

Control sciences for Neuroscience and Neurology

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1 Context and challenges

Neuroscience, and its associated clinical field of neurology, is concerned with the study of the structure and function of the nervous system which, in humans, includes the brain and spinal cord (the so-called *central nervous system*) as well as the peripheral system of neuron and nerves that innervate other organs.

Neurophysiological systems at different spatial scales: from individual neurons to the cortex

The physiology of the human nervous system, and that of the human brain in particular, involves several levels (or spatial scales) of organization (Fig. 1-top). These levels of interest correspond to different subfields of neuroscience, each with their own models and methodologies, and which do not always easily communicate with one another. **At the cellular level**, neuroscientists study the molecular and electro-chemical interactions between neural cells, which in the adult human brain include about 70-90Bn neurons and about as many supportive glial cells. Neurons are unique in their ability to send signals to other cells in the form of electrochemical pulses, called *action potentials*, transmitted over *axon* fibers that extend from their cell body and connect to other cells by electrochemical interfaces called *synapses*. There are many techniques available to record brain activity [106] – including electroencephalography (EEG), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI) or near-infrared spectroscopy (fNIRS) – but these do not allow for single-neuron resolution. Cellular mechanisms (e.g. synaptic transmission, action potential generation) were historically studied in-vitro, but now mostly with in-vivo single-unit recordings, in which microelectrodes record changes of voltage in the extracellular space close to the cell membrane, with a field of view of about $1\mu\text{m}$ (1 cell).

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At the population level (i.e. ensembles of 100s or 1000s of neural cells), neuroscientists study the emergent mesoscopic activity of interconnected neurons, such as their firing rate and local field potentials, and how it is modulated by excitatory or inhibitory connections from other populations of neurons in their neighborhood. In humans, although progress in high-resolution imaging (e.g. ultra-high field fMRI) offers hopes to image populations of neurons non-invasively, population recordings are typically done using surgically-implanted electrodes (stereoencephalography, SEEG) or devices (deep-brain stimulation, DBS, which can also be used as a sensor), which have a field of view of 50-500 μ m (10-100s of cells) but can so far only be used for research on patients who have a pre-existing medical condition that require such surgery (typically pharmacoresistant epilepsy for SEEG; movement disorders such as Parkinson's disease and neuropsychiatric conditions like obsessive-compulsive disorder for DBS).

Finally, **at the organ level** (i.e. whole brain), neuroscientists study how large networks of neural populations cooperate macroscopically to implement such high-level cognitive functions as learning, memory, behaviour, perception or consciousness. Research at that level often involves recordings of sensory inputs (e.g. sounds or images presented to freely behaving participants) and behavioral outputs (e.g. speech, facial expressions, subjective reports) simultaneously with brain activity, using non-invasive imaging techniques such as EEG, MEG, fMRI or fNIRS. Whole-brain, non-invasive imaging techniques allow more experimental flexibility, but vary in their temporal (milliseconds to seconds) and spatial (millimetric to centimetric) resolution. A current frontier of neuroscience research even aims to extend such research **at the organism level**, by studying the two-way interactions between the brain and other organs such as the heart (e.g. heartbeat-evoked potential, a brain response to each heartbeat thought to be linked to internal body awareness) or the gut nervous system (using electrogastrograms, the stomach/intestine equivalent of EEG).

Some challenging properties of neurophysiological systems for control engineering

From a control engineering perspective, neurophysiological systems at each of these spatial scales have a number of complex features that make them both interesting and challenging research objects.

Multiphysicallity: Neurophysiological systems communicate internally and externally via an intricate network of electrical, chemical/molecular signaling. When an electrical signal arrives at a chemical synapse, neurotransmitter molecules are released and then bound to specific receptor proteins in postsynaptic cells, causing the generation of electrical or chemical signals which further propagate down the network. The behavior of synapses (their so-called short-term plasticity) is further modulated by other signaling from surrounding neurons and, as is becoming increasingly apparent, supporting glial cells [112].

