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Adaptive Internal Models in Neuroscience

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Contents

Adaptive Internal Models in Neuroscience

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ABSTRACT

This monograph examines in mathematical terms an open question in neuroscience on the function of the cerebellum, a major brain region involved in regulation of the motor systems, speech, emotion, and other cognitive functions of the body. Reasoning from the perspective of control theory, we make a hypothesis that the primary function of the cerebellum is disturbance rejection of exogenous reference and disturbance signals. This brings to the fore the internal model principle of control theory: that any good controller must include a model of its environment.

The monograph is structured around a pursuit of the validity of this hypothesis. Given the system level architecture and the measurement structure of the cerebellum, is disturbance rejection mathematically feasible? Second, is a disturbance rejection interpretation consistent with experiments? Specifically we investigate the possibility that the cerebellum provides adaptive internal models of signals generated by the environment. After a brief historical overview of computational theories of cerebellar function and of the relevant parts of control theory in the area of regulator theory, we carry out a more or less chronological review of subjects in control theory that impinge on our investigation.

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We begin with classical regulator theory with its characteristic features of a known plant and known frequency content of disturbance and reference signals. We then pause to examine classical regulator theory from the perspective of modeling the cerebellum, finding that several aspects are not well suited to this endeavor. Foremost is the unrealistic assumption that the plant and exosystem parameters are apriori known. More subtle issues arise from the fact that classical regulator theory developed in a setting where output and error measurements are regarded as persistent, an assumption not valid in the brain. Next, we review adaptive control theory, organized in terms of error models. The main control theoretic tools appear in Section 5, as a synthesis of classical regulator theory and adaptive control, where we present several adaptive internal model designs.

To test our hypothesis on cerebellar function, we apply adaptive internal model designs to several motor systems regulated by the cerebellum. These include the slow eye movement systems: the vestibulo-ocular reflex, gaze holding, smooth pursuit, and the optokinetic system. We also study discrete time behaviors regulated by the cerebellum: the saccadic eye movement system and, more generally, visuomotor adaptation. The results from these modeling studies suggest that an interpretation of cerebellar function in terms of disturbance rejection is compelling, with the potential to provide a unifying framework to explain how the cerebellum can contribute to so many different systems in the body. The monograph concludes with suggestions for future research directions.

1

Introduction

This monograph makes contributions to the field of *systems neuroscience*. Systems neuroscience aims to understand the brain at a systems or behavioral level, particularly considering the interactions between different brain regions and the rest of the body. By way of contrast, *systems biology* regards the study of biological processes, particularly at the cellular level.

When one peruses the literature on systems neuroscience one rather quickly stumbles upon terms such as *motor control*, *adaptation*, *learning*, *perception*, *consolidation*, and *internal models*, among others. All words that pique the curiosity of the control theorist. Questions that arise are: what control architectures does the brain use to solve problems of motor control and adaptation? Are these control architectures the same as the ones already employed in robotics and engineering? Where are these internal models in the brain? How does the brain deal with disturbances? What control problems has the brain already solved through its evolutionary advantage that control theorists with their engineering models and principles have not?

This monograph initiates an investigation into some of these questions. We were particularly intrigued by the pervasiveness of discourse on internal models in the brain in the neuroscience literature, contrasted with a void regarding internal models of control theory. This dichotomy was highlighted in a session at the 2018 IEEE Conference on Decision and Control (Huang *et al.*, 2018), with the hope that the two research areas could be brought closer together.

Our working hypothesis is that the internal model principle of control theory is operating in one or more areas of the brain. This is not a wild conjecture since neuroscientists have been discussing internal models for at least 40 years. Rather it shifts the focus from the role of internal models to replicate the dynamics of a system to be controlled (Jordan and Rumelhart, 1992; Wolpert and Kawato, 1998) to a role of internal models to replicate exogenous signals (Francis and Wonham, 1975). This shift of interpretation brings into view developments in control theory on the design of internal models, developments which have, up to now, not been regarded as relevant to brain modeling by either research community.

