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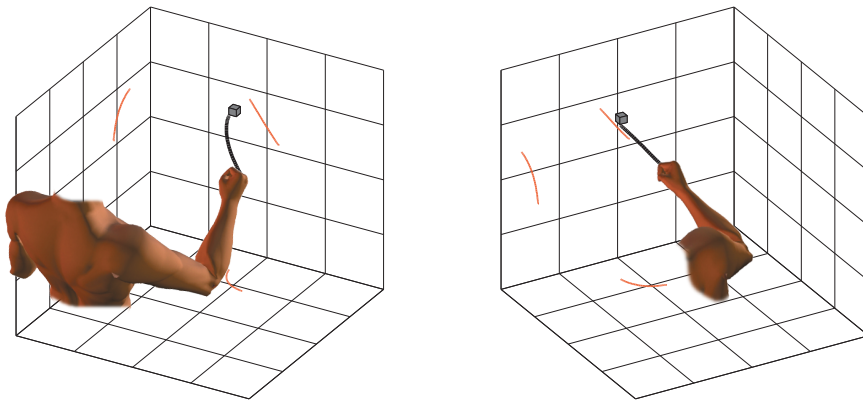
HABILITATION À DIRIGER DES RECHERCHES

Computational and neural principles for human motor control

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Preface

The present document provides a summary of studies on computational motor control elaborated in collaboration with Pierre Baraduc and Michel Desmurget (Centre de Neurosciences Cognitives, CNRS UMR 5229, Bron, France) between 2002 and 2008 at INSERM ANIM U742 (lead by Pr Marc Maier). I thank Pierre Baraduc, Michel Desmurget, Marc Maier, and Philippe Souères for helpful discussions and continuous support.

1 Introduction

Motor control is a fantastic challenge for the central nervous system. In fact, efficient motor coordination theoretically requires the mastering of the laws of Newtonian mechanics, and it is well known, from any textbook, that the equations of motion for systems with many degrees of freedom (DOFs), as it is the case for the human body, are nonlinear and complex (Bernstein 1967). Furthermore, ongoing actions can be unexpectedly disrupted by deterministic (e.g. obstacles) or stochastic (e.g. noise) perturbations. Yet, we know that humans are capable of highly skillful motor behaviors (e.g. dancing, riding a bicycle, ...). In the view that the brain should face unconquerable difficulties and incredible computational burden to faithfully represent the laws of movement, it is tempting to suggest that some "simplifying" strategies have been discovered, e.g. through phylogenetic processes, to alleviate the "cost" of motor control (Lee 1984; Macpherson 1991; Mussa-Ivaldi and Bizzi 2000; Latash et al. 2007). We have identified at least four (more or less formalized) approaches to motor control that concur with the idea of simplification. Following a thorough analysis and discussion, we conclude that none of the proposed strategies actually tackle the overall problem of motor coordination. Then we present a principled approach that provides an overarching account to motor control.

The scope of this review is restricted to the case of discrete movements (as defined in Hogan and Sternad 2007). We do consider, following recent theoretical and experimental works (e.g. Schaal et al. 2004, 2007; Huys et al. 2008), that discrete and rhythmic movements are subserved by distinct control mechanisms. Thus conclusions drawn for one type of movement are likely to be irrelevant or even wrong for the other type.

2 Motor control: What needs to be solved

We start with a brief description of some well-known problems in the framework of motor control.

2.1 The Bernstein's problem

Despite multiple levels of redundancy, noisy sensors and actuators, and the complexity of biomechanical elements to be controlled, the nervous system elaborates well-coordinated movements with disconcerting ease (Bernstein 1967). In fact, Bernstein (1967) observed that a motor goal can be successfully reached although each attempt to reach this goal has unique, nonrepetitive characteristics. To succeed in this daunting control task, powerful mechanisms should be at work in brain circuits. Their properties should encompass the capacity: 1. to reach a goal with little error and small energy expenditure, i.e. to choose an appropriate set of motor commands among an infinite number of solutions (degrees-of-freedom problem); 2. to face deterministic (e.g. change in goal, force applied on the moving limb) and stochastic (e.g. noise in motor commands) perturbations (variability problem). The Bernstein's problem which encompasses both the degrees-of-freedom and variability problems, is illustrated in Fig. 1 for a reaching movement. In this example, the moving arm has three degrees of freedom (Fig. 1A; shoulder, elbow, wrist), and moves in a two-dimensional space to reach a target (Fig. 1B). Thus there exists an infinite number of articular displacements which are appropriate to capture the target (Fig. 1C). In the presence of noise, the reaching movements are successful, but have different characteristics (Fig. 1D).
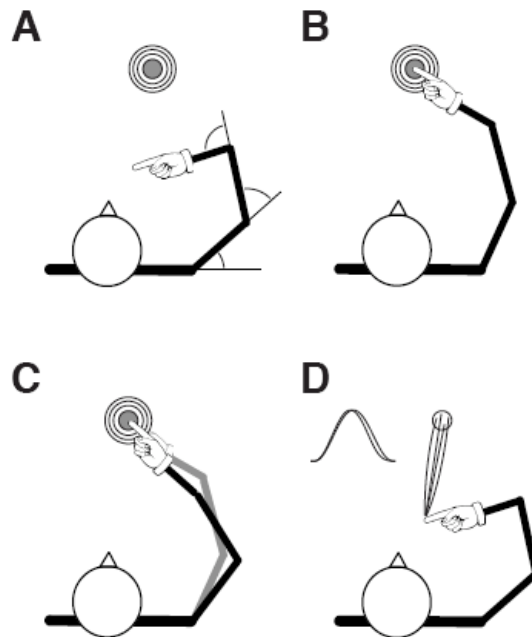
Figure 1. Illustration of the Bernstein's problem. **A**. Planar reaching movement with a redundant arm (3 DOF). **B**. A successful movement reaches the target region (central gray circle). **C**. Two successful movements with different final postures. **D**. Several successful movements with different spatiotemporal characteristics. Inset: velocity profiles.