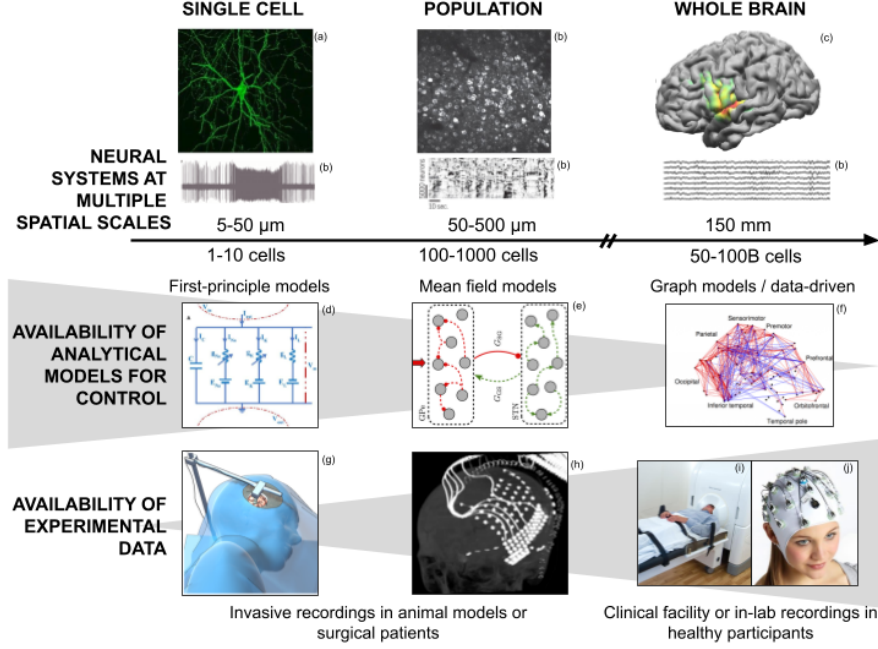


Figure 1: **The multiple spatial scales of neural systems.** The physiology of the human brain involves several spatial scales of organization, which correspond each to specific methodologies and challenges for the science of control. At the cellular and population level (left), rich analytical models exist (such as, as illustrated here, the Hodgkin-Huxley model of axon signaling [63] and the Wilson-Cowan [113] field model). However, data and opportunities to experiment at these scales are scarce and constrained by considerable ethical, regulatory, and practical barriers. At the other extreme (right), data at the whole-brain scale have never been more accessible: non-intrusive imaging and affordable EEG systems allow the rapid collection of neural signals in healthy participants, often under lightweight ethical oversight and at minimal cost. However, dynamics at these scales cannot be succinctly represented by first-principle models, and instead require data-driven representations, which remain an active domain of study. *Credits for illustrations: (a) Piatkevich et al. 2019 [83]; (b) Stringer & Pachitariu, 2024 [99]; (c) source: www.amnahyder.com (d) Fang et al. 2021 [39]; (e) Madadi Asl et al. 2022 [73]; (f) Achard et al 2006 [1]; (g) Coughlin et al 2023 [32]; (h) Hill et al. 2012 [62], (i) source: clevelandclinic.org; (j) source: brainproducts.com.*

Non-linearity: The building block of neurophysiological systems, the individual neuron, is an intrinsically non-linear system. Its input-output mapping (current in, membrane potential out) essentially has an integrate-and-fire phenomenology, and has given rise to a large variety of mathematical models in the form of nonlinear dynamical equations (derived from the seminal work of Hodgkin & Huxley [63]). At the population level, the microscopic behaviour of neurons interconnected with excitatory or inhibitory connections also gives rise to coarse-grain non-linearity when modeled as a mean field (e.g., Wilson & Cowan [113]). The extent whether such macroscopic and/or whole-brain dynamics can be described/predicted/controlled with linear models is the topic of much current research [79].

Feedback: Backward connections (i.e. that re-ascend the information-processing pathway) are ubiquitous in the human cortex and play a central role in computational formulations of brain function, because they are necessary to explain macroscopic phenomena such as event-related potentials [50]. At the behavioural level, the brain also *implements* important feedback functions, in which e.g. efferent signals (motor commands, speech) are compared continuously to reafferent monitoring signals to compute prediction errors and achieve a target, i.e. essentially a form of optimal control [105].

Strong intrinsic activity: The brain has a key function in homeostatic regulation, which means it is continuously monitoring and modulating various aspects of the organism's metabolism, such as food intake, energy expenditure and cardiorespiratory activity [68]. This activity manifests itself as an intrinsic oscillatory activity (so-called 'resting-state' activity) which, at any level of observation, accounts for a substantial fraction of variability in e.g. single-unit firing rates, population mean-field activity or event-related responses to external stimuli. In terms of system identification, this means that the 'perturbation' signal acting on any input-output relationship may be several orders of magnitude greater than the stimulus' influence, and have a non-random structure with strong spatio-temporal correlations (e.g. traveling waves; [88]).

Stochasticity: Noise is pervasive at every level of the nervous system, from thermodynamic/quantum noise acting on sensory receptors (e.g. photons hitting retinal photoreceptors at random rates), variability in the strength and timing of neuronal action-potential transmission (e.g. 'background' spontaneous neurotransmitter release in synapses), up to macroscopic variability in motor actions and behaviour [38]. Whether such variability is intrinsically stochastic or results from a deterministic process that is too complex to grasp (and thus better modeled as random), advances in the analysis and control of stochastic dynamical systems are of relevant use in the neuroscience context. In particular, the functional role of noise in sensory systems is an active research question in biology, with mechanisms

such as stochastic resonance showing that the addition of an optimal level of noise to a weak input can enhance its detectability [89].