Validating our hypothesis requires working both on the control theory side and on the neuroscience side. The task involves carefully examining the experimental record in neuroscience for any evidence of behavior that reflects the internal model principle. On the other side, we review developments in control theory to determine if available internal model designs are suitable for brain modeling (see Section 3). This monograph offers a curated and condensed view of two major thrusts of the last 50 years in control theory: *regulator theory*, discussed in Section 2, and *adaptive control*, discussed in Section 4. The synthesis of these two areas (a process still ongoing) has resulted in *adaptive internal models*, discussed in Section 5.

On the neuroscience side we have particularly focused on experimental results for the *oculomotor system*. Study of the oculomotor system proves to be immensely gratifying because the brain structures and the neural circuits are reasonably well known; the experimental record is thorough and unrelenting; the oculomotor research community has a history of outstanding modelers (Robinson, 1981; Zee, 2018); and finally, the oculomotor system is widely regarded to provide the blueprint for all other motor systems. Results for the oculomotor system as well as visuomotor adaptation are found in Sections 6–9. These sections draw upon our prior work (Battle and Broucke, 2021; Broucke, 2020; Broucke, 2021; Gawad and Broucke, 2020; Hafez *et al.*, 2021).

1.1 Internal Models in Control Theory

Regulator theory and the associated *regulator problem* regard a control specification to make an error signal of a control system tend to zero asymptotically, despite the presence of persistent, exogenous disturbance and reference signals entering the control loop. A key assumption is that the disturbance and reference signals can be modeled by a linear *exosystem*. A controller that satisfies the requirements of the regulator problem is called a *regulator*.

Starting from the 1970s, regulator designs progressed from multi-input multi-output (MIMO) linear time-invariant (LTI) systems with known plant and exosystem parameters, to uncertain nonlinear systems (Byrnes *et al.*, 1997), and finally to regulator designs when neither plant nor exosystem parameters are known. Of particular relevance are regulator designs based on *adaptive internal models*, which appeared in the control theory literature in the mid 1990s to early 2000s (Bodson *et al.*, 1994; Bodson and Douglas, 1997; Nikiforov, 1996; Nikiforov, 1997a; Marino and Tomei, 2000; Marino and Tomei, 2003a; Serrani and Isidori, 2000; Serrani *et al.*, 2001). We present highlights of this progression for linear systems.

Known Plant and Exosystem. When both the plant parameters and exosystem parameters are known, the solution is given in Davison (1976), Francis and Wonham (1976), and Francis (1977), where necessary and sufficient conditions for regulation are provided. The solution relies on the design of an *observer* or a *servocompensator* that asymptotically reconstructs exogenous signals using an internal model. The internal model is not adaptive. These developments are reviewed in Section 2.

Known Plant and Unknown Exosystem. In the case when the plant model is known and only the dimension of the exosystem is known, then the adaptive internal models in Nikiforov (1996) and Marino and Tomei (2003b) provide an asymptotic estimate of exogenous signals. If only an upper bound on the dimension of the exosystem is available, but the plant is minimum phase, asymptotically stable, and has known relative degree, then the adaptive internal model in Marino and Tomei (2007) asymptotically reconstructs exogenous signals. For this design, persistent excitation guarantees exponential convergence of observer and parameter estimation errors. Linear systems with known parameters but subject to unknown time delays in the control loop were studied in Gerasimov *et al.* (2020), Gerasimov *et al.* (2019a), Gerasimov *et al.* (2019b), and Nikiforov *et al.* (2020). In the case of discrete-time systems, a design based on averaging theory is developed in Guo and Bodson (2009). A different approach for discrete-time systems appears in Fiorentini *et al.* (2006) but requires the online solution of a Sylvester equation at each time-step.

Unknown Plant and Known Exosystem. It is possible that uncertainties are limited to the plant, while the exosystem is known perfectly. If the plant is stable, then an adaptive internal model design is given in Marino and Tomei (2015). It uses knowledge of the signs of the DC gain and either the real or imaginary part of the frequency response at the frequencies of the exosystem.

