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Gesture planning integrating knowledge of the motor plant's dynamics: A literature review from motor control and speech motor control

Pascal Perrier

Gipsa-lab, UMR CNRS 5612, Grenoble INP, Grenoble, France

Abstract:

In order to study how dynamical properties of the motor plant are accounted for in movement planning, an optimal motor planning hypothesis was proposed in the late eighties. It suggested that forward and inverse internal models of the dynamics of the motor plant are learned in the brain, and that these models are used to compute and minimize a cost along the movement sequence. In this paper, the original form of this optimal motor planning hypothesis is described in detail in order to introduce the main issues that have since been investigated in relation to this hypothesis. A selected number of experimental studies carried out in the context of arm and speech movements are presented and analyzed. It is shown that while models of the motor plant's dynamics seem to be used in arm movement planning, no evidence currently exists in support of this hypothesis for speech movement. In general for both arm and speech movements, recent findings suggest that representations of the motor plant's dynamics in the brain could be spatially local or dedicated to a specific task. This raises the question of whether these representations are based on models or on motor memory. These findings are discussed more specifically in the context of speech motor control. Updates of the original hypothesis are given and some alternative hypotheses are briefly introduced.

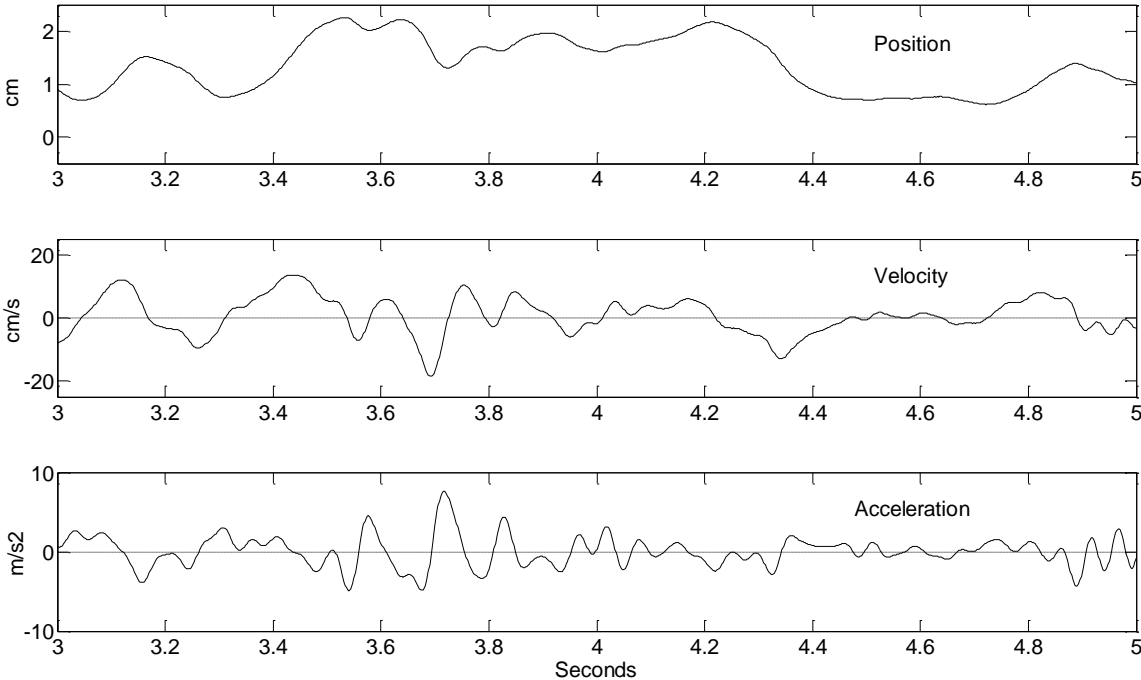
1 Introduction

Speech communication is based on the transmission of acoustic signals from speakers to listeners. Hence, speech is acoustics. However, to generate the acoustic signals, the speakers move their jaw, their tongue, their lips, and their vocal folds. Listeners also use facial movements when perceiving speech in a face-to-face interaction with a speaker. Hence, speech is undoubtedly movements. Because of the bimodal nature of speech, the literature is full of debates related to the deep nature of the speech goals: are they primarily in the acoustics (e.g. Stevens, 1972) or in the articulatory domain (Browman & Goldstein, 1990)? From a cognitive perspective, one can argue whether speech movements are determined by the necessity to produce specific desired goals in the acoustics or whether speech movements are the goals of speech production, which are made perceivable to listeners via the acoustic signal. However, from a purely physical perspective, speech movements precede the acoustic signal. Speech movements are the causal factors that determine the time variation in vocal tract geometry and, consequently, the spectro-temporal characteristics of the acoustic speech signal. In that sense, speech movements are the basis of oral linguistic communication. To communicate with speech humans have to know how to generate the appropriate gestures in their vocal tract, independently of whether these gestures are the ultimate goals of the task or just the obligatory means of achieving the ultimate goals in the acoustics. This is why the focus of this paper is on the way humans plan sequences of gestures in their vocal tract to communicate with speech; we have already addressed in other papers the issue of the nature of the speech goals (Savariaux et al., 1995, 1999; Perrier, 2005; Brunner et al., 2009, 2011; Grimme et al., 2011).

From a physical perspective, these movements are a result of the actions of muscle forces on mechanical structures, namely the articulators of the vocal tract. The characteristics of movements, their spatial paths, their velocities and their accelerations, depend strongly on the intrinsic mechanical properties of the articulators and on the mechanical interactions that the articulators have with each other and with external mechanical structures, such as the palate, the teeth or the pharyngeal walls. Some of the articulators are rigid bodies (jaw and hyoid bone), and some of them are made of soft tissue (tongue, lips, velum, pharyngeal walls). Mechanical interactions among speech articulators or between articulators and external structures induce time-varying frictions or damping with a range of magnitudes, which in some cases can be considered equivalent to obstacles on the movement paths. Stiffnesses of

the articulators vary in time as functions of the activation of the muscles that act on them or that are part of them (in the case of soft tissues).

Kinematics



Dynamics

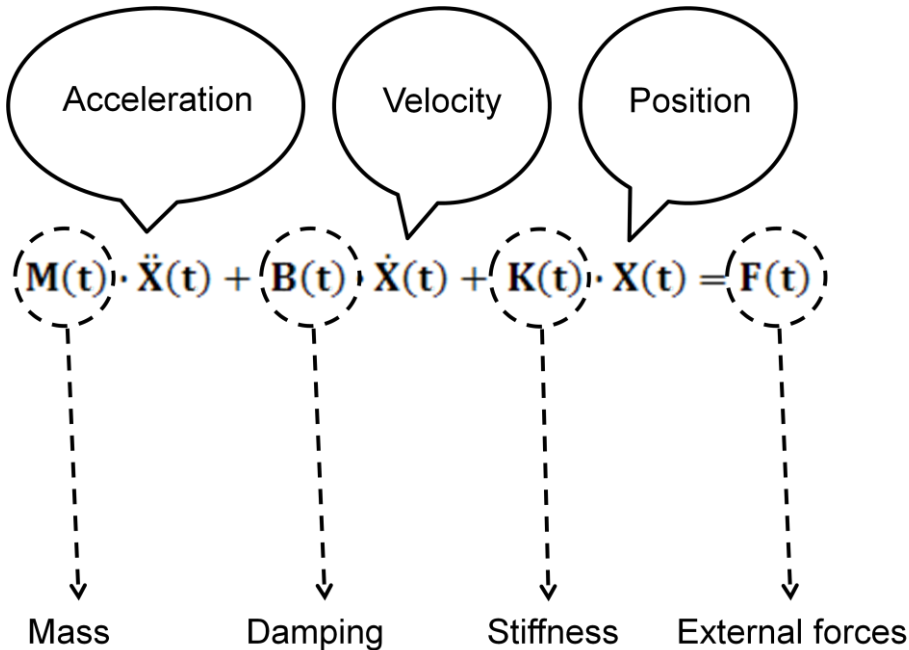


Figure 1: An illustration of differences and relations between kinematic properties (top panel) and dynamical properties (bottom panel) of movements.

All these complex mechanical phenomena, which initiate or influence movement properties, constitute the **dynamical properties** of the speech motor plant. The resulting observable movement properties, i.e. spatial paths, velocities and accelerations, without consideration of any forces that are involved in the generation of the movement, are its kinematic properties. Kinematic properties can relatively easily be recorded with video systems, ultrasound systems, dynamical MRI or motion capture systems such as the Optotrack or Electromagnetic Articulometers. The dynamics of a mechanism, in contrast, corresponds to the causes of its motion. The system's dynamics are the underlying mechanical processes that enable and constrain movements and determine their kinematic properties (see Figure 1 for a summary). Dynamical properties are not easy to measure directly during speech production. Investigating and analyzing them using easily available measures usually necessitates the use of models based on theoretical assumptions concerning the mechanical characteristics of the articulators of the vocal tract.

Some dynamical properties of the motor plant, such as muscle force intensity and direction and the stiffness of joints or tissues, can, to a certain extent, be controlled¹ by the Central Nervous System (CNS). Let us call these properties *controllable properties*. Other dynamical properties, such as friction, damping or weight, are intrinsic to the motor plant in its environment (henceforth called *the physical motor plant*) and they cannot be voluntarily modified. Let us call these properties *intrinsic properties*. By specifying controllable properties of a dynamical system, a controller can influence the kinematic properties of a movement. However, the actual influence strongly depends on the intrinsic properties of the system. Let us consider the simple theoretical case of a controller that is designed to control the duration of the first free oscillation of an undamped mass-spring system, starting from an initial stretched length different from its rest length. For an undamped mass-spring system it is well known that under these conditions the free oscillation duration (i.e. the period) is directly linked to the square root of the mass-normalized spring stiffness (i.e. the stiffness divided by the mass). Hence, if the controller knows the value of the mass that will be moved, it can control the oscillation duration of the movement by specifying the stiffness of the spring. However, if the mass-spring system is damped (due, for example, to external frictions), the duration of the first oscillation (i.e. the pseudo-period) is determined by both the mass-

¹ Muscle forces result both from descending inputs from the Central Nervous System to the brainstem or the spinal cord and from afferent inputs from the muscles (see Schmidt, 1988). Muscle force directions are strongly dependent on anatomy. Stiffness of a muscle is the result of combined influences of passive tissue properties and muscle activations (McMahon, 1984).

normalized stiffness and the mass-normalized damping factor. This damping factor is intrinsic to the system and cannot be controlled. Consequently, an accurate control of the first oscillation duration via the specification of the spring's stiffness is only possible if the mass and the damping factor are perfectly known, i.e. if the controller has a perfect knowledge of the intrinsic properties of the system.

This example illustrates the crucial issue that motor control studies in general, and speech motor control studies in particular, investigate with regard to the integration of the dynamical properties of the motor plant in motor control strategies. To what extent and in which forms are these dynamical properties taken into account in movement planning and movement execution? Is the motor control system able to learn the dynamical behavior of the motor plant and to predict the influences of the dynamical properties on movements? Does the motor control system know enough about the dynamical behavior to compensate for the impact on movement of intrinsic properties by tuning the controllable properties? Is it possible for the controller to precisely guide the motor plant along a specified spatial trajectory with a specified timing? If the motor control system does not know the dynamical behavior in its whole complexity, what minimal knowledge is required to ensure the achievement of the motor goals? If knowledge of the motor plant's dynamics is incomplete, how can feedback compensate for this deficiency, and ensure acceptable movement accuracy and stability?

