



**HAL**  
open science

# Optimalité et modularité du mouvement humain : du contrôle optimal aux synergies musculaires

Bastien Berret

► **To cite this version:**

Bastien Berret. Optimalité et modularité du mouvement humain : du contrôle optimal aux synergies musculaires. Neuroscience. Université paris-saclay, 2017. tel-04261033

**HAL Id: tel-04261033**

**<https://hal.science/tel-04261033>**

Submitted on 26 Oct 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**Ecole Doctorale 566**  
**Sciences du Sport, de la Motricité et du Mouvement Humain**

**OPTIMALITE ET MODULARITE  
DU MOUVEMENT HUMAIN :  
DU CONTROLE OPTIMAL  
AUX SYNERGIES MUSCULAIRES**

Habilitation à Diriger des Recherches

Soutenue le : **24/11/2017**

par

**Bastien Berret**

Devant le jury composé de :

|                       |                                       |            |
|-----------------------|---------------------------------------|------------|
| M. Benoît Bardy       | Professeur, Université de Montpellier | Rapporteur |
| M. Etienne Burdet     | Professeur, Imperial College London   | Rapporteur |
| M. Michel Desmurget   | Directeur de Recherche, INSERM        | Rapporteur |
| M. Michel-Ange Amorim | Professeur, Université Paris-Sud      | Examineur  |
| M. Frédéric Jean      | Professeur, ENSTA ParisTech           | Examineur  |
| M. Thierry Pozzo      | Professeur, Université de Bourgogne   | Examineur  |

---

## Avant-propos

Ce mémoire d'Habilitation à Diriger des Recherches (HDR) est l'aboutissement d'une dizaine d'années de réflexion. Les travaux qui ont conduit à ce document ont été effectués au sein de trois institutions.

La première est l'**Université de Bourgogne** où j'ai découvert la thématique du contrôle moteur pour ma thèse, courant 2005. Venant des mathématiques pures, j'avais envie de confronter mes connaissances à des questions concrètes et l'étude du mouvement humain m'a tout de suite intéressé. Cela s'est confirmé quand j'ai compris qu'un "mathématicien" pouvait y jouer un rôle central. Essayer de comprendre comment le cerveau parvient à contrôler nos mouvements, même les plus simples, est une problématique captivante mais si complexe qu'elle nécessite de croiser plusieurs champs scientifiques. Confiné aux constructions abstraites de la plupart des cours de mathématiques, j'avais alors d'importantes lacunes à combler en biomécanique et neurosciences ainsi qu'en modélisation et expérimentation en sciences du mouvement humain. Heureusement, l'environnement pluridisciplinaire du laboratoire dans lequel j'ai effectué ma thèse m'a permis de m'initier à la démarche scientifique expérimentale et à la recherche fondamentale en neurosciences du mouvement.

Après ces 3 années riches et intenses, j'ai eu l'opportunité de faire un séjour à l'**Institut Italien de Technologie** de Gênes à partir de 2009 où j'ai pu voir une autre organisation de la recherche et aborder des thématiques et des méthodes nouvelles en lien avec la robotique humanoïde et les neurosciences. Cette expérience à l'étranger m'a fait gagner en autonomie, en indépendance et a élargi ma culture scientifique.

Depuis 2012, je poursuis mes travaux à l'**Université Paris-Sud** dans un environnement scientifique exceptionnel qui m'a permis de rencontrer des chercheurs de premier plan dans de nombreux domaines liés aux sciences du mouvement humain (mathématiques, informatique, santé et handicap neuromoteurs, robotique et exosquelette, psychologie...) et venant d'horizons divers (ENSTA, Hôpital Raymond-Poincaré, CEA, Université de Versailles Saint-Quentin-en-Yvelines, CNRS...).

Cette proximité de compétences m'a permis d'envisager des projets de recherche ambitieux avec des finalités concrètes. Jusqu'à présent, mon travail m'avait surtout amené à traiter de questions fondamentales du contrôle moteur, mais les discussions avec ces collègues ont fait surgir de nouvelles idées, émerger de nouvelles questions et imaginer de nouvelles méthodes pour y répondre. Ayant travaillé avec des mathématiciens, des neuroscientifiques, des roboticiens, des psychologues et des médecins, j'ai pu mesurer la difficulté à se comprendre tant les modes de pensée, la philosophie et les objectifs de chacun peuvent différer. Dans un contexte pluridisciplinaire, la confrontation de cultures scientifiques divergentes peut parfois donner l'impression d'une progression laborieuse

---

mais ma conviction est que cela en vaut la peine. L'expérience a montré que les longues heures de brainstorming ont toujours été décisives pour l'élaboration d'un "bon papier". De fait, ce mémoire n'aurait pas la même teneur sans un travail collaboratif. Durant toutes ces années, j'ai eu la possibilité de rencontrer des collègues avec qui les collaborations furent souvent fructueuses et les discussions toujours passionnantes, ce qui à mon avis est une part essentielle de la vie du chercheur.

Ce mémoire est *in fine* l'expression de mon point de vue personnel dont le fil conducteur est l'utilisation de la modélisation mathématique comme outil pour tenter de mieux comprendre **comment le cerveau contrôle le mouvement humain**. Plusieurs niveaux d'analyse sont possibles sur une telle problématique, allant du plus microscopique au plus macroscopique. Le mien a toujours été macroscopique n'ayant pas expérimenté ni modélisé au niveau de la cellule ou de la population de neurones. Je me suis intéressé aux trajectoires des segments du corps humain sous l'effet de l'environnement (ex : la gravité) et de contractions musculaires volontaires. Pourquoi et comment le système nerveux central produit certains mouvements plutôt que d'autres a été mon principal questionnement scientifique. Dans un système mécanique où la commande est connue, il est possible de prédire les trajectoires à partir d'un principe de moindre action. Pour le mouvement biologique, où la commande n'est pas connue à l'avance, il serait intéressant de trouver des principes similaires permettant de faire des prédictions précises sur la cinématique ou la dynamique du mouvement, allant même jusqu'à prendre en compte les variations inter-individuelles. La citation de Maupertuis placée en épigraphe "*la Nature dans la production de ses effets agit toujours par les moyens les plus simples*" reflète bien la manière dont la problématique du contrôle moteur est envisagée dans ce mémoire d'HDR. La question centrale est alors de déterminer ce que l'on entend par "simple" ou "moindre action" pour le mouvement biologique. Cela peut avoir affaire aux **notions d'optimalité et de modularité**.

---

Ce document est organisé en **deux parties**. La première est la synthèse de mes travaux, projets et activités. La deuxième comporte une sélection d'articles complets.

Dans la première partie, on trouve **3 chapitres** :

Je commence d'abord par effectuer une **synthèse de mes principaux travaux antérieurs**, en faisant le lien entre deux théories répandues en sciences du mouvement humain mais finalement peu discutées simultanément dans la littérature, à savoir la théorie du contrôle optimal et la théorie des synergies musculaires.

Dans un deuxième temps, je présente un **projet de recherche autour de la théorie dite du "coût du temps"** afin d'essayer d'expliquer un fait assez simple mais intrigant : certaines personnes se meuvent beaucoup plus vite que d'autres dans des conditions pourtant similaires. Il semble exister un continuum entre les personnes les plus rapides et les personnes les plus lentes. Mais qu'est-ce qui motive et influence le choix de telle ou telle vitesse chez un individu dans une situation particulière ? Les causes peuvent être multiples et des réponses dans les domaines de la biomécanique, de la neurophysiologie et de la psychologie pourraient être apportées.

Enfin, le dernier chapitre est consacré à un **récapitulatif détaillé de mes activités académiques**, des publications issues de ma recherche jusqu'aux responsabilités académiques en passant par mes enseignements.

**NOTA BENE** : le choix de rédiger ce manuscrit en langue anglaise a été motivé par plusieurs raisons. D'une part, le Chapitre 1 est basé sur ce qui devrait faire l'objet d'un chapitre d'ouvrage prenant la forme d'une revue de littérature sur l'optimalité et la modularité du mouvement humain. Celle-ci s'appuie fortement sur mes travaux et correspond bien à l'exercice de synthèse de l'HDR. D'autre part, le Chapitre 2 est basé sur le projet de recherche que j'ai soumis à l'Institut Universitaire de France (IUF) et qui fut rédigé en Anglais dès l'origine. Le Chapitre 3 est lui aussi tiré de mon dossier IUF en grande partie.

---

## Remerciements

Je tiens à remercier ma famille pour son soutien et ses encouragements tout au long de ces années, et plus particulièrement Marie qui me suit depuis le début.

Je remercie également tous mes collègues et co-auteurs avec qui j'ai partagé ma vie d'apprenti chercheur puis d'enseignant-chercheur.

Enfin, je remercie mes rapporteurs et examinateurs d'avoir accepté de faire partie de mon jury d'HDR.

---

*”La Nature dans la production de ses effets agit toujours par les moyens les plus simples”*

**Pierre Louis Moreau de Maupertuis,**

*Accord de différentes loix de la nature qui avoient jusqu’ici paru incompatibles, 15 Avril 1744*

# Contents

|          |  |           |
|----------|--|-----------|
| <b>I</b> | <b>Research and academic activities</b>                                  | <b>5</b>  |
| <b>1</b> | <b>Synthesis of previous works</b>                                       | <b>7</b>  |
| 1.1      | Introduction . . . . .   | 8         |
| 1.2      | Optimal control hypothesis . . . . .                                     | 10        |
| 1.2.1    | Direct and inverse optimal control approaches to motor control . . . . . | 10        |
| 1.2.2    | Example of inverse optimal control results . . . . .                     | 12        |
| 1.2.3    | Remarks regarding optimal control theory . . . . .                       | 24        |
| 1.3      | Modular control hypothesis . . . . .                                     | 27        |
| 1.3.1    | Hierarchical modular control . . . . .                                   | 27        |
| 1.3.2    | A task-space perspective to modularity . . . . .                         | 32        |
| 1.3.3    | Remarks regarding modular control theory . . . . .                       | 36        |
| 1.4      | From optimality to modularity and vice-versa . . . . .                   | 38        |
| 1.4.1    | Optimality with modularity: theoretical ground . . . . .                 | 38        |
| 1.4.2    | Optimality versus modularity: paradox and causality . . . . .            | 39        |
| 1.5      | Conclusion and overall perspectives . . . . .                            | 41        |
| <b>2</b> | <b>Research project</b>  | <b>45</b> |
| 2.1      | Scientific positioning . . . . .   | 45        |
| 2.2      | Research objectives . . . . .  | 46        |
| 2.3      | Research significance . . . . .  | 47        |
| 2.4      | Research program . . . . .   | 51        |
| 2.4.1    | Fundamental research . . . . .   | 51        |
| 2.4.2    | Applied projects . . . . .   | 56        |
| 2.5      | Complementary research projects . . . . .                                | 59        |
| <b>3</b> | <b>Curriculum vitae</b>  | <b>61</b> |
| 3.1      | General information . . . . .  | 61        |
| 3.2      | Scientific education . . . . .   | 62        |
| 3.3      | Career . . . . .   | 63        |
| 3.4      | Supervision work . . . . .   | 63        |
| 3.5      | Teaching, pedagogic and administrative duties . . . . .                  | 66        |
| 3.6      | Scientific activity . . . . .  | 69        |

*Contents*

---

|   |           |
|---|-----------|
| 3.7 List of publications . . . . .            | 72        |
| 3.8 Five most relevant publications . . . . . | 77        |
| <b>Appendix</b>                               | <b>82</b> |
| <b>Bibliography</b>                           | <b>85</b> |
| <b>II Selection of full-text articles</b>     | <b>99</b> |

# List of abbreviations

|     |                                   |
|-----|-----------------------------------|
| OCP | optimal control problem           |
| OC  | optimal control                   |
| LQR | linear quadratic regulator        |
| LQG | linear quadratic gaussian         |
| DOF | degree of freedom                 |
| PCA | principal component analysis      |
| NMF | non-negative matrix factorization |
| ICA | independent component analysis    |
| VAF | variance accounted for            |
| BG  | basal ganglia                     |
| CNS | central nervous system            |
| CoT | cost of time                      |
| MT  | movement time                     |
| TPV | time to peak velocity             |
| EMG | electromyography                  |
| EEG | electroencephalography            |
| EOG | electrooculography                |

# List of Figures

|      |   |    |
|------|---|----|
| 1.1  | Predicted hand trajectories for two influential motor costs during planar reaching movements. . . . .   | 12 |
| 1.2  | Illustration of the inactivation principle. . . . .   | 13 |
| 1.3  | Illustration of the vertical asymmetries of speed profiles of comparable extent and duration. . . . .   | 14 |
| 1.4  | Structure of the optimal solution when minimizing a compromise between the absolute work and the integral of the squared acceleration. . . . .                    | 15 |
| 1.5  | Example of raw data for one subject performing full-extended arm pointing movements in the sagittal plane. . . . .  | 16 |
| 1.6  | Illustration of the difference between pointing toward a target point versus pointing toward a target bar/line. . . . .   | 18 |
| 1.7  | Experimental and simulated trajectories for a representative subject performing an arm pointing task with a uniform, long target bar in a vertical plane. . . . . | 19 |
| 1.8  | Reach endpoint formation question when ask a participant to reach to a line: an eye-hand coordination study. . . . .  | 22 |
| 1.9  | Emergence of an optimal duration within optimal control theory. . . . .   | 23 |
| 1.10 | Illustration of the hierarchical modular control architecture at the muscle activation level. . . . .   | 28 |
| 1.11 | Illustration of the space-by-time modularity and its relation to other typical extraction methods. . . . .  | 31 |
| 1.12 | Illustration of whole-body coordination during the study of modularity in motor control at the kinematic level. . . . .   | 32 |
| 1.13 | Differences between the robotic approach and the neuroscience approach regarding modularity for movement control. . . . .   | 33 |
| 1.14 | Single-trial decoding approach proposed by Delis et al. (2013). . . . .   | 34 |
| 1.15 | Complementarity between variance accounted for (VAF) and decoding scores. . . . .   | 35 |
| 2.1  | Amplitude-duration relationship for self-paced planar single-joint arm movements, in a pointing task. . . . .   | 50 |

|     |   |    |
|-----|---|----|
| 2.2 | Methodology to sample values of the CoT from experimental data. . . . .       | 54 |
| 2.3 | Lower-limb exoskeleton illustration (credit to S. Alfayad). . . . .           | 57 |
| 2.4 | Photo of the exoskeleton ABLE worn by P. Garrec (credit to CEA-LIST). . . . . | 58 |



## **Part I**

# **Research and academic activities**

---

The first part of the present manuscript is organized as follows. In Chapter 1, I present a critical synthesis of my past works and discuss optimal and modular control theories concurrently. In Chapter 2, I present my research project for the coming years. Finally, Chapter 3 gives a full CV of my academic activities.

