

Internal Models in Control, Biology and Neuroscience

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Abstract—This tutorial paper deals with the Internal Model Principle (IMP) from different perspectives. The goal is to start from the principle as introduced and commonly used in the control theory and then enlarge the vision to other fields where “internal models” play a role. The biology and neuroscience fields are specifically targeted in the paper. The paper ends by presenting an “abstract” theory of IMP applicable to a large class of systems.

I. INTRODUCTION

By the 1930s, thanks to research at the Bell Telephone Laboratories, the mathematical foundation of “classical” linear feedback control based in the frequency domain was soundly established. Its implications were the following:

- 1 Error feedback (i.e. output feedback followed by the precise differencing of output and input reference signals to form the tracking error) by itself can reduce parameter sensitivity, and final tracking error, but only at the expense of high loop gain.
- 2 Error feedback, plus an internal model of the reference signal generator, together reduce final tracking error to exactly zero (i.e. ensure perfect tracking), regardless of (reasonable) parameter perturbations, while requiring only moderate average loop gain.

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A familiar example is the “integrator” component of PID control used to track (specifically) step reference inputs. In general the price to be paid for perfect tracking was extra control complexity, including a stabilising compensator, specific to the reference signals to be tracked. Later, Otto Smith [68] incorporated an internal model in his scheme of predictive control, while from the 1970s the study of parameter-insensitive perfect asymptotic tracking led to the recognition of both error feedback and the internal model as necessary and sufficient structural features of “robust” linear multivariable systems. The IMP, in turn, was fully developed for linear multivariable systems in the 70s in the set of seminal works [16] and [13] in which the step reference generator of PID control was generalised to an arbitrary linear exogenous system (“exosystem”) as well as outputs of arbitrary vector dimension. The relevant aspect of the framework developed in those papers relies in the complete characterisation of necessary and sufficient conditions for the solution of the problem of output regulation in a *robust* way, namely in presence of uncertainties, appropriately defined, in the regulated plant. The principle, in turn, claims that asymptotic regulation is achieved in presence of plant parameter variations “only if the controller utilises feedback of the regulated variable, and incorporates in the feedback path a suitably reduplicated model of the dynamic structure of the exogenous signals which the regulator is required to process”. Generalisations to nonlinear systems (with a differential geometry perspective) were initially obtained in [22], [23] (see also [86]) mainly in case of step reference signals and then extended to general exosystems in [30], [25]. Since then, many attempts have been done to make the nonlinear framework even more general and constructive and nowadays output regulation is still an active research area in control theory (see in this regard Section VI).

In psychology and human experience generally the IMP is by no means new. According to Kenneth Craik [12], “Only an internal model of reality - this working model in our minds - enables us to predict events which have not yet occurred in the physical world, a process which saves time, expense, and even life. In other words

the nervous system is viewed as a calculating machine capable of modelling or paralleling external events, and this process of paralleling is the basic feature of thought and of explanation.” Mark Twain, apprenticed as a teenager to a Mississippi river pilot, later [78] reports his mentor as saying, “You only learn *the shape* of the river; and you learn it with such absolute certainty that you can always steer by the shape that’s *in your head*, and never mind the one that’s before your eyes”. We shall later indicate what that “shape of the river” might be (see Section V). Our mimicry of the IMP with automata (or discrete dynamics) is nothing new either; as Thomas Hobbes [24] declared, “For seeing life is but a motion of limbs ... why may we not say, that all automata (engines that move themselves by springs and wheels as doth a watch) have an artificial life?”

The idea that an appropriate model of the environment where the system operates is somehow incorporated in the system itself (not necessarily in a closed-loop fashion) whenever it shows special properties, such as the ability of adapting its behaviour to external stimuli or executing smart operations in presence of partial information, is then ubiquitous in many fields of science that go well beyond control theory. As presented in [71], the IMP, as with any “principle” in control theory and more generally in mathematics, is not a theorem but rather a “mold” for many possible frameworks and theorems declined in different ways according to the specific scientific field.

For instance, internal models are crucial for the proper functioning of many biological organisms that must be able to detect changes in their environment and adjust their internal states accordingly, a process commonly referred to as “homeostasis” or “adaptation” (see [71], [2]). For example, successful chemotaxis (movement towards high concentrations of chemical attractant) of *E. coli* depends on the ability of the bacteria to adapt to step changes in chemoattractant ([1]). In terms of terminology commonly used in control theory this capability is related to the presence of “blocking zeros” in the transfer function modelling such a bio systems.

Similarly, in neuroscience it is clearly observed that the brain allows vertebrates to act proactively rather than reactively, to acquire new skills and to maintain mastered skills in response to changes in the external environment and the motor systems. There are many reasons to believe that it does this by computing the expected sensory consequences of a given motor command, and producing sensory prediction error signals

when the actual sensory input does not match expectations. The expected consequences are indeed captured by an internal model that is rapidly updated to enable the motor system to learn to expect unexpected sensory inputs ([7]) and respond appropriately. Properties of this kind are observed also in invertebrates whose nervous system implements prediction of the sensory consequences of action ([82], [50]). In terms of control terminology, *forward models* are used to predict the sensory consequences of actions and *inverse models* are used to produce motor commands that adapt to the plant. These internal models, along with models of the environment, are thought to underlie the rapid, robust, and adaptive behaviour typically observed in vertebrates and invertebrates. Investigating the neural implementation of these computations is an active area of research.

In the paper we present an overview of the concepts and tools that are behind the IMP by bridging research skills and viewpoints from the above mentioned research areas. The main goal is to overview how the “mold” of the IMP developed in the control community and how it is declined in the two fields of bioengineering and neuroscience.

II. OUTPUT REGULATION FOR SYSTEMS MODELED BY ORDINARY DIFFERENTIAL EQUATIONS

A. Problem Formulation

The problem of robust output regulation aims at designing a feedback controller for an uncertain plant so that, in the resulting closed-loop system, all trajectories are bounded and the output asymptotically tracks a class of reference inputs (produced by an exogenous system), in the presence of a class of disturbances. To describe this problem, consider a (composite) plant described by

$$\begin{aligned} \dot{x} &= f(x, u, w, \mu) \\ \dot{w} &= s(w) \\ e &= h(x, u, w, \mu) \\ y &= h_m(x, u, w, \mu) \end{aligned} \tag{1}$$

with state $x \in \mathbb{R}^n$, control input $u \in \mathbb{R}^m$, exogenous input $w \in \mathbb{R}^r$, tracking error $e \in \mathbb{R}^m$, measurement output $y \in \mathbb{R}^{p_m}$, and uncertain constant parameter vector $\mu \in \mathcal{P} \subset \mathbb{R}^p$. It is assumed that the equilibrium at the origin of the exosystem $\dot{w} = s(w)$ is stable (in the sense of Lyapunov) and, for any $w(0)$, the solution of exosystem exists and is bounded over $t \in [0, \infty)$. It is also assumed that the nominal value of the uncertain

parameter μ is $\mu = 0$. The plant (1) is said to be known exactly if $\mathcal{P} = \{0\}$.

We consider the control law described by

$$\begin{aligned} u &= k(z, y) \\ \dot{z} &= f_z(z, y), \end{aligned} \quad (2)$$

with state $z \in \mathbb{R}^{n_z}$. The control law (2) includes the full information control when $h_m(x, u, w, \mu) = \text{col}(x, w)$, state feedback control when $h_m(x, u, w, \mu) = x$, and error output feedback control when $h_m(x, u, w, \mu) = e$ as special cases. Let $x_c = \text{col}(x, z)$ be the state of the closed-loop system with dimension n_c . Then, the closed-loop system can be written as

$$\begin{aligned} \dot{x}_c &= f_c(x_c, w, \mu) \\ e &= h_c(x_c, w, \mu) \end{aligned}$$

for some functions f_c and h_c . For convenience, it is assumed that all the functions here are sufficiently smooth and defined globally on the appropriate Euclidean spaces, with the value zero at the respective origins, and $f(0, 0, 0, \mu) = 0$, $h(0, 0, 0, \mu) = 0$ and $h_m(0, 0, 0, \mu) = 0$ for all $\mu \in \mathbb{R}^p$.

Various versions of the output regulation problem have been defined over the years. Here we unify these versions to the following.

Definition 1 (Output Regulation Problem) *For some subsets $X_c \subset \mathbb{R}^{n_c}$, $W \subset \mathbb{R}^r$, and $\mathcal{P} \subset \mathbb{R}^p$, which contain the origins of the respective Euclidian spaces, find a control law of the form (2) such that, for all $x_c(0) \in X_c$, all $w(0) \in W$, and all $\mu \in \mathcal{P}$, the solution of the closed-loop system exists and is bounded for all $t \geq 0$, and is such that*

$$\lim_{t \rightarrow \infty} e(t) = 0. \quad (3)$$

Definition 1 includes several special versions. For instance, when $\mathcal{P} = \{0\}$, the problem is a non-robust output regulation problem, when X_c , W , and \mathcal{P} are arbitrarily small neighbourhoods of the origins of their respective Euclidian spaces, the problem is called local robust output regulation problem, and when $X_c = \mathbb{R}^{n_c}$, and $W \subset \mathbb{R}^p$ and $\mathcal{P} \subset \mathbb{R}^r$ are arbitrarily large compact sets, respectively, the problem is called global robust output regulation problem. Finally, if the problem can be solved for arbitrarily large compact sets $X_c \subset \mathbb{R}^{n_c}$, $W \subset \mathbb{R}^p$, $\mathcal{P} \subset \mathbb{R}^r$, then the problem is called semi-global robust output regulation problem.

B. The Origin of Nonlinear Output Regulation

The output regulation problem was first studied for the class of linear time-invariant systems [13], [18], [17], to name just a few. The main tool for dealing with the output regulation problem is the IMP. By this principle, the robust output regulation problem of a given plant can be converted into an eigenvalue assignment problem of an augmented system composed of the given plant and a well defined dynamic compensator called internal model. In the mid 1970s, Francis and Wonham also considered the robust output regulation problem for a class of weakly nonlinear systems for the special case where the exogenous input is constant [17]. For this special case, they showed that a linear robust regulator designed based on the linear approximation of the plant can solve the local structurally stable output regulation problem for the nonlinear plant. Later, the output regulation problem of general nonlinear systems with the constant exogenous input was further studied in several papers [14], [22], [25]. In particular, Huang and Rugh related the solvability of the problem to the solvability of a set of nonlinear algebraic equations [25].