All these issues are crucial. In order to address them in motor control studies, the concept of *dynamical internal model* has been proposed, which provides hypotheses about the way the CNS integrates knowledge of the motor plant's dynamics in gesture planning. Internal models are extensively used in the literature to investigate issues in motor control in general and in speech motor control in particular. Internal models are mathematical models of the relations between the inputs and the outputs of a system. In the literature, they differ from one another in the extent to which they model the physical mechanisms underlying the relations between inputs and outputs, and in the way they account for the relations between inputs and outputs (static, time-varying, etc). Classic examples of internal models are models of the relations between the joint angles in the arm and the finger position in the space, models of the relations between joint torques and joint angles in the arm, of the relations between muscle activations in the vocal tract and spectral peaks of the acoustic speech signal, or models of the relations between articulatory positions in the vocal tract and spectral peaks in the acoustics. In this paper, the focus is on how the CNS integrates knowledge of the dynamics of the motor plant in gesture planning in general, and in speech gesture planning in particular. The general concept of *dynamical internal models* will be presented first and it will be shown how it helps

in formalizing and then clarifying the problem. To do this, we will first refer to the original proposals that were made at the end of the eighties. Since then, many changes have been made to these original proposals, because of a number of experimental studies that have challenged them. The following section is devoted to the presentation of some important published experimental studies of this kind that have investigated whether the CNS uses knowledge of the dynamical behavior of the motor plant to control it, and if it does, with what level of complexity and accuracy. More recent publications have been taken into account in this section. In the last section, the existence and the nature of *dynamical internal models* will be discussed in the specific context of speech motor control. As concerns speech production in particular, the work carried out with the DIVA model (Guenther et al., 1998; Tourville & Guenther, 2011) incorporating experimental data and functional brain imaging studies provided strong support for the existence of internal models linking articulatory positions in the vocal tract and spectral characteristics of the speech signal. It also found evidence for the cortical localization of this internal model (Bohland & Guenther, 2006).

2 Dynamical Internal Models

2.1 Basic principles

2.1.1 Internal models: Representations of the motor plant stored in the brain

To our knowledge, the *internal model principle* was originally proposed by Francis & Wonham (1976) in the field of robust control theory. The underlying idea was that a controller needs to use a model of how the system to be controlled reacts to perturbation and to change in control parameters to ensure robust control. This principle was introduced in the field of human motor control theory by Kawato et al. (1987) in order to explain how skilled human movements can be produced rapidly in spite of the intrinsic limitations of the biological feedback system:

There are substantial delays in the feedback loop; for example the transcortical loop requires 40-60ms (Evarts, 1981). Further, experimental results indicate that the contribution of the supraspinal loop to load compensation is insubstantial (Evarts, 1981). Feedback delays and small gains both limit controllable speeds of motions [if they are controlled using these feedback signals, Author's Note]. Consequently, in learning a movement, we first must execute the movement very

slowly, because otherwise the control system becomes unstable. (Citation from Kawato et al., 1987, p. 171)

Kawato et al. (1987) proposed that, in order to overcome these limitations and to precisely control rapid movements, the CNS would learn and use different kinds of generalized representations of the relations between motor commands, forces and the properties of movements. These learned models are stored in the brain and they are called *internal models*. Internal models can be of two kinds depending on their inputs and outputs: they are *forward* or *inverse* models.

2.1.2 Forward models: Causal representations of the motor plant from commands to sensory signals

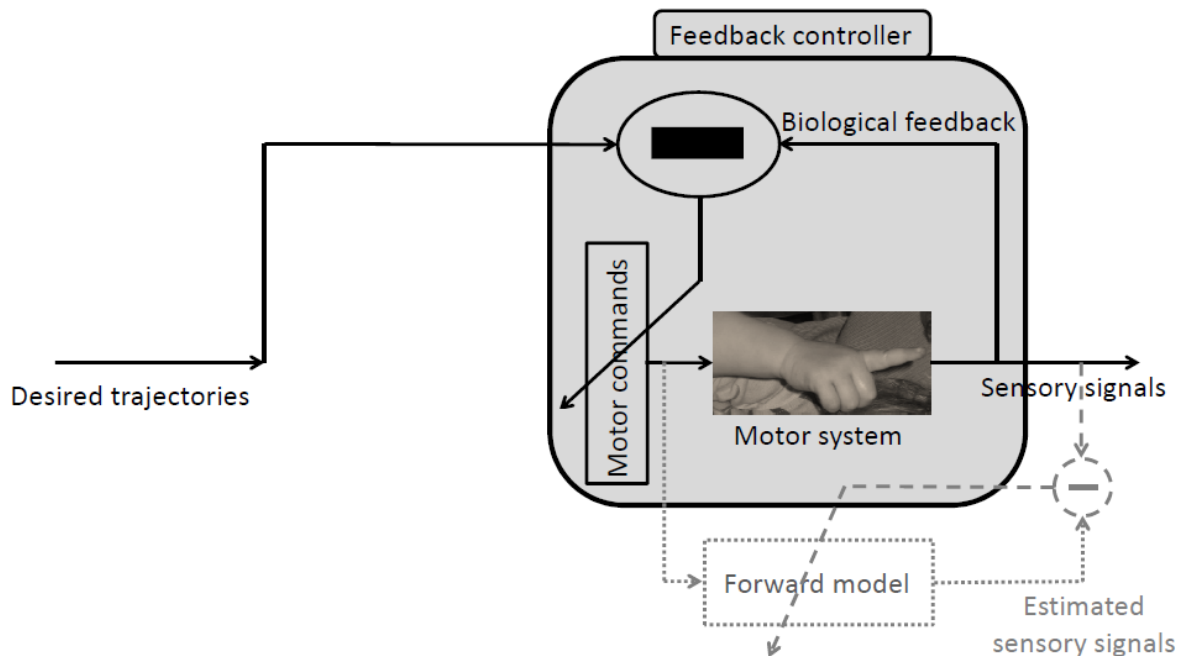


Figure 2: First stage of the motor learning process according to Kawato et al. (1987). The CNS specifies the motor goals in the form of desired trajectories and it adjusts the sequence of motor commands accordingly using the information that the biological feedback sends back about the state of the motor plant. Due to noticeable feedback delays, this adjustment cannot be done quickly. In parallel the CNS learns an internal model of the relation between motor commands and sensory signals, a so-called *forward model*.

For more details about the symbols used in this representation, see the Appendix.

Kawato et al. (1987) suggested that, in the first stage of the learning process of a skilled motor task (such as pointing, reaching, grasping, or speaking), movements would be executed slowly. Slow movements would be required in order for the CNS to adjust and correct the sequence of motor commands on the basis of the biological feedback, which provides information on the actual position of the motor plant, as compared to *desired trajectories*,

which are the motor goals specified by the CNS. This way of controlling movement is called *feedback control* (Figure 2).

To speed up the execution of the movement, according to Kawato et al. (1987), it would be necessary for the CNS not to have to rely only on the slow biological feedback. An efficient way to do so would be to learn an internal model that tells the CNS how the motor plant behaves in response to motor commands. Kawato et al. (1987) suggested that the CNS would use the first stage of the motor learning process, during which various slow movements are executed using a *feedback control*, to learn the relationships between the motor commands and the sensory signals that motor commands induce (described in terms of position, velocity, acceleration, forces or torques). These relationships would be stored in the brain in the form of an internal model, a so-called *forward model*, which mimics the motor plant and describes the relationships between motor commands and sensory signals (Figure 2).

The core hypothesis of the internal model framework for motor control suggests that thanks to this *forward model*, the CNS can predict the sensory signals that the real motor plant would generate in response to the motor commands. This prediction can be used by the CNS to evaluate the consequences of the motor commands without having to wait for the biological feedback to send back this information. Hence, the predicted sensory signals can be considered as *internal feedback*. With a *forward model*, the estimation of the sensory signals from the motor commands can be done prior to the execution of movement, since it relies on an internal simulation of the movement. These internal feedback loops are much faster than biological feedback loops arising from the true physical motor plant. Thanks to the *forward model*, the Central Nervous System can control and execute fast movements using a *feedback control* strategy based on the fast internal feedback loops (Figure 3) (see also Miall & Wolpert, 1996, for more details). Obviously, the accuracy of the control depends on the quality of the *forward model*. If the *forward model* simulates the true motor plant precisely, the internal feedback will be very close to the real sensory signals, and the control will be accurate. If the *forward model* simulates the motor plant poorly, the control will be worse. In this case, if the movement actually produced is too far from the desired trajectory, the biological feedback can be used to correct movement, but only if it is made slowly because of the time delay involved.

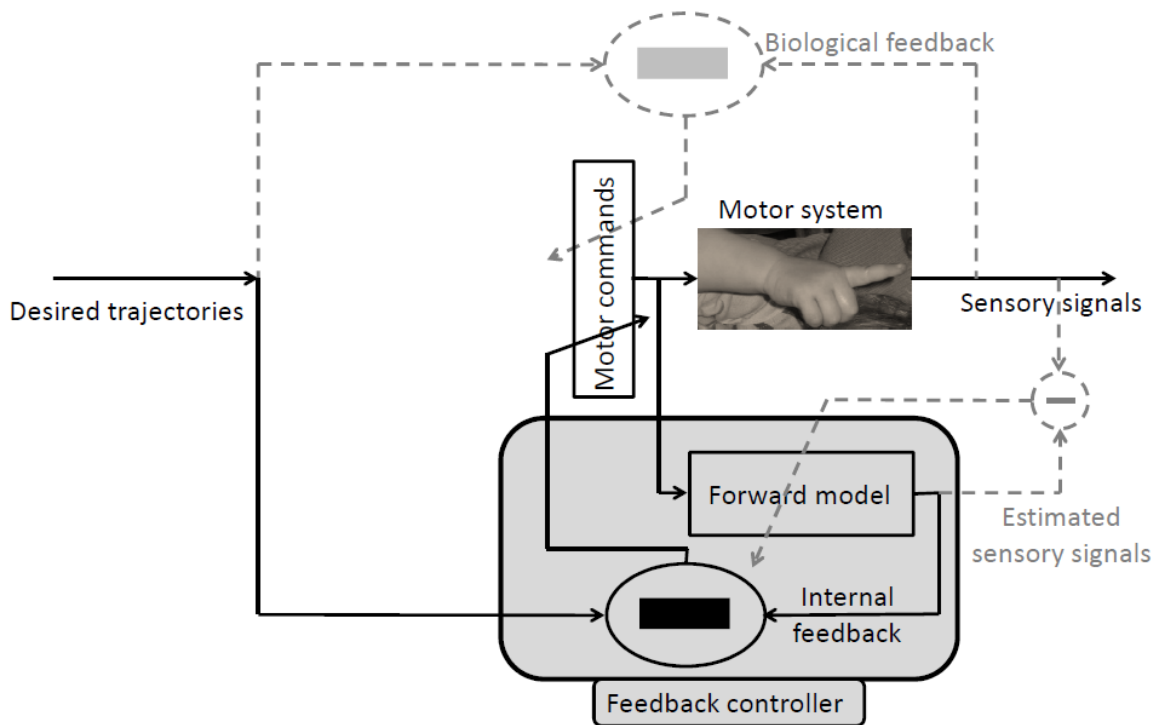


Figure 3: Second stage of the motor learning process according to Kawato et al. (1987). In order to control fast movements, the CNS uses the *forward model* and its internal feedback to adjust the commands in such a way that the motor plant moves along the specified desired trajectories. The CNS can still use the biological feedback (see Figure 2) if the *forward model* is not accurate enough or if external perturbations are applied to the motor plant. The *forward model* is continuously adapted, if necessary, on the basis of the comparison between the estimated and the actual sensory signals.