# 1

## Chapter 1

---

# Synthesis of previous works

**T**HIS chapter presents a critical synthesis of my research work, which has been very much multidisciplinary since my PhD thesis by integrating knowledge from mathematics, biomechanics, robotics, psychophysics or neuroscience. The study of the neural control of movement naturally leads to such a diversity of disciplines. In particular, at the modeling level, I employed approaches based on stochastic/deterministic optimal control theories, numerical optimization and machine learning methods such as dimensionality reduction and matrix factorization techniques. Experimentally, I used motion capture devices, force platforms, electromyographic (EMG) sensors, eye-tracking systems to collect human movement data during specific motor tasks designed on purpose. Along the course of my research, I also went through connected fields/questions such as humanoid robotics (e.g., emulating muscle co-contraction properties with variable stiffness actuators), neuro-rehabilitation (e.g., better understand muscle organization to help patients recovering lost sensorimotor gait functions) or sport sciences (e.g., optimization of performance in high-skill tasks such as overarm throwing). While I mainly focused on fundamental questions in agreement with my personal inclination, these more applied topics have been a fruitful source of inspiration. More recently, I have started to collaborate locally within Université Paris-Saclay with linguists to study French sign language, psychologists to investigate the cause of inter-individual differences in motion vigor, clinicians to better apprehend the reorganization of synergies after stroke or spinal cord injury, and roboticists to improve high-level control laws in exoskeletons. However, given that these studies are mostly ongoing work, I will not discuss them in the current chapter where I focus on already published studies related to my main stream of research.

Thus far, my main research activity investigated the motoric decisions that underlie the planning of human movement such as where to go, how to get there and with what speed etc. To this aim, in-lab experiments reflecting how the brain selects spatial trajectories or movement durations were

designed on purpose and explanatory models were developed, most of the times within optimal control theory. My research also considered a complementary theory of motor control, called the modular control hypothesis, which postulates that pre-coded muscle synergies may exist and simplify control of the numerous degrees of freedom (DOF) of the musculoskeletal system.

In the following, I give a comprehensive review and discussion of my past work that relates to the optimal and modular control hypotheses, two influential theories of the motor control literature.

## 1.1 Introduction

The vision neuroscientist David Marr, in his posthumous book, distinguished three levels of analysis in the field of computational neuroscience (Marr, 1983). In the context of computational motor control, the higher level (“theory”) addresses questions such as why humans displace their limbs the way they do or what goals they try to achieve (Shadmehr and Krakauer, 2008). Essentially, this level of analysis seeks to explain why human movement trajectories have certain signatures and what makes the elected movement better than another. By intuition and also by analogy with the principle of least action in classical mechanics, some researchers (including Marr himself) presumed that human behavior may be optimal in a sense that remains to be specified. Formulated in this way, the question turns out to be an *inverse optimal control* problem, a class of problems that mathematicians started to tackle a long time ago (e.g. Kalman, 1964) and has been recently applied to reaching (Gauthier et al., 2010), locomotion (Chittaro et al., 2013) or even flying (Ajami et al., 2013). Precisely, inverse optimal control is the process of recovering the optimality criterion (or cost function) according to which a bunch of *ex hypothesi* optimal trajectories are indeed optimal. It is an ill-posed problem in general, which is harder than direct optimal control (Bellman, 1957; Pontryagin et al., 1964). Direct optimal control consists in *a priori* guessing the cost function and computing the corresponding optimal trajectories, which can be a tricky mathematical problem in itself in many occasions. Importantly, at this level of analysis, no assumption is made about how the brain could manage to generate these optimal trajectories or whether it constantly solves optimal control problems from scratch<sup>1</sup>. This type of question is left to the second level of analysis called “algorithm” which investigates how observably optimal trajectories could be generated

---

<sup>1</sup>A useful analogy from classical mechanics is the principle of least action. For instance, trajectories of conservative systems are *extrema* of the *Action*, i.e. the time integral of the Lagrangian (kinetic minus potential energies), while it is hardly arguable that objects explicitly “optimize” their trajectories on purpose. In fact, finding whether a Lagrangian exists for a given system of differential equations has been the topic of numerous investigations in physics which date back to the works of Maupertuis, Euler or Lagrange. This refers to the inverse problem of calculus of variations (Douglas, 1941) and can be seen as the analog problem of inverse optimal control. Notably, inverse calculus of variations has been used in the context of motor control to investigate the origin of the two-thirds power law (Lebedev et al., 2001).

by the sensorimotor system. To this aim, several motor control theories have been proposed such as the ones based on active inference which do not even require the specification of a cost function to explain movement generation (Friston, 2011). However, active inference crucially requires prior knowledge about limb trajectories. As inverse optimal control precisely seeks to provide the rationale about why certain trajectories may be more valuable than others *a priori*, it can complement active inference models by informing why certain priors are used. Conceivably, through evolution and life-span development, the central nervous system (CNS) may have learned statistical descriptions of movement distributions or may have found simplified ways to trigger optimal or, say, good enough movements. By storing synergies (also called building blocks, primitives or modules<sup>2</sup>), it has been proposed that the CNS might have found clever ways to group and coordinate different DOFs (joints or muscles) so that only a few task-related variables would need to be tuned in order to produce adequate motor patterns and efficient movements. Modularity can be assumed at different levels: kinematic, dynamic, muscular or neural. When focusing on the muscle activation level, we usually talk about the muscle synergy hypothesis whose main appeal is to simplify neural motor control through the timely activation of pre-coded groups of muscles. However, what these “muscle synergies” are and according to what rules they are combined remains elusive. Very often these motor “building blocks” may take the form of muscle activation ratios or temporal waveforms, and are identified via dimensionality reduction such as PCA (principal component analysis), NMF (non-negative matrix factorization) or ICA (independent component analysis), i.e. unsupervised machine learning techniques applied to approximate motor signals (e.g. surface EMG data). Currently there is still a gap between theories investigating the structure of muscle activities and theories assuming that cost functions determine limb trajectories. Yet, the crucial pivot to both approaches is musculoskeletal modeling. In inverse and direct optimal control, a model of the musculoskeletal system is required because optimally driving a system requires some dynamical description of it (e.g. rigid body dynamics with more or less advanced models of musculotendon complexes). Musculoskeletal models are also required to test the modular control hypothesis in muscle space, especially for assessing the effectiveness of the extracted synergies (typically inferred from EMG signals) in controlling the musculoskeletal system; i.e. feeding back the EMG-based synergies into the controlled system, which is rarely done in motor control studies. A growing number of studies are interested in investigating the links between optimality - at the highest level of analysis - (according to Marr’s classification) and modularity - at the second level of analysis - in order to evaluate whether optimal (or at least good enough) trajectories can be obtained from the combination of a limited number of specific motor modules. Whether or not

---

<sup>2</sup>In this HDR manuscript, the terms synergy, primitive, module or building block are loosely treated as synonyms and will be used interchangeably. In the literature, a precise mathematical definition specifying the exact nature of each term is generally lacking. Different authors may thus have their own conception regarding the exact meaning of each term. This is something we addressed in Chiovetto et al. (2013) and Delis et al. (2014).

the algorithm used by the CNS to trigger “almost optimal trajectories” truly relies on some form of modularity is an open question but evidence is usually sought by tackling Marr’s third level of analysis, that is, the “implementation” level. In particular, finding synergies of a neural origin would strongly support the theory. However, the nature and shape of the building blocks to be found within the CNS critically depends on the hypotheses made by the framework used to infer them computationally. Therefore, research at the implementation level is linked to the algorithmic level; i.e. studies of the neurophysiological underpinnings of modular structures must be conducted in conjunction with candidate models of modularity.

In this chapter, I will mainly review and discuss optimal and modular control theories and underline their strengths and limitations. It is worth noting that the three levels of analysis put forward by Marr are complementary but address conceptually different questions. Therefore, the interplay between the first two levels will be discussed. In Section 1.2, I will review the (inverse) optimal control approach which aims at deciphering the high-level principles underlying motoric decisions. In Section 1.3, I will review works related to the muscle synergy hypothesis that assess the structure of muscle activity patterns from a dimensionality reduction perspective. Section 1.4 is dedicated to discussing the links between the two approaches and, finally, some perspectives for future research on these topics are proposed in Section 1.5.

## **1.2 Optimal control hypothesis**

### **1.2.1 Direct and inverse optimal control approaches to motor control**

The inverse optimal control problem (OCP) was first considered in a seminal paper by Kalman for linear-quadratic problems (Kalman, 1964) and extended in (Nori and Frezza, 2004). In motor control, few studies employed such an inverse approach to tackle the motor planning problem until recently. This is not to say that optimal control has not been used; on the contrary it has been applied extensively mostly since the 80s and has emerged as a leading theory in the human movement control literature (Engelbrecht, 2001; Todorov, 2004). The work of Nelson (1983) exemplifies the classical (direct) approach that was initially employed: several costs were tested separately and compared to find the best descriptor/predictor of human motion data. Then, the researcher suggested that the elected cost constituted an explanatory principle of biological motion. Since that time the computational theory of motor control has developed and become very popular. An account of all the main ideas and concepts like “optimal feedback control” and “internal models” can be found in specialized reviews (Todorov, 2004; Scott, 2004; Diedrichsen et al., 2009; Scott, 2012; Schwartz, 2016). The success of this computational theory of motor control may be

explained by two main reasons: first, once a cost function is defined, it captures everything about the possible trajectories of the system, thereby implementing an elegant dimensionality reduction from the infinite number of potential trajectories to cost functions (Berniker and Körding, 2015); second, it is readily implementable in artificial systems because the very same language is used by control theoretists and roboticists (Ivaldi et al., 2012). The point I want to make here is that most studies tended to *a priori* choose a cost function and to test its predictions subsequently, and hence, used a direct OC approach. Generally, researchers tried to match the standard LQR (linear-quadratic regulator) or LQG (linear-quadratic Gaussian) designs to make the problem easier to solve mathematically/numerically (Kappen, 2011; Todorov, 2006). Notable extensions were developed to deal with multiplicative (signal-dependent) noise that is relevant to the human motor apparatus (Todorov, 2005). Interestingly, these simple models were sufficient to explain several classical motor control phenomena (two-thirds power law, Fitts’s law; e.g. Harris and Wolpert, 1998). However, the true nature of the question “why do we move like that?” requires a reversed process, which brings *inverse* OC into play. An illustration of the difference between inverse and direct OC is given below (Eq. 1.1):

$$\begin{array}{ccc}
 \text{observed trajectories} & \xrightarrow[\text{control approach}]{\text{inverse optimal}} & \text{cost function} \\
 \text{cost function} & \xrightarrow[\text{control approach}]{\text{direct optimal}} & \text{compare observed vs.} \\
 & & \text{predicted trajectories}
 \end{array} \tag{1.1}$$

The need for inverse optimal control arises from the need to identify the most plausible (among all possible) cost functions in an automated or mathematical way. Mathematically, a cost function may take the form  $C(\mathbf{u}) = \int_0^T h(\mathbf{x}, \mathbf{u}, t) dt$  where  $\mathbf{x}$  is the controlled variable (e.g. system state such as velocity, position etc.),  $\mathbf{u}$  the control variable (e.g. joint torques or motoneuron inputs) and  $t$  is time<sup>3</sup>. If a cost function  $h$  accounts for some data, nothing precludes another cost of a different nature to perform equally well or even better. This has been at the origin of some controversy because in many occasions divergent costs were found to account for planar point-to-point reaching movements, a highly studied motor control paradigm. So, the following question would inevitably arise: which of these candidate costs is really relevant to human motor control? Innovative paradigms were thus required to disambiguate among candidate costs. This situation is exemplified in Figure 1.1 where a simple change of the target type allows better discriminating between cost functions.

Leaving aside the experimental design concern, inverse OC remains a difficult problem because

<sup>3</sup>In this manuscript, I only consider integral costs for simplicity but a terminal cost could be easily added in all the OCPs. Throughout the manuscript, I will mainly focus on deterministic OC models for which a final state (or manifold if the final state is not unique) is known in advance and can be attained exactly.