Unknown Plant and Unknown Disturbance. The most complex case is when both the plant model and the exosystem are uncertain. There are a number of results for this problem. *Kreisselmeier observers* and *backstepping* are proposed in Nikiforov (1997a) to design adaptive internal models to reconstruct exogenous signals assuming the order of the exosystem is known. More generally, novel techniques for designing internal models to reconstruct exogenous signals were presented in Nikiforov (2004a) and Nikiforov (2004b). The case of output tracking a measurable reference signal with unknown frequencies by an unknown single-input single-output (SISO) LTI system using output feedback was considered in Nikiforov (1997b).

If the plant is minimum phase with known relative degree and bounds on parameter uncertainties (for both the plant and exosystem) are known, then the design in Marino and Tomei (2011) may be used. In Marino and Tomei (2016), the design of Marino and Tomei (2015) was extended by estimating disturbance frequencies online. The design relies on averaging theory, and it is assumed that the plant is stable and the frequency response information previously mentioned is available. A discrete-time solution is given in Tomei (2017), also using averaging theory. An alternative design for discrete-time systems appeared in Hoagg *et al.* (2008) based on deadbeat control and employing a logarithmic Lyapunov function argument for stability and parameter convergence.

Uncertain plants and exosystems are considered in Basturk and Krstic (2012) and Basturk and Krstic (2014) when only state derivative feedback measurements are available to the internal model. Unknown time delays in the input or state are addressed in Basturk and Krstic (2015) and Basturk (2017). Finally, Yilmaz and Basturk (2019) considers unknown minimum-phase LTI systems with known relative degree and system order. Again using Kreisselmeier observers and adaptive backstepping as in Nikiforov (1997a), the internal model design in Yilmaz and Basturk (2019) rejects unknown sinusoidal exogenous signals while making the system output track a given reference trajectory using only output feedback.

1.2 Internal Models in Neuroscience

Many parts of the brain have been implicated in motor control and motor learning including, but not limited to, the *basal ganglia*, the *motor cortex*, and the *cerebellum*. What is of greatest interest to us is that neuroscientists have posited that the cerebellum, in particular, contains internal models. Here we review relevant theories of cerebellar function. Our review is not complete, but highlights theoretical model development since the 1970s, focusing on those theories that interpret cerebellar function in terms of adaptive control, adaptive filters, and internal models; see Barlow (2002) for a detailed discussion and Montgomery and Bodznick (2016) for a historical perspective.

In 1967, Eccles, Ito, and Szentagothai published a landmark book on the neuronal structure of the cerebellum (Eccles *et al.*, 1967). Their use of the term "neuronal machine" invited comparison with computer science and control theory. The striking uniformity of the cerebellum (see Section 3.2), despite the fact that it receives inputs from many parts of the cerebral cortex, inspired Marr (1969) and Albus (1971) to propose computational models of the cerebellar circuit as a spatial pattern classifier. The Marr-Albus theory provided significant detail concerning the neuronal circuitry and the specific wiring of the cerebellum, with a focus on modifiable synapses to account for learning. The Albus theory arguably provided the first neural network model of the cerebellum.

Following this, Calvert and Meno (1972) developed a spatio-temporal model of cortical activity and applied it to the cerebellum. They operated under the assumption that while the true input-output relationship is highly nonlinear (exhibiting such phenomena as saturation and refractory periods), the cerebellum may be modeled as a linear system since the ensemble behavior appears linear. To the best of our knowledge, this is the first attempt at using linear models to qualitatively describe cerebellar function and behavior, albeit at a neuronal level rather than at a higher behavioral level.

In Hassul and Daniels (1977), the authors observed discrepancies between experimental results and the predictions of Calvert and Meno (1972). They opted for a simpler model by treating the cerebellar cortex as a lumped linear system, bypassing the need to model the spatial structure of neuronal circuitry in the cerebellum. Their model predicted that the cerebellum implements a form of lead-lag compensation to maintain loop stability in spite of the substantial delays involved in signal paths to and from the cerebellum.