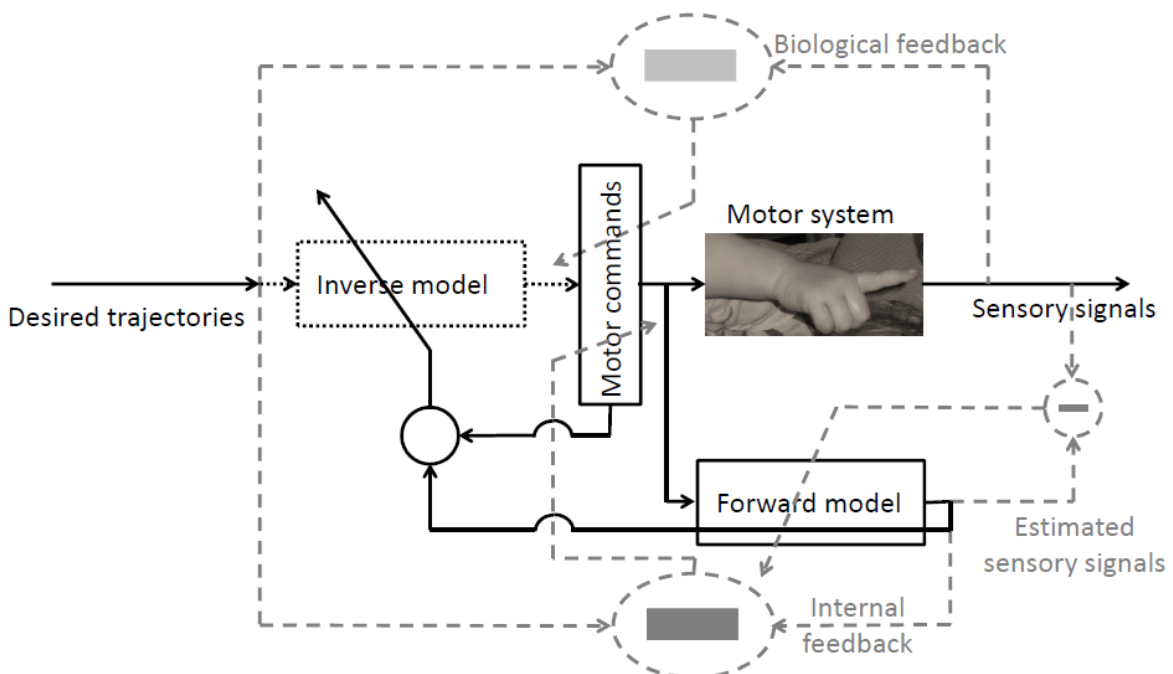


Figure 4: Third stage of the motor learning process according to Kawato et al. (1987). The CNS learns an internal model, called the *inverse model*, which allows inference of the sequence of motor commands from desired trajectories. This is made possible by an extensive set of movements simulated with the *forward model*. Biological feedback can also be used, but due to its long delay the learning would be less efficient.

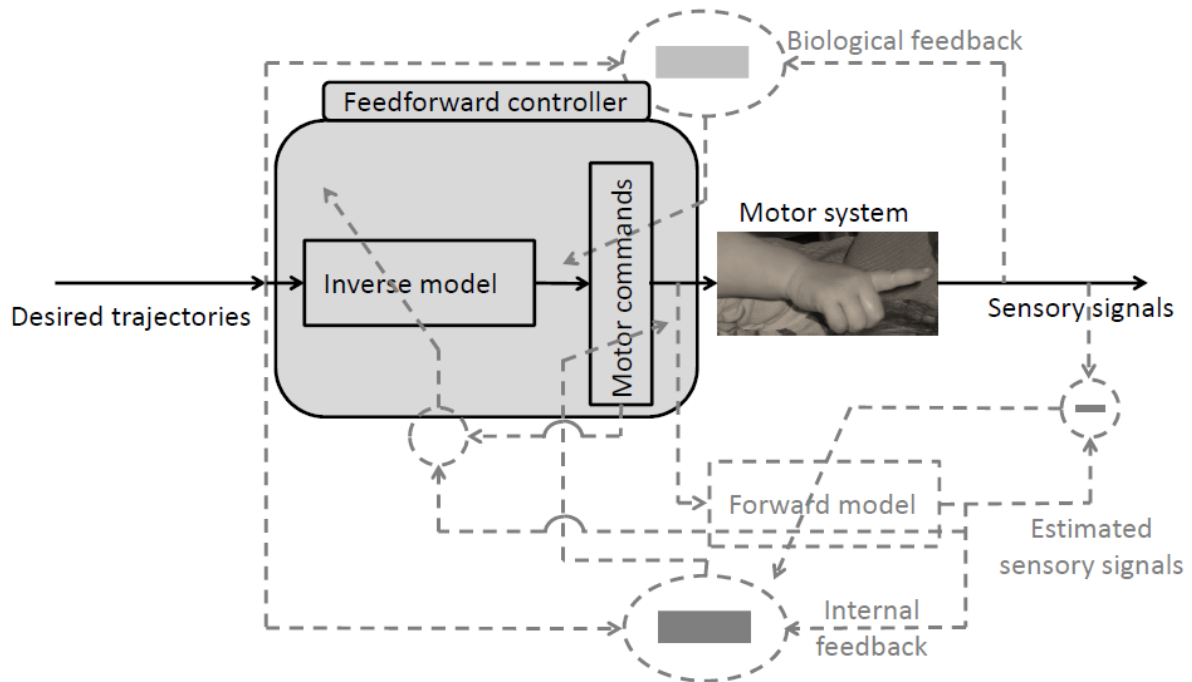


Figure 5: Last stage of the motor learning process according to Kawato et al. (1987). The *inverse model* has been learned and it is used to infer directly the sequence of motor commands from the desired trajectories. This is the so-called *feedforward control*. The CNS can still use the biological feedback if the *forward* and *inverse models* are not accurate, or if an external perturbation is applied to the motor plant.

2.1.3 Inverse models: Inverse mappings in the motor system that compute motor commands directly from motor goals

According to Kawato et al. (1987), after successfully achieving a very large number of various motor tasks, the CNS also learns how to infer the sequence of motor commands directly from the specification of a desired trajectory, and no longer requires corrective feedback. This relationship between the output of the motor plant, namely the trajectory of the end-effector, and the input of the motor plant, namely the sequence of motor commands, is stored in a second internal model, called the *inverse model*. An accurate learning of an *inverse model* requires a very large number of motor tasks. The actual achievement of all these motor tasks with the physical motor plant would take a very long time. Hence, Kawato et al. (1987) suggested (see also Miall & Wolpert, 1996) that the learning of the *inverse model* could be done more quickly and more efficiently by simulating these tasks with the *forward model*. Thus, the large number of required movements could be simulated internally and rapidly, instead of being physically and slowly generated (Figure 4). In this scheme, if the forward model is inaccurate, the inverse model that develops will obviously also be inaccurate, and the inferred sequence of motor commands not particularly appropriate to the actual achievement of the desired trajectory.

Once the *inverse model* has been learned, the sequence of motor commands can be directly determined from the specification of the desired trajectory; sequences of motor commands are the outputs of the *inverse model*, while the desired trajectory is the input to this model. This kind of control is called *feedforward control*, as opposed to *feedback control*, since there is no need for the controller to use any information sent back from the motor plant, or from its *forward model*, to the controller (Figure 5). In the absence of unexpected external perturbation, if the *inverse model* has been learned correctly, the *feedforward control* should ensure accurate achievement of the desired trajectory. In the presence of an external perturbation or if the model is inaccurate, the *feedback control*, based on the biological feedback, is required to correct the sequence of motor commands initially computed by the *inverse model*.

2.1.4 The “feedforward control and desired trajectories” scheme: The need for very accurate dynamical internal models

According to Kawato et al. (1987), by successively learning a *forward* and an *inverse internal model*, the CNS can, in the absence of any perturbation, accurately and rapidly guide the motor plant along desired trajectories using a *feedforward control*. This scheme provides a very strong and powerful theoretical model for investigating and understanding skilled human motor control. However, for this motor control scheme to be efficient, three strong key-hypotheses should be fulfilled:

The CNS specifies extensively the *desired trajectories* that are the goals of the movements.

The *forward model* is an appropriate simulator of the dynamical motor plant; if this were not the case, an inappropriate *inverse model* would be learned.

The *inverse model* accounts perfectly for all the dynamical properties of the system; if it did not, the computed sequence of motor commands would not be appropriate to the achievement of the desired trajectory.

The last two hypotheses seem to be quite unrealistic for most of the motor plants in humans. Human motor plants can have very complex dynamical properties and this is clearly true for the speech apparatus, since the majority of the speech articulators are made of soft tissues, where elasticity and damping can vary significantly with strain and muscle activation (McMahon, 1984; Gerard et al., 2005; Nazari et al., 2011a). Hence, it seems difficult to believe that the *forward* and *inverse internal models* can capture these dynamical properties in their whole complexity. In addition, more generally, learning the dynamical *inverse model*

requires access to errors at the level of the motor commands, and, according to Wolpert et al. (1998, p. 338) (see also Kawato, 1999), these errors are not directly available to the CNS. For all these reasons, it does not seem reasonable to assume that the CNS can achieve a perfect description of the motor plant in its entirety, either in its causal forward form or in its inverse form. Consequently, the theoretical model proposed in Kawato et al. (1987), based on the specification of desired trajectories and on the learning of a *feedforward controller*, does not seem to be realistic. In this respect, Kawato et al. (1990) have proposed interesting modifications based on the concepts of *trajectory formation* and *optimal motor planning*.

2.2 Trajectory formation and optimal motor planning

Kawato et al. (1990) modified the original hypothesis of the existence of motor goals in the form of fully specified desired trajectories. They suggested that motor goals could instead be specified by a limited number of discrete key-points in the task space. The task of the controller would be to ensure that the motor plant actually reaches the different key-points in the right serial order and with the appropriate timing, from the starting position all the way to the final position. Kawato et al. (1990) called these key-points *via-points*. For a given sequence of *via-points* there is an infinity of possible trajectories for the motor plant (see Figure 6). The emergence of a particular trajectory from the specification of the *via-points* is called *trajectory formation*. Kawato et al. (1990) proposed that *trajectory formation* is based on an optimization process that minimizes a certain cost for the motor plant along the whole trajectory in order to have maximum smoothness for the trajectory (“*maximum smoothness*” principle). For multi-joint arm movements, according to Kawato et al. (1990), two costs are suited to the achievement of the maximal trajectory’s smoothness: the integral of the square of the jerk (the jerk is the derivative of the acceleration) as proposed by Hogan (1984) in his *minimum jerk model*, or the integral of the square of the derivative of the torques at the arm joints as proposed by Uno et al. (1989) in their *minimum torque-change model*. The minimum jerk model optimizes trajectory smoothness by acting directly on kinematic characteristics of the movement: position, velocity, acceleration and jerk. It does not require an explicit formulation of the dynamical characteristics of the motor plant. The minimum torque-change model acts at the level of the muscle force generation mechanism and requires, to be effective, a detailed knowledge of the torque distribution at the joints and of the way these torques influence movement. Thus, the minimum torque-change model requires a detailed representation of the dynamics of the motor plant.