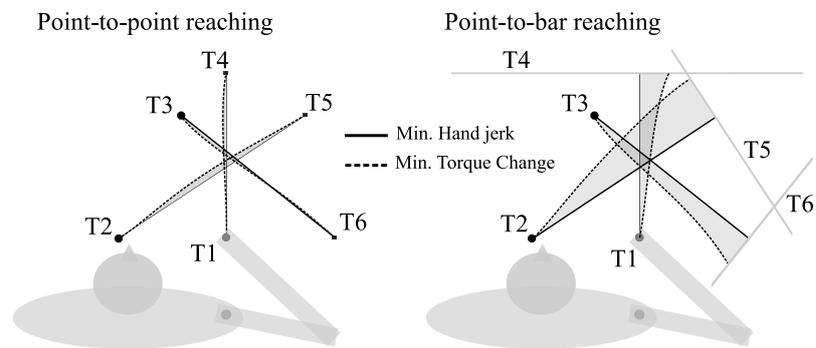


Figure 1.1: Predicted hand trajectories for two influential motor costs during planar reaching movements. *Left panel:* when reaching to a **target point**, the minimum jerk (Flash and Hogan, 1985) and torque change (Uno et al., 1989) models predict highly similar and therefore equally plausible trajectories, whereas the two models are very different in nature (kinematic cost for the former and dynamic for the latter). *Right panel:* when replacing the point with a **target line or bar**, the two costs lead to different trajectories, and may thus be distinguished empirically. Shaded areas indicate the difference between the trajectories predicted by the two models. Taken from Berret et al. (2011a).

it is primarily ill-posed mathematically unless very careful conditions are imposed. In sum, to successfully study inverse OCPs, not only mathematical sophistication but also careful experimental designs or singular enough experimental observations are needed to distinguish putative cost functions.

### 1.2.2 Example of inverse optimal control results

In 2008, we identified a necessary and sufficient condition of optimality for fast enough arm reaching movement (Berret et al., 2008b,a; Gauthier et al., 2010). Namely, periods of simultaneous inactivation of opposing muscles - during the movement - were shown to be equivalent to the minimization of a cost *including* a term like the integral of the absolute power of muscle torques (termed “absolute work”). This principle is illustrated in simulation and for experimental data in Figure 1.2.

The strength of this result was the mathematical proof of an “equivalence” between a singular motion feature (muscular inactivation) and a cost feature (non-smoothness of the cost). This was a nice example of a fruitful collaboration between mathematicians and motor control researchers. Initially, we however used a direct approach by guessing what could be a physically-relevant cost function (Berret et al., 2008b). This is only later that the mathematical analysis allowed to establish this powerful inverse OC result, whereby we could infer certain properties of the cost function

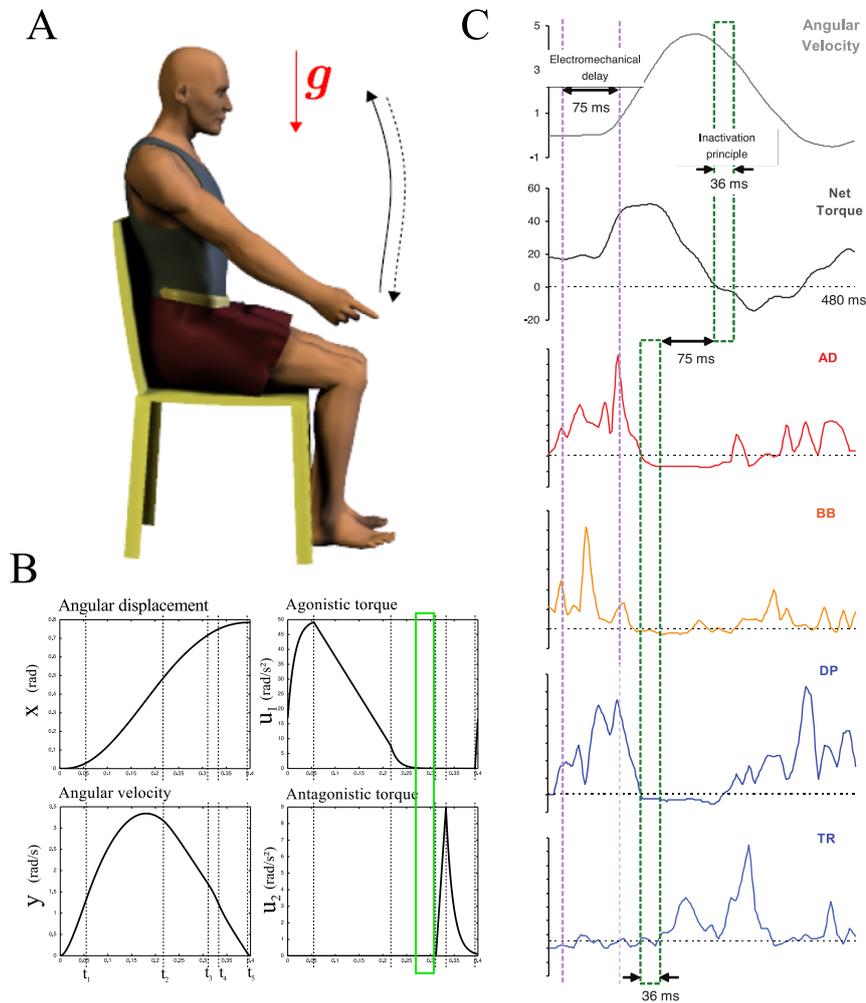


Figure 1.2: Illustration of the inactivation principle (Berret et al., 2008a). A. Task under consideration: single-joint pointing movements with a fully extended arm are studied in a vertical plane. B. Inactivation principle in simulations when optimizing a compromise between the absolute work of muscular joint torques and motion smoothness (squared angular acceleration). Some muscle dynamics is taken into account here and relatively large/fast movements are simulated to see the inactivation phenomenon. C. Raw experimental data of a single upward movement for a given subject. Angular velocity and net shoulder torque are depicted together with the rectified EMG activity whose tonic level has been removed (hence the negative parts in the EMG plots). Recorded muscles: AD=Anterior deltoid, BB=Biceps, DP=Posterior deltoid, TR=Triceps.

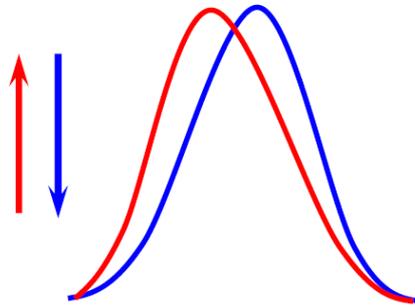


Figure 1.3: Illustration of the vertical asymmetries of speed profiles of similar extent and duration. One DOF arm pointing movements are considered, starting and ending at rest. Red: upward movement. Blue: downward movement. It is a strong and robust finding that the relative duration of the acceleration phase is shorter for an upward motion compared to a downward motion.

right from singular experimental observations (Gauthier et al., 2010). In practice, the work was motivated by a different intriguing experimental result: the kinematics of vertical arm movements was shown to depend on its orientation relative to gravity vector, therefore suggesting a potential imprint of gravity on human movement (Papaxanthis et al., 2003; Gentili et al., 2007; Gaveau et al., 2011). This directional dependence was quantified through an index of symmetry of hand speed profiles (often termed “time to peak velocity” - TPV - or “factor B” in some studies). Asymmetries were systematically observed between upward and downward motions, as illustrated in Figure 1.3.

Since then, a series of papers has shown that upward movements differed from downward movements of equal duration and amplitude (including 1-DOF motions during which only the sign of gravity effects change with movement direction; i.e. assists/resists the acceleration of downward/upward movements respectively) in that the acceleration duration was shorter in the upward compared to the downward direction (Papaxanthis et al., 2005; Gentili et al., 2007; Le Seac’h and McIntyre, 2007; Crevecoeur et al., 2009; Gaveau and Papaxanthis, 2011; Sciutti et al., 2012b; Gaveau et al., 2014; Yamamoto and Kushiro, 2014; Toma et al., 2015; Gaveau et al., 2016; Hondzinski et al., 2016). These directional asymmetries have been observed by independent groups of researchers so consistently that we could now employ the term “law of asymmetries” to refer to this phenomenon. In particular, minimizing the absolute work of muscle torques has been shown to robustly reproduce these vertical asymmetries for fast enough movements, despite differences in initial postures (Berret et al., 2008a), upper limb’s segment (Gaveau et al., 2014) or gravito-inertial context (Gaveau et al., 2016). An explanation of the reason why asymmetries are predicted by such a model is detailed in Figure 1.4 where the optimal motor strategy is decomposed; this has to do with the inactivation principle mentioned above and the force of gravity.

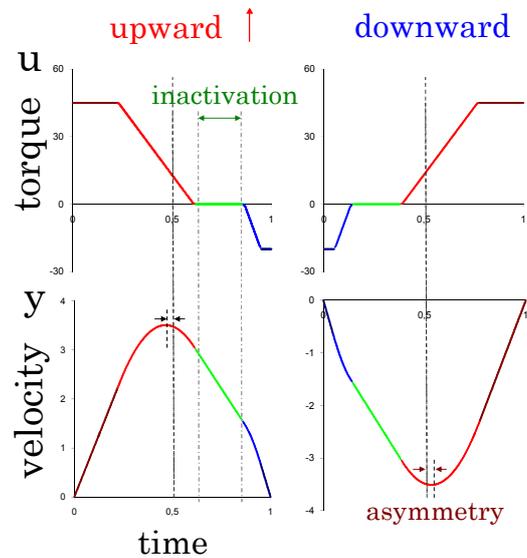


Figure 1.4: Structure of the optimal solution when minimizing a compromise between the absolute work of joint torques and the integral of the squared joint acceleration, during single-joint pointing movements in the vertical plane. Note that the green phase is a time period when the arm is in free fall (only gravity would be acting on it if we neglect all frictions) and this possible utilization of gravity accounts for the asymmetries in velocity profiles.

To further verify this result, experiments were conducted in microgravity during parabolic flights and revealed an adaptation of the hand kinematics during similar movements, as quantified through the TPV index. This adaptation progressively removed the hand kinematic differences between upward versus downward single-joint arm movements and emphasized the effect of gravity in 1-DOF movements in a parasagittal plane. It also ruled out any potential confound related to the observed up/down asymmetries on earth (e.g. different muscular groups acting etc.). An illustration of raw kinematic and EMG data obtained in microgravity is presented in Figure 1.5 and the reader is referred to Gaveau et al. (2016) for a deeper analysis at the kinematic level.

This led the authors to conclude about an optimal integration of gravity force during motion planning where gravity torque can be utilized to drive the limb during rapid movements. This interpretation is also corroborated by existing EMG analyses showing that, during a rapid movement, the (phasic) activity of anti-gravity muscles is clearly lower than the (tonic) activity that would be needed to maintain a static arm posture in the same position, in certain movement phases<sup>4</sup> (e.g. Buneo et al.,

<sup>4</sup>It is generally assumed that the muscle torque  $\tau$  acting at a given joint can be split into two terms such that  $\tau = \tau_{stat} + \tau_{dyn}$ , where  $\tau_{stat}$  is a static term which only depends on the system position and  $\tau_{dyn}$  is a dynamic term which depends on its velocity and acceleration (Hollerbach and Flash, 1982; Atkeson and Hollerbach, 1985). Gravitational torque is part of the static term which may also include other terms related to elastic forces. On

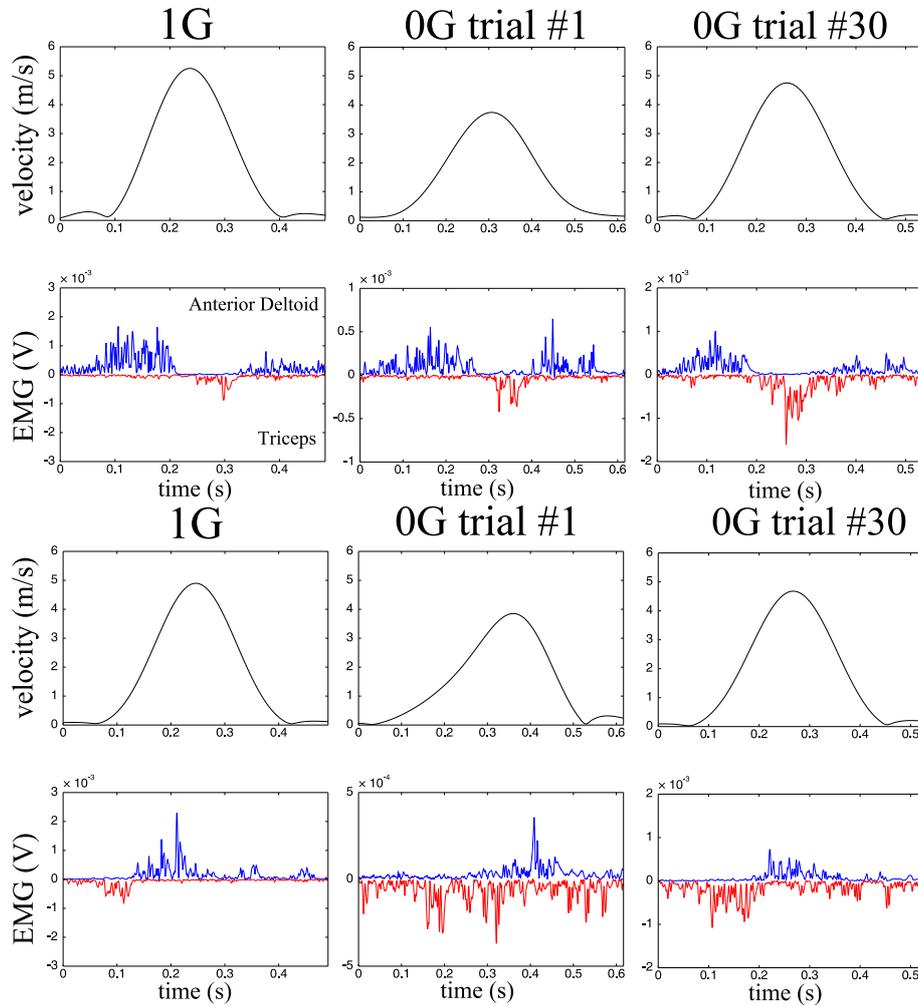


Figure 1.5: Example of raw data for one subject performing full-extended arm pointing movements in a parasagittal plane. Baseline behavior on earth before parabolic flight (left column), first trial ever in microgravity (middle) and behavior after 30 upward (*top*) and 30 downward (*bottom*) movements (right column). It is visible on these graphs that EMG patterns tend to become more “symmetrical” in 0g after adaptation, while the first trial is more noisy although the target was successfully attained. Initially, 0G movements tended to be slower, possibly to let the CNS process more feedback signals (see also Crevecoeur et al., 2010). A full study of the adaptation of EMG patterns in microgravity is still missing however.