Spatial structure & connectivity: Finally, one additional complex feature of brain dynamical systems is that their networks are strongly constrained by brain anatomy. Detailed anatomical studies have documented a complex mesh of pathways (bundles of axons) linking neurons between distant cortical areas (the so-called *connectome*; [98]), while sometimes restricting interactions between areas that are spatially (but not functionally) closer. This graph structure is, for a large part, shared across individuals (e.g. the *corpus callosum*, a large bundle of more than 200 million axons that connect the two hemispheres) but may also be genetically inherited and modulated during/by behavior. It constitutes a complex, only partly-understood substrate for the dynamic interactions between cell populations and, because these connections are mostly reciprocal, they largely determine what spatiotemporal correlations can be observed between populations. Even within populations, the non-local nature of brain dynamics has led to the development of analytical and numerical tools for the study of spatiotemporal patterns, based on partial differential equations (PDEs) or integro-differential equations [31].

The role(s) of control engineering in neuroscience

While not usually considered a mainstream research tool in neuroscience (as would e.g. signal processing or artificial neural networks/machine learning [90]), the theory and methodology of control science (and its subfields of modeling, analysis, identification, observers and control/command) offers important opportunities for the study of neurophysiological systems, both at the fundamental (understanding normal brain function) and applied/clinical level (diagnosing/curing abnormal brain function).

Because they are essentially dedicated to the study of complex non-linear systems, the control subfields of **modeling** and **analysis** provide a strong framework to understand neurophysiological systems, both at the level of the individual neuron and within-between cell populations. In addition to providing conditions for e.g. stability and controllability that may explain why such biological structures evolved the way they did, analysis may also provide causal explanations for emergent phenomena. For instance, models that include or don't include certain backward connection can be compared in their ability to generate mean field activity consistent with experimental data [50]. In such a role, control engineering shares a lot of similarity with research described as 'computational' or 'mathematical' neuroscience [93], although the two communities perhaps do not communicate as much as they could/should.

The control subfield of **system identification** offers important opportunities to study and model experimental data, as measured e.g. by single-unit, local-field or whole-brain recording. In addition to providing realistic parameter estimates for computational models (see Fig. 2 for an early example of nonlin-

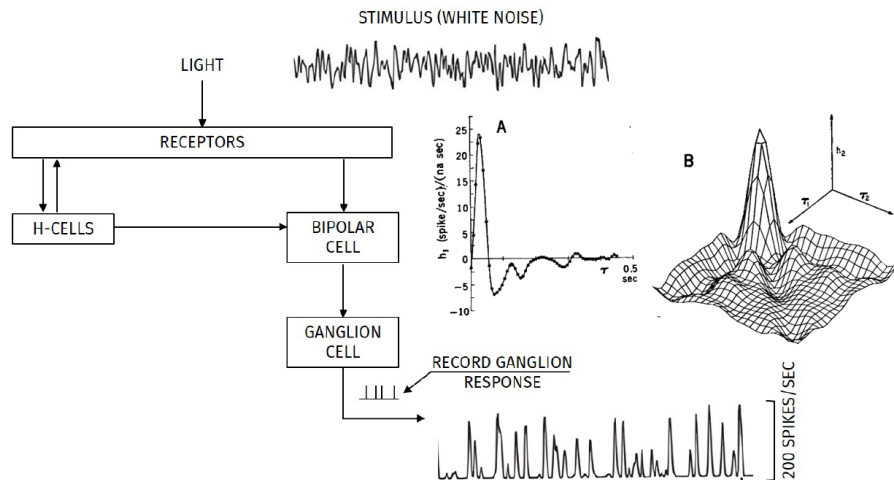


Figure 2: **White-noise system identification in an experimental chain of three retinal neurons.** An early 1970s example of using system identification to characterize the equivalent system of how the catfish retina converts light intensity to neural spikes in the visual ganglion. An in-vitro montage of the cells is stimulated experimentally with visual white noise, and the input-output system is modeled with Volterra kernels. The first order kernel (A) is the impulse response of the linear part of the transfer function of the chain. The second order kernel (B) describes the nonlinear behavior of the system. *Figure adapted from [75].*

ear system identification with white noise applied to a three-stage neuron chain in the catfish retina [75]), system identification also offers unique opportunities to extract parameters at the individual patient level and see if these parameter values can serve as biomarkers to e.g. differentiate patients from controls, or cluster different phenotypes of patients (see e.g. [2] for an application to cognitive deficits after a brain stroke). In such a role, the field of control appears especially close to the emerging so-called ‘data-driven’ methods in the field of psychophysics and sensory neurophysiology (reverse correlation [92]; temporal response functions [33]), which essentially (and somewhat confusingly) propose to identify impulse-response models - and would probably benefit from using a more consistent terminology.