2.2 Posture/movement

The apparent easiness of motor control hides the paradoxical problem of interference between posture and movement (Ostry and Feldman 2003). The central issue is why processes which are responsible for postural control do not appear to overtly interfere with movement control. Consider the following example: a mass which can move along a line and which is attached to two muscle-like actuators (Fig. 2A). Each actuator is represented by a muscle unit (Zajac 1989): a force generator and a parallel elastic element. The purpose is to capture two main features of muscular functioning: 1. The muscle generates force in response to a stimulation; 2. The muscle generates a restoring force when lengthened. Thus a more detailed model is not necessary here. The mass is initially in equilibrium due to the equal and op-

posite actions of the actuators' forces. The goal is to displace the mass to a new position (e.g. to the right), and maintain it in equilibrium at this position.
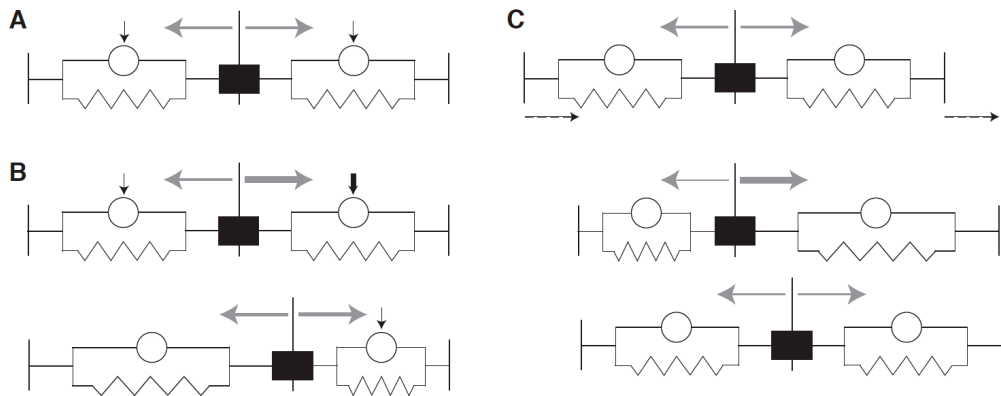

Figure 2. Illustration of the posture/movement problem. **A**. A mass is at equilibrium due to the equal and opposite forces of two muscles (*gray horizontal arrows*: actual forces exerted on the mass; *black vertical arrows*: control forces). **B**. To displace the mass, the equilibrium is modified by changing the control forces (more force to the right). **C**. To displace the mass, the equilibrium is modified by changing the origin of the muscles (displacement to the right).

We observe that activation of the rightward muscle displaces the mass to the right, but that the final position requires maintained activation of this muscle to compensate for the leftward restoring force induced by the displacement (Fig. 2B). In this case, posture interferes with displacement, and initial and final postures are not equivalent. This example shows that specification of a displacement by a force is not appropriate to manage the conflict between postural maintenance and initiation/termination of movement (Ostry and Feldman 2003). An alternative approach is to create a force through a change in the origin of the muscles (Fig. 2C). In this case, one and the same mechanism is used for posture and movement, and the initial and final postures are of the same nature.

These two examples raise the fundamental issue of the integration between posture and movement that should be addressed by any model of motor control.

3 Simplifications

We describe strategies at different levels in the brain/body system that could provide simplified solutions to the problem of motor control.

3.1 At the biomechanical and muscular level

Motor control arises from the interplay between processes at the neural and musculoskeletal levels. Although it is generally believed that the neural level has a dominant role in the control of movements, there is evidence that the mechanics of moving limbs in interaction with the environment can also contribute to control (Chiel and Beer 1997; Nishikawa et al. 2007). Raibert and Hodgins (1993) defended the view that "the mechanical system has a mind on its own" and that "the nervous system and the mechanical system should be designed to work together, sharing responsibility for the behaviour that emerges" (p. 350). For instance, Kubow and Full (1999) showed in a model that running in the cockroach can be generated by a feedforward controller with a self-stabilization against perturbations through mechanical feedback that alters leg moment arms. In this sense, mechanics can act to simplify the control task. The idea of "intelligent mechanics" has been developed mainly in the study of invertebrates, but related ideas can be found in the study of human movements (van Ingen Schenau 1989). Morphological computation can be performed by the tendinous network of human hand (Valero-Cuevas et al. 2007), and the mechanics of the ocular plant (Demer 2006). In the latter case, mobile soft-tissue sheats (pulleys) in the orbit influence the pulling direction of extraocular muscle. This organization could provide a mechanical basis for simplified oculomotor control by constraining eye movements to follow Listing's law (Quaia and Optican 1998).

It is also well known that muscles can play a self-stabilizing role during move-

ment due to their force-length and force-velocity properties (Brown and Loeb 2000; Jindrich and Full 2002; Richardson et al. 2005). For instance, an immediate restoring response can be elicited following a perturbation that stretches a muscle. Intrinsic muscular properties contribute to compensation for perturbation in human (Rothwell et al. 1982).

Although the premise that the neural and mechanical levels share the responsibility for emerging motor behaviors, is surely correct and makes sense for reactive control, it remains unclear how proper coordination and predictive motor control can be obtained with "two drivers in the car".

3.2 At the neuromuscular level

3.2.1 Synergies

The concept of synergy is a recurring theme in the framework of motor control (Bernstein 1967; Lee 1984; Macpherson 1991). Historically, a synergy has been broadly defined as a set of anatomical or functional elements acting together. Such a "lumping" was thought to simplify the coordination task of the CNS in the face of multiple levels of redundancy (motor units, muscles, degrees of freedom, ...). Macpherson (1991) addressed the issue of muscular synergies, and concluded that, if they exist, these synergies are not hard-wired, but highly flexible, versatile, and task-dependent (see also Soechting and Lacquaniti 1989; Maier and Hepp-Reymond 1995; Mercer and Sahrmann 1999). In a her view, a description of motor behavior in terms of muscular synergies is a way to say that there exists an underlying efficient, but inaccessible process of coordination.