The research on the nonlinear output regulation problem for the general case where the exogenous input is time-varying started in 1990 when Isidori and Byrnes formulated and solved the output regulation of nonlinear systems with $\mathcal{P} = \{0\}$ and solved this problem by a feedforward control approach in [30]. In particular, Isidori and Byrnes linked the solvability of the nonlinear output regulation problem to a set of nonlinear partial differential and algebraic equations of the form (4) known as regulator equations. As the regulator equations are the foundation for the research of the nonlinear output regulation problem, we make their existence an assumption as follows:

Assumption 1 *There exist sufficiently smooth functions $\mathbf{x}(w, \mu)$ and $\mathbf{u}(w, \mu)$ with $\mathbf{x}(0, 0) = 0$ and $\mathbf{u}(0, 0) = 0$ that satisfy, for all $w \in W$ and $\mu \in \mathcal{P}$, the following equations*

$$\begin{aligned} \frac{\partial \mathbf{x}(w, \mu)}{\partial w} s(w) &= f(\mathbf{x}(w, \mu), \mathbf{u}(w, \mu), w, \mu) \\ 0 &= h(\mathbf{x}(w, \mu), \mathbf{u}(w, \mu), w, \mu). \end{aligned} \quad (4)$$

Based on the solution of the regulator equations, Isidori and Byrnes showed that if there exists a feedback gain K such that $x = 0$ is a locally exponentially stable equilibrium of $\dot{x} = f(x, Kx, 0, 0)$, then the following

control law

$$u = \mathbf{u}(w, \mu) + K(x - \mathbf{x}(w, \mu)) \quad (5)$$

solves the local output regulation problem of (1).

The law (5) presumes the availability of the exogenous input w as well that of the parameter vector μ . If only the error output is available for measurement and μ is uncertain, in order to solve a problem of (robust) output regulation one has to establish an appropriate nonlinear version of the IMP. A first progress in this direction was made in [26] by Huang, who, inspired by an example in [8], realised that the steady-state tracking error in a nonlinear system is a nonlinear function of the exogenous signals, and that a good internal model should be able to “reproduce” the solution of the nonlinear regulator equations. Based on this observation, Huang conceived the concept of k^{th} order internal model that leads to the solution of the robust output regulation problem for an uncertain nonlinear system provided the solution of the regulator equations of the system is a polynomial in the exogenous input [27], [29]. Subsequently, the robust output regulation problem was further pursued in [9], [33], generating various techniques and insights on this important issue.

The role of the internal model conceived in [27], [26] as well as in [9] is to convert the local robust output regulation problem to an eigenvalue assignment problem for the linear approximation of an augmented system. A regulator designed in this way, though, is unable to handle the global or semi-global robust output regulation problem with large \mathcal{P} . Moreover, like the one in [13], [18], [17], it cannot deal with uncertainties in the exosystem.

Since the mid 1990s, the research on the output regulation problem has made further advancement in two directions. First, the solution of the local robust output regulation problem has been extended to cover the cases of semi-global or global robust output regulation, with arbitrarily large \mathcal{P} . Second, adaptive output regulation techniques have been developed for dealing with uncertain exosystems. For these purposes, the original concept of nonlinear internal model was not adequate. Efforts have been made to give a more general characterisation of the idea of internal model. The key elements for this generalisation are the concepts of immersion and steady state generator, first proposed in [9], and then further enriched and generalised in a sequence of papers, say, [10], [28], [43], leading to a variety of internal models for different scenarios.

C. General Characterisation of Internal Models

The cornerstone for generalising the internal model is the concept of *system immersion*, described as follows.

Definition 2 *Suppose Assumption 1 holds. The autonomous system (with output u)*

$$\dot{w} = s(w), \quad u = \mathbf{u}(w, \mu) \quad (6)$$

is said to be immersed into the system

$$\dot{\xi} = \phi(\xi), \quad u = \gamma(\xi). \quad (7)$$

defined on some set Ξ containing the origin of \mathbb{R}^q if there exists a smooth mapping $\tau : W \times \mathcal{P} \rightarrow \Xi$, satisfying $\tau(0, 0) = 0$ such that

$$\frac{\partial \tau(w, \mu)}{\partial w} s(w) = \phi(\tau(w, \mu)), \quad \mathbf{u}(w, \mu) = \gamma(\tau(w, \mu)). \quad (8)$$

If this is the case, the triplet (τ, ϕ, γ) is said to be a steady state generator.

One can see that, if a steady state generator exists, then the input solution of the regulator equations can be reproduced by the autonomous system (7), which is independent of the uncertain parameter μ . Thus it is possible to use (7) to reproduce $\mathbf{u}(w, \mu)$, which is the necessary information for solving the output regulation problem.

Having introduced the concept of steady state generator, we are ready to give a general characterisation of the concept of the internal model as follows. Consider a system

$$\dot{\eta} = \alpha(\eta, u) \quad (9)$$

in which $\alpha : \mathbb{R}^q \times \mathbb{R}^m \mapsto \mathbb{R}^q$ is a sufficiently smooth function vanishing at the origin.

Definition 3 *Suppose system (1) admits a steady-state generator (τ, ϕ, γ) . System (9) is an internal model candidate if*

$$\frac{\partial \tau(w, \mu)}{\partial w} s(w) = \alpha(\tau(w, \mu), \gamma(\tau(w, \mu))). \quad (10)$$

The composition of the plant and the internal model candidate characterises what is called the “augmented” system

$$\begin{aligned} \dot{\eta} &= \alpha(\eta, u) \\ \dot{x} &= f(x, u, w, \mu) \\ e &= h(x, u, w, \mu). \end{aligned} \quad (11)$$

A consequence of the definition of internal model candidate is that, in the augmented system, the manifold $\mathcal{M} = \{(\eta, x, w) \mid \eta = \tau(w, \mu), x = \mathbf{x}(w, \mu), w \in \mathbb{R}^p\}$ is rendered invariant by means of the control $u = \mathbf{u}(w, \mu)$ and on such manifold the error output is identically zero. In fact,

$$\begin{aligned} \frac{\partial \tau(w, \mu)}{\partial w} s(w) &= \alpha(\tau(w, \mu), \mathbf{u}(w, \mu)) \\ \frac{\partial \mathbf{x}(w, \mu)}{\partial w} s(w) &= f(\mathbf{x}(w, \mu), \mathbf{u}(w, \mu), w, \mu) \\ 0 &= h(\mathbf{x}(w, \mu), \mathbf{u}(w, \mu), w, \mu). \end{aligned} \quad (12)$$

To further illustrate the role of the internal model, let

$$\begin{aligned} \bar{\eta} &= \eta - \tau(w, \mu) \\ \bar{x} &= x - \mathbf{x}(w, \mu) \\ \bar{u} &= u - \gamma(\eta). \end{aligned} \quad (13)$$

Then we have

$$\begin{aligned} \dot{\bar{\eta}} &= \bar{\alpha}(\bar{\eta}, \bar{x}, \bar{u}, w, \mu) \\ \dot{\bar{x}} &= \bar{f}(\bar{\eta}, \bar{x}, \bar{u}, w, \mu) \\ e &= \bar{h}(\bar{\eta}, \bar{x}, \bar{u}, w, \mu), \end{aligned} \quad (14)$$

which has the property that, for all trajectories $w(t)$ of the exosystem, and all $\mu \in \mathbb{R}^r$,

$$\begin{aligned} \bar{\gamma}(0, 0, 0, w(t), \mu) &= 0 \\ \bar{f}(0, 0, 0, w(t), \mu) &= 0 \\ \bar{h}(0, 0, 0, w(t), \mu) &= 0. \end{aligned} \quad (15)$$

Thus, if an output feedback control law of the form

$$\bar{u} = \bar{k}(\xi, e), \quad \dot{\xi} = g_\xi(\xi, e) \quad (16)$$

locally or globally stabilises the equilibrium of the augmented system (14) at the origin, then the following controller

$$\begin{aligned} u &= \gamma(\eta) + \bar{k}(e, \xi) \\ \dot{\eta} &= \alpha(\eta, u) \\ \dot{\xi} &= g_\xi(e, \xi) \end{aligned} \quad (17)$$

solves the robust output regulation problem for the original plant (1) locally or globally. In other words, the robust output regulation problem of the composite system (1) has been converted into a robust stabilization problem of the equilibrium at the origin of the augmented system (14).

D. Construction of Internal Models

From the previous discussion, it follows that the design of an internal model has to fulfill two purposes: (i) to make sure that the identity

$$\phi(\tau(w, \mu)) = \alpha(\tau(w, \mu), \gamma(\tau(w, \mu))) \quad (18)$$

is fulfilled, and (ii) to make sure that system (14) is stabilizable by means of a feedback of the form (16).

An internal model candidate is called a local or global internal model if it is such that the equilibrium of (14) at the origin is locally or globally stabilizable. However, finding a global internal model for a general nonlinear system is at least as intractable as ascertaining the global stabilizability of a general nonlinear system. Therefore, a more practical approach is to find an internal model candidate with some good properties, such as being input-to-state stable (ISS) [69].

First of all, it is stressed that a simple strategy to fulfill identity (18) is to pick

$$\alpha(\eta, u) = \phi(\eta) + N[u - \gamma(\eta)] \quad (19)$$

in which N is a matrix of design parameters that could be used to make the design of the stabiliser (16) easier. If this is the case, the main issue in the design of the internal model is to find a steady state generator. In what follows, we will overview a few typical internal models widely used in practice. For simplicity, we assume $m = 1$.

1) *Canonical linear internal model:* The canonical linear internal model was first proposed in [55] and later formalised in [61] and [62]. Suppose the system (6) is immersed to the linear system

$$\dot{\xi} = \Phi \xi, \quad u = \Gamma \xi, \quad (20)$$

and the pair (Φ, Γ) is observable. Let $\tilde{M} \in \mathbb{R}^{q \times q}$ and $\tilde{N} \in \mathbb{R}^{q \times 1}$ be any controllable pair with \tilde{M} Hurwitz such that the spectra of the matrices Φ and \tilde{M} are disjoint. The Sylvester equation $T\Phi - \tilde{M}T = \tilde{N}\Gamma$ has a unique nonsingular solution, and hence (19) can be written in the form

$$\alpha(\eta, u) = M\eta + Nu. \quad (21)$$

in which

$$M = T^{-1}\tilde{M}T, \quad N = T^{-1}\tilde{N}. \quad (22)$$

If we perform a coordinate transformation $\tilde{\eta} = T\eta$, then it can be verified that

$$\dot{\tilde{\eta}} = \tilde{M}\tilde{\eta} + \tilde{N}u \quad (23)$$

is also an internal model candidate of (1) corresponding to the steady-state generator $(\tilde{\tau}, \tilde{\phi}, \tilde{\gamma})$ with $\tilde{\tau}(\xi) = T\tau(\xi)$, $\tilde{\phi}(\xi) = T\Phi T^{-1}\xi$, and $\tilde{\gamma}(\xi) = \gamma T^{-1}\xi$. A particular advantage of (23) is that it can handle uncertain exosystems, see, for example, [40], [55], [62], [90].