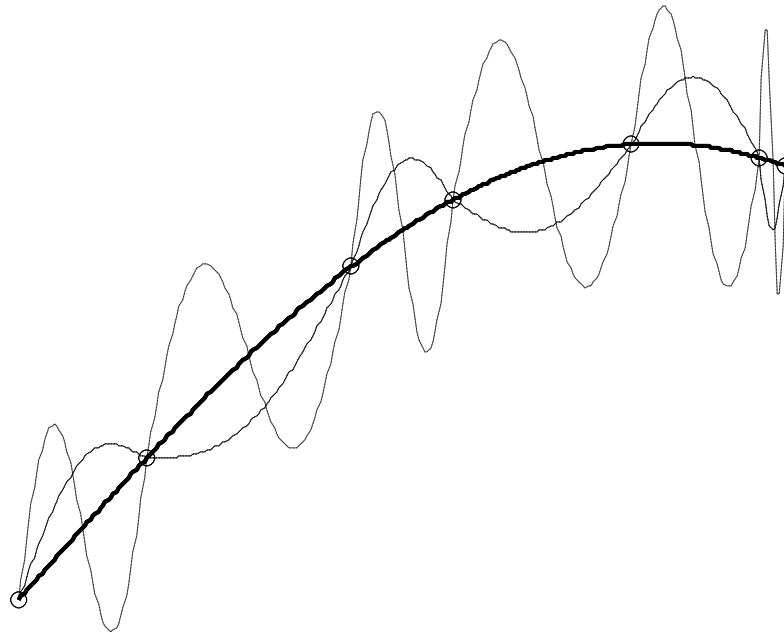


Figure 6: Via-points (circles) and examples of possible trajectories joining these via-points. The bold solid line corresponds to the trajectory with maximal smoothness.

The optimization process determines both the optimal trajectory joining the intended via-points and the sequence of motor commands enabling the motor plant to follow this trajectory. It is an *optimal motor planning* of the movement toward the successive intended via-points. According to Kawato et al. (1990), this kind of *optimal motor planning* uses a *forward model* of the motor plant in order to compute the cost via the prediction of the trajectory in response to a sequence of motor commands, and to determine how to change this sequence of motor commands in order to minimize the cost. This is summarized in Figure 7. Consequently the internal model should include a description of the sensitivity of the cost to local changes in motor commands. The optimal trajectories are intended trajectories, in the sense that the actual achievement of these trajectories by the motor plant will depend on the accuracy of the *forward model* and on the effectiveness of the optimization process. Once the CNS has found optimal sequences of motor commands and trajectories for a sufficiently large number of via-point sequences, it should be able, according to Kawato et al. (1990), to generalize to new sequences without going through the optimization process. In doing so the CNS learns an *inverse model* that determines the optimal sequence of motor commands and the corresponding intended optimal trajectories directly from the specification of the via-points

(see Figure 8). At this stage, the CNS uses a *feedforward control* to generate the appropriate movement. The actual achievement of the motor goals depends on the accuracy of the internal *forward* and *inverse models*.

Note that Jordan & Rumelhart (1992) made a similar proposal. Both Kawato et al. (1990) and Jordan & Rumelhart (1992) also showed that such an *optimal motor planning* is useful for determining motor commands from motor goals in motor plants with redundant degrees of freedom. For systems having degrees of freedom in excess, many different sets of motor commands can generate the same positions of the end-effector in the task space. For example, in a planar pointing task, the end-effector is the forefinger. The same position of the forefinger can be reached for a large number of joint angles at the shoulder, the elbow and the wrist, and for an even larger number of muscle activations at these joints. Hence, the specification of the forefinger position in the task space does not determine the motor commands. Such an excess of degrees of freedom is extremely important and useful in motor control, since it allows the elaboration of motor equivalence strategies, i.e. the selection of various strategies to reach the same goal in the task space. However, determining motor commands from the specification of the forefinger position in the task space only is not possible. This is an inverse problem with many solutions, and for this reason it is called an *ill-posed inverse problem* (see, for example, Marroquin et al. (1987), for an interesting explanation of the concept of ill-posed problems). Ill-posed problems can only be solved by taking into account additional constraints. Kawato et al. (1990) and Jordan & Rumelhart (1992) suggested that for a sequence of motor goals, this additional constraint could consist in looking for maximal smoothness for the trajectory connecting these goals, which means using an *optimal motor planning*.

In the context of *optimal motor planning*, some publications have proposed other costs. For walking, Anderson & Pandy (2001) proposed that the CNS would minimize the metabolic energy expenditure used per unit distance traveled. For target-oriented motor tasks, such as eye saccades or pointing tasks, Harris & Wolpert (1998) suggested that the sequence of motor commands could be determined so as to minimize the variance of the end-position across repetitions of the same task (the so-called *minimum of variance model*). Depending on the cost to be minimized during the *trajectory formation* and *optimal motor planning* process, different complexity is required for the *forward* and *inverse internal models*. In the context of the minimum jerk model, in which the cost is computed from kinematic variables, there is no need to have a very accurate model of the dynamical properties of the motor plant in interaction with its environment (see Jordan & Rumelhart, 1992). In the context of the minimum variance model, Harris & Wolpert (1998) simulated fairly realistic movement

patterns for eye saccades and planar arm movements by using simplified dynamical representations of the motor plant. However, if it is hypothesized that the torque-change is minimized, accurate internal models of the dynamical characteristics of the motor plant are required (Kawato et al., 1990; Wolpert et al., 1998; Kawato, 1999). In their model for walking control, Anderson & Pandy (2001) computed the energy expenditure with a model consisting of 10 segments controlled by 54 muscles and having 23 degrees of freedom! A fairly complex internal model! Hence, the choice of the cost to be minimized in *optimal motor planning* has strong consequences for the level of complexity that is required for the description of the motor plant in the *forward* and *inverse internal models*.

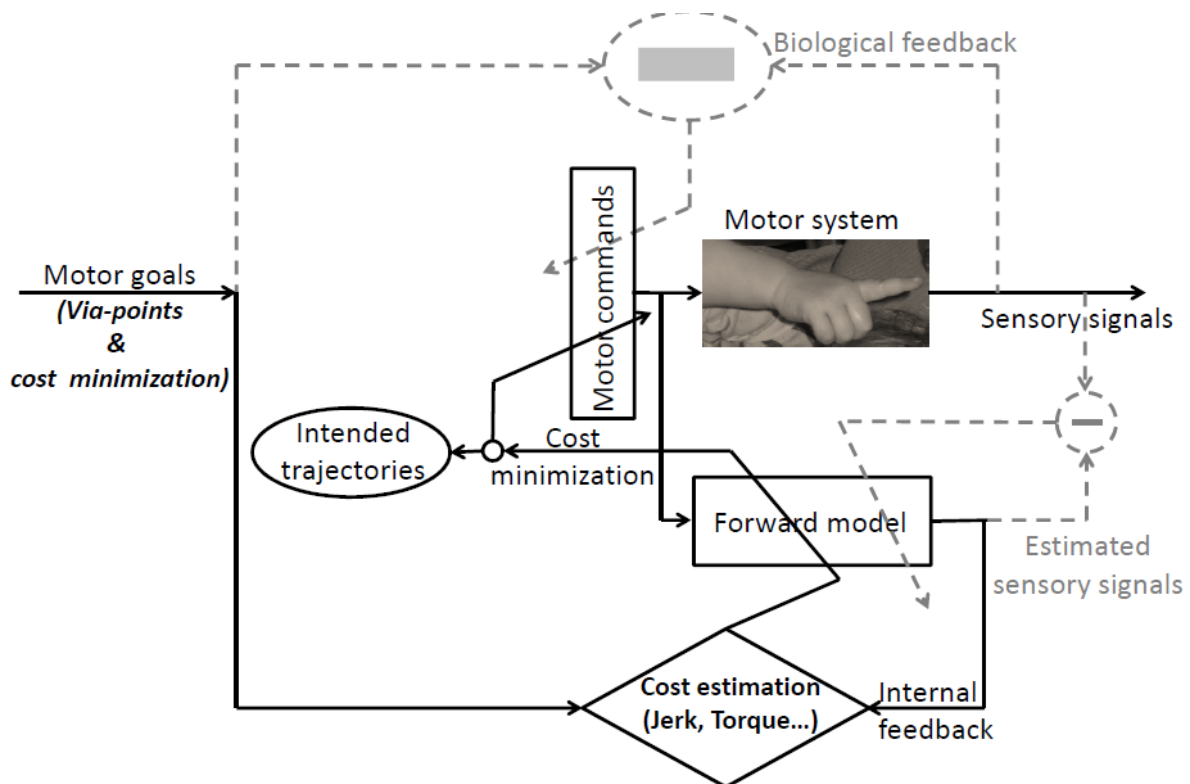


Figure 7: Optimal motor planning using a *forward model* according to Kawato et al. (1990). The *forward model* generates an estimation of the outputs of the motor plant, on the basis of which the CNS estimates the cost (jerk or torque). The CNS also uses the *forward model* to find how to change motor commands with the aim of minimizing the cost. Once the cost has been minimized, the optimal intended trajectory joining the via-points is determined together with the appropriate motor commands.

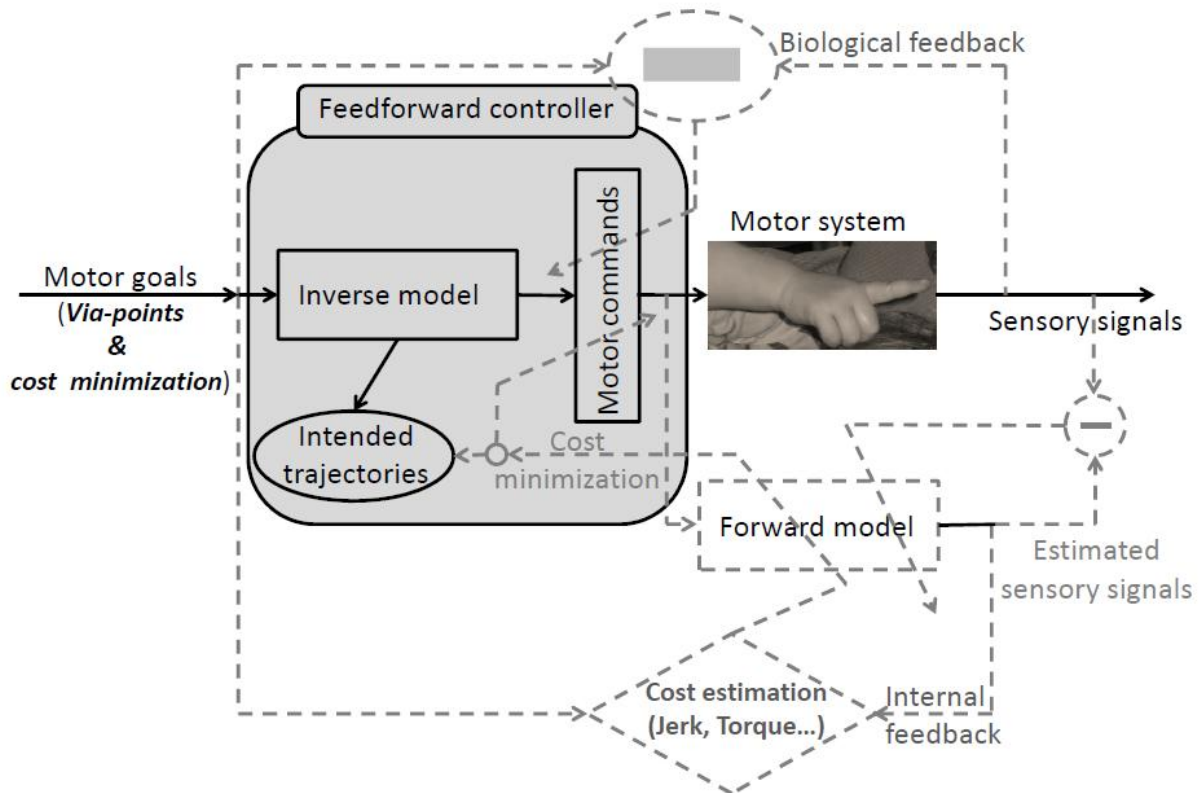


Figure 8: Feedforward control after optimal motor planning according to Kawato et al. (1990). After having found optimal trajectories and motor commands for a sufficiently large number of via-point sequences, the CNS generalizes and learns an *inverse model*; this inverse model determines the motor commands and the intended optimal trajectories directly from the specification of the via-points, according to a *feedforward control* scheme

2.3 Summary

In the original papers going back to the late eighties and the beginning of the nineties, two main motor control schemes were proposed to account for the potential existence of dynamical representations of the motor plant in the CNS. Both schemes apply to the control of fast movements, for which a feedback control based on the long-delay and low-gain biological feedback would not be appropriate. Both schemes also suggest that after motor learning and in the absence of unexpected external perturbations, motor control should be based on a *feedforward control* using a dynamical *inverse internal model* of the motor plant. The *inverse internal model* is considered to be learned on the basis of numerous movement simulations using a *forward internal model* of the motor plant.