In recent years, the concept has been redefined in more functional terms, but in at least three qualitatively different ways. One definition is derived from microstimulation experiments in the spinal cord which have identified a motor map

of convergent force fields, i.e. neural synergies that generate movements toward an equilibrium position (Bizzi et al. 2000; Mussa-Ivaldi and Bizzi 2000). These spinal modules that produce specific pattern of muscle activation, would form a set of "motor primitives", "building blocks", "basis functions" which could be combined to construct complex motor behaviors (Mussa-Ivaldi and Bizzi 2000). The feasibility of this idea has been assessed in a computational model (Mussa-Ivaldi 1997).

The second definition can be considered as an extension of the first one. It is based on the hypothesis that a small set of time-varying patterns is sufficient to generate, through appropriate scaling and time-shifting, the entire set of muscle patterns across a range of motor behaviors (d'Avella et al. 2003). This view has been widely used to describe dimensionality reduction in the motor system for different species (frog, cat, monkey, human, ...), tasks (posture, locomotion, grasping, ...), and conditions (perturbations, motor disorders, ...) (Krouchev et al. 2006; Klein Breteler et al. 2007; Torres-Oviedo and Ting 2007; Overduin et al. 2008). In these cases, as the natural behavior of freely moving animals was considered, it was not possible to directly ascertain the actual biomechanical effects of synergies. Yet, in some studies, the muscle synergies were shown to be correlated to the control of task-related variables (e.g. endpoint kinematics or kinetics, displacement of the center of pressure; Ivanenko et al. 2003; Krishnamoorthy et al. 2003; Ting and Macpherson 2005; Torres-Oviedo et al. 2006). Furthermore, a modular organization of movement control at the task level is consistent with observation of neural population recordings (Georgopoulos et al. 1993) and microstimulation experiments (Graziano et al. 2002; Lemay and Grill 2004). A central premise of this approach is to equate a synergy to an open-loop process that unfolds independent of feedback signals (i.e. a motor program; d'Avella et al. 2003). This hypothesis on the nature of synergies has been challenged by Kargo and Giszter (2008). They showed that distortion of

sensory feedback through muscle vibration modified the timing of burst signals that control wiping movements in the frog. More generally, control casted in termed of motor programs fails to reflect the flexible nature of motor behaviors (see below; Desmurget and Grafton 2000; Todorov and Jordan 2002).

The third definition is based on the Uncontrolled Manifold (UCM) approach, i.e. a technical procedure that identifies stable performance variables from trial-to-trial variability (Schöner 1995). This method makes a partition of the variance of a set measured variables (e.g. joint angles of a redundant limb) into two components: a component that modifies the value of a performance variable (e.g. the endpoint position of the limb) and one (the uncontrolled manifold) that does not affect it. The structure of the variability revealed by the UCM define synergies characterized by stability against perturbations and flexibility to solve concurrent tasks (Latash et al. 2007).

Overall, the identification of synergies is a meaningful step toward understanding which performance variables are controlled by the CNS, and how the CNS translates task goals into appropriate spatio-temporal patterns of muscle activation. Yet it remains that synergies are obtained as the outcome of a data processing/statistical analysis. The point raised by Macpherson (1991) of the actual coordination process that produces synergies remains an open issue: what computational mechanism could solve the problem of motor control by a reduction of dimensionality compatible with the characteristics of synergies?

3.2.2 Elimination

It has been proposed that a strategy to solve a redundant task is the freezing of supernumerary DOFs (Bernstein 1967; Newell 1991; Vereijken et al. 1992). This strategy would entail a radical simplification by drastically restricting the space of possible mechanical solutions. Yet, as mechanical coupling induce interaction forces be-

tween segments of a moving limb, freezing a DOF necessarily involves an active control. Gribble and Ostry (1999) showed that a pure forearm movement evokes EMG activity in shoulder muscles that stabilizes the upper arm and is proportional to elbow velocity.

A related strategy has been observed in the control of eye movements. According to Donders' law, possible gaze positions in 3D space are restricted to a plane (Wong 2004), i.e. eye torsion is automatically defined by the choice of horizontal and vertical displacements. We can make two remarks. First, Donders' law does not apply in general to arm movements (Gielen et al. 1997). Second, the mechanical origin of this law is debated (Angelaki and Hess 2004; Demer 2006; Tweed 2007). For instance, frequent violations of Donders' law are observed during the vestibulo-ocular reflex and sleep.

3.3 At the control level

The control level encompasses processes that convert task goals into muscle activations.

3.3.1 Equilibrium point theory

The equilibrium point theory (EPT) proposes that movement results from imbalance between the spring forces generated by a shift of the origin of the springs (Fig. 2C) (Feldman and Levin 1995). In this framework, movement is a series of continuous transitions between postures along an "equilibrium trajectory" defined by time-varying changes in the origin of the muscles. Postural maintenance is a natural product of the control scheme. A central tenet of the theory is that realistic movements can be generated without knowledge on the dynamics of the object to be controlled, i.e. the equilibrium trajectory is derived from kinematic characteristics

of the planned movement. The validity of this tenet is highly debated as the arguments for or against the theory are based on the nature of muscle models and level of stiffness considered (Gomi and Kawato 1996; Gribble et al. 1998; Kistemaker et al. 2006, 2007). Paradoxically, the debate on the EPT has focused on the problem of movement generation while its main weakness is probably on the postural side of the problem. In fact, according to the EPT, posture is a passive stiffness-based process, which raises at least two remarks. We first note that the geometry of muscular insertion can threaten postural stability (Shadmehr and Arbib 1992; Dornay et al. 1993). Second, the issue of the magnitude of stiffness is crucial, i.e. is stiffness sufficient to oppose the destabilizing effect of gravity (Winter et al. 1998; Morasso and Schieppati 1999)? Although agreement is still lacking on this point, converging evidence from recent studies on postural control indicates that ankle stiffness is too low for passive postural maintenance (Loram and Lakie 2002b; Morasso and Sanguineti 2002; Casadio et al. 2005; van Soest and Rozendaal 2008).