1994; Flanders et al., 1996; d'Avella et al., 2006, 2008; Russo et al., 2014, and Fig. 1.2).

Thus far, the absolute work of muscle torques was only shown to be one of the potential ingredients of a more general cost function that may underlie human movement planning (Berret et al., 2008a). Various researchers had already successfully proposed other cost functions in the literature as well as the idea of composite costs, which was explicitly tested later in Berret et al. (2011a). The idea of composite costs assumes that multiple complementary criteria may actually shape human trajectories. For instance, motion smoothness and energy expenditure are complementary criteria as minimizing one may well be detrimental to the other. This mixed nature of cost functions has been observed in various tasks such as reaching (Berret et al., 2011a; Vu et al., 2016b; Gaveau et al., 2016), landing after a jump (Zelik and Kuo, 2012) and walking (Yandell and Zelik, 2016). At this point, it is important to classify cost functions in two categories: the first category, “subjective” costs, depends on the subject’s choice; the second category, “objective” costs, depends on the task specification<sup>5</sup>. In general both objective and subjective costs are relevant to motor control. Forcing a subject to reach at maximal speed to a target, tracking an imposed trajectory, freezing a joint or throwing a ball as far as possible are examples of objective costs. Objective costs can be easily modeled in the OC formalism. Yet, even with such task objectives, most motor tasks are still redundant because there is an infinity of ways, i.e. motor control solutions, to perform them. Subjective costs come into play to resolve all residual task redundancy and provide the rationale about why the task is eventually performed as it is. Here, I want to underline this last statement. Reproducing or trying to explain empirical data with an OC model does not compulsorily mean that the nervous system does solve an OCP permanently or from scratch. It only means that the motor solutions the nervous system has developed, whatever the time scale, are advantageous in a sense that has been delineated. According to the objective/subjective cost dichotomy, one may suggest that, in order to eliminate the effects of objective costs in the identification process, experimenters should give maximal freedom to the participant and put as little task constraints as possible. In other words, considering highly redundant tasks with very few instructions given by the experimenter may help understanding the fundamental principles humans prefer to rely on during motor planning.

---

this basis, researchers have proposed to split EMG activity into tonic and phasic components (e.g. Flanders et al., 1996). To clarify my purpose, let me consider a single-joint upward movement here. If the static torques were to be compensated at all times, a phasic activity of the agonist muscle should come on top of its tonic activity during the entire motion duration. On the contrary, if the agonist EMG signal is found to be below its corresponding tonic level, it may suggest that gravity is not just counteracted but utilized as a driving force. This lack of tonic activity, already observed - but not fully considered - in several studies, actually echoes the inactivation principle mentioned in the main text. If observing proper inactivation may be tricky due to multiple factors such as the noisiness of EMGs, the predicted briefness of the phenomenon and the requirement of being under well-suited conditions of speed and amplitude, this lack of compensation of gravity torques, clearly apparent in EMG data, is additional evidence for an energy-related use of gravity in reaching movements.

<sup>5</sup>This terminology is borrowed from Knill et al. (2011). In Schwartz (2016), the terms internal and regularization are used for subjective costs while the term task-based is used for objective costs.

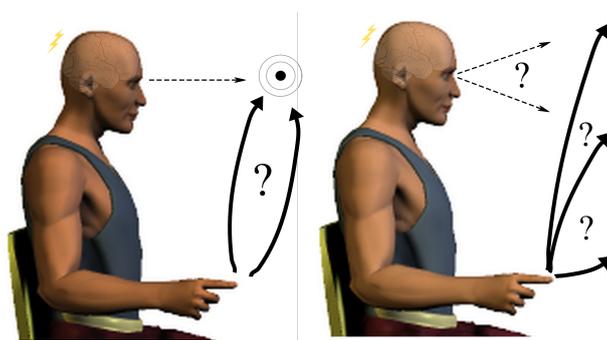


Figure 1.6: Illustration of the conceptual differences between pointing to a target point/dot (*left*) versus pointing to a target bar/line (*right*).

In goal-directed reaching tasks, one may envision two ways of making a task more redundant: either by adding intrinsic (body space) DOFs or extrinsic (task space) DOFs. To clarify my purpose, let me consider an arm pointing task where the only objective constraint is to touch a target with the fingertip. The target location commonly defines 3 constraints (in the 3-dimensional space) but to make the task more redundant one could consider adding other DOFs. For instance, by placing the target beyond arm's length, we could induce whole-body movements with more joints involved, which would likely be advantageous to emphasize subjective motoric decisions. However, it would also make the OCP considerably harder to solve computationally due to the complexity of the musculoskeletal plant being controlled. An alternative is to reduce the constraints imposed by the target itself (extrinsic DOFs). Instead of a dot, asking a subject to point to a line, or a surface, makes the task redundant even with a classical planar two-link arm model (e.g. Fig. 1.1). The appeal of this second approach is also to make explicit the *choice* problem faced by a subject in Cartesian space when planning a movement<sup>6</sup> (“where to go?” is often the first question one would resolve in motor control; in this type of task, the subject has to select an end point on his/her own). It also allows preventing the “curse of dimensionality” occurring in OC when adding more and more intrinsic DOFs to a system. How a subject moves when asked to point toward a line (not a point) may thus be instructive and has been studied in a couple of papers (Berret et al., 2011b; Nashed et al., 2012; Berret et al., 2014; Togo et al., 2017). This paradigm is illustrated in Figure 1.6.

An example of real experimental trajectories are reported in Figure 1.7 (left) for this task. The result obtained from a numerical inverse OC analysis shows the best-fitting simulated trajectories obtained from an OC model with composite costs (Berret et al., 2011a).

While considering such a class of tasks (called “manifold reaching paradigm” in Berret et al., 2011b) may appear strange or artificial at first, it is actually a rather ecological task. Imagine

<sup>6</sup>Notably, motor control has been conceived as a true (motoric) decision-making problem recently (Wolpert and Landy, 2012).

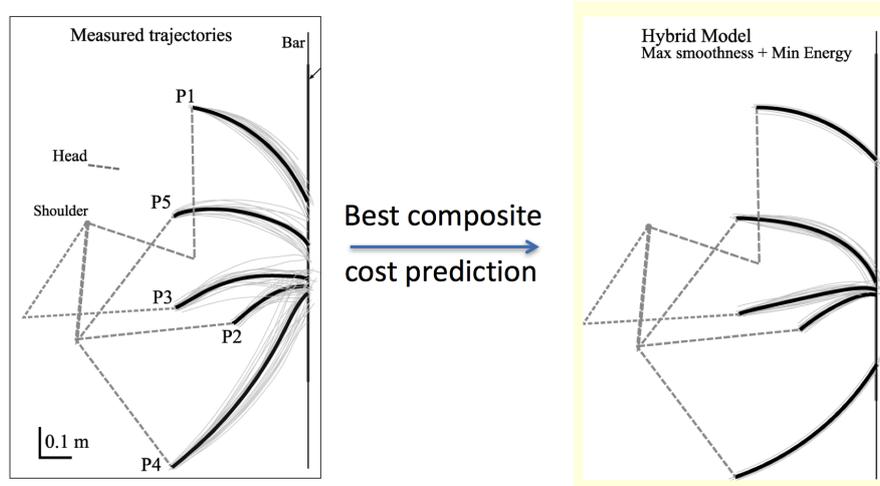


Figure 1.7: Experimental data for a representative subject performing pointing movements with 2 DOFs in a vertical plane toward a uniform, long target bar (*left*). Predicted trajectories optimizing a composite cost mixing the absolute work of torques and motion smoothness (integral of the squared angular jerk) (*right*). These predictions represent the best fitting solution found among a set of 8 classical cost functions proposed in the literature. From Berret et al. (2011a).

that, while reading those lines, you want to put your cup of coffee on your (clean and empty) desk; then, where to put the cup is a free choice and an infinity of end locations are compatible with the task achievement. We could say that the desk represents a horizontal plane of potential “targets”. However, your brain would eventually choose one particular location for the cup, for some reason. One may devise other examples such as opening a door by pushing it or grasping a stick. Analyzing how and why participants select certain reach endpoints in such tasks revealed itself interesting for addressing a variety of questions. In particular, this type of paradigm has been used to investigate eye-hand coordination (Berret et al., 2014), posture-movement coordination (Hilt et al., 2016), the nature of motor planning variables and the use of interaction torques during 3D movements (Vu et al., 2016b,a). Regarding the control of interaction torques in 3D movements, we used a similar paradigm (pointing to a horizontal surface from a flexed arm posture above it) to explore whether humans could exploit interaction torques, just as we had previously shown that they could exploit gravity torque during vertical movements. Here, exploitation of interaction torques changed the final hand location and thus induced substantial hand trajectory modifications, which were easily quantifiable from motion capture data. Regarding the nature of the variables taken into account during the planning of 3D movements, we could readdress old questions regarding the kinematic versus dynamic nature of motor planning variables (e.g. Wolpert et al., 1995), a question which can be rephrased within the normative framework of OC. Experimental evidence

had previously suggested a possible integration of upper limb's inertia during the planning of arm reaching movements (Bernardin et al., 2005; Gordon et al., 1994) and during the control of cyclical 3D arm rotations where participants exhibited spontaneous changes of rotation axis. Participants naturally switched from a geometrical rotation axis (shoulder-elbow axis; a kinematic strategy) to an inertia-based one (minimum principal inertia axis; a dynamic strategy) when speed increased (Isableu et al., 2009). Since OC can take into account limb's biomechanics and attempts to find controls that minimize the amount of muscle torques (or other related variables such as torque changes or mechanical energy), we were able to identify subject-specific composite costs predicting the adaptive behavior of each participant when executing the pointing task at different speeds using a numerical inverse OC approach. Overall, these studies contributed to give a rationale about why and how humans are influenced by the passive properties of the dynamical system under control. Eventually, the brain might just try to exploit all passive sources of motion when relevant and compatible with the task (at least gravitational or interaction torques in ecological settings). Regarding the study of posture-movement coordination, using a redundant target was also interesting because it allowed participants to choose among several goal-equivalent strategies, which however emphasized either postural or focal motor preferences. In fact, a large inter-individual variability was observed in a task which consisted of whole-body pointing movements toward a slightly inclined surface placed in front of the subjects, beyond arm's length. Some subjects favored stable dynamic equilibrium at the price of spending more energy and jerk to realize the reaching task, while other subjects favored reach efficiency even though it led to more unstable postures, with a center of mass projection typically moving closer to the limits of the base of support. Optimal control could again give an account of the experimental data by matching individual behaviors to certain weightings of cost functions. Regarding eye-hand coordination in the planning of goal-directed movements, the question was to better understand which of the eye or the hand would drive the reach endpoint selection process in such motoric decisions (i.e. the "where to go?" issue must clearly be addressed when pointing to such a redundant target). The usual view is from eye to hand when planning goal-directed movements towards a target (e.g. a luminous spot defining a unique 3D spatial position to reach to) (Desmurget et al., 1998). When pointing to a long uniform line instead of a dot, we devised two possible mechanisms: (1) the eye could first choose a final location for the hand and inform the hand motor system (just as in the usual view even though the eye should resolve a new problem before issuing a hand motor command) or (2) the hand could select its preferred location and inform the eye motor system subsequently. The conclusions were that the eye motor system procrastinated the eye movement onset, likely to gain more information about where the hand wished to go. When eye procrastination was long enough, only one accurate saccade landing on the correct upcoming hand position was triggered, before hand movement onset. When eye procrastination was shorter, multiple saccades were often triggered before hand

movement onset with a first (primary) saccade that was consistently inaccurate in the sense that its amplitude did not coincide with the future hand location on the target line. Figure 1.8 summarizes these observations.

Hitherto, all the above-mentioned modeling studies have considered that movement time was known<sup>7</sup> and the OC models were always formulated in fixed time  $T$  with a cost function of the form  $C(\mathbf{u}) = \int_0^T l(\mathbf{x}, \mathbf{u})dt$  where  $l(\mathbf{x}, \mathbf{u})$  could be the squared jerk, torque change, absolute power of muscle torques etc., or any linear combination of such ingredients (i.e. composite costs, see above). However, motor redundancy is not only spatial but also temporal in most motor tasks. In particular, the total amount of time required to reach a desired goal is practically another DOF. Why are some subjects faster than others or what determines someone's movement vigor<sup>8</sup> are questions that were more recently addressed (Shadmehr, 2010; Baraduc et al., 2013; Qian et al., 2013; Shadmehr et al., 2016; Berret and Jean, 2016; Huh and Sejnowski, 2016). Different models and formulations have been proposed to account for duration of hand movements, such as the isochrony principle (Viviani and Flash, 1995), the speed/accuracy trade-off in relation to constant and multiplicative noise (Harris and Wolpert, 1998; Tanaka et al., 2006; Qian et al., 2013; Wang et al., 2016), the constant effort principle (Guigon et al., 2007), the constant motor range principle (Baraduc et al., 2013) or the conservation of drive (i.e. constant Hamiltonian) (Huh and Sejnowski, 2016). Some authors have put an explicit cost on time in OC models to explain the emergence of a preferred duration in biological movement. The most simple OC model assumed a linear cost of time (Hoff, 1994). Basically, adding a cost of time (CoT) to the cost function of an OCP may ensure the emergence of a finite movement time for the intuitive reason illustrated in Figure 1.9. If the optimal total cost exhibits a "U" shape as a function of movement time, it will clearly yield an optimal duration. The question would be whether it is the correct duration.