In the first scheme, motor goals are defined as fully specified desired trajectories in the task space. Part of the planning, namely that of the desired trajectories, is done at a high level (it is not clear which), and does not take into account any information about the dynamical properties of the motor plant. Only the choice of the motor commands appropriate for the

achievement of the desired trajectories integrates information about these dynamical properties. In this context, controlling the motor plant with accuracy requires both the *forward* and the *inverse internal models* to be extremely accurate and to correspond to complex descriptions of the physical motor plant.

In the second scheme, motor goals are described less extensively with a limited number of via-points discretely distributed in the task space, between the starting point and the end point of the movement. Determining the intended continuous trajectory connecting the via-points, the so-called *trajectory formation* process, is part of the motor planning since this trajectory is the output of an optimization process, which minimizes a certain cost. The choice of the appropriate motor commands is the other output of this *optimal motor planning*. The proposed framework for this *optimal motor planning* is based on the learning and the use of a *dynamical forward model* of the motor plant, and its last stage consists of the learning of a *dynamical inverse model* that will be used afterwards in the *feedforward controller*. However, depending on the cost to be minimized in the optimization process, various levels of complexity can be considered for the dynamical representation of the motor plant which is included in the *forward*, and then the *inverse, model*. In addition, the consequences of potential inaccuracies or simplifications in this dynamical representation are not as strong as in the first motor scheme, based on the specification of desired trajectories. The planned intended trajectories are not the goals of the motor task; their formation is just one step in the motor planning process that aims at achieving the true motor goals, namely the via-points. Hence, a certain amount of difference between the actual trajectory and the intended optimal one can be tolerated, as long as via-points are reached with the required amount of accuracy.

In the second part of this paper, a number of experimental findings will be presented. These have contributed to investigating whether dynamical representations of the motor plant do exist in the brain, and with what level of complexity. They will be interpreted in the context of the *optimal motor planning scheme* that has been described above.

3 Experimental findings

Biological evidence has been found in support of the existence of inverse models in the cerebellum (Wolpert et al., 1998). For example, Gomi et al. (1998) found that, during reflex eye movements, the Purkinje cells that exist in the cerebellum react to inputs related to the position, the velocity and the acceleration of the eyes: their firing rate varies as a function of these inputs. Since it is known that these cells send information to the motor cortex, they

could undoubtedly be the basis for the implementation of inverse internal models. However, it is not clear whether the information about position, velocity and acceleration is actually processed and used in a way compatible with the computation of a cost and the learning of a dynamical inverse model of the motor plant. Hence, additional experimental evidence is needed to confirm the internal model and optimal motor control hypotheses.

There are numerous examples of experimental studies of how the CNS integrates the dynamical properties of the motor plant to determine motor commands. In this section we do not claim to be exhaustive by summarizing all these works. Only a few studies that illustrate our own understanding and interpretation of a very rich and controversial literature are presented. This presentation is organized along three main issues:

Does the CNS learn about the dynamics of the motor plant to ensure gesture accuracy?

Does the CNS learn about the dynamics of the motor plant to optimize gestures?

Does the CNS learn generalized dynamical internal models or does it learn simpler and more local information about dynamics in the context of a specific motor task?

In each case, examples from limb motor control studies and from orofacial motor control studies are presented.

3.1 Integrating dynamics to control movement accuracy

3.1.1 Arm movement: Inertial sensitivity is taken into account in trajectory planning

Sabes et al. (1998) studied the role of inertial sensitivity in motor planning during an obstacle avoidance experiment in three dimensions. In this experiment, the subjects were placed in a 3D virtual environment where they could see on a screen two small virtual spheres, representing the starting and end positions of the movement, a virtual cylindrical obstacle located between the two spheres, and a virtual cube displaying the actual position of their hand. The main axis of the cylindrical obstacle was orthogonal to the plane defined by the two spheres and the center of gravity of the cylinder. The position of the center of gravity of the cylinder was the center point of the workspace. The subjects could not directly see their arm and the only visual feedback was given via this 3D virtual environment. The subjects were asked to move their finger from the starting point to the end point going around the obstacle and making sure to avoid hitting it. The experiment was run under three different conditions as regards the orientation of the main axis of the obstacle in reference to the body. The main axis of the cylinder was either vertical, or horizontal and oriented from the right to the left, or horizontal and oriented in the front-back direction. The movement was essentially done in the

plane orthogonal to the main axis and passing through the two spheres. Hence, the different orientations induced different arm postures during the execution of the movement, and thus, different dynamical properties of the arm. Movement directions were specified in such a way that they turned from 0 to 360° around the obstacle. Many trials were considered for all directions in the three orientations of the plane of movement. The task was done for both the right and the left hand.

The authors measured the spatial distribution of the point of the trajectory which was the closest to the obstacle, the so-called “near-point,” in relation to the center of gravity of the virtual cylinder obstacle (center point). This near-point is important from a motor control point of view, since it corresponds to the point where collision with the obstacle could easily happen if control is not accurate or if the movement is sensitive to slight changes in dynamical constraints. The authors observed that, for each orientation of the main axis of the obstacle, the near-points clustered for all movement directions in the same location of the workspace and along the same direction from the center point. The main orientation of the cluster changed according to the orientation of the main axis of the obstacle, i.e. according to the posture and the dynamical properties of the arm during movement execution.

According to Sabes et al. (1998), the constancy of the near-point cluster’s orientation across movement directions together with its variability with obstacle orientation could be attributed either to perceptual factors, corresponding to anisotropy in the visual perception of the task space, or to factors intrinsically related to the arm posture and the arm dynamics during movement execution. If perceptual factors were the explanation for the patterns of near-point distribution, the same patterns should be observed for the right and the left hand movements. This was not the case. The patterns of distribution observed for the left hand were mirror images of those of the right hand reflected about the midline of the workspace. Hence, the orientations of near-point clusters seem not to have their origins in perceptual factors but in factors intrinsically related to arm posture and arm dynamics, during movement.

Sabes et al. (1998) measured the 3D mobility of the left and right arms at the center point of the task space (i.e. at the location of the center of gravity of the virtual cylindrical obstacle in the experiment). This was done by applying local force perturbations to the arm in all directions and by looking at the amplitude of the arm displacements caused by this perturbation. The arm mobility was characterized in the plane of movement by an ellipse whose minor axis describes the direction in which the arm provides the best resistance to perturbations. The authors found that for both arms, and for the three orientations of the obstacle, the near-point distribution was located in relation to the center point along a

direction that matches the direction of the minor axis of the mobility ellipse quite well. This suggests that the point of the trajectory where accuracy and stability is required, namely the near-point, is planned so as to ensure the best possible resistance to factors that could affect the distance between the trajectory and the obstacle. Thus, it seems that intrinsic dynamical properties of the arm are taken into account by the CNS in trajectory planning in order to ensure maximum stability of the movement at the location where stability requirements are the strongest to avoid collision with the obstacle.

3.1.2 Jaw movement: Speech motor control does not seem to integrate the influence of gravity

Shiller et al. (1999) investigated how gravity is taken into account in speech motor control. This question is well justified and important, since every human is able to speak clearly in the upright, supine or inclined position of the body, while, depending on the orientation of the head, weight exerts its influence along different directions relative to the head. Consequently, it is logical to assume that changes in dynamical conditions associated with changes in head orientation are taken into account by the CNS in order to compensate for their consequences and make sure that the perceptually relevant acoustical characteristics are actually produced.

Shiller et al.'s (1999) methodological approach consisted in analyzing simulations generated with a 2D biomechanical model of the jaw and hyoid bone complex (see Laboissière et al., 1996) and experimental data. The goal of the simulations was to provide an objective characterization of how jaw movements change with head orientation (upright, supine and prone) within the gravity field, in the absence of any modification of the motor commands. The empirical study consisted in recording acoustic signals and articulatory data (in the mid-sagittal plane) from subjects speaking either in upright, in supine or in prone head orientations, and to observe how movement patterns change with orientation. The comparison of the predictions with the experimental data was the means of assessing to what extent the CNS adjusts the motor commands in order to compensate for the influence of gravity: if data and simulations match, it can be assumed that nothing is done at the level of the CNS to take into account orientation.

Shiller et al. (1999) reported a generally good match between the changes in jaw movements that they observed experimentally and the changes predicted with the model assuming no changes in motor commands. Compared with the upright condition, in the prone orientation the jaw moved closer to the palate, whereas in the supine orientation the jaw moved further away from the palate. Compared with the prone condition, in the supine position the jaw

trajectory was located further back in the head. In the acoustics, they observed that the first formant (an indicator of vocal tract aperture) was higher in the upright orientation, and that the second formant (an indicator of the front/back position of the tongue) was higher in the prone orientation. These results support the hypothesis that the CNS does not adjust the motor commands in order to compensate for the influence of gravity, in spite of the fact that changes in head orientation in the gravity field have a significant impact on movements and acoustics. Shiller et al. (1999) interpreted the absence of compensatory adjustments as evidence that the CNS does not learn about the new dynamical conditions, in spite of the fact that the preservation of the task's goal would have required this learning. Their interpretation was based on the fact that the spectral changes associated with changes in head orientation were systematic and significant. However, the amplitude of the spectral changes was within a range of variation compatible with the correct perception of the vowels. Hence, another explanation is possible for Shiller et al.'s (1999) observation: the CNS did not adjust the motor commands simply because the changes in the articulatory paths due to the change in gravity orientation did not endanger the goal of the task, which is the correct perception of the sounds. In this case, the differences between Sabes et al.'s (1998) observations for arm movements and Shiller et al.'s (1999) observations for speech movements would be due to differences in the impact of the inertial constraints on the achievement of the task, and not to the inability of the CNS to achieve a dynamical learning for speech movements. At this stage, it is not possible to discard one or the other of these two possible explanations. However, Shiller et al.'s observation is important in itself: in speech production the CNS does not seem to take into account the influence of gravity when setting up the motor commands suited for the achievement of the desired motor goals.

3.1.3 Arm movements: The stiffness of the motor plant is controlled to increase stability

Franklin et al. (2007) investigated how the end-point stiffness of the arm varies in planar pointing tasks when the arm has to move under the influence of an external force field. The end-point stiffness of the arm corresponds to the resistance to displacements measured at the hand when the arm is in a stable posture and when external forces are applied to the end point from all possible directions. When there is a high degree of stiffness, the displacement induced by the external force is small. When there is a lower degree of stiffness, the displacement induced by the same force is large. The representation of stiffness for forces arising from all possible directions in the task plane, 360° degrees around the hand, is an ellipse, the so-called "*stiffness ellipse*." The major axis of the stiffness ellipse represents the

direction in which the stiffness (i.e. the resistance to external forces) is the largest, while the minor axis corresponds to the direction in which the stiffness is the smallest. The direction of the major axis is called the *orientation* of the stiffness ellipse.