We can also ask whether EPT really entails a simplification of motor control, since compensation for loads applied during arm movement requires information about the loads and arm dynamics (Gribble and Ostry 2000). In the same way, it is unclear how anticipation of the effects of interjoint coupling can occur without knowledge of limb inertia (Shapiro et al. 1995; Gribble and Ostry 1999).

3.3.2 Dynamical systems theory

The dynamical system approach to motor control attributes emergent behaviors to regularities of nonlinear dynamical systems (Schöner and Kelso 1988). In this framework, spatiotemporal patterns can emerge spontaneously from interactions between coupled subsystems. If applicable, this approach entails a clear-cut simplification in control as computation is merely replaced by a natural evolution in space and time. This could be the case for rhythmic movement patterns which are

observed in a wide variety of coordinated behaviors (e.g. finger tapping, locomotion, ...). Application to discrete movements is more controversial as it is widely held that discrete and rhythmic movements are subserved by distinct control mechanisms (Schaal et al. 2004, 2007; Huys et al. 2008). Schöner (1990) proposed a model for discrete movement generation in which movement kinematics emerged from the alternation of a fixed-point regime and a limit-cycle regime in the same dynamical system. The model was able to produce the timing properties of discrete movements of a mass point in a single dimension (spatial coordination was not described). This model was extended to a nonlinear redundant biomechanical system by Martin (2006), yet with a glaring loss in the expected simplification. We note that an important limitation of the dynamical system approach to discrete movements is to define posture as a fixed point attractor, i.e. posture is an asymptotically stable behavior, unlike what has been observed experimentally (Kiemel et al. 2002; Bottaro et al. 2005).

3.3.3   Muscular strategies

Discrete movements are characterized by typical and reproducible electromyographic (EMG) patterns. For instance, fast arm movements are accompanied by a triphasic agonist/antagonist EMG (Hallett et al. 1975). Analysis of the relationship between EMG characteristics (intensity, timing) and movement kinematics (amplitude, duration, velocity) and dynamics (load) has lead to propose descriptive rules for EMG, i.e. how to build the proper EMG given movement characteristics [speed control hypothesis (Freund and Büdingen 1978), pulse-step control (Ghez 1979), impulse timing theory (Wallace 1981), dual strategy (Gottlieb et al. 1989), ...]. We will not enter into the details of these strategies, but simply note that they only apply to single-joint movements. Extension to multijoint movements would require complex rules to deal with interaction forces, and directional anisotropy of inertia and

velocity-dependent forces. A simple scaling rule is not sufficient in the case of two-joint arm movements as the fine details of motor coordination and timing can hardly be embedded in a rule (Buneo et al. 1995).

3.4   At the functional level

Various experimental data point to a necessary dissociation between posture and movement control (Frank and Earl 1990; Massion 1992). The timing of anticipatory postural adjustments can vary independently from the onset of focal movement (Brown and Frank 1987; Schepens and Drew 2003). The timing also varies with the importance of the destabilizing effect of the focal movement on balance (Zattara and Bouisset 1986). These results suggest that the postural and movement components may be controlled and planned separately. A possible scenario could involve a canonical, predefined postural synergy that would guarantee the maintenance of upright stance during performance the focal movement (Nashner and McCollum 1985; Frank and Earl 1990).

It should be noted that authors arguing for specialized posture and movement processes, basically argue against a single process, and fail to propose a clear computational scheme that would illustrate the duality of posture and movement. In particular, it is unclear how proper coordination can be guaranteed in a separation scheme (Latash et al. 1995).

3.5   Is it possible to simplify?

If we try to find what is common to the preceding proposals, we see that simplification is frequently discussed in relation to *simplified* motor control problems. For instance, discrete hard-wired synergies have been described for postural control in the sagittal plane (Rushmer et al. 1983; Nashner and McCollum 1985), but such

a description is not valid for the general case of postural sway in the horizontal plane (Macpherson 1988; Moore et al. 1988). The EPT has addressed the control of single- (St-Onge et al. 1997; Gribble et al. 1998; Kistemaker et al. 2006) and two-joint (Flash 1987; Flanagan et al. 1993) arms, but not kinematically redundant systems (although it has been claimed to be feasible; Balasubramaniam and Feldman 2004). These remarks lead the following conclusion: if simplification is a solution to motor control, it remains to be proven in a case that encompasses the main and difficult issues of motor control.

4   Control with internal models

Although simplification should remain an objective, it should also be in keeping with a general solution to motor control. A general solution should not be a mere description of all the complex problems that the CNS faces to generate motor actions and a catalogue of mechanisms that could solve these problems, but a principled approach that captures the spirit of motor coordination and provides computational processes that create it. The equilibrium point theory and the dynamical systems theory could be candidate solutions, but they fail to be comprehensive enough (see above).

In fact, from a design perspective, it would seem necessary that motor control processes should incorporate detailed knowledge on the functioning of the object to be controlled. This view has lead to the notion of internal models, i.e. structures that define the relationship between commands and outcomes (*forward models*), or desired outcomes and commands (*inverse models*). Two kinds of architecture have been proposed that exploit internal models.

4.1 Inverse dynamics and impedance control

This architecture involves: 1. a feedforward controller that translates a *desired trajectory* into appropriate control signals; 2. a feedback controller that can correct deviations between the actual and the desired trajectory (Kawato 1999; Fig. 3). The feedforward controller is an inverse model of the dynamics of the object to be controlled which guarantees an efficient guidance of the object toward its goal. The feedback controller exploits the viscoelastic properties of the neuromuscular system to compensate for unexpected perturbations exerted on the controlled object (Shadmehr and Mussa-Ivaldi 1994; Franklin et al. 2003).