If we consider that an explicit cost related to the passage of time exists, the question turns out to be *again* an inverse optimal control issue, but in a free-time setting now. More precisely, assuming a linear separability between the time and state/control cost functions, i.e.  $C(\mathbf{u}) = \int_0^T h(\mathbf{x}, \mathbf{u}, t)dt = \int_0^T g(t) + l(\mathbf{x}, \mathbf{u})dt$ , the question would be to recover  $g(t)$ . If  $g$  is a constant function, the CoT would be linear (or affine) as mentioned above. Actually, we do not need to guess the CoT in such settings. It was shown that it is indeed possible to accurately sample  $g(t)$  for different times  $t$  from experimental movement vigor data (Berret and Jean, 2016) (see also Chapter 2 of this manuscript for more details). In particular, this approach requires having knowledge of both the subjective and

<sup>7</sup>When I say that movement time is known, modeling-wise, I mean that time is set by the user (often simply taken from experimental data). Therefore, time is an input to the model, preset by the modeler. Note, however, that total movement time can also be a free variable that emerges from optimality properties just as the limb's spatiotemporal trajectory does.

<sup>8</sup>Vigor loosely refers to the time, speed, extent or frequency of movement (Dudman and Krakauer, 2016). It is often characterized by relationships between amplitude and velocity or duration.

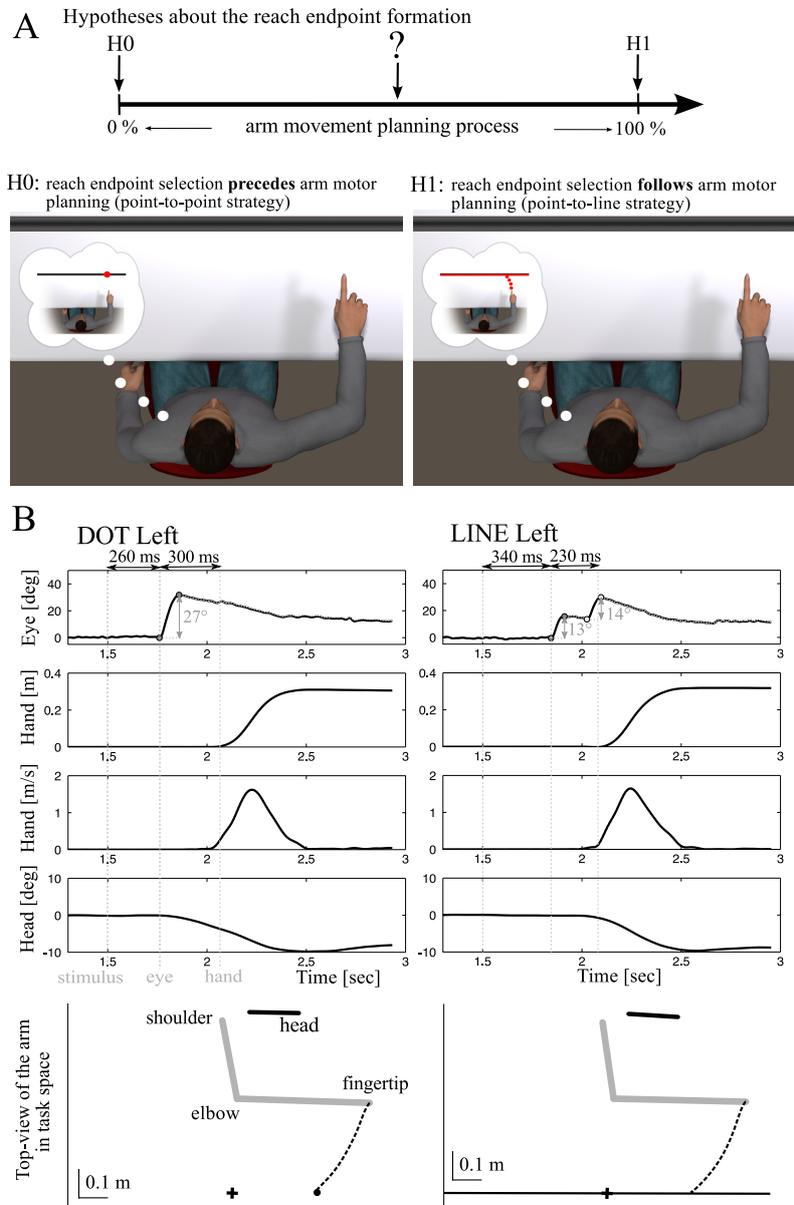


Figure 1.8: Reach endpoint formation question when reaching to a line. A. Different hypotheses that can be made regarding which of the eye or the hand leads the motor planning process and in particular the selection of the upcoming final hand position. B. Eye-hand coordination data (using an EOG system to measure the kinematics of horizontal saccades). The main differences between pointing to a DOT versus pointing to a LINE are as follows: (1) on average, the first saccade is delayed in LINE compared to DOT; (2) when the onset of the first saccade is little delayed, it hardly predicts the upcoming hand position in LINE and multiple saccades are more often observed *before* hand movement onset or transcortical feedback processing (estimated about 100 ms, Scott, 2012). This establishes a link between eye procrastination and the accuracy/latency of the primary saccade, suggesting that the eye motor system may be waiting for additional information about the upcoming final hand position. Taken from Berret et al. (2014).

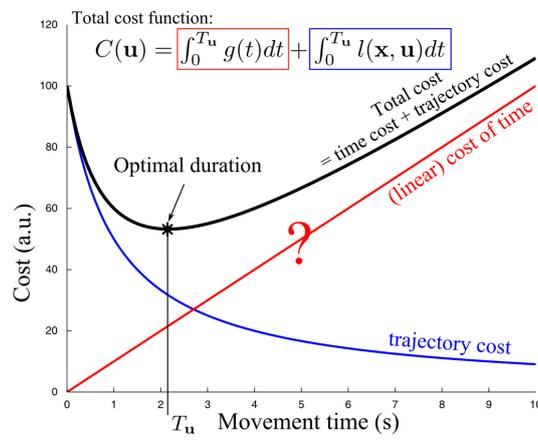


Figure 1.9: Consider a reaching task from a given state to another. Classical OC models assumed that there is a trajectory cost (e.g. effort, accuracy, energy, jerk, torque change, denoted by  $l(\mathbf{x}, \mathbf{u})$ ) whose minimization shapes the arm trajectories and accounts for how people will select a given system trajectory  $\mathbf{x}$  joining initial and final states in a given time  $T_u$ . Yet the trajectory cost is usually decreasing with time (blue curve) such that very slow movements are less costly than very fast ones. Taken alone, it cannot predict a finite movement duration in free time unless some cost of time is assumed. Here a linear cost of time is illustrated and its infinitesimal expression is denoted by  $g(t)$ . The sum of both time (red) and trajectory (blue) costs yields an optimal duration. The problem is that we cannot know in advance how the brain values the passage of time (hyperbolically, quadratically, exponentially, linearly...?)

objective terms of the trajectory cost  $l(\mathbf{x}, \mathbf{u})$  before one is able to recover  $g(t)$ . The nice property of this formulation is that it extends naturally all known results that have been obtained in fixed time previously (due to the linear separability, the optimal trajectories in free and fixed times coincide). It particularly rationalizes all the previous works done in fixed time that aimed at identifying  $l(\mathbf{x}, \mathbf{u})$  (see above). Given these assumptions and different simple models of the musculoskeletal plant, it was found that the CoT exhibited a sigmoidal growth during simple arm reaching movements. This shape would have been hardly predictable without an (inverse) OC approach. Indeed previous researchers assumed linear, quadratic, exponential or even hyperbolic time costs (Shadmehr et al., 2010; Haith et al., 2012; Huh and Sejnowski, 2016; Hoff, 1994) but never sigmoidal ones in their investigations. This model of self-paced movement formation raised additional questions such as: how would the CNS proceed to depart from its spontaneous pace choice when speed instructions are given to a subject (such as “move fast”)? A complex interplay between trajectory and time costs, but also between objective and subjective costs, may be hypothesized. Indeed, it was shown that speed instructions were most plausibly captured by adding objective trajectory criteria to  $l(\mathbf{x}, \mathbf{u})$  (Jean and Berret, 2017) rather than modifying  $g(t)$  itself, and that subjective trajectory costs appeared to be quite insensitive to speed instructions (Vu et al., 2016b). Therefore, time, energy/effort, smoothness but also accuracy may be relevant in general to biological motion planning and control (Missenard and Fernandez, 2011). The relative weights associated to each cost element may then depend on the task characteristics. The composite and multivariate aspect of the cost function and the addition of task-dependent costs make the identification problem quite hard, even though these results may indeed capture some fundamental high-level goals/properties of the motor system.

### 1.2.3 Remarks regarding optimal control theory

In general, posing an inverse OCP problem remains difficult as it requires several choices to be made. Indeed, both devising the class of cost functions and the dynamical system to use are modeling choices. First, the choice of which functional space of cost functions to consider is mostly left to the experimenter. Once such an infinite dimensional space is chosen, however, a sort of discretization is required to make the problem numerically tractable and to only have a finite number of parameters to be inferred in practice<sup>9</sup>. One may distinguish basis costs that are chosen for mathematical reasons (e.g. polynomials) from those that are chosen for their physical/biological meaning (e.g. energy, effort...). While the former costs can be good for fitting or reproducing

---

<sup>9</sup>For example, a researcher might decide to work in the space of cost functions that depend on position and speed variables, or might wish to include acceleration variables (e.g. Chittaro et al., 2013). Other assumptions could be made such as working with polynomials (e.g. Terekhov et al. 2010; Pauwels et al. 2014). However, a numerical implementation would necessitate restricting to some degree  $n$  or working with a finite number of basis costs belonging to the function space under consideration.

anthropomorphic motion, they do not allow to explain it and, thus, do not answer Marr's top level question which constitutes the main appeal of the use of OC for motor neuroscience in my view. Second, the choice of the (sensorimotor) level of investigation is a related concern. It contributes to specify the dynamical system under consideration, thereby constraining the variables that can be included in the cost function. Overall, the CNS has a hierarchical organization from task space to muscle space. Thus, the CNS may first care about what happens in task space and work with a simplified model of the musculoskeletal dynamics. Accordingly, cost functions could be defined at a kinematic level, at a dynamic level or could even attempt to minimize the overall motoneuronal activity. What level of description/investigation is best suited remains uncertain. Nevertheless, it seems that, in many cases, we can get reasonably good predictions of human movement trajectories by simple models that capture the essence of the system being controlled. For example, rigid body dynamics with some very basic muscle dynamics implementation are sufficient to capture several important motor phenomena as discussed above. Yet, more involved models of the musculoskeletal apparatus have been considered too (e.g. Li and Todorov, 2007). While this is a valuable and complementary approach, this raised questions regarding the confidence one can put in the "optimality" of the solutions found by numerical methods and in the dependence of the solutions on the relative uncertainty about the model parameters such as muscle time constants, pennation angles, length/velocity force dependencies, the physiological cross-sectional area and so on, and which are difficult to know precisely for a given individual. Solving an OCP is generally a tricky task (doing the optimal synthesis<sup>10</sup> even for simple problems may illustrate this; Pontryagin et al., 1964). Quite often, we may only find sub-optimal solutions and get stuck in local minima when using numerical tools. Therefore, working with very high-dimensional and non-linear systems may be challenging also for this reason. The need for stochastic extensions of OC models may further complexify the picture although some clever formulations lead to efficiently solvable problems (e.g. Todorov, 2009b; Kappen, 2011).

I must mention that, like with any theory, the question of falsifiability must be posed. Because inverse OC is a form of data fitting (at least its numerical implementation), one shall always find some functions that fit a given set of data. Thus, special care must be taken regarding overfitting: Occam's razor principle should be applied for numerical inverse OC especially when composite costs (i.e. combinations of multiple cost functions) are considered. If the CNS truly relies on certain composite costs and if one imposes the constraint that a limited number of costs should explain a variety of tasks, falsifiability could then be addressed. This would suppose that the same (subjective) cost functions should be relevant to a variety of tasks in the sense of generalization and cross-validation. If, in contrast, a given mixture of costs allows to account for motor performance in a given task but not in other tasks, then it would mean that the model must be modified or even

---

<sup>10</sup>Formally, this is the set of all the optimal trajectories joining any initial state to any terminal one.

reconsidered more globally. To address this level of questioning, it is likely that researchers should consider ecological (common/overlearned) motor tasks; otherwise the question of whether and how the CNS may solve novel OCPs would be the actual topic of investigation.