2) *Two Nonlinear Internal Models*: The existence of the canonical linear internal model requires the system (6) be immersed to a linear system, which essentially requires that the nonlinearity in the plant (1) be of polynomial type. To weaken this restriction, two nonlinear models were developed later. The first one was given in [28] under the assumption that the system (6) can be immersed into a nonlinear system of the form (7) with $\phi(\xi) = \Phi\xi$ for some matrix Φ . Moreover, this assumption can be verified by the solution of the regulator equations. The particular form of this immersed system also leads to a nonlinear internal model of the form (19) with

$$\alpha(\eta, u) = (M + N\Gamma)\eta + N(u - \gamma(\eta)) \quad (24)$$

where Γ is the gradient of γ at the origin, the pair (Ψ, Γ) is assumed to be observable and the pair (M, N) is the same as (22). Under some assumption on γ , (24) is globally ISS.

Another nonlinear internal model was proposed in [10] under the assumption that there exist an integer q and a sufficient smooth function g vanishing at the origin such that (here L denotes the Lie derivative):

$$L_{\mathbf{u}}^q s(w) + g(\mathbf{u}, L_{\mathbf{u}}^q s(w), \dots, L_{\mathbf{u}}^{q-1} s(w)) = 0. \quad (25)$$

In fact, in this case, the system (6) can be immersed the nonlinear system of the form (7) with $\phi(\xi) = \text{col}(\xi_2, \dots, \xi_q, g(\xi_1, \dots, \xi_q))$ and $\gamma(\xi) = \Gamma\xi = \xi_1$. If g is bounded, N can be chosen in such a way that the internal model is ISS. This internal model has been used to handle semi-global output regulation.

3) *A Generic Internal Model*: All the previous three internal model candidates are constructed under various assumptions on the solution of the regulator equations. Recently, a generic internal model was proposed in [43]. Suppose that the exosystem satisfies the property of Poisson stability on some compact subset $W \subset \mathbb{R}^p$. Then, there exist a sufficiently large integer q , a controllable pair $(M, N) \in \mathbb{R}^{q \times q} \times \mathbb{R}^{q \times 1}$ with M Hurwitz, and a continuous map $\gamma : \mathbb{R}^q \rightarrow \mathbb{R}$, such that, for all $w \in W$ and all $\mu \in \mathcal{P}$ with \mathcal{P} a compact subset of \mathbb{R}^r , $\gamma(w, \mu)$ satisfies (8) with $\phi(\xi) = M\xi + N\gamma(\xi)$. That is, system (6) is immersed to a system of the form (7). As a result, the following dynamic compensator

$$\dot{\eta} = M\eta + Nu \quad (26)$$

is an ISS internal model of (1).

The applicability of the internal model (26) relies on the explicit construction of the function γ . But this function is only known to exist. Some discussion on approximately finding the function γ which is locally Lipschitz was given in [44]. It is noted that this internal model was used to study the semi-global robust output regulation problem for some non-minimum phase nonlinear systems in [43].

III. THE INTERNAL MODEL PRINCIPLE IN SYSTEMS BIOLOGY

Organisms depend critically, for their adaptability and survival, on their capability to formulate appropriate responses to chemical and physical environmental cues, distinguishing “background” signals from informative inputs. They must maintain a narrow range of concentration levels of vital quantities (homeostasis, adaptation) while at the same time appropriately reacting to changes in the environment (signal detection). This is achieved by regulatory changes in metabolism and gene expression, which are in turn mediated by signal transduction and gene regulatory networks in individual cells which process sensed chemical (for instance, nutrients or chemokines) or physical inputs (such as temperature, pressure, or electric potentials). Much theoretical, modelling, and analysis effort has been devoted to the understanding of these questions, traditionally in the context of steady-state responses to constant or step-changing stimuli.

One says that a system Σ regulates against all external input signals u in a given class \mathcal{U} of time-functions (for example, \mathcal{U} might be the class of all constant inputs, or of all inputs that are periodic with a certain period) if a certain quantity $y(t)$ associated to the system (the “output” in control-theory terms) has the property that $y(t) \rightarrow y_0$ as $t \rightarrow \infty$ whenever the system is subject to an input signal from the class \mathcal{U} (Figure 1), where y_0 is a fixed value which does not depend upon the particular input $u \in \mathcal{U}$. In control

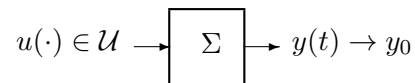


Fig. 1. Given system, regulated output $y(t)$ when inputs in \mathcal{U}

theory, this would be called a disturbance rejection property (or, if the output is the error signal with respect to a desired reference input, a tracking problem).

In biology, one often uses the term *adaptation* for this property. An example studied in [91] from a control-theoretic viewpoint is that of bacterial *E. coli* chemotaxis, where adaptation against constant inputs (chemoattractants) plays a central role in enabling motion in the directions of nutrient change. If the nutrients being sensed do not change much during a time interval, they are sensed as constant, and no directed motion happens. In this example, and simplifying a little to give the intuitive idea, “ y_0 ” is the internal concentration of a kinase, a chemical signaling protein. At this special value y_0 , the bacterium moves purely at random, instead of actively trying to move in a directed fashion. Adaptation against constant inputs is achieved by an integrator embedded in the system, in which the methylation state of a receptor serves as a memory (integrator) and the “error” is the average kinase activity relative to its basal value.

The question that the IMP asks is: if a system Σ is seen experimentally to regulate against all inputs in \mathcal{U} , then what can it be said about its internal structure? Answers to this question may help guide experimentalists and modelers, by ruling out putative mechanisms and suggesting the search for components responsible for adaptation.

A bit more formally, the IMP states, roughly, that if the system Σ adapts to \mathcal{U} then it necessarily must contain a subsystem Σ_{IM} which can itself generate all disturbances in the class \mathcal{U} . The terminology arises when thinking of Σ_{IM} as a “model” of a system which generates the external signals. For example, if $y(t) \rightarrow y_0$ as $t \rightarrow \infty$ whenever the system is subject to any external constant signal (i.e., the class \mathcal{U} consists of all constant functions), then the system Σ must contain a subsystem Σ_{IM} which generates all constant signals (typically an integrator, since constant signals are generated by the differential equation $\dot{u} = 0$). If, instead, $y(t) \rightarrow 0$ as $t \rightarrow \infty$ whenever the system is subject to a sinusoidal signal at frequency ω (i.e., the class \mathcal{U} consists of all functions of the type $A \sin(\omega t + \phi)$, for some fixed ω but different possible amplitudes A and phases ϕ), then Σ should have a subsystem Σ_{IM} which generates these signals (such as a harmonic oscillator $\dot{x}_1 = x_2, \dot{x}_2 = -\omega^2 x_1$), and so forth. In addition, the IMP specifies that, in an appropriate sense, the subsystem Σ_{IM} must only have y as its external input, receiving no other direct information from other parts of the system nor the input signal u . One intuitive interpretation is that Σ_{IM} generates its “best guess” of the external input u based

on how far the output y is from zero. Pictorially, if we have the situation shown in Figure 1, then there must be a decomposition of the system Σ into two parts, as shown in Figure 2, where the system Σ_{IM} (with $y \equiv 0$)

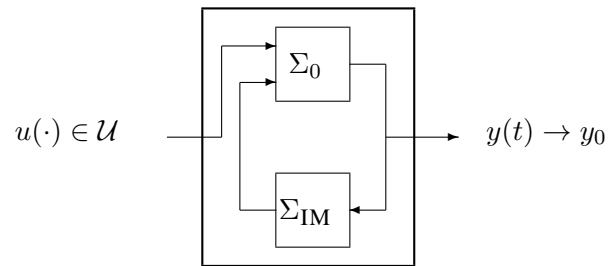


Fig. 2. Decomposition of Σ into Σ_0 and Σ_{IM} , the latter driven by $y(t)$

is capable of reproducing all the functions in \mathcal{U} . The IMP originates in the biological cybernetics literature, and like any “principle” it is not a specific result, but rather is a guide for different theorems, which hold under different technical assumptions and whose conclusions will depend upon the precise meaning of “class of external signals,” “reproducing all functions,” and so on.

The Francis/Wonham theory applies to systems Σ which are already partitioned into a “plant” plus a “controller”. The robustness assumption amounts to the requirement that the given controller should perform appropriately (in the sense that the regulation objective $y(t) \rightarrow y_0$ is achieved) even when the plant subsystem – but most definitely not the controller subsystem – is arbitrarily perturbed. The conclusion is that the controller is driven by y and incorporates a model of the external signals. (It is obvious that some additional condition, such as structural stability, must be imposed, since otherwise the trivial system Σ which simply outputs “ $y \equiv y_0$ ” for every possible input signal u adapts, yet does not contain any subsystem generating the signals in \mathcal{U} .)

In biological applications, it is very difficult to think of a “plant” and “controller” as different objects – the system regulates itself, and therefore robustness is arguably not a natural condition. In addition, few biological systems behave in even approximate linear regimes. Thus, it is desirable to have theorems which (a) apply to nonlinear systems Σ , (b) do not require the system Σ to be split between “plant” and “controller” subsystems, and (c) do not require structural stability (robustness) in the sense of the Francis/Wonham theory.

We will review here a result from [71], illustrated

with an example from [67], which shows that, under certain Lie-algebraic conditions on the system and assuming that the inputs in \mathcal{U} are not “too unstable”, the IMP holds when we impose instead of robustness a condition which amounts to a *signal detection* property, namely that the output must reflect sudden changes in the input (thus ruling out the trivial solution $y \equiv y_0$). One perhaps surprising fact is that, while for linear systems the class of inputs for which the IMP can be proved is quite arbitrary (the IMP for linear systems can be easily understood in terms of transfer function pole/zero cancellations, as discussed in [71]), for nonlinear systems there are counterexamples, when inputs are unstable.