We can make two remarks on this architecture. First, it is unclear how one and the same neuromuscular unit can produce the appropriate combination of feedforward and feedback commands. On the one hand, the feedforward command is a direct specification of the force (or torque) to be produced by the neuromuscular system. On the other hand, the feedback command, which is a visco-elastic term that depends on actual and desired state of the controlled object, must be produced by force-length and force-velocity mechanisms at the neuromuscular level, independently of and without interference with the feedforward command. Thus control requires a combination of force- and position-based commands (Ostry and Feldman 2003) that has never been precisely described. Second, the notion of desired trajectory, which is central to the robustness of this approach, has been strongly criticized as it fails to account for the flexibility of motor behavior (Bernstein 1967; Sporns and Edelman 1993; Todorov and Jordan 2002).

4.2 Control and estimation

This architecture involves: 1. a controller that elaborates appropriate control signals to reach a *desired goal* for a given state of the system; 2. a state estimator that con-
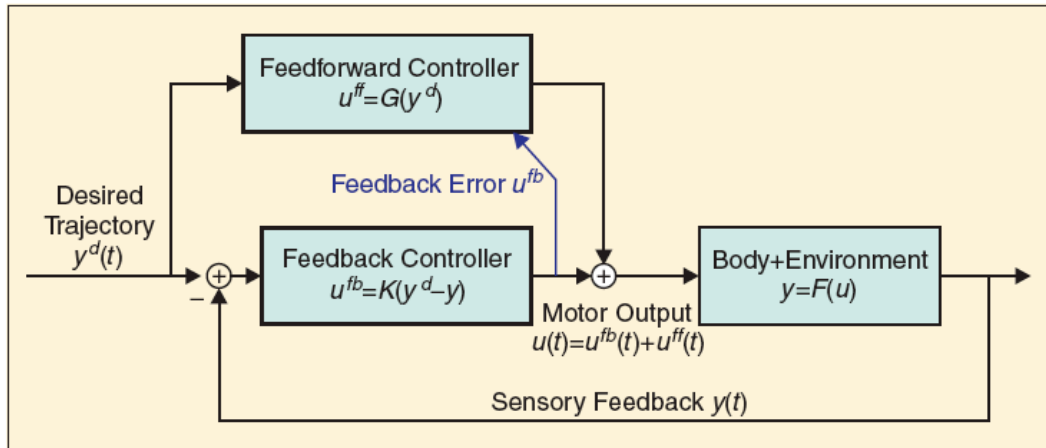
Figure 3. Architecture for inverse dynamics and impedance control.

structs an estimated state of the system based on commands and sensory feedback (Fig. 4).

A rationale for a control/estimation architecture in the framework of motor control has been developed recently by Todorov and Jordan (2002). Central to their analysis is the observation that, for reaching a behavioral goal, the CNS is directly pursuing it rather than trying to reproduce a predetermined pattern that would fulfill it. This fact was already noticed by Bernstein (1967), and formalized by Abbs et al. (1984):

> "A program is more likely the representation of the dynamic processes whereby the appropriate sensorimotor contingencies are set up to ensure cooperative complementary contribution of the multiple actions to a common, predetermined goal".

To capture this notion, Todorov and Jordan (2002) proposed a computational mechanism (stochastic optimal feedback control, SOFC; see also Bryson and Ho 1975; Stengel 1986; Todorov 2004, 2005) that precisely accounts for the goal-directed nature of motor actions. The recipe has three components. First, it is based on
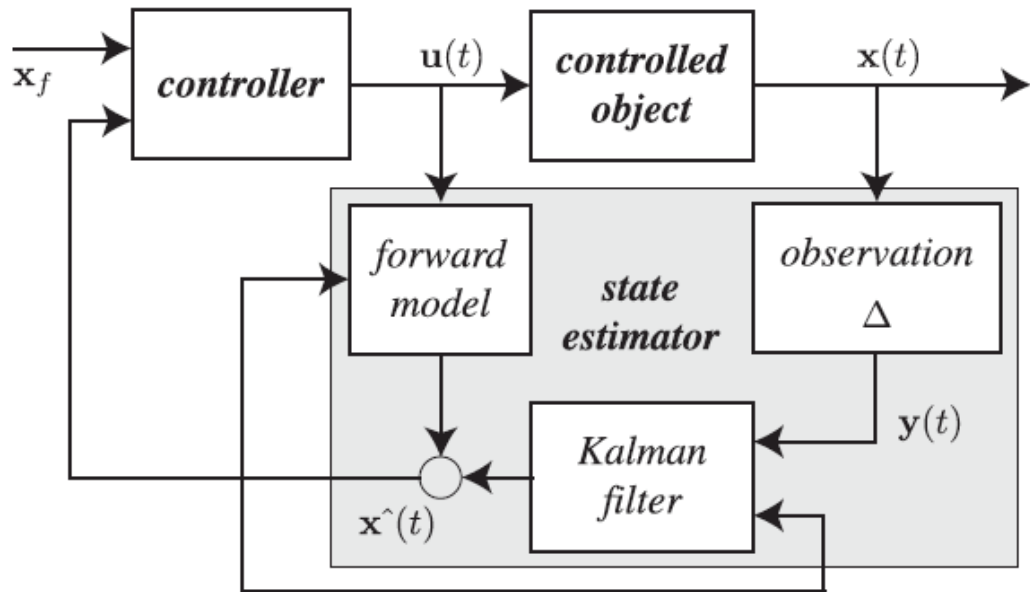
Figure 4. Architecture for control and estimation.

feedback control. This component is a ubiquitous feature in the field of motor control (Houk and Rymer 1981), but is generally used in the sense defined in classical control theory (e.g. PID control), with its well-known limitations (e.g. necessity of high gains, oscillatory behavior for long feedback delays). In the framework of SOFC, the feedback control is defined by time-varying gains elaborated from a full knowledge of the properties of the object to be controlled, and does not suffer the same limitations as classical feedback. The second component is an optimality principle, which is also frequently encountered in computational motor control to solve redundancy problems (review in Todorov 2004). Interestingly, optimality not only solves redundancy, but also implements a "minimum intervention principle": the controller does not compensate for a deviation that does not interfere with the success of the task not to incur an unjustifiable cost. The third component is stochastic control, i.e. the capacity to control a system in the presence of uncertainty (e.g. noise).