Some authors have argued that motor control is “good enough” instead of really optimal (Loeb, 2012). Actually, saying that a system is not behaving optimally can be considered a stronger claim than saying it is behaving optimally because it is always possible to find a cost replicating a given experimental trajectory (a trivial - admittedly meaningless - counterexample would be a cost tracking the specific trajectory to be reproduced). Yet, being good enough may be sufficient for the sensorimotor system for most motor tasks, especially if one thinks of the existence of muscle synergies or primitives that restrain the repertoire of available motor commands. In any case, saying that a behavior is good or favorable implies that it offers some advantages against others, which can be theoretically translated in terms of cost functions. Even though some behavioral strategy is a local, not global, optimum (Ganesh et al., 2010; de Rugy et al., 2012), it is nevertheless an *extremum* of a certain cost function (e.g. satisfying the necessary conditions given by Pontryagin Maximum Principle; Pontryagin et al., 1964), whose nature would be useful to characterize. In the end, saying that something is good enough or even optimal (reciprocally not good enough or not optimal) makes no sense without adding “with respect to” some well-defined cost function<sup>11</sup>.

Other theories such as the passive motion paradigm (Mohan and Morasso, 2011) have also been opposed to optimal control. The core idea in this paradigm is to replace cost functions with endpoint force fields and assume that the mechanical system is moved by a virtual force acting at the level of the end-effector (e.g. like strings moving a puppet’s limbs). This is seen as a means to maximally exploit the spontaneous dynamics of the musculoskeletal system. However the nature of the underlying force field has to be given (by choosing some free parameters) and, once one is chosen, it could still be interpreted as arising from a certain optimality criterion (e.g. optimal feedback control arising from LQR/LQG settings typically leads to static or time-varying force fields, in Cartesian or joint space depending on the control system under investigation). The same point could be made regarding dynamical system theory (Turvey, 1990; Kelso, 1997) as, once a control law is defined, the musculoskeletal system may appear to be self-organized and governed by some ordinary differential equations. Inverse OC theory mainly seeks to justify why certain force fields or dynamical attractors would be utilized rather than others. In practice, relying on learned dynamical patterns, or basis force fields, can be viewed as an efficient algorithmic way to solve the degrees of freedom problem (Bernstein, 1967) and to generate effectively coordinated limb movements (Mussa-Ivaldi, 1997). However, this level of investigation rather addresses Marr’s second level of analysis (algorithm).

---

<sup>11</sup>A biomechanical analogy would be to talk about the “moment of a force” without precisising the fixed reference point with respect to which it is calculated.

From a robotic perspective and towards an anthropomorphic motion factory, inverse OC is also appealing as it may allow roboticists to produce an infinity of human-like movements just from the knowledge of a relevant cost function. Indeed, cost functions (together with a model of the plant) allow to plan movements that have not been tested or encountered previously. Yet, the difficulty to resolve quite involved OCPs in real time for robots with numerous DOFs limits the appeal of its generalization power. Besides classical linear-quadratic formulations, we lack ways to quickly solve such problems. Model predictive control might partly resolve this issue. Although this is an increasingly popular approach, it remains however unknown whether its control architecture is biologically plausible (Mehrabi et al., 2016). Modularity may contribute to efficiently solving OCPs in a bio-inspired way but further research efforts are needed to figure out whether and how the CNS may actually implement the control of limb movement in such a way.

## 1.3 Modular control hypothesis

### 1.3.1 Hierarchical modular control

Another significant body of the motor control literature has focused on the idea of compositional or modular motor control, such as the muscle synergy hypothesis on which I focus in this manuscript. This body of literature suggests that the CNS stores certain muscle synergies and is able to combine them adequately to generate a motor command that would allow accomplishing a given motor task. A useful metaphor to illustrate the concept of modularity for spatiotemporal motor signals is to depict movement generation as music playing. Music is created by combining “modules” such as a melody (notes) and a rhythm (tempo). Similarly, coordinated movement may be the outcome of the combination of such stereotyped motor building blocks. The idea of hierarchical modular control is illustrated in Figure 1.10.

The computational appeal of this theory is that, if pre-coded invariant modules can be used as motor building blocks, the CNS would only have to coordinate them to execute consistent movements, thereby simplifying the control problem by, *de facto*, implementing a dimensionality reduction. Therefore, at this level of analysis (the second Marr’s level of analysis), one attempts to elucidate how the CNS builds motor commands that generate limb’s trajectories that display all the good (enough) properties indicated by inverse OC studies (which is not necessarily via muscle synergies but could relate to active inference or other means as mentioned above).

A first step for deciphering how motor building blocks may be stored within the CNS consists in defining a plausible modularity model. The model parameters can then be inferred from experimental data and correlated with their putative neural underpinnings. This is again a modeling

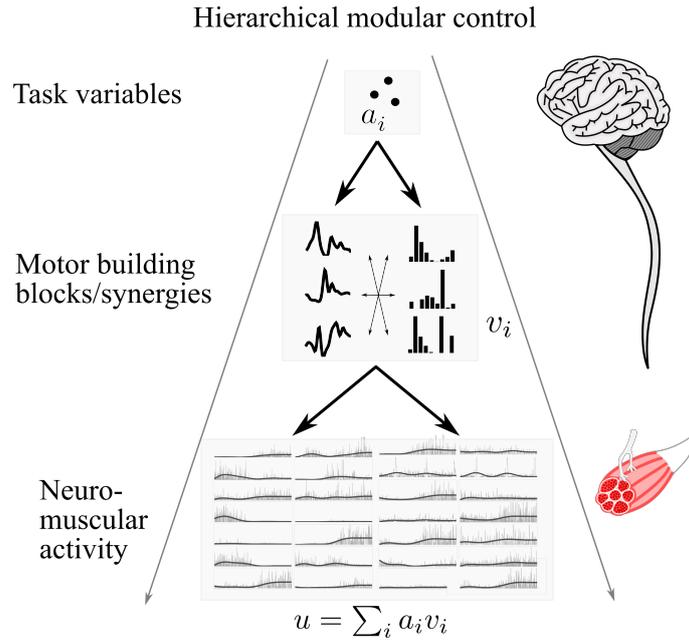


Figure 1.10: Illustration of the hierarchical modular control architecture at the muscle activation level. The scheme goes from task parameters (in a lower-dimensional space yielding some activations  $a_i$ ), via combinations of pre-coded and stored motor modules (here loosely denoted by  $v_i$ ), to neuromuscular inputs (in a higher-dimensional space, e.g.  $u = \sum_i a_i v_i$  for a linear model). Dependencies on time/state and distinction between vector/scalar quantities are not specified on purpose. The precise nature of the modules and their combinations depend on the underlying model: they can be temporal waveforms, vectors of muscle activation ratios, spatiotemporal activity profiles, feedforward and/or feedback elementary control actions, and can be combined in a linear or nonlinear fashion etc. In all cases, their task-dependent modulation is assumed to account for the formation of genuine muscle patterns.

choice. To implement this first step, several models of motor modularity have been proposed in the literature, mainly differing in their assumptions about a) what quantities are stored by the motor system as invariant “modules” which can be reused in different movements and b) what quantities are determined by the descending neural drives that recruit the modules in single movements (Tresch et al., 1999; Ivanenko et al., 2004; d’Avella and Tresch, 2001). Modules have been hypothesized to represent spatial, temporal or spatiotemporal invariant patterns in motor signals (Alessandro et al., 2013b; Chiovetto et al., 2013). Notably, we developed a unifying space-by-time extraction method to reconcile existing methods within a single framework (Delis et al., 2014). Figure 1.11 summarizes the approach. The new model seeks to extract separately yet concurrently invariant spatial and temporal modules from recorded muscle patterns. The decomposition can be viewed as a generalization and unification of existing models as it expresses any muscle pattern  $\mathbf{m}^s(t) \in \mathbb{R}_+^{T \times M}$  as the following double sum ( $T$  and  $M$  being the number of time frames and muscles, respectively):

$$\mathbf{m}^s(t) = \sum_{i=1}^P \sum_{j=1}^N w_i(t) a_{i,j}^s \mathbf{w}_j + \text{residual}, \quad (1.1)$$

where  $w_i(t) \in \mathbb{R}_+^{T \times 1}$  and  $\mathbf{w}_j \in \mathbb{R}_+^{1 \times M}$  are the temporal and spatial modules respectively, and  $a_{i,j}^s \in \mathbb{R}_+$  is a scalar activation coefficient. The parameters  $P$  and  $N$  correspond to the number of temporal and spatial modules respectively. To extract these spatial and temporal muscle synergies in practice, we developed a specific algorithm called sample-based non-negative matrix tri-factorization (sNM3F) that aims at minimizing the Frobenius norm of the residual in Eq. 1.1. We also considered some variants of this model. The most important variant attempted to capture variability in time, which may be inherent to the CNS’s modular control strategy, or which may simply result from the time-normalization procedure of the EMG data or by any intrinsic fluctuation in the timing of muscular activations (e.g. sensorimotor noise). Specifically, we extended the model to take into account time-shifted versions of temporal modules in the spirit of time-varying synergies (d’Avella et al., 2003), as follows (Eq. 1.2):

$$\mathbf{m}^s(t) = \sum_{i=1}^P \sum_{j=1}^N w_i(t - \sigma_{i,j}^s) a_{i,j}^s \mathbf{w}_j + \text{residual}, \quad (1.2)$$

where  $\sigma_{i,j}^s$  is the time-shift corresponding to sample  $s$ , temporal module  $i$  and spatial module  $j$ . All the formulations of muscle-level modularity make hypotheses about the formation of muscle patterns within the CNS and usually suffer from several simplifications (e.g. linearity, time normalization etc.). Hence, while such models perform a good job at describing ensemble muscle activities, they may not be able to reflect the actual neural mechanisms underlying the formation of muscle patterns. This latter point has been the question of many muscle synergy

studies, irrespective of the proposed modularity model, and it revealed itself relatively tricky to answer (see below).

It is worth mentioning that modularity has also been assumed to exist at different levels of the motor hierarchy (e.g. kinematic, Santello et al., 1998; Berret et al., 2009; dynamic, Thomas et al., 2005; Chhabra and Jacobs, 2006; Russo et al., 2014; neural, Overduin et al., 2015; Churchland et al., 2012). An example of a study investigating modularity at the kinematic level using PCA has been conducted to better understand how posture and movement are combined during reaching while standing (Fig. 1.12 and Berret et al., 2009).

However, even though it is valuable to investigate modularity at kinematic and dynamic levels, most of the studies looked at modularity at the muscle activation level because this is the closest non-invasive measure to the motor command (Tresch and Jarc, 2009; Ting and McKay, 2007; Ting et al., 2015; d'Avella and Bizzi, 2005). In this vein, modularity at the muscle level during whole-body movements in various directions has been investigated (Chiovetto et al., 2010; Hilt et al., 2017). Regarding the mathematical formulation, models of motor modularity are typically linear because it was found that the force fields resulting from the activation of two spinal motor modules are linear combinations of the individual force fields according to the seminal frog studies conducted in Bizzi's lab (Mussa-Ivaldi et al., 1994). Thus, the algorithms used to identify putative modules are almost always based on linear dimensionality reduction methods such as PCA or NMF and the extracted modules are assumed to be combined by feedforward motor mechanisms. Recently, techniques for the identification of modules of feedback nature have also been proposed for isometric tasks (Razavian et al., 2015). In sum, it is worth noting that modeling choices include both the nature of the modules (spatial, temporal, feedforward, feedback etc.) and the combination rules (linear or not) and make hypotheses about the type of modularity that should be sought for within the CNS.

At the second step of this approach, motor signals recorded during a large number of motor tasks have been successfully fitted by modularity models suggesting that performance of such motor behaviors relies on a few invariant (and thus storable) motor modules (e.g. reaching, d'Avella et al. 2006; Tresch et al. 2006; Chiovetto et al. 2013; Delis et al. 2014; Muceli et al. 2010; grasping, Overduin et al. 2008; Brochier et al. 2004; Weiss and Flanders 2004; walking, Ivanenko et al. 2003, 2004, 2005; Dominici et al. 2011; Lacquaniti et al. 2012; Cappellini et al. 2006; pedaling, Hug et al. 2011, 2010; reflex movements, Tresch et al. 1999; Cheung et al. 2005; Perreault et al. 2008; d'Avella et al. 2003; postural control, Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007, 2010; Chvatal et al. 2011; Ting and Macpherson 2005 etc.). Furthermore, modular structure in muscle activity has been shown to be preserved or adjusted after different types of brain injuries (Cheung et al., 2012, 2009; Gizzi et al., 2011; Roh et al., 2013, 2015; Clark et al., 2010).