Like system identification, the **observer** subfield potentially provides an important framework to uncover brain states from experimental data. Measurements from brain imaging (e.g. up to 256 EEG sensors distributed across the scalp) are typically high-dimensional and highly redundant, and provide only a poor proxy to the state of the underlying dynamical system. Much recent research in neuroscience has focused on learning lower-dimensional ‘state-space’ embeddings of brain imaging data in which one can uncover causal links with other physiological signals (e.g. auto-encoders to learn a 1-d embedding of arousal that’s common to both pupil size and neuronal calcium-imaging time series [87]), or better separate phenotypes of patients than with surface features [85]. In such a role, the field of control appears close to recent neuroscientific

applications of ‘scientific machine learning’ [19], which aim to learn state-space representations, or even complete functional descriptions (i.e. ODEs) of a dynamical system in a purely data-driven manner (e.g. using symbolic regression [26]). The subfield of observers is also linked to the notion of compressed or virtual sensing, a topic especially relevant for neuroscience applications where the number of sensors may be practically limited and one would like to estimate hidden state variables [111].

Finally, the subfield of **control design** opens opportunities to construct control signals adaptively, either in the form of electric or sensory stimulation, in order to bring neurophysiological systems into a desired trajectory or regime. While an experimental science such as neuroscience requires the ability to test the consequences of experimentally-manipulated variables, such manipulations are typically only done in a simple open-loop way (e.g. inhibiting the activity of a neural population by applying transcranial magnetic stimulation - [82]) or, at best, with discrete stimulations triggered by predefined threshold on the output. For instance, in the sleep-neuroscience method confusingly called ‘closed-loop stimulation’, short bursts of acoustic noise are triggered in synchrony with the onset of EEG slow waves occurring in deep sleep, in an attempt to accentuate their amplitude and test their role for memory consolidation, often with limited success [5]. The objective of altering, or even controlling, the response of neuronal ensembles in a genuine closed-loop manner, notably by exploiting the stimulation capacity of implanted SEEG or DBS systems, would open the door to a wide range of possible therapeutic interventions, including in Parkinson’s disease or epilepsy. In such a role, the field of control appears close to the research concerns of the *brain computer interface* (BCI) and *neurofeedback* communities, although the latter tend to focus on letting individuals learn to induce certain patterns of brain activity, (which are then detected and transcoded into some form of feedback), rather than on techniques that directly manipulate that activity [114].

2 Contributions of the French Control community to the field of Neuroscience

As early as the 1950s and 1960s, French researchers in the spirit of cybernetics began to conceptualise the brain as a regulatory system, with pioneers such as Louis Couffignal exploring analogies between nervous function and machine feedback [71]. In the decades that followed, the community of French control scientists increasingly engaged with questions at the interface of neuroscience and neurology and, with the advance of brain imaging technology in the 2000s, contributions from this community have become both more frequent and more diverse. We review here a number of research topics that appear particularly active in the current French community.

Parkinson’s disease

Parkinson’s disease (PD) is a neurodegenerative disease which causes the progressive degeneration of nerve cells in the subcortical region of the *substantia nigra*, with the consequence of deregulating neuronal dynamics in the *striatum*, another subcortical region involved with voluntary motor control, and to which the substantia nigra normally provides dopamine neurotransmitter. This deregulation cause a variety of motor symptoms, such as tremor, rigidity and bradykinesia (slowness of motion), as well as non-motor disorders, such as dementia.

Significant efforts have been made by the French control community to counteract motor symptoms in PD. The main developments rely on Deep Brain Stimulation, a symptomatic treatment developed by the team of Prof. A.L. Benabid in Grenoble in the early 1990’s [7]. This treatment consists in inserting electrodes in deep brain regions to deliver low-voltage high-frequency electrical impulses (3-5 V, 130 Hz).

In clinical practice, the electrical signal is delivered in open loop, i.e. it is the same regardless of the patient’s brain state or macroscopic activity. As reviewed in [21], several attempts have been made to go closed-loop, namely to adapt the stimulation signal based on real-time measurements of the patient’s brain activity. Until recently, most of these attempts have been confined to fundamental research, either of a computational or experimental nature. However, closed-loop systems have recently come closer to medical practice since the first device allowing for closed-loop DBS (BrainSense, by Medtronic) has received CE mark approval in January 2025, which may also create larger opportunities for experimentation for control research.

Contributions from the French control community first aimed at analyzing the mechanisms by which parkinsonian brain activity is generated. It is well documented that motor symptoms severity correlates with the intensity of specific brain waves in deep brain regions, particularly in the beta frequency band (13-30 Hz) [14]. By relying on computational models of the neuronal populations involved, notably derived from biophysical models of the subthalamic nucleus (STN) – globus pallidus pars externa (GPe) network [64], the link between these pathological oscillations and the synaptic weights between STN-GPe has been formally evidenced, with explicit account of axonal propagation delays [54, 56] and of the spatiotemporal nature of the neuronal populations [17]. A resonance effect, which may explain the amplification of activity in the pathological frequency band, has also been studied with incremental stability techniques [22]. From a more microscopic viewpoint, the synchrony properties of an assembly of interconnected neurons has also been addressed, in which each neuron is modeled by an oscillator [47, 49, 48].