The setup. We study dynamical systems with inputs and outputs in the standard sense of control systems theory [70]:

$$\dot{\mathbf{x}} = F(\mathbf{x}, u), \quad y = h(\mathbf{x}), \quad (27)$$

where F, h are functions which describe respectively the dynamics and the read-out map. Here, $u = u(t)$ is a generally time-dependent input (in biology, an input is typically called a “stimulus” or “excitation”) function, $\mathbf{x}(t)$ is an n -dimensional vector of state variables, and $y(t)$ is the output (in biology, “response” or “reporter” variables). In order to describe positivity of variables as well as other constraints, we introduce the following additional notations. States, inputs, and outputs are constrained to lie in open subsets, which we call \mathbb{Z}, \mathbb{U} , and \mathbb{Y} respectively, of Euclidean spaces $\mathbb{R}^n, \mathbb{R}^m, \mathbb{R}^q$. For example, $\mathbb{U} = \mathbb{R}_{>0}$ means that the input values must be scalar ($m = 1, \mathbb{U} \subset \mathbb{R}^1$) and positive. The functions F, h are differentiable. We will assume that for each piecewise-continuous input $u : [0, \infty) \rightarrow \mathbb{U}$, and each initial state $\xi \in \mathbb{Z}$, there is a (unique) solution $\mathbf{x} : [0, \infty) \rightarrow \mathbb{Z}$ of (27) with initial condition $\mathbf{x}(0) = \xi$, and the corresponding output $y : [0, \infty) \rightarrow \mathbb{Y}$ is $y(t) = h(\mathbf{x}(t))$. More specifically, in order to review the results from [71], we will restrict to scalar-input scalar-output n -dimensional systems for which the input appears to first order:

$$\dot{\mathbf{x}} = f(\mathbf{x}) + ug(\mathbf{x}), \quad y = h(\mathbf{x}). \quad (28)$$

The vector fields f and g are smooth, and h is a smooth function.

We will illustrate the main result by means of the incoherent feedforward loop (IFFL) model studied often in the systems biology literature:

$$\dot{x} = \alpha u - \delta x, \quad \dot{y} = \beta \frac{u}{x} - \gamma y \quad (29)$$

with $h(x, y) = y$, where u, x, y are assumed to evolve in the set of positive real numbers. In vector form, this is $\dot{\mathbf{x}} = f(\mathbf{x}) + ug(\mathbf{x})$, where the vector fields are:

$$f(x, y) = \begin{pmatrix} -\delta x \\ -\gamma y \end{pmatrix} \quad \text{and} \quad g(x, y) = \begin{pmatrix} \alpha \\ \beta/x \end{pmatrix}. \quad (30)$$

In an IFFL, the input u directly helps promote formation of the reporter y and also acts as a delayed inhibitor, through an intermediate variable x . This “incoherent” counterbalance between a positive and a negative effect gives rise, under appropriate conditions, to adaptation. There are many models of IFFL’s, but this is one of the simplest ones. IFFL’s are ubiquitous in systems biology. The reference [34] provides a large number of incoherent feedforward input-to-response circuits, which participate in EGF to ERK activation [58], [53], glucose to insulin release [47], [54], ATP to intracellular calcium release [41], [45], nitric oxide to NF- κ B activation [57], microRNA regulation [76], and many others. A variation of the model studied in [67] was given in [77], [72], and appears in slightly modified forms in models for *Dictyostelium* chemotaxis and neutrophils [89], [38], microRNA-mediated loops [88], and *E. coli* carbohydrate uptake via the carbohydrate phosphotransferase system [36] and other metabolic systems [79]. The work [6] shows experimentally and analytically that IFFL’s are especially well-suited to controlling protein expression under DNA copy variability.

We will say that the system (28) *adapts to inputs in a class* \mathcal{U} if for each $u \in \mathcal{U}$ and each initial state $x^0 \in \mathbb{Z}$, the solution of (28) with initial condition $x(0) = x^0$ exists for all $t \geq 0$ and is bounded, and the corresponding output $y(t) = h(x(t))$ converges to a fixed value $y_0 \in \mathbb{Y}$ (which does not depend on the particular input $u \in \mathcal{U}$) as $t \rightarrow \infty$. As usual in control theory, we describe the class of inputs \mathcal{U} with respect to which adaptation holds through the specification of an “exosystem” that produces these inputs. An exosystem is simply any autonomous system Γ :

$$\dot{w} = Q(w), \quad u = \theta(w) \quad (31)$$

with the following property: the input class \mathcal{U} consists exactly of the functions $u(t) = \theta(w(t))$, $t \geq 0$, for each possible initial condition $w(0)$. For example, if we are interested in step responses, we pick $\dot{w} = 0$, $u = w$. This means that the possible signals are the solutions of $\dot{w} = 0$, i.e. the constant functions of time; that is, \mathcal{U} is the set of functions $u(t)$ for which $u(t) = \bar{u}$ for all t for some $\bar{u} \in \mathbb{U}$. On the other hand, if we are interested

in sinusoidals with frequency ω then we would use $\dot{x}_1 = x_2, \dot{x}_2 = -\omega^2 x_1, u = x_1$.

A technical assumption for stating the result from [71] is that the signals in \mathcal{U} do not grow without bound. Specifically, the exosystem is assumed to be *Poisson-stable*, meaning that for every state w^0 , the solution $w(\cdot)$ of $\dot{w} = Q(w)$, $w(0) = w^0$ is defined for all $t > 0$ and it satisfies that w^0 is in the omega-limit set of w . In other words, the exosystem is almost-periodic in the sense that trajectories keep returning to neighbourhoods of the initial state. Both the constant and sinusoidal examples mentioned above are generated by Poisson-stable systems. In contrast, ramps (linearly growing signals) are not generated by Poisson-stable systems, since they require an unstable second-order system $\dot{w}_2 = 0, \dot{w}_1 = w_2, u = w_1$ to generate them. Thus, adaptation to ramps is not included in the scope of the theorem to be stated. The exosystem is assumed to have states that evolve on some differentiable manifold, Q is a smooth vector field, and θ is a real-valued smooth function.

The IMP claims that a copy of this exosystem must be embedded in the system (28). More precisely, one says that the system *contains an output-driven internal model of \mathcal{U}* if there is a change of coordinates which brings the equations (28) into the following block form:

$$\begin{aligned} \dot{z}_1 &= f_1(z_1, z_2) + u g_1(z_1, z_2) \\ \dot{z}_2 &= f_2(y, z_2) \\ y &= \kappa(z_1) \end{aligned} \quad (32)$$

so that the subsystem with state variables z_2 is capable of generating all the possible functions in \mathcal{U} . Namely, for some function $\varphi(z_2)$, and for each possible $u \in \mathcal{U}$, there is some solution of

$$\dot{z}_2 = f_2(y_0, z_2) \quad (33)$$

which satisfies $\varphi(z_2(t)) \equiv u(t)$. “Change of coordinates” means that there is some integer $r \leq n$ and two differentiable manifolds Z_1 and Z_2 of dimensions r and $n - r$ respectively, as well as a smooth function $\kappa : Z_1 \rightarrow \mathbb{R}$ and two vector fields F and G on $Z_1 \times Z_2$ which take the partitioned form

$$F = \begin{pmatrix} f_1(z_1, z_2) \\ f_2(\kappa(z_1), z_2) \end{pmatrix}, \quad G = \begin{pmatrix} g_1(z_1, z_2) \\ 0 \end{pmatrix}$$

and a diffeomorphism $\Phi : \mathbb{R}^n \rightarrow Z_1 \times Z_2$, such that $\Phi'(x)f(x) = F(\Phi(x))$, $\Phi'(x)g(x) = G(\Phi(x))$, and $\kappa(\Phi_1(x)) = h(x)$ for all $x \in \mathbb{U}$, where Φ_1 is the Z_1 -component of Φ and prime indicates Jacobian. Intuitively, the signal z_2 computes an integral of a

function of the output $y(t)$, and when $y(t) \equiv y_0$, z_2 is (up to the mapping φ , which may be interpreted as a sort of rescaling) a signal in \mathcal{U} . For example, if \mathcal{U} consists of constant functions (adaptation to steps), then for $y \equiv y_0$ one obtains (for different initial conditions) the possible constant signals.

In order to prove a theorem justifying the IMP, several technical conditions are imposed in [71]. The first is a signal detection or “sensitivity” property: (1) for some positive integer r , called in control theory a finite uniform relative degree, $L_g L_f^k h \equiv 0$, $k = 0, \dots, r - 2$ and $L_g L_f^{r-1} h(x) \neq 0 \forall x \in \mathbb{Z}$. Generally, $L_X H$ denotes the directional or Lie derivative of a function H along the direction of a vector field X : $(L_X H)(x) = \nabla H(x) \cdot X(x)$, and one understands $L_Y L_X H$ as the iteration $L_Y(L_X H)$. (In the special case that $L_g h(x) \neq 0$ for all x , the relative degree is $r = 1$, since the condition for $k < r - 1$ is vacuous.) Given that the relative degree is r , one may consider the following vector fields:

$$\begin{aligned} \tilde{g}(x) &= \frac{1}{L_g L_f^{r-1} h(x)} g(x) \\ \tilde{f}(x) &= f(x) - \left(L_f^r h(x) \right) \tilde{g}(x) \\ \tau_i &:= \text{ad}_{\tilde{f}}^{i-1} \tilde{g}, \quad i = 1, \dots, r, \end{aligned}$$

where ad_X is the operator $\text{ad}_X Y = [X, Y]$ = Lie bracket of the vector fields X and Y , and $\text{ad}_{\tilde{f}}^{i-1}$ is the iteration of this operator $i - 1$ times (when $i = 1$, $\tau_i = \tilde{g}$). One says that a vector field X is complete if the solution of the initial value problem $\dot{x} = X(x)$, $x(0) = x^0$ is defined for all t and for any initial state x^0 . Two vector fields X and Y are said to commute if $[X, Y] = 0$. The final assumptions, then, are that (2) τ_i is complete, for $i = 1, \dots, r$ and (3) the vector fields τ_i commute with each other. (In the special case $r = 1$, condition (3) is automatic, since every vector field commutes with itself.) These assumptions are satisfied for linear systems. The assumptions are also satisfied, for example, for the IFFL system (29). Indeed, since $L_g h = (0, 1) \cdot (\alpha, \beta/x)^T = \beta/x$ is everywhere nonzero, we have that $r = 1$. Thus we need only check that

$$\tau_1 = \tilde{g} = \frac{1}{L_g h(x)} g(x) = \frac{x}{\beta} g(x) = \begin{pmatrix} \frac{\alpha}{\beta} x \\ 1 \end{pmatrix}$$

is complete, which is true because \tilde{g} is a linear vector field.