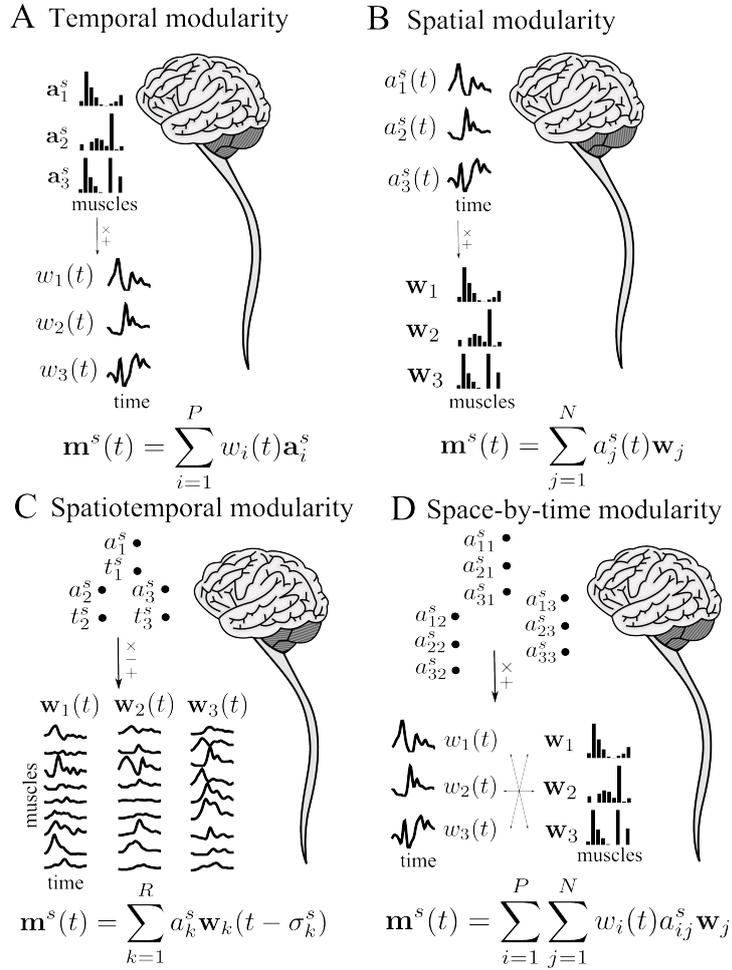


Figure 1.11: Illustration of the space-by-time modularity model and its relation to other typical extraction methods. Taken from Delis et al. (2014). Here  $\mathbf{m}^s(t)$  represents the spatiotemporal activity of a set of recorded EMGs during a single trial (i.e. movement). The indice  $s$  stands for “sample”. Previous methods focused on temporal, spatial or spatiotemporal invariance (A-C). The unifying method (D) emphasized that concurrent spatial and temporal invariance may exist in muscle patterns. A dedicated algorithm aiming at extraction such concurrent spatial and temporal modules was developed on purpose (called sNM3F for sample-based non-negative matrix tri-factorization).

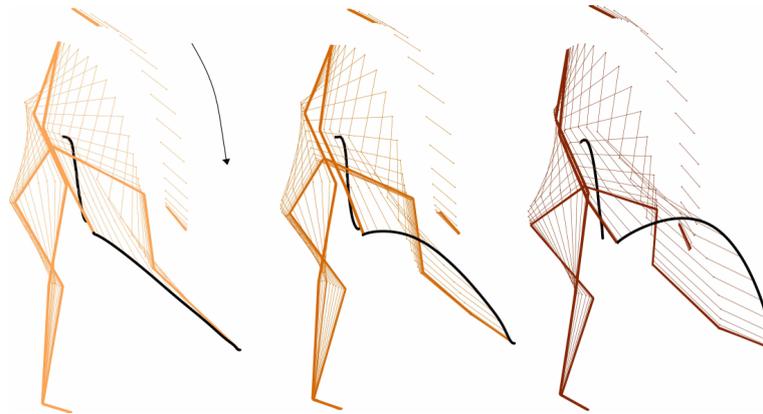


Figure 1.12: Illustration of whole-body coordination during the study of modularity in motor control at the kinematic level. From Berret et al. (2009).

At last, in order to probe the neural basis of modularity, the model parameters learned from the motor signals can be used as proxies of modular mechanisms, so their correlations with neural signals can be investigated. Several studies have identified potential neural bases of modules or their activations, both at the cortical level (Holdefer and Miller, 2002; Kargo and Nitz, 2003; Overduin et al., 2012; Desmurget et al., 2014; Overduin et al., 2015) and in spinal structures (Hart and Giszter, 2004, 2010; Giszter and Hart, 2013; Saltiel et al., 2001). Crucially, such analyses can serve to disentangle a) the nature and structure of modules, thereby informing the design of suitable modularity models and b) the level of the neural hierarchy where modules may be encoded, thereby addressing Marr's third level of analysis (the neural implementation). In this vein, Kargo and Giszter (Kargo and Giszter, 2008) showed that, at the spinal level of motor organization, premotor pulses (i.e. temporal modules) are more likely to be encoded than time-varying synergies (i.e. spatiotemporal modules). Also, Roh and collaborators (Roh et al., 2011) showed that medulla and spinal cord are sufficient for the expression of most (but not all) muscle synergies (i.e. spatial modules), which are likely activated by descending commands from supraspinal areas.

### 1.3.2 A task-space perspective to modularity

Most studies have tested modularity models based on the extent to which they allow to reconstruct the recorded muscle activation patterns for a number of task conditions using a limited number of invariant modules (input space assessment). Recently, a regain of interest to relate modularity to task space performance has been observed. A recent review of literature emphasizes this shift of paradigm (Alessandro et al., 2013b). The rationale is that, to be a plausible control scheme which could be of interest also in robotics, it must be proven that compositional motor control gives

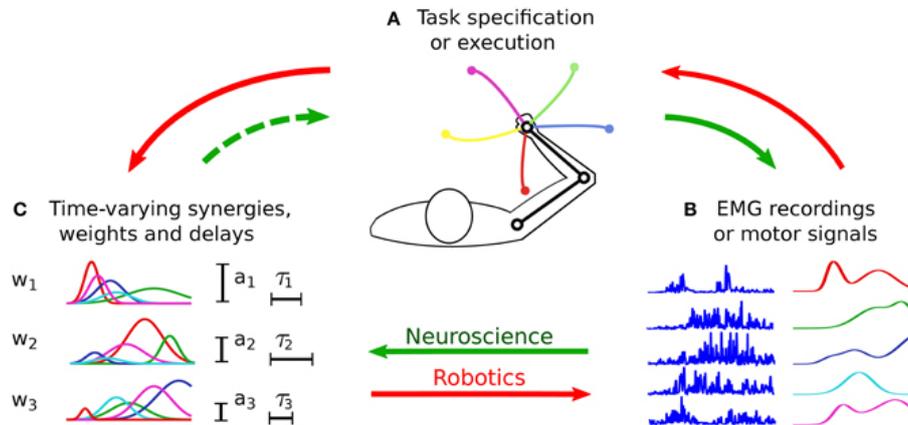


Figure 1.13: Illustration of the classical workflows in muscle synergy studies: differences between the robotic and the neuroscience approaches. In neuroscience, researchers typically start with the measurement of motion data during the execution of a variety of motor tasks (e.g. pointing in various directions). Motor synergies are then extracted using some dimensionality reduction methods. Finally, researchers try to see the extent to which the inferred synergies relate to the task specificities, both in terms of the nature/shape of the synergies themselves and in the way those synergies are activated/recruited on a single-movement basis. In robotics, basically a reverse approach is employed as researchers are more interested in the synthesis of motor commands (i.e. to create effective and efficient controls quickly and flexibly) rather than in reverse-engineering the functioning of the CNS.

acceptable results in task space (Fig. 1.13).

As already mentioned, muscle synergies are commonly extracted from recorded EMG data using unsupervised algorithms implementing dimensionality reductions. Typically, the quality of this process is evaluated through the variance accounted for (VAF) or  $R^2$  ( $R$  being the correlation coefficient) values. However, this assessment has some limitations. First, VAF or  $R^2$  values are somewhat arbitrary and defining an absolute threshold that indicates what is good fitting performance is a sensitive subject. Several absolute thresholds have been proposed (e.g. 90%) and other heuristics have been employed (e.g. looking at an “elbow” in a VAF curve). Second, the musculoskeletal system being largely nonlinear, small errors in input space can lead to large errors in task space and undermine task achievement. Therefore, we should evaluate how putative motor synergies and their activations relate to task parameters. This idea has recently been put forward by many authors (Allen and Neptune, 2012; de Rugy et al., 2013; Delis et al., 2013b,a; Sponberg et al., 2015). Mostly three approaches were taken: (1) using isometric tasks for which a virtual mapping from muscle space to task space can be defined by the experimenter, (2) quantifying the extent to which task identity is encoded in synergy-space so as to test whether the way synergies are

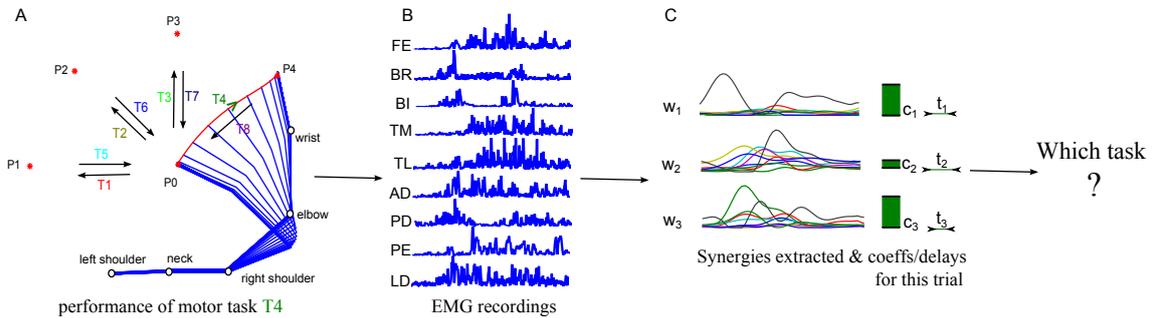


Figure 1.14: Illustration of the single-trial decoding approach proposed by Delis et al. (2013b). A. Experimental task specification, here planar arm reaching movements in various directions. B. EMG recordings of several muscles. C. Extracted synergies, according to a given model, here time-varying synergies (d’Avella et al., 2003). Eventually, single-trial decoding analysis are employed to estimate the extent to which it is possible to recover the task identity from the way synergies are combined on a single trial (movement) basis. Typically, the result is given as a percentage of successfully decoded trials.

activated unequivocally determines the task at hand, as postulated by the theory, and (3) grounding on realistic musculoskeletal models to test whether experimentally-driven synergies can effectively be used for control.

In a series of papers, de Ruyg and collaborators evaluated “the usefulness of muscle synergies [...] in terms of errors produced not only in muscle space, but also in task space” (de Ruyg et al., 2013). They showed that even for what could appear as a relatively high VAF, control with muscle synergies could lead to unacceptable errors in task space.

In a series of papers, we argued that single-trial task decoding/information techniques could be used to evaluate whether modularity can guarantee task performance in single trials (Delis et al., 2015). We showed that VAF and single-trial decoding are complementary parameters that should both be high for supporting the modularity hypothesis. An illustration of the decoding approach is given in Figure 1.14 and the complementarity between VAF and decoding scores is illustrated in Figure 1.15.

The rationale was the following: if the performed movement cannot be discriminated in the reduced-dimension synergy space, this would cast serious doubts about the effectiveness of the proposed hierarchical modular control scheme (indeed, it is possible to have a large VAF with a low decoding score, which would invalidate a modular decomposition although it is doing a good job at reducing dimensionality). We concluded that complex and comprehensive data sets should be considered in general to conduct such analyses, in the spirit of large-scale neuroscience endeavors (Gao and Ganguli, 2015). This is a relevant approach as it was shown that the number and efficiency of

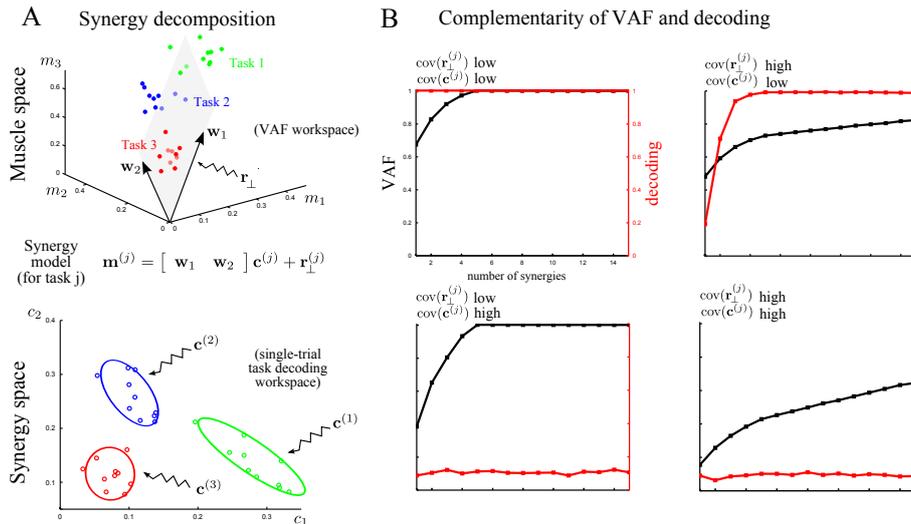


Figure 1.15: Illustration of the complementarity between the variance accounted for (VAF) and the decoding scores. Once viewed in synergy space, EMG patterns underlying the generation of single movements correspond to points in that (finite and low-dimensional) space. Theoretically, we should be able to decode which movement has been performed only from the location of that point in synergy space. Indeed, from a point in synergy space, we are able to reconstruct a genuine muscle patterns that should in turn drive the arm unequivocally toward the expected target. If it is impossible to distinguish the task identity in synergy space, this would mean that the synergistic structure cannot ensure task achievement on a single trial basis, and thus, cannot reasonably be used as an effective control scheme. The key point in these analyses is to focus on inter-trial variability and not average data, which is a common practice in synergy studies. High-decoding score is thus a prerequisite for a plausible synergy decomposition. However, using this methodology requires many task conditions and movement repetitions, and therefore, dedicated experimental protocols with rich enough data sets.

muscle synergies depends on the scope of the original database and on the complexity of the tasks under investigation (de Rugy et al., 2013; Steele et al., 2013).