Based on these analytic results, some feedback-control strategies have then been developed to attenuate parkinsonian brain activity. Control in PD is made challenging by both practical and theoretical aspects of the disease. Practically, available data and opportunities for experimentation (e.g. during electrode positioning) are scarce in order to limit surgical intervention time, and safety

concerns also require bounded control, for stimulation not to propagate to neighboring regions. Theoretically, models for pathological neuronal dynamics remain imprecise, and present several control-theoretical challenges such as the presence of time delays due to axonal propagation and the high spatial heterogeneity of the considered neuronal populations.

At the microscopic scale, it has been shown that a feedback proportional to the mean activity of the neurons is enough to desynchronize them [43, 45, 44, 46, 47]. At the mesoscopic scale, it has been shown that stimulating the subthalamic nucleus (an excitatory deep brain region) proportionally to its own activity is enough to disrupt oscillations [55, 23, 36, 24]. Moreover, this proportional gain can be adaptively adjusted in order to limit the stimulation influence when oscillations are in a non-pathological frequency range [81, 80, 42] (Figure 3). It has also been shown that this stimulation can be made less energy consuming and more physiologically respectful by using observers to estimate averaged synaptic weights and the activity of unmeasured populations [16].

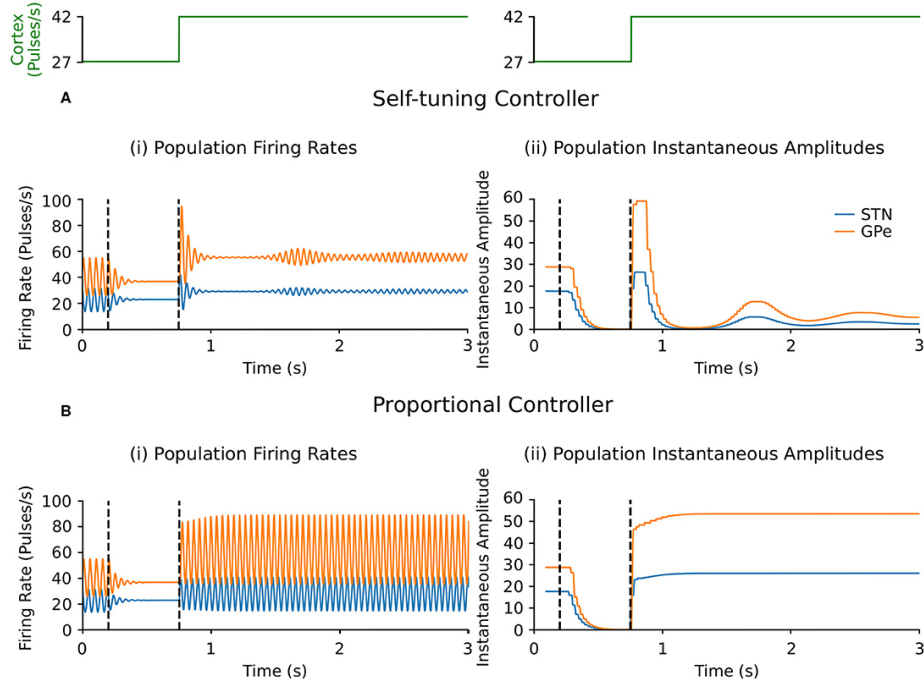


Figure 3: Controlling pathological dynamics in models of Parkinson's Disease (PD). Synaptic weights between populations of neurons modeling the STN and GPe brain regions can simulate pathological beta oscillations associated with PD. Closed-loop control algorithms simulating the effect of deep-brain stimulation (DBS) devices acting on the STN can attenuate these oscillations. Shown here: a comparison between proportional (bottom) and self-tuning controllers (middle), after being switched on ($t=200$ ms), and after the introduction of additional oscillations at $t=750$ ms. While the self-tuning DBS automatically adapts the proportional gain to maintain the attenuation of beta oscillations, pure proportional DBS is unable to do so. *Figure reproduced from [42].*

Epilepsy

It has already been mentioned that most neuroscience mathematical models, although sharing a common formalism with those typically used for control purposes, are developed by researchers who would probably not claim to belong to the control-theory community, such as computational neuroscientists or physicists. Epilepsy models do not escape the rule, whether they are operating at the level of phenomenology [66], biophysics [35] or mean-field dynamics [77] (for a review, see [34]). One notable exception is [3], in which authors from the French control community propose to model the considered brain region as a network of interconnected sub-regions, each modeled by a nonlinear oscillator. Seizures then occur due to the activation of short-term plasticity mechanisms, whose threshold would be abnormally low for epileptic patients, opening the possibility to control seizures with a closed-loop stimulation architecture.