The main theorem in [71] says the following: *Suppose that assumptions (1)-(3) hold for the system (28). If (28) adapts to inputs in a class \mathcal{U} generated by a*

Poisson-stable exosystem, then it contains an output-driven internal model of \mathcal{U} .

The proof of the theorem consists of showing that there is, under the stated conditions, a change of variables as claimed. The map producing the change of variables is obtained by solving a first-order partial differential equation.

Let us now illustrate this change of variables with the system (29), or (30) in vector form. This system adapts to steps (constant inputs): it is easy to see, for any constant (positive) input $u(t) \equiv u$, there is global asymptotic stability of the steady state $x_0 = \alpha u / \delta$ and $y_0 = \frac{\beta \delta}{\alpha \gamma}$, and y_0 is independent of u . We already checked properties (1)-(3), and the system, so the theorem says that it should be possible to recast it integral feedback form. The proof in [71] asserts the existence of a mapping $\varphi(x, y)$ whose Lie-derivative along g solves the following first-order linear PDE:

$$L_g \varphi = \nabla \varphi \cdot g = \alpha \varphi_x(x, y) + \frac{\beta}{x} \varphi_y(x, y) = 0.$$

Generally, such an equation may be solved using the method of characteristics. However, in our example the solution is immediate: $\varphi(x, y) = \alpha y - \beta \log x$. The map

$$(x, y) \mapsto (z_1, z_2) = (y, \varphi(x, y)) = (y, \alpha y - \beta \log x)$$

is a diffeomorphism whose inverse is $y = z_1$ and $x = e^{(\alpha z_1 - z_2) / \beta}$. We obtain the following equations in the new coordinates (z_1, z_2) :

$$\begin{aligned} \dot{z}_1 &= \beta u e^{(z_2 - \alpha z_1) / \beta} - \gamma z_1 \\ \dot{z}_2 &= \beta \delta - \alpha \gamma z_1 \end{aligned}$$

with output $y = z_1$. This has the desired internal model form $\dot{z}_1 = f_1(z_1, z_2) + u g_1(z_1, z_2)$, $\dot{z}_2 = f_2(z_1, z_2)$, $y = \kappa(z_1)$, if we define: $f_1(z_1, z_2) = -\gamma z_1$, $g_1(z_1, z_2) = \beta e^{(z_2 - \alpha z_1) / \beta}$, $f_2(z_1, z_2) = \beta \delta - \alpha \gamma z_1$, and $\kappa =$ identity. Thus z_2 is the variable that integrates the error: when $y = y_0 = \frac{\beta \delta}{\alpha \gamma}$, the equation for z_2 becomes $\dot{z}_2 = 0$, whose solutions are all the possible constant signals. We can also write this system in terms of the coordinates $x = e^{z_2 / \beta}$, $y = z_1$ as follows:

$$\dot{x} = c x (y_0 - y), \quad \dot{y} = \beta u x e^{-\frac{\alpha}{\beta} y} - \gamma y \quad (34)$$

with $c := \frac{\alpha \gamma}{\beta}$. See [67] for more details. This system has the generic form $\dot{x} = x F(y_0 - y)$, $\dot{y} = G(x, y, u)$ of “nonlinear integral feedback systems” in [66]. Bacterial chemotaxis models often can be shown to have this form.

When the IMP fails. Interestingly, the Poisson stability of the exosystem seems to play a key role. To see this, we now show the two-dimensional IFFL in (29) has the property that it adapts to polynomial inputs of any degree, and in fact to any subexponential inputs, even though the IFFL cannot contain as a factor a system of arbitrary dimension (as needed to generate arbitrary-degree polynomials). These remarks are from [74], see [73] which should be consulted for more details. Consider (assume $u(t)$ differentiable)

$$v(t) := \frac{d}{dt} \ln u(t) = \frac{\dot{u}(t)}{u(t)}$$

and its limsup and liminf as $t \rightarrow \infty$:

$$\underline{\lambda} := \liminf_{t \rightarrow \infty} v(t), \quad \bar{\lambda} := \limsup_{t \rightarrow \infty} v(t)$$

We will assume that v is bounded, so both are finite. We also denote

$$\underline{y} := \liminf_{t \rightarrow \infty} y(t), \quad \bar{y} := \limsup_{t \rightarrow \infty} y(t)$$

Then one can prove:

$$\frac{\beta}{\alpha \gamma} \max\{0, \delta + \underline{\lambda}\} \leq \underline{y} \leq \bar{y} \leq \frac{\beta}{\alpha \gamma} \max\{0, \delta + \bar{\lambda}\}$$

This implies that if u is a sub-exponentially increasing input, such as a polynomial of any order, so that $(d/dt) \ln u = 0$, then $\lambda = 0$ and thus

$$\lim_{t \rightarrow \infty} y(t) = \frac{\beta \delta}{\alpha \gamma}.$$

Thus the output $y(t)$ converges to the same constant independent of the input as if the input was constant.

Interestingly, if there is exponential growth, $\frac{\dot{u}(t)}{u(t)} \rightarrow \lambda$ as $t \rightarrow \infty$, for example if u is an exponential function $u(t) = \beta e^{\lambda t}$, then

$$\lim_{t \rightarrow \infty} y(t) = \frac{c}{\alpha \gamma} \max\{0, \delta + \lambda\}$$

so $y(t)$ converges to value linear on the logarithmic growth rate. This convergence is hypothesised to play a role for this adapting circuits in recognising the speed of change of a tumor or infection [74].

IV. INTERNAL MODELS IN NEUROSCIENCE

Sensorimotor integration, the transformation of sensory information into motor actions, is one of the most studied functions of the nervous system. Producing context-appropriate movement for foraging, escaping from predators, or mating, is critical to animal survival. Moreover, since the output of this computation (movement) and many of its inputs (sensory stimuli)

can be measured from behaviour alone, sensorimotor integration can be studied in humans as well as a variety of animal species.

Many of the early studies focused on reflexive movements, in which sensory stimuli directly drive stereotypical motor actions in response. However, it has been clear for a long time [80] that many sensorimotor transformations in nature do not fall in this category but display predictive and adaptive features. The framework of control theory has been very influential in developing insight into the computations underlying these features and to guide experimental investigations of their neural implementation.

Whenever it is observed that a control system is capable of perfect (asymptotic) tracking of the reference signals produced by an exogenous system, the internal model principle implies that the controller must include an internal model of such exosystem (in addition to feedback control). Similarly, a control system capable of closing a sensorimotor loop with no apparent delay (or significantly smaller than the sensory and actuation lags) must include an internal model of relevant parts of the sensorimotor plant within a feedforward or predictive control scheme. Theoretical considerations such as these can be translated into experiments that probe the use of internal models in the nervous system.

Here we review some of the experimental evidence that the sensorimotor transformations performed by humans and many animal species are in fact consistent with the use of internal models of the plant and the environment. A variety of techniques and experimental preparations have been effectively employed to functionally probe these models, but revealing the neural mechanisms underlying these computations has proved challenging, with progress limited to a few special preparations. Some of the fascinating questions that remain open for investigation include (i) to what extent internal models are explicitly represented in the nervous system, as opposed to implicitly computed, (ii) whether there are separate neural substrates for different types of internal models and for feedback control and (iii) to what extent neural mechanisms implementing internal models have been conserved across species.

While this tutorial paper focuses on the internal model principle, which classically refers to the internal model of an exogenous system, most of the focus in neuroscience has been placed on internal models of the plant. Hence, we will mostly discuss what is known about these types of internal models, with special emphasis on forward (direct) models of the plant.

However, we will conclude with evidence for internal models of the environment in which the organism operates, for example of the feasible trajectories of a moving target, which are directly relatable to exosystems in the context of the internal model principle.

A. *Internal models of the plant*

Humans and animals can perform motor gestures which require exquisite temporal and spatial precision, such as hitting a baseball or catching evading prey. While this is theoretically achievable via pure feedback control (with the right sequence of fast reflexive corrections), the sensorimotor delay is usually large relative to the task. For example, visual processing alone takes a minimum of 20ms in insects such as dragonflies, and 100ms or more in humans. Significant delays are also introduced in the loop by neural computations and muscle contractions to generate forces. It is hard to imagine how a purely feedback-based controller with these lags could enable a hunting dragonfly to catch its prey within 150ms, or a professional baseball player to hit a ball within 500ms. Moreover, any sensory apparatus has limited resolution, and the sensory information driving the feedback loop (e.g. the prey or ball position) must be isolated from a variety of noise sources. In particular, the nervous system must distinguish useful sensory information about the external world from self-motion artifacts, which every motor gesture produces. Finally, it is unclear how context-dependent movements could be implemented in a purely reflexive system. For example, insects have an innate *optomotor* reflex that maintains their body orientation aligned with the horizon, but this reflex would prevent a dragonfly from performing banked turns while in pursuit of a prey.

It is thus posited that the nervous system combines some form of model-based predictive control to sensory-driven feedback loops. As the nervous system plans and executes a motor action, a copy of the motor command (*efference copy* [80]) is thought to be processed through a **forward model** of the plant and combined with incoming delayed sensory input (*afferent input*). Such a control architecture (Figure 3) resolves the limitations of pure feedback control. The nervous system can avoid the large sensorimotor lag by closing the loop with predicted sensory input or with some predicted internal state, computed using the forward model within a state observer (by using a Kalman-filter-type architecture, for example). Moreover, the sensory consequences of self-motion can be predicted and canceled from the incoming sensory stream to

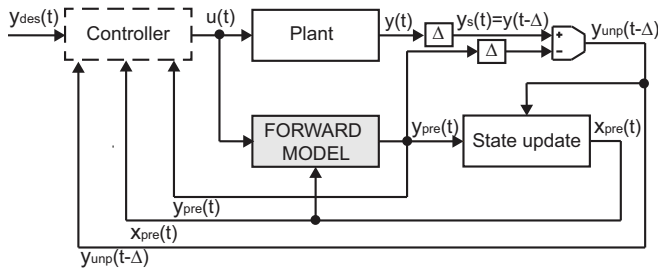


Fig. 3. A forward model of the plant can be used to predict upcoming sensory inputs ($y_{pre}(t)$), identify the unpredicted information ($y_{unp}(t - \Delta)$) within the raw sensory signals ($y_s(t)$), or estimate internal states ($x_{pre}(t)$). The controller may use $y_{pre}(t)$ or $x_{pre}(t)$ to close the loop without being subject to the sensorimotor lag Δ .

improve the ability to extract sensory information about the external world. This cancellation can occur by adding to the sensory input a signal equal and opposite to the predicted contribution of self-motion (“software cancellation”) or by moving the sensory apparatus, e.g. the eyes, in a way that counteracts the effect of self-motion (“hardware cancellation”). Similar mechanisms can be used to guarantee that reflexive responses are activated only by unexpected sensory inputs and not by self-motion artifacts.