During this experiment, the forearm of the subject was coupled to the handle of a robotic manipulandum that constrains the arm to move in the horizontal plane and can apply forces to the arm at anytime and in any direction of the task plane. Subjects were asked to perform a point-to-point reaching task between two small circles located directly in front of the subject and on a line orthogonal to the line joining the two shoulders of the subject. Under perturbed conditions, three divergent force fields were applied to the arm during movement. These force fields were oriented along three directions that were specifically selected because they correspond to directions in which, according to a modeling study, end-point stiffness can be specifically increased by the activation of a specific pair of antagonist muscles. If the subject was moving her/his arm along the straight line joining the circles used as starting point and goal in the reaching task, no perturbing force field was applied. However, if the subject deviated from this straight line, a divergent force field was applied, which was proportional to the amplitude of the deviation. Hence, the duration, the nature and the amplitude of the perturbation were unpredictable. End-point stiffness was measured for the three force field conditions and in the absence of force field. Electromyography (EMG) signals were also recorded from the 3 muscle pairs that were considered to act specifically on the stiffness in one of the 3 force fields conditions.

After learning all subjects were able to properly achieve the reaching task in the absence of perturbation and for the three different force field conditions. It was found that after training, under perturbed conditions, the main orientation of the end-point stiffness was close to the orientation of the force field orientation. Hence stiffness was specifically increased in the direction of the force field. In addition, the patterns of EMG activation revealed that the activated muscles were those of the pair that could increase the stiffness in the direction of the force field: this suggests that the CNS knows enough about the dynamics of the arm in its physical environment to selectively activate the muscles that increase the stiffness in the direction where the perturbation is the strongest. In doing so, the CNS increases the stability of the motor plant.

3.1.4 Jaw movements: Kinematic variability coincides with intrinsic stiffness patterns

From Franklin et al.'s (2007) study, it can be concluded that in limb motor control the CNS is able to adjust stiffness in order to control kinematic variability according to the accuracy

requirement of the task. In this context, it is interesting to know whether the CNS is able to do the same in orofacial motor control, and more specifically in speech motor control. Shiller et al.'s (2002) study provides interesting information to deal with this question. Indeed, these authors investigated the relation between stiffness and kinematic variability in jaw movements, in speech and non-speech conditions. Measures of the jaw stiffness were measured during the production of steady-state vowels by applying small perturbing forces to the jaw. These forces were applied in the sagittal plane and in all directions via a computer-controlled robotic device connected to the lower teeth. Four vowels of English corresponding to four different jaw heights were considered. The results of these measures were depicted in the sagittal plane in the form of 4 stiffness ellipses, as described above, each of which is associated with a specific vowel and thus with a specific jaw height. It was found for all vowels that the major axis of the stiffness ellipse is oriented along the jaw protrusion-retraction direction and the minor axis along the jaw raising-lowering direction. Globally the stiffness was higher for high than for low vowels.

Variability of jaw positioning was also measured, in speech and in non-speech conditions. In speech conditions, the subjects were asked to pronounce several repetitions of different consonant-vowel-consonant sequences, in which the vowel was one of the four vowels for which jaw stiffness was to be measured. For each of these sequences, the variability of the jaw position was measured for the inter-consonantal vowel. In non-speech conditions, two kinds of movements were considered, vertical movements between positions similar to the ones of the lowest and highest vowels used in the speech production experiment, and protrusion movements for a high jaw position similar to that of the highest vowel. For all these jaw movements, the variability of the jaw position was measured at the upper and lower turning point of the jaw trajectory. The results were displayed in the sagittal plane in the form of ellipses, whose major axes represent the directions of maximum variability, and whose minor axes depict the directions of minimum variability. In both speech and non-speech conditions the major axes of the ellipses (i.e. the directions of maximal variability) were along the jaw raising-lowering direction, and the minor axes along the jaw protrusion-retraction directions. Both for speech and non-speech tasks, these ellipses were oriented orthogonally to the stiffness ellipses measured for speech production.

At this stage, two important observations deserve emphasis: (1) the patterns of jaw variability do not depend on the nature of the task, speech *versus* non-speech, and (2) the patterns of variability are consistent with the stiffness patterns measured in speech production. These observations can be interpreted in two ways: either stiffness patterns have been learned for

speech production to match accuracy requirements, and they have been generalized to non-speech movements, or the stiffness patterns have not been learned and are the result of natural and intrinsic properties of the orofacial system. In order to know more about the stiffness patterns linked with intrinsic properties of the orofacial system, Shiller et al. (2002) used a 2D biomechanical model of the jaw and hyoid bone complex (see Laboissière et al., 1996). The stiffness ellipses were computed for different jaw heights, similar to the experimental one, and for different levels of muscle activations. The authors computed these ellipses under these different conditions for various geometries of the jaw. In all cases, the patterns of stiffness ellipses were found to be very close to those measured experimentally in speech production. In conclusion, Shiller et al.'s (2002) study suggests that in jaw movements involved in speech and non-speech production, contrary to the observations made for arm motor control by Franklin et al. (2007), the CNS does not adjust motor commands in order to control jaw stiffness and to match accuracy requirements imposed by the motor task. On the contrary, it seems that jaw positioning accuracy measured in speech production could be a simple consequence of the intrinsic physical properties of the jaw associated with muscle anatomy, muscle force generation capabilities and the geometry of the jaw.

3.2 How knowledge about dynamics is used to generate a specific trajectory

3.2.1 Arm movements: Adaptation to a velocity-dependent force field seems to involve the learning of internal models and an optimization process

Shadmehr & Mussa-Ivaldi (1994) asked their subjects to produce reaching movements in the right part of their workspace while grasping the handle of a robotic manipulandum. During the course of the movement no visual feedback was given to the subjects about the position of their hand, so that they could not follow a visible trajectory. The manipulandum constrained the arm to move in the horizontal plane but it did not limit freedom of movement in the plane, except in the case where it applied a force field to the hand varying in direction and amplitude. This force field was a function of the velocity of the subject's shoulder and elbow joints during the movements. Hence, when this field was active, its strength was maximum in the middle of the movement (velocity profiles are essentially bell-shaped) and it was zero at the beginning and end of the movement. In the absence of an external force field, the trajectories of the hand were gently curved. This geometrical characteristic has been shown to be the possible consequence of an optimization process (see Flash & Hogan, 1985, or Gomi & Kawato, 1996).

Introducing the force field means modifying the dynamical properties of the motor plant in interaction with its environment. If it is correct to assume that movement trajectory results from an optimization process based on the combination of forward and inverse dynamical models, movement trajectory should change dramatically when the force field is applied. The authors observed that during the first trials following the onset of the perturbation, the trajectories were indeed very different from the normal path: the hand deviated strongly from the direction of the targeted end point, before quickly returning to it at the end of the movement. This induced the emergence of a strongly curved hook in the very last part of the trajectory. The more the task was repeated under perturbed conditions, the more this hook disappeared, up to the stage where all the subjects were able to compensate for the perturbation and to follow movement paths that were very similar to the normal ones, i.e. gently curved and without any hook, matching the characteristics of an optimized movement. In addition, once the perturbation had been removed, after-effects were observed, in the sense that the subjects did not immediately return to the trajectories that they had followed before the perturbation had been introduced.

After-effects are interpreted by Shadmehr & Mussa-Ivaldi (1994) as evidence that for all subjects the adaptation to the mechanical perturbation involved the learning of internal models which took into account the new dynamical conditions of the motor plant associated with the introduction of the force field. The fact that trajectories after learning are gently curved is consistent with the hypothesis that the internal models are used in an optimization process.

3.2.2 *Jaw movements: Adaptation to a velocity-dependent force field provides evidence that dynamics is taken into consideration in movement planning and/or execution*

A similar study was carried out by Tremblay et al. (2003) with the jaw, in speech and non-speech conditions. With a robotic device connected to the lower teeth and controlled by computer, Tremblay et al. (2003) also delivered velocity-dependent mechanical perturbations to the jaw during lowering movements. Perturbing forces were applied in the sagittal plane in the direction of jaw protrusion. Three different conditions were tested: production of the utterance [siat] slowly and clearly with vocalization; articulation of the same utterance without vocalization (silent speech) and still slowly and clearly; and non-speech jaw movement that matched the amplitude and duration of the two speech conditions. For each condition the task was first performed several times without perturbation; it was then

performed several times with perturbation, and finally the perturbation was removed and the task was again repeated several times.

The results were as follows. In the first trials following the introduction of the perturbing force field, a noticeable modification of the trajectory of the jaw was observed for all subjects and for the three conditions: its curvature increased significantly in the front direction. After training, for the two speech conditions (vocalized and silent), an adaptation to the perturbation was observed and the motion path of the jaw became similar to the one produced without the perturbation. This adaptation was not observed in the non-speech condition. In addition, for the two speech conditions, an after-effect was noticed: once the perturbation was removed, a few trials were necessary for the subjects to go back to the jaw trajectories observed before the onset of the perturbing force field. An acoustical analysis of the vocalized speech signals and perception tests on these signals did not reveal any significant differences between the normal, the perturbed and the post-perturbation conditions. It would seem that the adaptation process observed in speech conditions is not guided by some kind of desired trajectory specified in the acoustic or perceptual domain.

The results obtained with speech movements are consistent with Shadmehr & Mussa-Ivaldi (1994). They suggest that the CNS is able to learn about the new dynamics of the jaw under perturbed conditions in order to generate the same trajectories as under normal conditions. Differences observed between speech and non-speech movements can be attributed neither to differences in muscle mechanics and jaw dynamics, nor to differences in the learning capabilities of the CNS, since both tasks used the same articulators in very similar ranges of displacement and duration. According to Tremblay et al. (2003), these differences reflect differences in the specification of the motor goals. In the context of the optimal planning hypotheses, we can suggest another interpretation, namely that optimal planning is not universal for all tasks or that the criteria to be optimized vary across tasks. However, it should be noted that Tremblay et al. (2003) did not in any way suggest that their data would provide evidence that either speech or non-speech movements were optimized.

Overall, the experimental observations of Shadmehr & Mussa-Ivaldi (1994) and Tremblay et al. (2003) that are summarized above suggest that the CNS learns about the dynamics of the motor plant and assimilates this knowledge in order to shape trajectories. These results are consistent with the internal model and optimal planning hypotheses, but they do not provide clear evidence for them. Curved paths have been shown to be potentially explained by anatomical factors and muscle mechanics, for arm movements (Flanagan et al., 1993, Gribble

et al., 1996, or Gribble et al., 1998) as well as for orofacial movements (see Perrier et al., 2003 or Perrier & Fuchs, 2008). In addition, they show that the CNS can integrate changes in dynamics, but only locally, i.e. for the very gestures for which the subjects were trained in the presence of the force field. The results summarized above do not show that the CNS stores a model of the dynamics that could be used for other gestures or in other locations in the space. In the following section, experimental studies related to this question are described.

3.3 Learning: Generalized models, local learning or task specific learning?

Kawato et al.'s (1987, 1990) original papers suggested that a comprehensive model of the dynamics of the motor plant could exist in the brain. Since then, numerous studies have been carried out for arm movements to study the complexity of the knowledge that is actually stored in the brain. The large majority of these studies tend to show that the knowledge is not stored in the form of a generalized model of the dynamics. With a generalized model, we understand a model that was learned for a certain task and in a certain location in the task space, and that could then apply to another task or to another location in the task space. For speech movements, there are not many studies in this domain, but those that have been conducted also tend to reject the hypothesis of a generalized model of the dynamics of the vocal tract articulators. In this section only two studies are presented, one for the arm and one for speech. They have been selected because they illustrate well the debate and the experimental paradigms used in this investigation.