Beyond modeling, most of the recent contributions on epilepsy in the French control community have exploited observer theory. In [30, 29], the authors rely on neural mass models to estimate hidden state variables, such as the mean membrane potential of neuronal populations, based on EEG measurements. A local, but probably more constructive, approach was proposed in [57] by relying on linear parameter-varying systems techniques. A hybrid approach, mixing continuous and discrete dynamics, has also been proposed and additionally allow to estimate synaptic weights [28]. While all these approaches aim at precise estimation of specific state variables or parameters, seizure onset detection and prediction are mainly concerned by a qualitative shift in the brain region dynamics: evolving from a normal state to a pathologically excited one. This idea gave rise to the notion of qualitative detection [104], which aims at estimating the overall dynamical behavior of the considered system (resting, oscillating, bursting, spiking, etc.) regardless of the exact value of the parameters which underlie them.

Vision and perception

The primary visual cortex (V1) is a brain area involved in the processing of visual information transmitted by the retina. It is organized in columns, that code not only the intensity and color, as would a television screen, but also for the orientation of contours. A mathematical model of V1 has been proposed by A. Sarti, G. Citti and J. Petitot, in which each point in the perceived image is enriched with information about local contour orientation, thus embedding the image in the higher dimensional manifold $SE(2)$, which corresponds to translations and rotations in the plane [91].

By relying on this model, the French community has developed neuro-inspired image processing algorithms by relying on control-theory tools. In particular, the state of each image point (containing both contrast and direction) can be combined to diffusion dynamics in order to restore a significantly degraded image [86] or for object recognition [12]. By combining this model with a spatio-temporal version of Wilson-Cowan model mentioned above, a mathe-

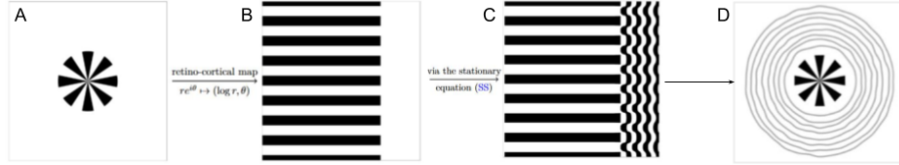


Figure 4: **Mathematical analysis of neural field models of the visual correct explains visual hallucinations.** The so-called “MacKay” family of visual illusions induces the illusory perception of concentric rings in the visual periphery (right), when one fixates a funnel-shaped stimuli in the center of the retinal field (A). By converting stimuli to a retino-topical model of how the visual cortex encodes visual scene (middle-right), and analysing how a neural field model (of the Cowan-Wilson family) propagates that stimuli, one can simulate cortical representations that correspond to the illusory percept. *Figure adapted from [103].*

mathematical analysis of the neural processes involved in the generation of visual hallucinations (Fig. 4) has also been proposed [9, 10, 101, 103], including a controllability analysis aiming at identifying the type of hallucinations that can be emulated by this model [102]. A similar approach was adopted for sound reconstruction [15].

Circadian rhythms and homeostasis

One primary function of the central nervous system is to maintain homeostasis - i.e. control over the internal environment of the organism - and circadicity - i.e. its adaptation to external environmental cycles. Because they are essentially bistable dynamical phenomena, these processes have attracted a number of mathematical modeling efforts, which typically model circadian and homeostatic drives as coupled non-linear oscillators (for sleep/wake cycles, see e.g. S. Strogatz’s PhD Thesis [100]), or - more generally - simplified cubic systems (Fig.5) that bifurcate, potentially stochastically, between states [65].

Unsurprisingly, this modeling framework has provided a fruitful playground for control-theoretic approaches. Recent work in the French control community have focused for instance on system identification, where techniques were proposed to characterize the adaptation speed of the circadian system based on temperature measurements [13], and on analysis, where the impact of homeostasis regulation processes have been included in population models of neural dynamics [59].

Locomotor rehabilitation

Beyond the cortex, neural injury at the brainstem or spinal-cord level may lead to severe locomotor deficits, or even complete limb paralysis. In the past 5-10 years, progress in stimulation neurotechnology has made it possible to deliver trains of electrical stimulation directly to the spinal cord, on demand, letting patients regain some level of voluntary control over previously paralyzed muscles [109].