There are two main limitations to the control/estimation architecture and the SOFC approach as currently applied to motor control. First, it deals purely with movement, and says nothing on the integration of posture and movement. Second, it does not take into account low-level characteristics of the neuromuscular system (reflex, stiffness).

4.3 Are there internal models in the brain?

Although the concept of internal models is a widely used theoretical construct in the framework of motor control (Kawato 1999), its cogency has been questioned. Early on, Turvey et al. (1978) were concerned with the possibility to perform movement coordination through a detailed central specification of muscular operations. They raised the issue of the coordination of multiple degrees of freedom (Bernstein's problem), and the problem of context-conditioned variability, i.e. the fact that muscles can have context-dependent mechanical actions. Incidentally they noted that the presence of sensory feedback information can alleviate the issue of context-conditioned variability, an observation that anticipated the necessary role of online feedback control (Desmurget and Grafton 2000). More recently, Ostry and Feldman (2003) discussed the failure of control based on internal models to properly address the posture-movement problem (see Fig. 2B). This issue is fundamental all the more because it is generally ignored in the field of computational motor control (Hoff and Arbib 1993; Wolpert and Ghahramani 2000; Todorov and Jordan 2002; Todorov 2004). We will return to this point in the following section.

5 Principles for motor control

On the basis of the preceding observations we describe several principles that provide a unified basis for motor control (Guigon et al. 2007a, 2007b, 2008a, 2008b).

5.1 Optimality

Optimality as an overarching principle for motor control is a well-substantiated idea (review in Todorov 2004). From a theoretical point of view, it provides an efficient solution to the Bernstein's problem as it generates realistic movements in the face of spatial, temporal, kinematic and muscular redundancy (Todorov and Jordan 2002; Guigon et al. 2007a). The idea applies equally well to different motor tasks involving the hand, the arm, the eye or the whole body (Harris and Wolpert 1998; Tweed 2007). There is also empirical evidence that humans behave according to optimal laws (Arechavaleta et al. 2008), or can learn to discover near optimal solutions to real-world tasks (Inooka and Koitabashi 1990; Engelbrecht et al. 2003; Chhabra and Jacobs 2006; Izawa et al. 2008; Sherback and D'Andrea 2008).

5.2 Efficiency

Optimality entails the choice of a cost function, which indicates a quantity to minimize. The nature of the cost function is a highly debated issue. Part of the confusion arises from the fact that all the proposed cost functions (jerk, energy, torque change, ...) make similar predictions on basic qualitative characteristics of movement, e.g. trajectories, velocity profiles (Flash and Hogan 1985; Uno et al. 1989; Alexander 1997; Harris and Wolpert 1998; Todorov and Jordan 2002; Guigon et al. 2007a). Yet, a thorough quantitative analysis is in general lacking, and could provide more contrasted results. For instance the minimum torque change model fails

to produce the observed quantitative characteristics of velocity profile (Engelbrecht and Fernandez 1997), and the appropriate curvature of 2D movements (Soechting and Flanders 1998).

With the minimum variance model, Harris and Wolpert (1998) have drastically changed the viewpoint on the cost functions. Their proposal is to use a behaviorally relevant measure (variance) rather than an arbitrary and behaviorally meaningless quantity (e.g. acceleration derivative) as a cost. This is a radical departure from the previous optimal control models in the sense that characteristics of motor behavior emerge from a general principle rather than from a level-specific (e.g. kinematic, dynamic, muscular), effector-specific (e.g. arm, eye) or task-specific (e.g. posture, locomotion, ...) criterion (see Todorov 2004, for a review). This analysis was further refined by Todorov and Jordan (2002), leading to an error/effort cost function, where the effort is the size of central signals that eventually generate the movement. The rationale for this choice is discussed in Kawato (1996). In a series of studies, Guigon et al. (2007a, 2007b, 2008a, 2008b) have used a cost function with a single effort term, error being considered as a constraint to be fulfilled. The two types of cost function have been able to explain a wide range of observations on motor control (Todorov and Jordan 2002; Saunders and Knill 2004; Todorov and Li 2005; Li 2006; Guigon et al. 2007a, 2007b; Liu and Todorov 2007; Guigon et al. 2008b). Yet, the two approaches differ on what is considered as a cost and what is considered as a constraint (Guigon et al. 2008a). This point raises subtle and interesting issues if one is to identify the actual cost function that governs motor behaviors (O'Sullivan et al. 2009). The mixed error/effort function would predict that subjects can make a trade-off between error and effort, e.g. sustain a larger error in order to minimize their effort. This issue could likely be tested in an experiment.

5.3 Feedback

Feedback is probably one of the oldest notion used for the formal description of motor control. Yet there is some confusion on the nature and role of feedback. The nature of feedback is clearly illustrated in the stretch reflex (e.g. Houk and Rymer 1981). Muscle lengthening leads to increased afferent discharge through Ia and II fibers on the one hand, and increased motoneuronal discharge and muscle force on the other hand. One component of feedback has a sensory dimension, and can carry information on the state of the muscle. This information is transmitted through ascending tracts to the cortex and the cerebellum, and can contribute to central representations of posture and movement. The other component has a motor dimension which can be exploited to compensate for perturbations, but also to produce movements (Houk and Rymer 1981; Feldman and Levin 1995).