For challenging goal-oriented tasks, such as catching prey or hitting a baseball, the nervous system may also exploit internal models of the external world, to predict the future position of the goal. We will discuss these models in the next subsection, whereas here we focus on models of the plant.

Significant insight into sensorimotor integration, at least at the computational level, can be obtained even without neural recordings, by tracking the sensory inputs and motor behaviour in well-designed experimental conditions. Wolpert et al. [84] used this approach to show that humans are able to optimally combine internal model predictions and sensory feedback to estimate the current state of their arm. Human subjects were asked to move a computer-controlled manipulandum and to report the estimated state of their arm at the end of a movement performed in the dark. Assistive or resistive forces were applied to the manipulandum in some of the trials. The bias and variance of the estimates in the different conditions were inconsistent with pure feedback (in this case proprioception, the sense of relative position between body parts) but were well described by an optimal linear estimator employing a forward model (Kalman filter). Mehta and Schaal [48] found similar results when they asked subjects to control a virtual inverted pendulum via

a manipulandum with and without visual feedback. Controlling an inverted pendulum requires real-time control (the control sequence cannot be memorised), but subjects were able to successfully perform this task even during 500ms periods of visual blackout, suggesting that a forward model was used to provide a persistent estimate of the pendulum state. There is also behavioural evidence for the use of forward models to predict the consequences of self-motion. For example, the latency of eye movements in tracking a moving target, which is usually 130ms, disappears when the target is manually controlled by the subject [60] - a “hardware cancellation” of self-motion effects.

While behavioural evidence for forward models in the human brain is relatively rich, the investigation of their neural implementation is limited by the lack of available neural recordings. Indirect evidence, however, points to the cerebellum as a possible locus for these computations. Perturbation of the cerebellum via transcranial magnetic stimulation during a reaching task [49] produces performance deficits consistent with the use of a delayed estimate of the arm position instead of the real-time estimated position. Similar motor deficits are observed in cerebellar patients [75].

Direct neural evidence for forward models has been found in the cerebellum of non-human primates, in the context of vestibular sensing of head movement. Brooks et al. [7] recorded the neural activity of the deep cerebellar nuclei, which send the output of the cerebellum to the rest of the brain, when the head of a monkey rotated actively towards a target and when it was rotated passively by a torque motor. They found neurons that responded only to passive rotations of the head but not to active (voluntary) rotations, reflecting a “software cancellation” of the sensory consequences of self-motion. When a passive rotation was added during active head rotations, the activity of the neurons was proportional to the passive component alone - the unexpected sensory input. Even more interestingly, if the same passive rotation was added to every voluntary movement, the neurons gradually reduced their activity to zero, consistent with adaptation of the forward model responsible for computing the expected consequences of self-motion, which now included the added passive term. The output of the cerebellum may thus represent the difference between predictions, made by a rapidly-adaptive forward model, and actual sensory inputs. This output may be used as an “innovation term” (like in the Kalman filter) by other brain regions that are thought to hold the current estimate of the body state, such as

the posterior parietal cortex (PPC) [64]-[51].

But is the forward model itself - which transforms motor signals and current state signals into predicted sensory signals - fully implemented within the cerebellum? After all, the forward-model-related signals in the cerebellum reported in [7] may be inherited from upstream regions, or may reflect a distributed computation involving not only the cerebellum but also other regions (including the PPC, as argued in [52]). While this question has not been definitely answered, there are anatomical, computational and experimental considerations [83] which suggest that the forward model may be implemented within the cerebellar cortex itself (not to be confused with the cerebral cortex, of which PPC is one part). The main neurons in this region (*Purkinje cells*) receive thousands of sensory inputs and efference copies of motor commands, organised in a strikingly regular fashion that could favour learning complex associations between these inputs. The “regular” high-frequency spiking patterns of these neurons (*simple spikes*) encode the expected sensory inputs better than the true ones [15]. Moreover, Purkinje cells also produce special *complex spikes* when a mismatch occurs between expected and actual sensory inputs, e.g. when there is an unexpected sensory input after movement. Complex spikes are thought of as teaching signals, and there is evidence (at least in specific domains, e.g. eye movements [46]) that they may induce changes in the pattern of activity of simple spikes - perhaps reflecting an adaptation of the forward model.

The closest to a mechanistic explanation for how a forward model may be implemented, comes from a *cerebellar-like* region in a very different family of organisms, the *Mormyrids* electric fishes [59]. These animals sense the presence of other fishes (conspecifics, prey, etc.) by creating weakly electric fields around their bodies, and monitoring changes in these fields. However, the own activity of these fishes affects the electric field they use to sense the environment. Their movement in the water affects the electric field, and so do the active electric pulses they emit for electrolocation and communication. So these animals must be able to cancel the sensory consequences of their own actions to be able to sense the environment, and in fact they do. Through a combination of complex experimental perturbations and measurements, Sawtell and colleagues could observe the emergence of “software cancellation” signals in the output of Purkinje-like cells after repeated stimulation of the inputs of these cells during specific bouts of activity. This suggests

that the strengths of the synapses (input connections) to these cells are highly adaptive and the forward model implementation may be in these synapses along with the biophysical properties of the cells themselves and their downstream connections.

As illustrated by the electric fish case, there are animal species that may be more experimentally advantageous than primates to study the implementation of forward models of the plant (or any other internal model). Mice are becoming increasingly popular in the sensorimotor field, as it is now possible to combine genetic techniques for measuring and perturbing neural activity in the brain, with complex behavioural paradigms (e.g. [21]). Insects are also particularly appealing for their smaller nervous system, individually identifiable neurons and available genetic tools in some species (the fruit fly *drosophila melanogaster*). It has long been known, e.g. in crickets during singing [56], that efference copies of motor commands are used to modulate sensory inputs, but this could be through a much simpler mechanism than a forward model [82]. Recent behavioural and neural data, however, appears consistent with the hypothesis that internal models may also be implemented in the nervous system of insects. A behavioural study of dragonfly hunting flights [50] showed that dragonflies predictively steer their head while they are maneuvering, to keep the image of the prey in a fixed region of the eyes. In experimental conditions with constant speed of the prey (a computer-controlled bead), the head rotation almost perfectly canceled “in hardware” the effect of self-motion as well as the predictable movement of the prey. This suggests that the head control circuitry includes a forward model and a model of prey motion, perhaps very simple (see [81] for a possible neural substrate). Moreover, a neurophysiological study of the fruit fly [35] revealed that during fast, voluntary flight maneuvers, visual neurons receive motor-related inputs which are consistent in magnitude, sign and latency, with what would be needed to cancel “in software” the sensory consequences of the maneuver.

In addition to forward models of the plant, which transform motor commands into their predicted sensory consequences, the human brain is thought to implement **inverse models** of the plant to achieve the opposite transformation. An inverse model transforms a desired trajectory in sensory coordinates (needed to achieve a certain goal in the environment) into a motor command that can accomplish such an outcome. It is thus a very useful component of the controller - either within a pure

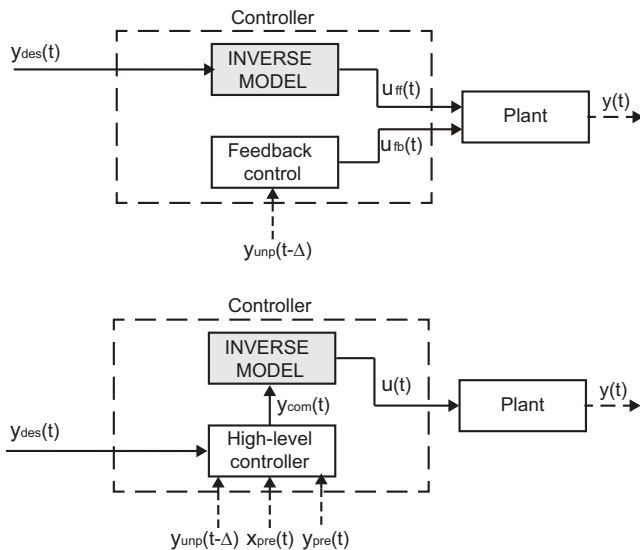


Fig. 4. An inverse model of the plant can be used in the controller, along with feedback control, to achieve a desired trajectory $y_{des}(t)$. In one possible scheme (top) the inverse model produces a feedforward control command $u_{ff}(t)$, whereas feedback corrections $u_{fb}(t)$ are driven by a separate pathway when unexpected sensory signals ($y_{unp}(t)$) are detected. An alternative scheme (bottom) uses the inverse model to convert high-level commands in extrinsic coordinates ($y_{com}(t)$, based on feedback, predictions or both) into appropriate motor commands to the plant ($u(t)$). If the desired trajectory $y_{des}(t)$ is produced by an exogenous system, the controller may also include an internal model of the exosystem (not shown).

feedforward pathway parallel to feedback control, or as a common stage for both feedforward and feedback pathways (Figure 4).

The best behavioural evidence for inverse models comes from classical “force field” experiments, in which human subjects were asked to control a robotic manipulandum towards a virtual goal, while external forces were systematically applied to the robot [63]. The subjects were initially affected by the force field, with their trajectories missing the goal. However, over the course of the experiment they learned to compensate for the force field and to produce successful trajectories which reached the goal. When the force field was unexpectedly removed, the trajectories produced by the subjects missed the goal with directional errors opposite to those produced when the force field was first experienced. This suggests that the control algorithm in the brain included an inverse model of the plant, which had adapted during the experiment to include the force field effects (an alternative interpretation would be that the brain had created an internal model of the experimental environment).

It is not fully understood where the inverse models

are implemented within the nervous system. Studies of cerebellar activity in primates during eye movements have been interpreted in the past as evidence that the cerebellum also implements inverse models in addition to forward models [65]–[83]. Other studies [20], however, have argued that the role of the cerebellum is only consistent with a forward model even in the context of eye movements, whereas the inverse model of the eye dynamics may mostly reside in the brainstem. For forelimb movements, instead, the locus of inverse model may be in the cerebral (not cerebellar) cortex. Force field experiments in monkeys [39] have revealed neurons in the motor cortex that adapt to the introduction of the force field perturbation, consistent with the behavioural adaptation results. However, while these neurons reflect the output of an inverse model, consistent with their role as limb controllers, the actual inverse model may reside upstream of motor cortex. As in the case of forward models, uncovering the neural implementation of inverse models may be more tractable in animal models such as mice or insects, by combining the right behavioural paradigm (e.g. force field adaptation) with genetic tools for recording and perturbing neural activity in multiple brain regions.