This emerging clinical context has opened an opportunity for the devel-

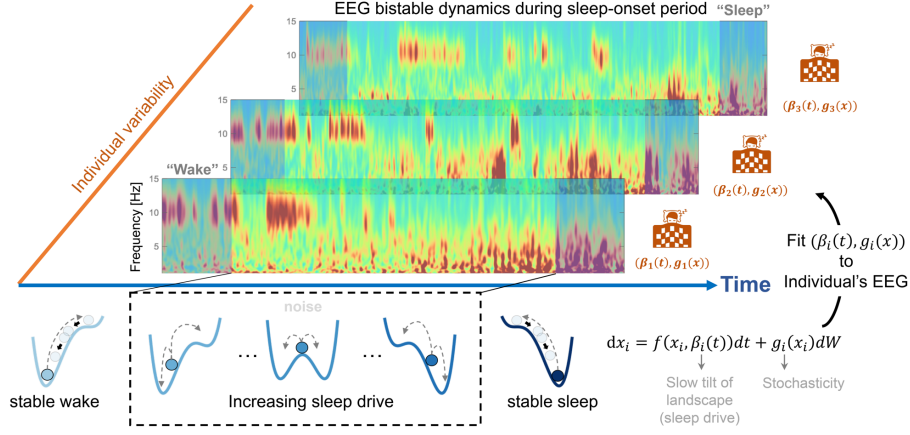


Figure 5: **Cortical dynamics during the transition to sleep modeled by a stochastic bistable system.** The sleep-onset period has a strongly bistable phenomenology, marked by a non-monotonous decrease of the electroencephalogram (EEG) frequency and high inter-individual variability, seen here in wavelet spectrograms of three illustrative participants' EEG (top). For control purposes, these dynamics can be modeled as the motion of a noisy overdamped particle in a slowly tilting bistable landscape. *Figure reproduced from [65].*

opment of closed-loop control strategy for locomotor rehabilitation, for which some authors of the French control community have started contributing. For instance, closed-loop control strategies have been developed to reduce the time-variance of muscle response under functional electrical stimulation [60]. Closed-loop approaches were also developed to control diaphragm of patients with *cervical spinal cord injury* [115].

Hemodynamic response

Finally, a number of neuroimaging methods such as fMRI or fNIRS estimate neural activity by measuring metabolic proxies, such as the increase of cerebral blood flow that support this activity. Estimating the brain hemodynamics response - essentially a transfer function - is key to the precision of such methods, and has seen a number of control-theory contributions, both in terms of modeling (e.g. coupled ODE-PDE models [6]) and identification (e.g. time-varying autoregressive models [97]). More generally, the hemodynamic response is at the core of closed-loop strategies for *transcranial direct current stimulation* (tDCS) [97].

3 Perspectives and open questions

The “dynamical renaissance” in neuroscience is an opportunity for control science

The field of neuroscience is undergoing a profound conceptual shift toward frameworks rooted in dynamical systems theory which, although reminiscent of early achievements such as the Hodgkin–Huxley and FitzHugh–Nagumo models, has been described as a “dynamical renaissance” [40]. Notions such as latent states [20], bifurcations [95], embeddings [87] and attractors [108] are increasingly used to describe neural computations and brain states in mainstream neuroscience work. Yet, these concepts are often invoked qualitatively, as observations made from empirical data, without being connected to formal modeling or analysis as dynamical systems – tools that control theory can provide. This convergence presents the control community with a pivotal moment and an opportunity to integrate control-theoretic principles such as stability analysis, feedback design, observability, and controllability into emerging dynamical models of brain function [70, 25, 67].

A critical trade-off between the need for models and the need for data

The field of control-engineering approaches to neuroscience faces a fundamental tradeoff between the need for models and the need for data (Fig. 1-bottom). On one hand, experimental data is indispensable: it provides inspiration for model formulation and allows the calibration of parameters; beyond access to pre-recorded data, the opportunity to experiment is also needed for identification purposes and to validate control procedures. On the other hand, control science, both for analysis and command, has historically relied on first-principle mechanistic models, typically expressed as systems of ordinary or partial differential equations. Such biophysical models of brain function, however, are usually only available at the neuronal-population level, where data are scarce and experimentation is constrained by considerable ethical, regulatory, and practical barriers. For instance, although theoretical work has explored the control of the subthalamic nucleus–globus pallidus externus (STN–GPe) network in Parkinson’s disease, advancing beyond simulation would require access to pre-recorded deep-brain stimulation data or, ideally, the ability to test control schemes in live patients, both of which remain formidable challenges.

At the other extreme, data at the whole-brain scale have never been more accessible: affordable EEG systems and brain–computer interface toolkits allow the rapid collection of neural signals in healthy participants, often under lightweight ethical oversight and at minimal cost. However, such data do not lend themselves naturally to classical model-based analysis, as whole-brain dynamics cannot be succinctly represented by low-dimensional ODEs or PDEs, but instead require data-driven representations such as NeuralODEs [27]. For these recent data-driven models, much work remains to be done in the domain

of analysis and control: for instance, providing strong evidence for the dynamical properties of the learned systems, developing procedures to enforce physical laws (e.g. stability) during training, or developing methods for uncertainty quantification and robustness to noise.

In short, the field faces a methodological gap: where data is abundant, the tools remain underdeveloped; where these tools exist, data is scarce.

Progress will likely require movement along one of two complementary paths: first, finding new, ethically and practically accessible experimental paradigms at the cellular-population scale (e.g., organ-on-chip models, which are increasingly being developed in academic engineering departments and could provide opportunities for easier collaboration); or developing a new methodological corpus that integrates control theory with scientific machine learning, enabling principled analysis and control of complex, data-driven models [8].

A two-way theoretical opportunity

The application of control-science principles to neuroscience presents a two-way opportunity for novel theoretical contributions in both fields.