On this basis, the possible role of feedback can be addressed. On the motor side, feedback can contribute directly to movement production as in the equilibrium point theory (Feldman and Levin 1995), or indirectly by correcting deviations from a desired trajectory (Shadmehr and Mussa-Ivaldi 1994). This view is not backed up by observations in deafferented patients showing that they move somewhat normally under visual feedback (Ghez et al. 1990). Although the general motor behavior of deafferented patients is strongly affected, the basic capacity to move appears to be preserved (Forget and Lamarre 1987). On the sensory side, feedback provides information on the state of the body, and is the basis for the widely acknowledged role of state estimation (Wolpert et al. 1995; Shadmehr and Krakauer 2008). The tight link between estimation and control has lead to the idea that motor commands are continuously updated by internal feedback loops (Desmurget and Grafton 2000), and to the notion of optimal feedback control (Hoff and Arbib 1993; Todorov and Jordan 2002; Guigon et al. 2008a).

5.4 Posture/movement

Integration of posture and movement is a central and debated problem of motor control (Ostry and Feldman 2003). The controversy is generally centered on two hypotheses. On the one hand, it has been proposed that movement results from continuous transitions between postures (Feldman and Levin 1995). In this framework (equilibrium point theory, see 3.3.1), a unique and coherent operation based on shifts in the equilibrium position of the moving limb, is responsible for maintaining steady postures and creating smooth displacements. This view is supported by computational models (e.g. Gribble et al. 1998). The limitations of this approach have already been discussed (3.3.1). On the other hand, separate processes could subserve posture and movement (Massion 1992; Kurtzer, Herter, and Scott 2005; Chew et al. 2008), although no formalized model has been proposed to support this view (see 3.4).

From a mechanical point of view, posture is related to the presence of static forces (e.g. gravity). In the absence of static forces, posture is simply maintained by zeroing applied forces. Several interesting observations have been made on the influence of static forces on motor control. The experiment of Nishikawa et al. (1999) showed that the terminal posture of 3D redundant movements is independent of movement velocity. Because the relative contribution of antigravity and dynamic torques varies with velocity, optimization of the total torque pattern would predict variations of terminal posture with velocity. This result suggests that dynamic forces are optimized independent of static forces. Kurtzer, DiZio, and Lackner (2005) showed that adaptation to a multiforce environment composed of a velocity-dependent force and a constant force was well described by a mechanism that processes velocity-dependent force separately from the total applied force. Psychophysical studies showed that velocity profiles remain unchanged when moving

in a known constant (Mustard and Lee 1987; Welter and Bobbert 2002), or a known elastic force field (Ghez 1979; Bock 1990; Flash and Gurevich 1992; Gottlieb 1996; Milner 2002; Levin et al. 2003; Rand et al. 2004). Taken together, these results suggest that the central nervous system processes static and dynamic forces separately (Flanders and Herrmann 1992; Buneo et al. 1994; Guigon et al. 2007a). Interestingly, optimal control models perform properly in the absence of static forces (Guigon et al. 2007a), but poorly in the presence of static forces (Soechting and Flanders 1998; Thoroughman and Feller 2003). We emphasize that separation of static and dynamic forces is not separation of posture and movement because static forces (gravity, muscular elastic forces) are present during both posture and movement.

In the debate on posture and movement, the separation principle suggests that the two elements are tightly related (Fig. 5). In this framework, motor control would be subserved by a 3-component architecture: 1) a *dynamic controller* (in fact, an optimal feedback controller), which calculates, for given target (goal) and estimated states, the appropriate control to master the dynamic forces and progress toward the goal (dashed arrow on the left); 2) a *static controller*, which calculates for each estimated state the appropriate control that maintains equilibrium against the static forces (dashed arrow on the right); 3) a *state estimator* (in fact, an optimal state estimator), which calculates a state estimate from sensory inflow and motor outflow (gray arrows). This view is consistent with the observation that posture likely results from a high-level, active, anticipatory process rather than from a low-level, passive, feedback process (Morasso and Schieppati 1999; Loram et al. 2001), although it remains to be proven that postural control (e.g. Loram et al. 2001; Loram and Lakie 2002a; Loram and Lakie 2002b; Lakie et al. 2003; Loram et al. 2004; Loram et al. 2005a; Loram et al. 2005b; Lakie and Loram 2006; Loram et al. 2006; Loram et al. 2007a; Loram et al. 2007b) can be explained using the proposed principles of motor

control (see Kuo 1995; Kiemel et al. 2002; Kuo 2005; Martin et al. 2006; Lockhart and Ting 2007; Qu et al. 2007 for some evidence). The impressive series of studies by Loram, Lakie and collaborators put strong, but underestimated constraints on the relationship between posture and movement.
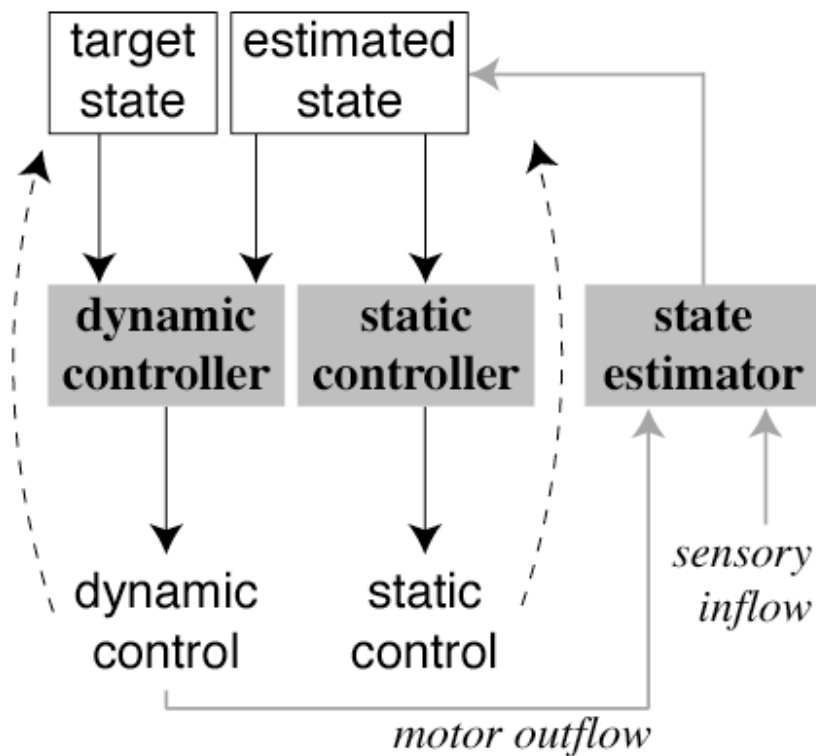