B. Internal models of the environment

The survival and success of an animal is tied to the environment in which it operates, and is particularly dependent on the interaction with external actors such as prey, predators and mates. It is thus not surprising that the nervous system of most animals is also capable of internalising regularities in the environment to improve perception and action selection. Having an internal model for how passive objects are physically bound to move (e.g. due to gravity) or how active external actors are likely to move (e.g. how a prey trajectory is likely to evolve in the next future) gives the nervous system similar advantages to having an internal model of its own plant. It enables an animal to properly weigh noisy sensory information against prior expectations (as in a Kalman filter) and to perform real-time control based on predicted sensory inputs or estimated state of the environment. This avoids the large sensorimotor lag that would render pure feedback-based control ineffective, and makes goal-oriented motor actions possible even when sensory inputs are unavailable or unreliable (e.g. when a prey that is being pursued is visually occluded).

Here we focus on the internal models of a moving object in the context of interception or visual tracking. This is only a subclass of all the internal models of

the environment that are likely present in the nervous system, but one that is tractable experimentally since predictions and measurements can be easily compared.

To track and intercept a falling inanimate object, the human brain uses an internal model of physical properties of the world, including gravity and momentum. When preparing to intercept a free-falling ball dropped from different heights, muscle activity at the elbow and wrist joints (measured via EMG recordings) was shown to precede contact by a fixed amount of time (about 100ms), suggesting a correct estimate of time-to-contact in the brain [37]. Moreover, when balls of different mass were dropped, the amplitude of preparatory activity was proportional to the expected momentum of the ball at impact. Internal models of gravity may be innate rather than learned, and somewhat hard-coded in the nervous system. In fact, astronauts in space are still biased towards expecting objects to fall according to gravity, which leads to incorrect interception behaviours [42], despite prolonged exposure to a 0g environment. Similar results have been observed in simulated visual 0g experiments on Earth [92]. Subjects were asked to intercept a ball falling behind a projector screen (when it reached the bottom edge of the screen) based on the visual cues provided by a constant speed (hence 0g) target projected on the screen. The speed of the projected target and the timing of ball release were coordinated so that the positions of the physical and virtual target would match at the interception point below the screen. The performance of the subjects in this task remained well below baseline (assessed with 1g virtual targets) even after many repetitions, and were consistent with the subjects not fully abandoning the assumption of gravity when computing the expected time-to-contact.

The brain can, however, switch between different internal models of a moving object depending on the context. In another experiment presented in [92], subjects were able to correctly intercept the 0g virtual target if the task was changed so that the physical ball was removed, and the interception was performed with the click of a mouse. Interestingly, in this task the subjects performed better when trained on 0g than on 1g virtual targets. These results may be accounted for by the existence of separate internal models for passive and active targets - the gravity model may have been engaged in the task with the physical ball, but not in the virtual interception task.

There is strong behavioural evidence that the nervous system can predictively track the movement of a self-

propelled (e.g., prey) or externally controlled target, provided it is sufficiently smooth and regular. For example, human subjects engaged in a manual interceptive task can track without delay targets moving along sinusoidal trajectories up to 2Hz [19]. These results are well accounted for by a computational model which augments optimal state feedback (enabled by a state predictor and a Kalman filter, as discussed for forward models of the plant) with a “disturbance observer” that plays the role of the internal model of an exosystem producing the sinusoidal trajectories. Similarly, monkeys can visually track complex trajectories (circles, Lissajous curves in 2D) with a delay of only a few ms (2-20 ms), much smaller than the full visuomotor lag observed in response to unpredictable shifts of the target (80-100ms) [32].

There are very few physiological studies of internal models of the environment, but the available results are similar to those described for forward models of the plant. Cerminara et al. [11] recorded neural activity from the cat’s cerebellum during a visually guided reaching task, with the target moving at constant speed and disappearing for 200-300ms in the middle of the task. They found that the simple spike activity of certain Purkinje cells was significantly modulated by the onset of target motion, and this activity remained modulated (higher or lower firing rates compared to baseline) until the target stopped moving. Crucially, the modulation of simple spikes during target motion persisted even when the target was not visible. Since the activity of those cells did not appear to encode limb or eye movements, these results suggest that Purkinje cells may have been encoding the predicted (rather than the sensed) target motion produced by an internal model. As in the case of forward models of the plant, computational models have suggested that the cerebellar cortex may be the locus of the internal model computation [32].

While the experimental evidence is much too scarce to draw conclusions, it is tempting to speculate that the similarities between neural data recorded in the context of forward models of the plant and models of target motion (e.g. simple spike activity encoding predictions in both cases) may result from a common mechanism for learning and executing internal models. Studying the neural implementation of internal models of the environment could be a tractable alternative to studying forward models of the plant, since the complexity of the environment can be controlled experimentally. The internal model principle would provide a useful theoretical framework for this kind of investigation. In the

context of target tracking, for example, one approach could be to systematically increase the complexity of the exosystem producing the trajectories to be tracked, and search for neural activity that adapts to match the increased complexity of the exosystem. If the nervous system can predictively track the given trajectories, the internal model principle proves that an internal copy of the exosystem must in fact be embedded in the neural controller.

V. AN ABSTRACT INTERNAL MODEL THEORY

As discussed in Sections III-IV, the concept of internal model is ubiquitous, and the internal model principle can be an important conceptual framework in a variety of fields. However, the technical machinery of the IMP in control theory (Section II) may not be easily translated to every other field. In this section, we thus introduce an abstract version of the internal model theory that is applicable to a large class of systems.

Since the achievement of “robustness” or structural stability of perfect regulation with respect to parameter variations is largely a matter of technology, we shall consider only the converse questions:

- Is error feedback a necessary condition for “good” regulation (i.e. perfect tracking)?
- Is an internal model a necessary condition for “good” regulation?

If “Yes”, shouldn’t these statements hold for a very wide class of regulator systems, linear or nonlinear?

Thus we shall assert as the IMP: For a very general class of systems:

- **Assertion 1.** Error feedback + Perfect regulation \Rightarrow Internal Model
- **Assertion 2.** Structurally stable (or “robust”) perfect regulation \Rightarrow Error feedback + Internal Model

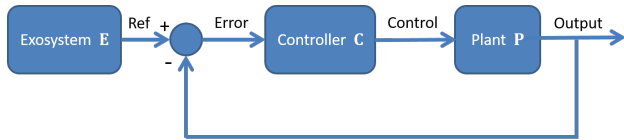


Fig. 5. Total System S.

Our goal is to establish the IMP in a general but rudimentary discrete-time framework, using just ordinary sets and functions, without any sophisticated technical or geometric machinery. We begin with the easier Assertion 1. Referring to Fig 5, we consider the total system $\mathbf{S} = \text{Exosystem} \times \text{Controller} \times \text{Plant} = \mathbf{E} \times \mathbf{C} \times \mathbf{P}$, with state space the set $X = X_{\mathbf{E}} \times X_{\mathbf{C}} \times$

$X_{\mathbf{P}}$, say. While there’s no need to distinguish sharply between Controller and Plant, we do so here for the sake of intuition and control tradition. Bring in the total one-step transition function $\alpha : X \rightarrow X$. We consider $X_{\mathbf{C}} \times X_{\mathbf{P}}$ to be α -invariant, and $X_{\mathbf{E}}$ the corresponding factor with induced map $\alpha_{\mathbf{E}} : X_{\mathbf{E}} \rightarrow X_{\mathbf{E}}$. Thus $(X_{\mathbf{E}}, \alpha_{\mathbf{E}})$ is the dynamic model of the exosystem or “outside world”, providing the reference signal for tracking by $\mathbf{C} \times \mathbf{P}$. Think of \mathbf{E} as “driving” $\mathbf{C} \times \mathbf{P}$.

For the total system \mathbf{S} we need to define internal stability, error feedback, and exosystem detectability. For internal stability we assume that X is a finite set and that $(X_{\mathbf{E}}, \alpha_{\mathbf{E}})$ induces an α -invariant subset of X via an injection $i_{\mathbf{E}} : X_{\mathbf{E}} \rightarrow X$ as shown in the (commutative) diagram of Fig. 6. Thus $\alpha \circ i_{\mathbf{E}} = i_{\mathbf{E}} \circ \alpha_{\mathbf{E}}$. Write $\tilde{X}_{\mathbf{E}} := i_{\mathbf{E}}(X_{\mathbf{E}})$ and assume (crucially) that $\tilde{X}_{\mathbf{E}}$ is a global attractor, namely that, for every initial state x_o in X , there is an integer N with $\alpha^n(x_o) \in \tilde{X}_{\mathbf{E}}$ for all $n \geq N$. [For simplicity we omit the technical details in case X is infinite.] Think of \mathbf{E} as an orchestra and $\mathbf{C} \times \mathbf{P}$ as an attentive but passive audience.

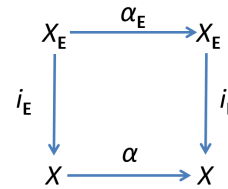


Fig. 6. Internal stability commutative diagram.

To define error feedback, first let $K \subseteq X$ be the target subset for regulation: in the standard case K is exactly the subset where tracking error is zero. Also let $\gamma : X \rightarrow X_{\mathbf{C}}$ be the natural projection defining state of the controller. Error feedback is then the property that the controller \mathbf{C} is externally driven only when state of \mathbf{S} deviates from the target K , namely the dynamics of \mathbf{C} are autonomous as long as $x \in K$, or “tracking remains perfect”. Suppose $x \in K$, so the controller state is $x_{\mathbf{C}} = \gamma(x)$. By feedback the next controller state $x'_{\mathbf{C}} = \gamma(\alpha(x))$ depends only on $x_{\mathbf{C}} = \gamma(x)$, i.e. for $x \in K$, $\gamma \circ \alpha(x)$ is computable from $\gamma(x)$. Formally $\ker(\gamma|_K) \leq \ker(\gamma \circ \alpha|_K)$, where $\ker(\cdot)$ denotes equivalence kernel of the functional argument and \leq means “is a refinement of”. Note that K itself need not be α -invariant and usually isn’t.

Lack of space prohibits formally defining exosystem detectability (see [85], [87]); just recall that detectability is “local observability” on an invariant subspace, defined here as the property that the global observer

congruence for the pair (γ, α) reduces to “full observation” (bottom element) on \tilde{X}_E . Intuitively this means that the controller is effectively coupled (via error feedback) to the exosystem, namely the latter is observable by the controller as long as regulation is perfect. This requirement could be dropped by replacing the exosystem by its “observable factor”.