While the Marr-Albus model has been highly influential both on subsequent theory and experimentation, it did not account for the temporal aspect of adaptation and learning, considering that information in the central nervous system (CNS) is conveyed by continuous time (analog) signals that are frequency-modulated by nerve impulses. To address this shortcoming, Fujita (1982) proposed an *adaptive filter* model inspired by the least mean square algorithm in adaptive signal processing (Widrow and Stearns, 1985). This model built on the work in Hassul and Daniels (1977) to provide a mechanism by which the lead-lag compensator could be made adaptive in order to account for the learning capabilities attributed to the cerebellum. If some performance metric is defined on the output of the cerebellum by way of some reference or target output, then the adaptive filter minimizes the mean square error of this performance metric. Using the adaptive filter model, Fujita was able to successfully simulate the vestibulo-ocular reflex (Fujita, 1982), a critical step in translating neuronal models to tangible motor behavior. A comprehensive review of this work can be found in Ito (1984). The adaptive filter model has been further developed by Dean, Porrill, and co-workers to account for experimental discoveries on synaptic plasticity and noise cancellation (Dean *et al.*, 2010); see below.

The idea that the cerebellum contains internal models appears to originate in the work of Ito and Kawato (Ito, 1970; Kawato *et al.*, 1987). Internal models are defined as neural mechanisms that can mimic the input-output characteristics (or their inverses) of the motor apparatus (Kawato, 1999; Miall and Wolpert, 1996; Wolpert *et al.*, 1998). *Forward internal models* predict sensory consequences from *efference copies* of issued motor commands, whereas *inverse internal models* calculate feedforward motor commands from desired reference trajectories.

The inverse model interpretation of the cerebellum was elaborated in Gomi and Kawato (1992) and Kawato and Gomi (1992) as *feedback error learning*, related to the *computed-torque method* in robotics (Spong *et al.*, 2005). The cerebellum builds an inverse model of the part of the motor system to be controlled. It takes desired reference trajectories which are assumed to be available as measurements and converts them to feedforward motor commands. The difference between actual motor commands (which include feedback terms) and feedforward motor commands generates a *motor error*, which drives the adaptation process to improve the estimate of the inverse model.

The forward model interpretation of the cerebellum has been elaborated over a series of papers (Dean *et al.*, 2002; Porrill *et al.*, 2004; Dean and Porrill, 2008; Dean *et al.*, 2010). The forward model transforms motor commands (available as efference copies) to predictions of motor action. These predictions of motor action are compared to the actual system response to generate an output (sensory) error, which, in turn, is used to train the cerebellum to generate improved motor commands. Dean and Porrill further interpret the function of the cerebellum to decorrelate sensory signals from error signals. This interpretation fits well within the mathematical framework of regulator theory in which exogenous (sensory) signals must be removed or “rejected” from errors, if those errors are to be driven to zero.

Several other theories of cerebellar function have been proposed. A Smith predictor model of the cerebellum was suggested in Miall *et al.* (1993). A *Smith predictor* is a compensator that counteracts long delays in the feedback path (Smith, 1959). Such a control mechanism would allow to overcome the long transport delays from visual feedback to motor command, for instance. Other theories propose that the cerebellum is a *Kalman filter* (Paulin, 1989), an *optimal controller* (Jordan and Todorov, 2002) or a *Bayesian state estimator* (Paulin, 2005). Despite numerous proposals, there is no consensus, to date, on a computational model of the cerebellum.

This monograph describes a different approach to modeling the cerebellum. We delegate to the cerebellum a primary role of satisfying the internal model principle of control theory (Francis and Wonham, 1976). On this basis, we then apply adaptive internal models from the control literature on regulator theory. Despite a different angle of attack, our approach and resulting models may be regarded as an extension of the class of models that derive from the adaptive filter interpretation of cerebellar function.

