexibility

Low-dimensional constraints provide global unity and coherence, yet the brain must also remain susceptible to a variety of external stimuli while remaining attentive to the most salient. Importantly, a system's dimensionality may differentially affect its susceptibility. For example, a system strongly coupled to a global signal may not be able to distinguish subtle stimuli, which a system with strong recurrent connectivity may enhance (and vice versa).

Once again, neural mass models offer a convenient means for exploring this effect [15]. If a square-wave stimulus is delivered to a peripheral cortical node in the corticothalamic model described above (Figure 2, bottom row), the amount of global coupling in the model has a demonstrative impact on the manner in which that impulse is transmitted throughout the network. If stimulated within the low coupling regime, the activity dies away following its onset. If the stimulus is applied in the hypercoupled regime, stimulation has a huge excitatory effect, activating the whole network, yet different inputs are effectively indistinguishable. However, in the intermediate regime, the balance of local and subtle diffuse excitatory signals means that different signals can be teased apart, in effect an indirect signature of the heightened information processing capability inherent within a system organised in this regime. Similar effects are also observed in the cellular-level model, which speaks to the generalisability of this effect [22,28].

Diffuse inputs to a system can also shape the manner in which dynamics propagate across a network over time [45]. In a neural mass model similar to the version described above, albeit with additional anatomical constraints [29], artificially stimulating regions of the cerebral cortex that indirectly recruited diffusely projecting nuclei within the thalamus caused a striking alteration in the spatial evolution of travelling waves across the cortex following stimulation: diffuse projections caused waves to travel in parallel, whereas targeted-projections enforced serial wave propagation [29].

A system with heightened susceptibility is effectively open to respond to as wide a range of inputs, as it can permit (in order to maximise its ability to survive and facilitate the next set of potentially spiking neurons). In engineering settings, the breadth of a systems responsiveness is often quantified by calculating the dynamic range: the strength of the output as a function of a range of different input strengths. Systems with broad dynamic ranges are capable of discerning both soft and loud noises or a wide range of both low- and high-frequency inputs. Using the cellular-level model described above (Figure 2b), we were able to demonstrate that the dynamic range of a simulated cellular network (imbued with the features of neuroanatomy characteristic of layer 5 pyramidal neurons) is directly related to the extent to with which the model neurons receive diffusely projecting inputs. This finding extends the biophysical claims of earlier arguments that the criticality of the brain enhances the dynamic range [46].

At the microscale, similar diffuse projections afforded the capacity for burst firing pyramidal neurons to recruit other connected neurons into a 'train' of bursting coalitions that conformed to scale-independent rules [28]. In this way, the model instantiated a key prediction of Dennett's 'multiple drafts model' [47], which likens conscious perception as an emergent property of a process analogous to speciation or 'fame in the brain' [48]. That the diffuse projections in this same model also lead to increases in network integration and integrated information [22], both of which have been previously suggested as signatures of intransitive consciousness provide further confidence in the importance of this neurobiological organising principle.

Conclusions and future directions

The brain is replete with diffusely projecting neurons that fundamentally alter the manner in which the brain processes information. Here, we have highlighted how implementing diffuse neural projections into computational models can demonstrate two key implications of this organisation: namely, low-dimensional coherence and heightened susceptibility. Furthermore, both of these features were invariant to the scale at which the models were designed (i.e. they occurred at both macroscopic and microscopic scales). There is early evidence to suggest that the brain is indeed an example of a complex, heterarchical system that demonstrates both of these features [49]; however,+++++++ further work is required in order to tease apart the logical relationship between neural structure and the emergent dynamic expression of systems-level behaviour.

Interestingly, most physical systems in which there have been clear examples of control parameters for critical order involve control parameters that are external to the system itself. For instance, consider the impact of an externally applied temperature source to a glass of water: the temperature causes a change in the kinetic energy of the water molecules, which then cause an abrupt state change at the systems boiling point (from liquid to gas). In contrast, the brain is an example of an internally controlled communication network [50], in which the control parameters are an inherent property of the system itself. As they are a part of the system they are controlling, the control nodes are themselves likely susceptible to operating in different regimes that depend on the state of the system itself. Neuronal control nodes are also susceptible to inputs that change their functional operating regimes, both on short-term (following both glutamatergic and GABAergic inputs from connected structures), medium-term (following neuromodulatory inputs onto the control nodes from other neurochemical systems), and long-term timescales (following genetic and developmental regulation of cellular activity dynamics). Whether a system organised in this way follows the same universal rules as a system with externalised control is an exciting open question for future research [51,52].

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Author Contributions

JMS wrote the first draft of the manuscript. All authors edited the final content.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors report no conflicts of interest.

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