With X_E as defined above, write $\tilde{\alpha}_E := \alpha|_{\tilde{X}_E}$, $\tilde{\gamma}_E := \gamma|_{\tilde{X}_E}$. Now we can prove

Theorem 1 Internal Model Principle: Assertion 1 above

Assume that **S** satisfies internal stability, perfect regulation, error feedback, and exosystem detectability. Then

- 1) There exists a unique mapping $\alpha_C : X_C \rightarrow X_C$ determined by $\alpha_C \circ \gamma|_K = \gamma \circ \alpha|_K$
- 2) $\alpha_C \circ \tilde{\gamma}_E = \tilde{\gamma}_E \circ \tilde{\alpha}_E$
- 3) $\tilde{\gamma}_E$ is injective

Statement 1 defines the controller’s dynamics, as autonomous under the condition of regulation. Statement 2 identifies these controller dynamics as a copy of the dynamics of **E** on the global attractor (i.e. exosystem dynamics). Statement 3 asserts that this copy is faithful, namely incorporates fully the exosystem dynamics. The result is shown in the commutative diagram Fig. 7. The proof (omitted) amounts to building up the commutative diagram Fig. 8. To formalise Assertion 2 above

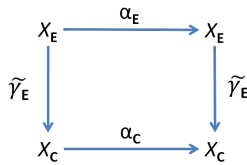


Fig. 7. Commutative diagram for Assertion 1.

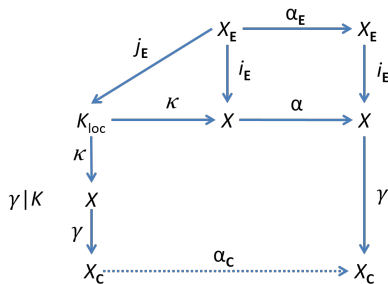


Fig. 8. Commutative diagram for Theorem 1.

we enlarge the state structure by forming products with a parameter set M ; and require that internal stability, perfect regulation, and exosystem detectability hold for every element μ in M . For realism and to avoid overkill we specialise $M = M_E \times M_C \times M_P$, $\mu = (\mu_E, \mu_C, \mu_P)$, resulting in the commutative diagrams of Fig. 9. The resulting perturbation model (Fig. 10) leads in turn to the equation

$$\alpha_C[R(\mu_E)(x_E), S(\mu_P) \circ i_P(x_E), T(\mu_C) \circ i_C(x_E)] = T(\mu_C) \circ i_C \circ \alpha_E(x_E)$$

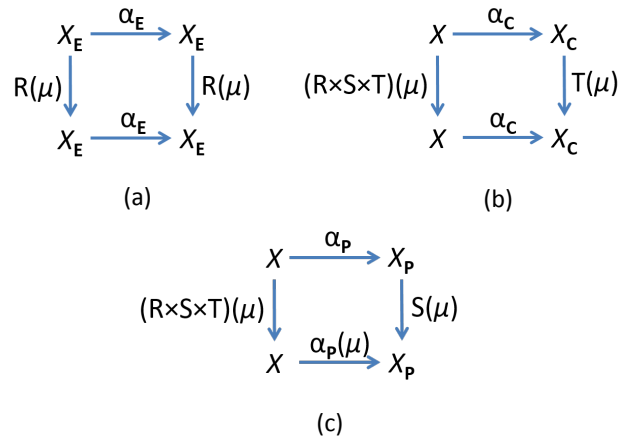


Fig. 9. Admissible transformations.

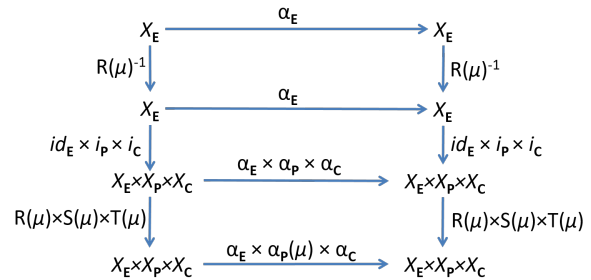


Fig. 10. Perturbation model commutative diagram.

We must make the final crucial assumption of Rich Parameter Perturbation:

For each fixed x_E , as μ_E varies through M_E and μ_P varies through M_P , $R(\mu_E)(x_E)$ varies through X_E and $S(\mu_P) \circ i_P(x_E)$ varies through X_P . It follows that

$$\alpha_C[R(\mu_E)(x_E), S(\mu_P) \circ i_P(x_E), T(\mu_C) \circ i_C(x_E)]$$

depends only on $T(\mu_C) \circ i_C(x_E)$. In other words, for each fixed parameter value μ , the system **S** has feedback structure on the attractor $\tilde{X}_E(\mu)$, namely for

every μ the controller \mathbf{C} is autonomous when regulation is perfect. As before, we deduce that \mathbf{C} contains an internal model of \mathbf{E} , establishing Assertion 2 above.

So what is “the shape” of Mark Twain’s river (which wanders about under perturbation)? Note that in Fig. 9, $\alpha_{\mathbf{E}} \circ R(\mu) = R(\mu) \circ \alpha_{\mathbf{E}}$, where $R(\mu)$ is in fact an automorphism. Thus a “small” perturbation μ merely shifts the current state of \mathbf{E} to one on a “neighbouring” trajectory of the same dynamics $(X_{\mathbf{E}}, \alpha_{\mathbf{E}})$. For “the shape” take any “nominal” trajectory you like!

The scheme above may provide a basis for versions of the IMP in a variety of more structured technical settings, for example bang-bang or sliding mode. Not to mention refinements topological, metric, differentiable, etc., where (essentially) the same commutative diagrams ought to work.

VI. CONCLUSIONS AND RESEARCH DIRECTIONS

This tutorial paper has the objective of presenting fundamental concepts about the internal model principle and how it is declined in different scientific areas, starting from control theory where the principle has been formalised around the 70s, and then overviewing the biology and neuroscience areas in which the principle is a driving concept. The goal of the paper was not to find a common formal perspective but simply to objectively present the different visions and problems as tackled in the different areas, by arousing the curiosity of the reader on how the same “principle” finds declinations in the presented scientific areas. The abstract perspective presented in Section V, in turn, can be seen as an attempt to formalise a primitive “intelligence” not biased on a specific area. Issues on how this “intelligence” is declined in different scenarios by addressing problems of adaptation, learning, computing power, and “real” problem-solving intelligence are definitely open for investigation and characterise the research challenges nowadays addressed in the different areas.

As for control theory, the research area of internal model-based design is still very active with many challenges that are now under the spotlight. Two accompanying papers to this tutorial ([5], [3]) provide more insight on some research aspects that are now considered. One of the main challenges is related to how the “primitive intelligence” declines for multivariable (i.e. with many inputs, measured outputs, and regulation errors) nonlinear systems not necessarily possessing special normal forms. The multivariable nature of the problem shows how internal model-based architectures devel-

oped so far in the context of output regulation for single input-single error nonlinear systems (see Section II) are somehow limitative and must be called into question. In this respect, the distinction that clearly emerged in the last years (see [31]) is between pre-processing and post-processing architectures, with the former typically proposed for single input-single error nonlinear systems and the latter that are typically adopted for linear systems in a general multivariable context. A pictorial sketch of the two architectures is shown in Figure 11. While post-processing architectures are definitely more

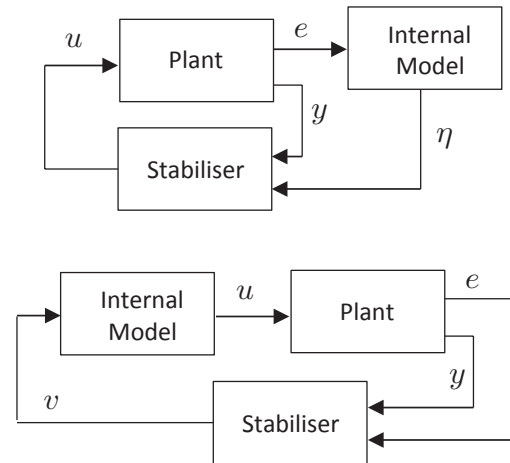


Fig. 11. Pre- and Post-processing internal model-based control architectures.

appealing for handling general multivariable systems, they pose some structural problems in the constructive design of the regulator for nonlinear systems (in this way justifying the research drift towards pre-processing schemes observed so far). In fact, a “chicken-egg” dilemma arises in the design of the stabiliser and the internal model, with the former that depends on the latter (since it is expected to stabilise the cascade between the plant and internal model) and the latter that depends on the former (since the cascade of the two is expected to provide the ideal steady state input), see [5]. While for linear systems a “sequential” design of the two units is possible since the harmonics of the ideal state inputs are known a-priori (as coincident with the exosystem modes) and are independent of the stabiliser, the nonlinear case is definitely more challenging. In plain words, while in the linear framework the internal model is just linked to the exosystem, in the nonlinear setting it is affected by the exosystem, the regulated system and the stabiliser. This fact, in turns, motivates a “synergistic” design of the stabiliser and internal model in which both are “simultaneously” designed to guaran-

tee the invariance of steady state manifold associated to a zero regulation error (typically demanded to the internal model unit) and the attractiveness of the latter (typically demanded to the stabiliser), with the internal dynamics of the steady state manifold that jointly depends on the exosystem and regulated plant. The adoption of a mix of adaptive and identification tools is a possible way investigated in [4] (see [5]). The quest for robustness is also a further fundamental research topic when dealing with the design of the regulator for multivariable nonlinear systems. As stressed in the accompanying paper [3], the formal requirement of robustness necessarily asks to specify which property must be preserved under system uncertainties (with “zero asymptotic regulation error” that is only one, often quite idealistic, possible property) and which kind of topology is used to model system uncertainties. For instance, for linear systems it is known that the linear regulator is robust when considering the property “zero asymptotic regulation error” and when considering arbitrary plant uncertainties that do not destroy the linearity of the system (and the closed loop stability). In the case of nonlinear systems the fact of insisting with the ideal property of zero regulation error in presence of arbitrary plant uncertainties seems to be unrealistic to the point that the paper [3] conjectures that finite dimensional robust regulators do not exist. This observation justifies research directions aiming to identify the strongest (i.e. “as close as possible” to zero regulation error) property that is preserved under the weakest topology constraining plant uncertainties, opening to internal model principles that depends on the adopted property/topology.

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