3.3.1 Arm movements: Learned models of dynamics seem to be local

In the study described above (Section 3.2.1), Shadmehr & Mussa-Ivaldi (1994) also investigated the issue of whether or not the CNS learns a generalized model of dynamics. With this aim, they asked their subjects to do reaching movements in the left part of the workspace, after they had learned how to compensate for the influence of the force field in the right part of the workspace (see Section 3.2.1). As in the right part of the workspace, they observed after-effects in the left part, since the trajectories after learning were different once the perturbation had been removed. This observation is consistent with the hypothesis that subjects have learned an internal model of the new dynamics that generalizes to the whole workspace, from the right part to the left part, solely on the basis of the training done in the right part. However, the after-effects in the left part of the workspace were different from those in the right part, and the differences were consistent with the changes in joint geometry

associated with the displacement of the arm from the right to the left part of the workspace. The authors interpreted this last observation as evidence for the fact that the generalized dynamical internal models had been learned in relation to the arm joints, which are the same in the displacement from the right to the left part, and not in relation to the absolute position of the hand in the space. However, another explanation can be proposed. These findings are also consistent with the “rote learning” hypothesis according to which the CNS would not learn a generalized internal model, but, more simply, a set of sequences of motor commands that allow the subject to compensate for the perturbation in a given task and in a given arm configuration. In the context of Shadmehr & Mussa-Ivaldi’s (1994) study, the “rote learning” hypothesis would suggest that subjects have learned how to compensate for the perturbation in a certain angle configuration at arm joints and that they use the same strategy for the same angles at elbow and wrist joints in spite of the change in the angle at the shoulder. Learning would explain after-effects, and the local nature of learning would explain the differences in after-effects between movements made in the right and the left parts of the workspace.

In this context, the study carried out by Conditt et al. (1997) is interesting. The authors used the same experimental setup as Shadmehr & Mussa-Ivaldi (1994) with the same kind of perturbing force field. The differences were in the task required from the subjects. A group of subjects was asked to perform a drawing task. As in the reaching task of Shadmehr & Mussa-Ivaldi (1994), subjects were able after learning to compensate for the perturbation and to reproduce in perturbed conditions the same drawing patterns as in normal conditions. After-effects were also observed. Another group of subjects was asked to perform a reaching task and to draw a circle. During the adaptation phase in the presence of the force field, the subjects executed only the reaching task. However, after learning, both the reaching and the circle drawing tasks were considered. The authors observed a transfer of learning from the reaching task to the circle drawing task. After learning, based only on the reaching task, subjects were able in the presence of the force field to draw a circle the shape of which was similar to the one they had drawn in the absence of the force field. After-effects were also observed for both tasks. These results tend to rule out the “rote learning hypothesis,” and support the hypothesis that an internal model which is not task specific has been learned. However, both tasks were executed in the same location of the workspace, in the same range of positions. Hence, there is still no evidence supporting the hypothesis that a generalized internal model, which would be valid everywhere in the space, had been learned during the adaptation phase.

Mattar & Ostry (2010) investigated this issue, also for arm movements. Again the experimental setup was similar to the one used by Shadmehr & Mussa-Ivaldi (1994). The perturbation consisted in a clockwise force field that pushed the hand toward the right of the trajectory described under normal conditions. The subjects were asked to do reaching movements toward 2 targets located in front of them, along the midline of their body, at two different distances, 15cm and 30cm. Subjects were split into two groups. In the first group, subjects learned how to compensate for the perturbing force when moving toward the closest target (15cm), and transfer of learning was assessed in movements toward the more distant target (30cm). In the second group, the experiment was reversed: the training phase was done with the more distant target (30cm), and transfer of learning was evaluated in movements toward the closer target (15cm). The results showed that transfer of learning did not systematically occur for the first group of subjects. It only occurred when movements toward the 30cm target were achieved at velocities in the range of the velocities observed in the movements toward the 15cm target. In contrast transfer of learning was systematically observed in the second group, from the movements toward the 30cm target to the movements towards the 15cm target. According to the authors, this result shows that there was no generalization of dynamics learning beyond the range of the dynamical conditions (here, the relations between perturbing force, velocities and positions) that were experienced in the learning phase.

3.3.2 Jaw movements in speech: Dynamics learning seems to be task specific

Generalization of dynamics learning in speech production was studied by Tremblay et al. (2008). These authors used the same experimental setup as in the study of Tremblay et al. (2003), which is described above, consisting of a computer-controlled robot connected to the lower teeth of the subject. Three different experiments were run. In the first experiment, the subjects were trained to adjust motor commands in order to compensate for the deviating force field applied to the jaw for the production of the speech sequence /siæs/ only. After this training, transfer of learning was assessed for the speech sequence /suæs/, which essentially requires the same jaw movements as /siæs/. In the second experiment, a group of subjects was trained to compensate for the force perturbation during the speech sequence /siæs/ (downward jaw movement) only and another group was trained during the speech sequence /sæis/ (upward jaw movement) only. For both groups, transfer of learning was assessed for the speech sequence /siæis/ (downward and upward jaw movement). In the third experiment, a

group of subjects was trained to compensate for force perturbation during the speech sequence /siæs/ articulated with vocalization, and the transfer of training was evaluated on the same sequence articulated silently, while the order was reversed for a second group of subjects. It was found in the 3 experiments that, in general, the subjects were able to properly adjust the motor commands for the learned sequence in order to compensate for the force perturbation (in agreement with Tremblay et al., 2003). However, transfer of learning was not observed in any of the three experiments: the force field perturbed the task chosen to assess transfer of learning in exactly the same way as it had perturbed the other task before learning, and no after-effect was observed after the removal of the perturbation for the task that was not learned. Hence, not only does dynamics learning in speech seem not to be generalized, a result which accords with what has been found in arm movements, but it seems to be task specific, even if the learned task and the test task share the same motor plant and the same location in space.

4 Discussion

In the first part of the paper, it was shown that the concept of *dynamical internal model* is powerful and useful in order to concretely understand how the CNS can learn about the dynamical properties of the motor plant and how it can use this knowledge in movement planning. In its original form, the hypothesis had strong implications and requirements since it assumed (1) that dynamical internal models are accurate and realistic descriptions of the physical motor plant in its entirety, and (2) that internal models are used either to guide the motor plant along *desired trajectories* specified by the brain as motor goals, or to determine *optimal trajectories* and then guide the motor plant along these trajectories. This last assumption, which corresponds to an *optimal motor planning*, seems to be more realistic since it provides explanations about the principles underlying the emergence of the intended trajectories as consequences of planning principles. Various modeling studies using dynamical internal models and optimal motor planning to control biomechanical models of the arm have simulated movements that have strong similarities with real arm movements recorded in humans (see, for example, Kawato et al., 1990, Gomi & Kawato, 1996, Kawato, 1999). These results undoubtedly support the hypothesis that optimal motor planning based on internal dynamical models is used for arm movement. This model is a potential explanation for the characteristics of human arm movements. However, the results of these simulations do not demonstrate that humans actually control their movements in this way. To

confirm this hypothesis, experimental evidence is required and this was the aim of numerous studies in the last decade.

In the second section of the paper, a number of selected experimental studies were described and interpreted. Obviously the proposed selection is not exhaustive, but it is, from our point of view, reasonably representative of the state of the art. This literature review shows that in arm movements the CNS takes dynamical properties of the motor plant into account when planning the motor task: Sabes et al. (1998) showed that inertial constraints are taken into account to avoid collision in obstacle avoidance; Franklin et al. (2007) found evidence for the fact that the CNS adjusts the end-effector stiffness in order to increase stability and gestural accuracy; Shadmehr & Mussa-Ivaldi (1994) found that new dynamical constraints can be learned in order to achieve the same trajectory as before these new constraints were introduced; and Conditt et al. (1997) even showed that this learning can be extended to other kinds of movements produced with the arm in similar positions. However, no or very little evidence has been found for the arm supporting the hypothesis that learning consists in building up full and generalized models of the motor plant's dynamics (Mattar & Ostry, 2010). It does not therefore seem realistic to assume that motor planning of arm movements could rely on accurate and complex models of the dynamics of the motor plant in its entirety. This statement is now widely accepted, in particular by Kawato and colleagues:

Considering the number of objects and environments, and their possible combinations, that can influence the dynamics of the motor system, the controller must be capable of providing appropriate motor commands for a multitude of distinct contexts, such as different tasks and interactions with objects, that are likely to be experienced. Given this multitude of contexts, there are two qualitatively distinct strategies to motor control and learning. The first is to use a single controller that uses all the contextual information in an attempt to produce an appropriate control signal. However, such a controller would demand enormous complexity to allow for all possible scenarios. (Wolpert et al., 1998, p. 344-345)

This explains why in the last decade the focus of studies investigating the nature of dynamical internal models was shifted from the investigation of their existence in the form of generalized models to the investigation of how multiple localized or specialized models could be learned and used to control different tasks in various contexts. Wolpert & Kawato (1998) proposed a neural architecture based on multiple paired forward-inverse models. In this architecture, for a given motor task, the CNS would first evaluate which one of the different

forward models best predicts the dynamical state of the motor plant in interaction with its environment. Once the best forward model has been selected, the corresponding paired forward and inverse models would be used to control the task. Imamizu & Kawato (2009), using functional brain imaging, found evidence for this modular structure of the representation of the motor plant's dynamics in the brain. For example, they observed that when their subjects were trained to interact with a computer using different kinds of mice (a normal mouse, a mouse rotated in direction, or a velocity-dependent mouse), different brain regions were activated. Krakauer et al. (2006) studied the influence of the context on the generalization of internal models learned for a given motor task to another motor task. They concluded that generalization depends on the history of prior motor behavior. In parallel, Mattar & Ostry (2010) proposed that simplified generalized models could be built up in the CNS by interpolating between local models learned in the regions of the motor space that have been already reached by the motor plant.

All these studies suggest that for arm movements a representation of the dynamics of the motor plant does exist in the brain, and that this representation is local and/or task specific. However, the issue of whether this representation is used in the context of an optimal motor control is still unsolved. Hence, if these representations are used in the context of an optimal motor planning, it is likely that the optimality is limited to a part of the task space and influenced by the nature of the task. The curvature of the experimental arm trajectories (Flash & Hogan, 1985, Gomi & Kawato, 1996) and the relation between this curvature and movement speed (Viviani & Flash, 1995) are consistent with the assumption that planning is optimal. However, simulations carried out with accurate biomechanical models of the arm have shown that these experimental results are also consistent with the influence of arm dynamics in the context of a non-optimal motor control (Flanagan et al., 1993). Hence these kinematic characteristics are not a convincing demonstration that trajectories actually result from any kind of optimal motor planning. In addition, it has been shown that, in some cases, when complex perturbations are applied to the arm during its movements, simple and non-optimal strategies, using very rough representations of the dynamics of the motor plant, are selected to maintain gesture accuracy. This phenomenon was observed among others by Franklin et al. (2008), who found that the adaptation of arm motor commands to time-varying changes in the environmental dynamics could be attributed “*to a single adaptive process, without explicit calculation of inverse dynamics or impedance,*” (p.11172) i.e. to a “simple” increase in the arm stiffness.

In conclusion, for arm movement, there is considerable evidence that dynamics is taken into account in planning to ensure gesture accuracy, but certainly not in the form of generalized and comprehensive internal models, and there is no convincing evidence that motor planning uses these dynamical representations in order to optimize a physical cost.