1.3 Control Theory and Systems Neuroscience

Control theory has contributed to understanding many biological processes, but the application of control theory in system-level studies of the brain is a relatively new endeavor. One must grapple with what level in the hierarchy of neurological processes to focus for a specific modeling problem (Gernstner and W. Kistler, 2014). Single neurons or small groups of neurons are modeled using the Hodgkin-Huxley model of action potential propagation, or larger groups of neurons comprising neural circuits of modest size may be modeled using population dynamic models such as the Wilson-Cowan model. Next come studies of brain regions such as the visual cortex, the hippocampus, and the thalamus, which likewise draw upon neural network and population dynamic models. At the highest level is the study of networks of brain regions and their interaction with the body, as in the study of the motor systems, of Parkinson's disease, and so forth. See Gernstner and W. Kistler (2014) and Dayan and Abbott (2001) for further discussion on computational methods. The emerging interface between control theory and systems neuroscience is further discussed in Madhav and Cowan (2020), Schiff (2009), and Schiff (2012).

This monograph attends to the highest level of the hierarchy by exploring the functional role of the cerebellum and how it contributes to motor systems in humans. However, a number of other themes are being explored at the interface between systems neuroscience and control theory.

- In addition to the work of David Robinson and others on the oculomotor system (Robinson, 1981), fundamental concepts of *linear system theory* such as feedback and controllability have been applied to clarify and understand the brain at a systems level. For example, Gu *et al.* (2015) explore the degree to which the network structure of the brain determines the level of brain activity in connected brain regions. To make precise their idea, the authors utilize a discrete-time linear system whose state vector captures neural activity in distinct brain regions. The controllability Gramian is used to obtain quantitative predictions on brain activity based on network structure. Khalil and co-workers studied micro-stimulation of the *basal ganglia* and Parkinson's disease by using using ideas from MIMO linear system theory (Liu *et al.*, 2010; Liu *et al.*, 2011).

- *Optimal control theory* has been applied to clarify how the brain manages redundant degrees of freedom of the limbs to achieve repeatable, energy efficient movements (Jordan and Todorov, 2002). The interactions between the motor cortex (M1), basal ganglia, and motor periphery to produce multi-joint movements such as arm reaches have similarly been explored using optimal control theory (Scott, 2004). Optimal control theory was also applied in Gu *et al.* (2017) to understand how the brain makes transitions through different brain states - states of neural activity within discrete brain regions.

- *Dynamical system theory* has held a prominent place both in systems neuroscience and systems biology (Iglesias and Ingalls, 2009). For instance, Slotine and co-workers utilized nonlinear contraction analysis to model action selection by the basal ganglia (Girard *et al.*, 2008). Dynamical system theory has been applied to large scale models of the cerebral cortex, for instance, to model epileptic seizures, sleep, and anesthesia (Breakspear, 2017).

- *Network theory* is another key contributor to the study of the brain at a systems level, taking inspiration from the area of network biology (Barabasi and Oltvai, 2004). Hierarchically organized networks of neurons combined with linear threshhold population models were utilized in Nozari and Cortes (2021a) and Nozari and Cortes (2021b) to analyze the emergent behavior of selective attention. Many other works treat the brain from a network perspective.

Finally, it is worth mentioning that while this monograph focuses on the application of the internal model principle to understand the cerebellum, the principle has also found application in systems biology. Doyle and co-workers (Yi *et al.*, 2000) applied the internal model principle to show robustness to disturbances in bacterial chemotaxis. Their analysis specifically regards disturbance rejection of constant exogenous signals using integral feedback.

1.4 Notation

Let $\mathbb{R}$ denote the real numbers, $\mathbb{R}^+$ denotes the non-negative real numbers, and $\mathbb{C}$ denotes the complex numbers. For a matrix $A \in \mathbb{R}^{n\times n}$, $\sigma(A)$ denotes its *spectrum*; the elements of $\sigma(A)$ are the eigenvalues of A. For a symmetric matrix $A \in \mathbb{R}^{n\times n}$, $\lambda_{max}(A)$ denotes the largest real eigenvalue of A. Also for symmetric $A \in \mathbb{R}^{n\times n}$, we write $A > 0$ if A is positive definite.

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