Figure 5. Architecture for the separation of static and dynamic forces.

The neural bases for the separation principle are still elusive. The separation principle is consistent with, but more general than, a separation of reciprocal activation and coactivation (Humphrey and Reed 1983; De Luca and Mambrito 1987). At the cortical level, putative correlates of static and dynamic controls were previously described in primate primary motor cortex as tonic and phasic-tonic patterns of discharge (Kalaska et al. 1989; Sergio and Kalaska 1998; Sergio et al. 2005). However, other types of discharge have been reported that could be considered to

contradict the separation principle (Cheney and Fetz 1980; Kalaska et al. 1989; Kurtzer, Herter, and Scott 2005). At the spinal level, it is expected that the two commands are additive, i.e., the force generated in a muscle by the sum of the commands is the sum of the forces generated by each command. Although additivity has been observed in some circumstances (Sergio and Ostry 1994; Rimmer et al. 1995; Sergio and Ostry 1995; Farley and Koshland 2000), it may not be a general case because of the threshold behavior in motoneurons.

5.5 Effort

In motor control models, a movement is generally specified by its amplitude and duration. Yet, although humans can performed timed actions, for instance rhythmic movements, not all their actions are actually timed, e.g. ambulatory locomotion movements, movements around postural states or reaching movements are not in general specified to have a particular duration (Schöner 2002). Psychophysical studies have shown that movement duration depends on movement parameters, e.g. amplitude/duration scaling (Fitts 1954; Wadman et al. 1979; Gordon, Ghilardi, Cooper, and Ghez 1994), load/duration scaling (Bock 1990; Hatzitaki and McKinley 2001), and systematic direction/duration variations (Gordon, Ghilardi, Cooper, and Ghez 1994; Pellegrini and Flanders 1996). Furthermore, subjects fail to adapt to time-dependent perturbations, e.g. force fields that explicitly depend on time (Conditt and Mussa-Ivaldi 1999), and they do consider time-dependent force fields as state-dependent force fields.

If duration is not specified for a given movement (defined its initial position and its amplitude), it should arise from a computational process. The constant effort principle proposes to calculate actual duration from a desired level of effort using the relationship between amplitude, duration, and effort prescribed by the optimal-

ity principle (Guigon et al. 2007a, 2008a), i.e. for a given amplitude and effort there exists a unique duration such that the optimal movement for this amplitude and duration is associated with this (minimum) effort. This principle provides a quantitative account of amplitude/duration and load/duration scaling, and direction-dependent changes in movement duration (Guigon et al. 2007a). A related idea is time minimization to match a given level of terminal variability (Meyer et al. 1988; Harris and Wolpert 1998). However, this solution predicts that scaling is associated with constant terminal variability. Experimental observations show that variability can increase with movement amplitude for series of movements obeying an amplitude/duration scaling law (Gordon, Ghilardi, and Ghez 1994; van Beers et al. 2004). A competing proposal to explain direction-dependent changes in movement duration is that the nervous system fails to compensate for the inertial anisotropy of the arm (Gordon, Ghilardi, Cooper, and Ghez 1994; see Todorov 1998 for a model). Yet, this view is not backed up by experimental observations (e.g. Flanagan and Lolley 2001).

6 Conclusion and perspectives

The idea that the nervous system could solve problems of motor control through simplifications was thoroughly reviewed. No appropriate strategies was persuasively and unambiguously identified that could actually address the complex issue of movement coordination. Putting simplification aside, a set of principles was presented based on the idea that the nervous system should possess detailed knowledge on the functioning of the objects to be controlled. Although these principles appeared highly successful for a computational description of motor control, it should not lead to forget the good reasons that have driven the search for simplifications (Turvey et al. 1978; Ostry and Feldman 2003). First, finding a solution to optimal

control problems is a highly demanding issue in computer science (Bryson 1999), and it is unclear how it could be discovered and realized by a neural hardware. More generally the neural substrate for the proposed principles remains elusive. Second, the problem of posture/movement integration is only partially and unpersuasively addressed. In particular, the lack of consideration for low-level characteristics of the neuromuscular system (reflex, stiffness) is problematic, and prevents the study of perturbation-induced changes in motor behavior. These limitations provide directions for future developments in the framework of computational motor control.

Two perspectives are interesting. First, the principles were applied to the control of the humanoid robot HRP2 (Tuan et al. 2008). Interesting preliminary results were obtained on the coordination of 7 and 9-DOF configurations involving the trunk and the arm. On the one hand, the application of biologically-inspired principles to robotics can offer an alternative to classical control techniques that are robust, but less flexible than the solutions discovered by the nervous system. On the other hand, the study of robotic systems could help validating the principles on more realistic kinematic chains (larger number of DOF). Second, the principles could apply to understand the neuroanatomy of motor control and associated motor disorders (e.g. Shadmehr and Krakauer 2008). For instance, the concept of effort could play a central role in inferring the functions of basal ganglia (Shadmehr and Krakauer 2008), and explaining behavioral disorders in Parkinson's disease (Mazzoni et al. 2007).

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