Our review of the literature suggests that speech motor control and arm motor control are different from the point of view of the integration of dynamical constraints in motor planning. We did not find any evidence supporting the idea that dynamical properties of the speech production system are learned by the CNS:

- Gravity does not seem to be integrated in speech motor planning (Shiller et al., 1999; see also Buchaillard et al., 2009).
- Jaw variability in speech production seems to be the passive consequence of the intrinsic stiffness of the jaw (Shiller et al., 2002), which is not specifically controlled.
- There is no transfer of learning between motor tasks for the jaw, even if these motor tasks share the same location in the task space (Tremblay et al., 2008).
- The fact that, in speech production, the CNS compensates for the impact of a perturbing force field (Tremblay et al., 2003) applied to the jaw can be explained without any dynamical learning. According to the authors themselves and consistent with Franklin et al.'s (2008) suggestion for arm motor control, a compensation based on a stiffness increase is possible, and this does not require any complex dynamical representation (Tremblay et al., 2008; see also Nasir & Ostry, 2006).

Thus, contrary to what could be concluded from experimental observations in arm movements, it does not seem necessary for speech motor control to integrate the dynamical properties of the speech motor plant in the form of a model even for the control of movement accuracy.

A first explanation for this difference between arm movement planning and speech movement planning could lie in the fact that the number of experimental studies of dynamical internal models in speech motor control is significantly lower than the number of studies regarding arm motor control. Hence, this difference could be an illusion due to a lack of knowledge about speech motor control. However, this difference can also be explained by a number of intrinsic differences between speech and arm motor control:

- (1) the motor goals of speech production are more tolerant to gestural inaccuracy than arm movements, because they are cognitive and not physical in nature;

(2) the dynamical properties of the orofacial motor plant are extremely complex (see, for example, Koolstra & Van Eijden, 2005, for jaw dynamics, Buchaillard et al., 2009, for tongue dynamics, and Nazari et al., 2010, for face dynamics); thus it is likely that speech motor control can only adapt roughly to these properties and can neither learn nor integrate them accurately.

When accuracy is an issue, a global control based on stiffness increase could be used in speech motor control in order not to endanger speech perception (as suggested for lip protrusion by Nazari et al., 2011a), as is done in arm movements. However, other strategies exist that could rely on the use of external mechanical structures (like the palate in high vowels and in alveo-palatal and palatal consonants, see Stone & Vatikiotis-Bateson, 1995) or on the use of saturation effects in the relation between articulation and acoustics (Perkell et al., 2000).

Speech production is certainly optimal in a way, since it has been shown that speakers can adapt to various speaking conditions (fast speaking rate, noise, non-native listeners...) in order to ensure an efficient communication with listeners (Lindblom, 1990). However, we could not find in the speech literature in general and in our own studies in particular any convincing evidence that speech gestures are controlled in order to optimize any physically measurable cost. Nelson (1983) proposed that the bell-shaped velocity profiles observed in jaw movements for speech are consistent with a minimum jerk model. Löfqvist & Gracco (2002) also suggested that the curved paths observed in vowel-consonant-vowel sequences support the minimum jerk model. Tasko & Westbury (2004) and Perrier & Fuchs (2008) found relations between speed and curvature in speech movements that have been shown to be consistent with the minimum jerk model (Viviani & Flash, 1995). However, we were able to reproduce all these different patterns using a biomechanical model of the tongue that was not controlled optimally in any way (Payan & Perrier, 1997; Perrier et al., 2003; Perrier & Fuchs, 2008). This suggests that these patterns could arise from the intrinsic dynamics of the speech articulators.

Hence, for motor control in general, and for speech motor control in particular, it is still unclear whether motor planning aims at optimizing any measurable physical cost (global torque change, minimum of jerk, minimum of variance...). Alternative models of motor control have been elaborated. All these models are controversial, just as optimal motor control models are. However, they offer interesting ways to think further about the way the CNS integrates dynamical constraints and uses this knowledge in gesture planning.

Feldman and colleagues have, for many years, been strong opponents of the idea that motor control is guided by optimality and that it relies on internal models of dynamics (see, for example, Ostry & Feldman, 2003, or Feldman, 2009). Their criticisms are based mainly on two points: (1) force, which is by nature the output of a dynamical internal model, cannot be a controlled parameter, since it is the result of combined influences arising from the CNS and from the motor plant itself via different kinds of afference; and (2) feedback can be tuned by the CNS, so learning complex dynamics on the basis of comparisons between desired outputs and feedback signals (see Figures 2 and 3) does not seem to be a realistic hypothesis. Feldman (1986) proposed a motor control model, the so-called λ model, based on the Equilibrium Point Hypothesis. The λ model assumes that movement is generated by continuously shifting the mechanical equilibrium point of the motor plant along relatively simple paths between specified target equilibrium positions. This is done by controlling the muscle length λ above which the muscle starts to generate an active force. According to this model the trajectory of the motor plant is determined by the combined influences of the motor commands and of reflex loops that ensure that the movement reaches the successive locations of the target equilibrium positions. In this context, none of the kinematic properties of the movement would result from any optimal process and there is no need for any explicit representation of the dynamics of the motor plant. In addition the λ model proposes an interesting way to control stiffness via a co-contraction parameter, C . In the context of the experimental findings listed above, which suggest an important role of stiffness in accuracy and stability control, this model deserves special attention. Proponents of optimal control models based on internal models of dynamics have developed numerous arguments against the λ model. For example, Wolpert et al. (1998) argued that this model would require unrealistic mechanical and neural feedback gains; Gomi & Kawato (1996) considered that the model would necessitate much too complex time variations of the motor commands; and Hinder & Milner (2003) showed for goal-directed wrist flexion movements that the patterns of variability at the end of the movements were not compatible with the basic hypotheses of the λ model. Now, our own implementations of the λ model in the context of speech articulators have provided interesting similarities between simulated movements and experimental data (Perrier et al., 1996, Perrier et al., 2003, Buchaillard et al., 2009). However, this speech production modeling work has also shown how difficult it is to properly define a co-contraction parameter for complex and deformable motor plants (tongue, lips, etc.). Work is in progress in our research group

(Winkler et al., 2011, Nazari et al., 2011b) to further evaluate the usability of this model in the context of speech motor control.

Recently, Kawato contributed to an article (Ganesh et al., 2010) in which the authors suggested that the search for optimality could be secondary in motor planning. Asking their subjects to achieve motor tasks that are more complex than reaching tasks (i.e. maintaining the wrist within a certain angle amplitude under the influence of vibratory disturbances), they observed that their subjects (1) did not all use the same motor control strategies to compensate for the perturbation, and (2) did not in general adopt any optimal strategy even if they had previously realized the optimal movement. Their investigations of the different strategies used by their subjects led them to assume that, instead of looking for a globally optimal movement, the CNS would instead remember a previously used solution that enabled the task to be achieved in a satisfactory way, and then look for a locally optimal movement around this solution. Thus, Ganesh et al. (2010) suggested that motor memory, and not optimal motor planning, would play the major role in the determination of motor strategies. The search for optimality would come after, in a second stage, and it would be local. This finding is consistent with the conclusion that dynamical internal models, if they exist, are first local. The finding is also compatible with a major criticism made by Friston (2011) of the optimal motor control hypothesis: there is no realistic way of thinking of a process with which the CNS could compute and minimize a global cost such as the jerk or the torque change during a movement. Instead of cost minimization Friston (2011) suggested that motor control strategies could be guided by *prior beliefs* characterizing expectations of the consequences of movement in the perception domain, based on the principle of *active inference*. In this context, the CNS would select the motor control strategies that have the highest probability of achieving the goals in the perception domain, according to Bayesian inference principles and using probabilistic forward models linking motor commands and perceptual parameters. This is an interesting alternative to the hypothesis of optimal motor control based on forward and inverse internal models of complex dynamical motor plants for two reasons: (1) it avoids the computation of a valued cost that would require some kind of measurement of physical parameters; and (2) it proposes a functional way to account for the dynamical properties of the motor plant, which globally and statistically relates motor commands and their impact in the perception domain. All together this direct link with perception instead of with physical parameters and the absence of any computation of physical costs makes less crucial the question of the accuracy of the dynamical internal models in motor planning. This is particularly interesting in the context of speech motor control, in which movements are not

produced with the aim of reaching clearly specified physical goals, but with the cognitive aim of producing a signal that can be perceived and identified by a listener. The probability approach is well adapted to the intrinsic variability of speech signals, in which the same percept can be associated with different physical signals, depending on the context, the speaking style or the speaker.

5 Conclusion

The review of the literature in this article has shown that little experimental support exists in favor of motor sequence planning based on optimal control and learned generalized dynamical internal models in the brain. While evidence was found in support of the integration, at least partial, of some dynamical properties of the motor plant in arm movement planning, no evidence was found in support of this hypothesis in speech production. We cannot discard the possibility that this absence of evidence may be due to the paucity of studies investigating this issue in speech production. However, some specific aspects of speech production as compared to other motor tasks could also explain why dynamical properties of the speech production apparatus do not need to be modeled in the brain.

In arm as well as in speech movements, experimental findings have shown that the assumption that generalized internal models of the physical motor plants could exist in the brain is not realistic at all. Recent researches have proposed that internal models of the dynamics would rather be local and sometimes task specific. Current studies are investigating how transfer can operate from internal models learned for a given task and in a given location in the task space to other tasks.

Internal models of the dynamics are usually considered in the context of an optimal motor planning in which the predictions provided by the forward model are used to optimize a certain cost in the physical domain, while optimal solutions are stored in the inverse model. A number of kinematic properties of arm and speech movements are consistent with the optimization of costs, such as minimum of effort, minimum of jerk or minimum of torque. However, simulations using non-optimal motor planning have been shown to generate similar kinematic properties. Hence, there is little convincing evidence that arm and speech movement are controlled as to minimize such a cost. The debate is still open.

Alternative hypotheses that have been shown to be biologically plausible and do not require cost computation do exist. However, further evaluation of these hypotheses is still required in the context of speech sequence planning. In speech the control of time is crucial, since

segmental duration can be associated in speech with meaning. Since motor plant dynamics influences the time behavior of the motor plant, hypotheses about speech motor planning should be evaluated more precisely in relation to time control. Experimental studies investigating this issue could open new doors to the clarification of the role of articulatory dynamics and optimal control in speech production.

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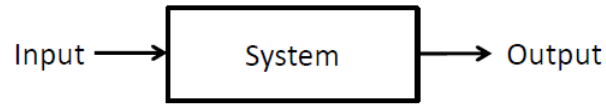
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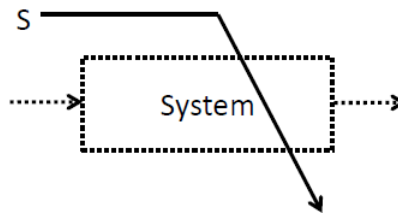
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7 Appendix: Symbols used in Figures 2, 3, 4, 5, 7, 8

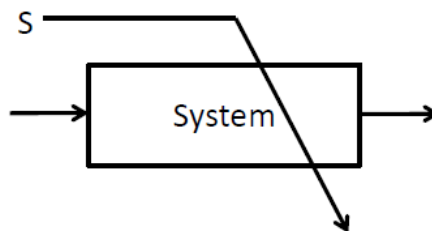
System (processes the input to generate the output)



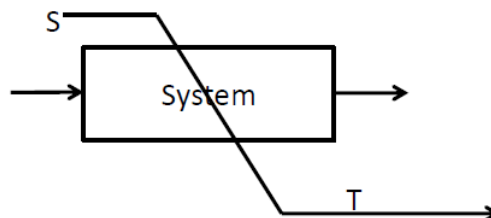
Learning of a system based on signal S



Adaptation of an active system based on signal S



Use of a system to execute task T based on signal S



Lines and contours used for the **main active process**



Lines and contours used for a **secondary active process**