For the field of neuroscience, the ‘internal model’ principle [4] is one illustration of how control theory can help understanding neuronal mechanisms and guiding experimental design to test biological hypotheses. Many sensorimotor mechanisms (e.g. producing and monitoring one’s own speech, [84]) are indeed consistent with the use of internal models of either the organism or its environment. Knowing the mathematical ground of internal models allows to predict fundamental ingredients of their neuronal implementation [11, 18]. A close collaboration between experimental neuroscientists and control theorists has the potential to address fundamental questions pertaining to the level at which internal models are explicitly coded in the nervous system and whether internal models and feedback control are coded on separate neuronal substrates.

Another key theoretical neuroscience question is whether the brain, or some of its structures, operates close to a critical state, meaning at the edge of qualitatively different behaviors. While some experimental evidence pleads for this hypothesis [61], other authors object that the employed statistical signatures of self-organized criticality (such as the power-law distribution of neuronal avalanches) can be reproduced far from any critical behavior [107]. In mathematical terms, self-organized criticality can be translated as the ability of a dynamical system to autonomously tune its parameters to a bifurcation value. It is thus a feedback mechanism, thus particularly well suited to control theory tools, the challenge lying mostly in the distributed nature of the control law implementation (each neuron adapting only its own dynamics, with a very limited knowledge of the overall population dynamics). Despite this familiarity, the control community has not yet devoted significant effort to this question, with the notable exceptions of [78, 37].

Conversely, biological neuroscience can be of great inspiration to advance control theory [74]. Precision, rapidity, robustness to uncertain and fluctuating environment, energy efficiency, adaptability, redundancy, distributed comput-

ing, ...: the brain is by far the greatest controller device we can think of. Progresses in the understanding its working mechanisms can therefore be of decisive inspiration for enhanced control design. A promising avenue in that direction lies on the specificity of the elementary brain computation primitive: the action potential or spike. This fast response of a neuron to a sufficient stimulation constitutes a continuous-time signal. Yet, it also endows a digital component, as the number of spikes generated by a neuron can be counted. This hybrid nature could provide a fundamental bridge between automata (discrete events) and physical systems (continuous time). The idea of post-digital computing devices relying on spikes and rhythms, rather than bits and clocks, is not new [76], yet spiking control systems is recently receiving a growing attention [94]. Systematic control design tools and performance guarantees are still needed in that framework.

The promise of clinical applications in neurorehabilitation

Recent neuroscientific work at the interaction with machine-learning has produced spectacular proofs of concept in neuroprostheses able e.g. to restore the capacity of walking [58] or speaking [72] in patients with severe paralysis. Many of the obstacles separating these prototypes from mainstream applications - issues of safety, robustness, adaptation to inter-individual differences and intra-individual plasticity - are topics related to control theory. Two particular domains where we see opportunities for important contributions of control engineering are brain-machine interfaces and neuromodulation.

Brain-machine interfaces (BMI) relate to developments aiming to allow direct interaction between the central nervous system and a computer or a robot. In these applications, neural activity is measured, decoded, and exploited by decoder to send appropriate commands to the artificial device. Feedback is most often visual [96], although more elaborate sensory feedback is sometimes employed for research purposes [51]. Brain-machine interfaces have a wide scope of possible applications, covering rehabilitation, diagnosis, assistive technology, robotics, and gaming. They fit ideally the classical framework of control theory, in which the controller is the brain, the control signal is the neural activity, the system is the machine, and the measurement results from the considered biofeedback. Despite this analogy, control theory is not yet fully exploited to enhance brain-machine interfaces, particularly in terms of robustness to the non-stationarity of brain signals, safety, shared control between the brain and a possible artificial control device and appropriation of the prosthesis.

A related topic that still requires deepened investigations is neuromodulation, meaning the ability to steer neural activity in specific brain regions. Different types of actuation can be used for that purpose, including electrical stimulation, magnetic stimulation, and optogenetics. The possibility to artificially influence brain activity is a key instrument for fundamental brain research, for instance to determine the role of a given brain structure on a specific function. Neuromodulation proves also useful for medical applications, including spinal cord injury [110], epilepsy [41], Parkinson's disease, essential tremor,

depression, and obsessive compulsive disorders [69]. More and more research effort is devoted to its use in more advanced cognitive processes, such as attention and memory [53]. While neuromodulation has traditionally been achieved in open-loop, strong benefit is expected from a closed-loop approach in which the delivered stimulation signal is adapted in real time to measurements from the brain or other body parts [52, 21]. As already mentioned, the first medical device allowing for closed-loop deep brain stimulation has been approved just a few months ago in Europe. Here also, the relevance of control theory catches the eye: the plant is the targeted brain structure, the actuator is the stimulation device and the sensor is the recorded biofeedback. Significant collaborative effort is still needed to go beyond the envisioned on-demand approaches, in which a predefined stimulation is delivered upon the detection of some specific biomarker.

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