Another way to test the modular control hypothesis is to build an accurate musculoskeletal model, as done in Neptune’s works (Neptune et al., 2009; Allen and Neptune, 2012). The authors of these studies focused on walking and showed that EMG-based synergies can be used as rough starting point solutions that need to be fine-tuned to elicit adequate walking patterns. Hence, this reaffirmed that the analysis of motor modularity should ideally consist of a closed loop between the recorded motor signals and their associated limb trajectories. This can be summarized as follows (Eq. 1.3):

$$\begin{array}{ccc}
 \text{real muscle patterns} & \xrightarrow[\text{engineering}]{\text{reverse}} & \text{extracted muscle synergies} \\
 \text{extracted muscle synergies} & \xrightarrow[\text{musculoskeletal dynamics}]{\text{forward}} & \text{reconstructed trajectories}
 \end{array} \quad (1.3)$$

The first step allows to extract the potentially stored modules via some machine learning technique, the choice of a particular model being not insignificant. In this vein, it is likely that switching from unsupervised to supervised learning algorithms taking into account the underlying biomechanics and trajectories in task space could lead to more advanced synergy extraction methods and models. However, the choice of unsupervised versus supervised learning algorithms is often neglected in practice because the simplicity of standard methods such as NMF is preferred. The second step consists in “playing back” the synergies into the musculoskeletal apparatus to test the produced motor behavior and evaluate the proposed control model in task space by analyzing the reconstructed limb trajectories.

### 1.3.3 Remarks regarding modular control theory

In reality, the questions of what the bricks of motor commands are, what model should be used to describe them and how motor commands are combined have not been resolved yet. It is likely that the models currently used are too simple to define a suitable framework from a control theory standpoint and to allow finding explicit neural correlates of the putative modules. In particular, most EMG-based identification models do not consider feedback processes whereas muscle synergies or coordination patterns may be posture-dependent as suggested in a couple of studies (Razavian et al., 2015; de Rugy et al., 2012). Therefore, the state of the biomechanical system should possibly be taken into account during the synergy identification process. Another restriction is that current synergy extraction algorithms require equal movement durations across trials to simultaneously extract synergies from different movement conditions whereas actual movement duration fluctuates across tasks and repetitions of the same task. At last, except in some studies where multiple layers of modularity have been considered, thereby leading to nonlinear reductions of dimensionality

(Berniker and Körding, 2015), most existing approaches are linear, which might be a good first-order approximation but might be limiting in practice to control a nonlinear plant.

A major criticism of the modularity hypothesis is that, for a given task or set of tasks, it will always be possible to reduce dimensionality to a certain extent or to account for muscle patterns if a sufficient set of modules is extracted. As a consequence, the extracted modules may be inherently task-dependent and may reflect the biomechanical constraints imposed by the human body (especially for neighboring muscles that control the same joint) (Kutch and Valero-Cuevas, 2012; Valero-Cuevas et al., 2009). Moreover, if optimality drives human trajectory formation and/or optimization guides muscle pattern creation, it is conceivable that small task variations (e.g. changing a target's position) will only produce small muscle activity variations. Overall, this would lead to certain commonalities in muscle patterns, which could always be isolated by machine learning or statistical techniques. Similarly to optimal control, generalization should be tested and special care should be taken with regard to the conclusions that can be reached via such EMG-driven analyses. In other words, while describing the organization of muscle patterns is valuable to provide synthetic views of how ensemble muscle patterns are structured, relating this structure to underlying active neural mechanisms is tricky and highly speculative. In practice, the existence of circumstantial evidence, as described above, combined with the possibility that any deviations from the theory can be attributed to either a coarse model of modularity or alternative neural pathways/mechanisms (e.g. allowing individual muscle control) make the modularity hypothesis hard to falsify (Tresch and Jarc, 2009).

Consequently, although the muscle synergy hypothesis is popular in human motor control, it remains rightly debated. At the core of the debate is whether EMG-based synergies are just a descriptive low-dimensional representation of expectedly well-structured motor outputs or whether they have a real neural basis. To better address this important point, some researchers hypothesized that such a representation in terms of synergies exists and examined what this would imply (d'Avella and Pai, 2010). Assume that a control action achieving a given motor task is hypothetically built from the combined activation of a given set of stored synergies. Therefore, performing a new task should just require adjusting the way synergies are combined until a suitable one is found. If no combination of synergies allows to execute the new task, it may be because it requires non-habitual muscle patterns or patterns that have not been experienced and stored before. Therefore, new synergies may need to be learned, which should take a longer amount of time than simply combining differently already stored synergies. By the way, this process would be compatible with the observation that muscle patterns are habitual rather than optimal (de Rugy et al., 2012). Remarkably, this logical reasoning predicts a testable hypothesis: learning a task that is incompatible with a currently available set of synergies should take a longer time. d'Avella and collaborators nicely investigated the predictions of such a theory along these lines (Berger et al., 2013). This approach of a) formulating predictions of

the modularity hypothesis and b) designing experiments to critically (and, if possible, quantitatively) test them might provide more direct evidence either supporting or falsifying the theory even though the neural code is not directly accessed (Ajemian and Hogan, 2010). Studying behavior and its adaptation to new tasks designed on purpose represents a very valuable, although indirect, approach to motor neuroscience (Krakauer et al., 2017).

## 1.4 From optimality to modularity and vice-versa

### 1.4.1 Optimality with modularity: theoretical ground

Optimality and modularity theories have often been treated separately yet some studies have attempted to combine the two concepts. Theoretical works are of particular interest among those studies. Interesting frameworks have been derived to understand if (and in what contexts) optimal controllers can be built from a limited set of elementary control actions (possibly optimal themselves). Most of the times, the mathematical analyses aiming at reconciling the two approaches were conducted from a control theory perspective. The link between optimality and modularity may be envisioned as follows (Eq. 1.1):

$$\begin{aligned}
 \text{Dynamics : } \quad \dot{\mathbf{x}} &= \mathbf{f}(\mathbf{x}, \mathbf{u}) \\
 \text{Optimality : } \quad C(\mathbf{u}) &= \int_0^T h(\mathbf{x}, \mathbf{u}, t) dt \\
 \text{Modularity : } \quad \mathbf{u}(\mathbf{x}, t) &= \sum_{i \in \mathcal{I}} a_i \mathbf{v}_i(\mathbf{x}, t)
 \end{aligned} \tag{1.1}$$

where  $\mathbf{u}$  is the control action that can drive the system state  $\mathbf{x}$  according to some dynamical constraints specified by  $\mathbf{f}(\mathbf{x}, \mathbf{u})$  and which is built from certain motor primitives or basis modules  $\mathbf{v}_i(\mathbf{x}, t)$ <sup>12</sup>,  $h$  is the infinitesimal cost whose integral should be minimized and the  $a_i$ 's are called the activation coefficients or combinator<sup>13</sup>. The main open question concerns the existence of motor building blocks allowing to effectively control the system for a given set of tasks. The basis modules may constitute a finite set of mixed feedforward and/or feedback control actions (Nori and Frezza, 2005; Alessandro and Nori, 2012; Alessandro et al., 2013a). Linearity is often central to modularity studies because of experimental findings showing linear summation properties of spinal force

---

<sup>12</sup>The basis modules  $\mathbf{v}_i(\mathbf{x}, t)$  might be separated into spatial and temporal components  $\sigma_i(t)\mathbf{w}_i(\mathbf{x})$  such as in Mussa-Ivaldi (1997) or Loeb et al. (2000), and in a way which is reminiscent of the modularity model proposed in Delis et al. (2014). In this case, spatial (state-dependent) modules, or muscle synergies, would be feedback-dependent as suggested in Razavian et al. (2015). Analogously, this time-space separation is also apparent in the optimal control of finite-horizon LQR/LQG problems (e.g.  $\mathbf{u}(t, \mathbf{x}) = K(t)\mathbf{x}$  where  $K$  is the time-varying feedback gain).

<sup>13</sup>The latter coefficients have to be set for each single movement to specify a complete motor signal  $\mathbf{u}$  (they could be computed “on-line”). The  $\mathbf{v}_i(\mathbf{x}, t)$  are assumed to be stored somewhere (or/and computed “off-line”) and invariant on a relatively short time scale.

fields (see Section 1.3). Interestingly, it can also be thought as a first-order approximation which simplifies the mathematical derivations. Notably, it allowed researchers to obtain elegant results for a restricted class of problems such as linear or feedback linearizable systems with quadratic costs or control-affine stochastic systems with control-quadratic costs that lead to a linear Bellman equation under suitable assumptions regarding noise properties (Nori and Frezza, 2005; Todorov, 2009b,a). These works showed that new optimal controls may be constructed from linear combinations of a finite number of elementary optimal control actions. However, the problem may be more complex when thinking of the human motor system as a whole because of the hierarchical nature of the neuromusculoskeletal system. Optimal control may indeed occur at different levels in the hierarchy (kinematic, dynamic, muscular or neural levels). It is, apropos, particularly remarkable how relatively simple OC models (e.g. minimum jerk model) capture the hand/joint kinematics although they neglect fine muscle properties (e.g. speed/length dependencies, concentric/eccentric contractions, slow/fast twitch muscle fibers etc.). Therefore, optimal control may conceivably apply in a low-dimensional space (task space or joint space) and lower level neuromuscular activity may subsequently conform to these higher level constraints already specifying the major spatiotemporal characteristics of the movement. In the spirit that approximate optimal motor commands are acceptable, a hierarchical control framework has been proposed (Todorov et al., 2005), thereby providing a theoretical link between task parameters and motor synergies. Other approaches based on deep learning schemes have also been considered by acknowledging that an OCP readily implements a (nonlinear) dimensionality reduction (Berniker and Körding, 2015), which could lead to very effective movement representations in neural networks. Although defining motor building blocks in the compositional sense of Equation 1.1 seems harder in those frameworks, they nevertheless nicely capture the idea of dimensionality reduction resulting from the concept of motor synergies and address important questions such as whether the monitoring of a restricted number of task-related variables can yield suitable coordination of the complex and nonlinear musculoskeletal plant.

#### **1.4.2 Optimality versus modularity: paradox and causality**

At first sight, the coupling between optimality and modularity may seem paradoxical as the constraints imposed by modularity might severely compromise or restrict optimality. If one assumes existence of synergies, two seemingly competing questions arise: (1) whether modularity constrains and shapes the type or degree of optimality that can be attained in higher-level variables (i.e. end-effectors or joints) and (2) whether optimality naturally leads to an apparent modularity at the lower level (i.e. neuromuscular). On the one hand, a number of studies have analyzed the extent to which motor synergies may arise from optimal control. Since optimal control and/or

optimization may give *de facto* a structure to the associated muscle patterns according to variations of the task demand, it can reasonably be expected that empirical motor synergies are just a by-product of optimality conditions. Accordingly, motor synergies have been shown to emerge from optimal feedback control theory (Todorov and Jordan, 2002). Furthermore, numerical studies have provided interesting insights regarding what kind of time-varying synergies would result from optimal control policies applied to planar reaching movements (Chhabra and Jacobs, 2006). On the other hand, the authors reversed the process to verify what kind of arm trajectories could be achieved via the extracted time-varying synergies (Chhabra and Jacobs, 2006). Interestingly, these numerical experiments demonstrated that task constraints (reaching to targets in a plane) together with optimality objectives could be fulfilled with a small number of hypothetical motor synergies. In the same vein, other authors have investigated a similar issue for different tasks and subsystems. Computational studies based on musculoskeletal modeling showed that a simplified construction of motor commands via modularity (either experimentally inferred using dimensionality reduction techniques or synthesized) could significantly affect optimality and lead to sub-optimal solutions in terms of effort costs during balance control (McKay and Ting, 2012) and to a limited ability to minimize energy but also to tune endpoint stiffness during an isometric upper-limb task (Inouye and Valero-Cuevas, 2016). It is worth mentioning that these studies relied on optimization rather than optimal control<sup>14</sup>. Other studies involving optimization techniques are also relevant here as they implemented the whole loop mentioned in Eq. 1.3 using EMG-driven virtual biomechanics (de Rugy et al., 2013; de Rugy et al., 2012). They could quantify how muscle synergies affected energy consumption and aiming errors in task-space. Numerical studies about modularity have also been conducted in robotics (Nori and Frezza, 2005; Alessandro and Nori, 2012; Taïx et al., 2013), in which errors in task-space were also evaluated. Overall, it may be concluded that the nature of the motor building blocks (feedback/feedforward) and the type of system and cost (linear-quadratic) is critical for effective and efficient motor control using modularity. As such, modularity may be favorable to reduce the computational burden of behaving rigorously in an optimal way at the price of sacrificing some optimality but remain good enough.

Besides the question of the neural origin of muscle synergies, which is crucial to motor neuroscience (as already discussed) and proved difficult to answer (Hirashima and Oya, 2016), thinking about the chicken-and-egg situation of modularity versus optimality is interesting. Assuming that both optimality and modularity are present in the sensorimotor system, which one drives the other remains unclear. It is likely that developmental studies could help disentangling how optimality and modularity emerge during growth and whether one constrained the other or vice-versa. For example,

---

<sup>14</sup>Optimization and optimal control should not be confused although they may be related when one comes to numerical resolution of OCPs. The former only deals with a standard function while the latter deals with a functional, i.e. a function of a function.

Dominici et al. (2011) analyzed the development of motor primitives in newborn babies but the energetic efficiency of their locomotion was not estimated simultaneously. On the other hand, evolutionary studies have investigated the energetics of bipedal versus quadrupedal locomotion (Sockol et al., 2007). Mixing the knowledge gained from such type of studies might be insightful with respect to the question posed. It is possible that, if stored muscle synergies are really hardwired in the CNS, they would limit the kind of optimality that can be attained (unless perhaps they have been precisely shaped to match the desired optimality conditions); this would suggest that motor development is the parallel process of finding both efficient limb trajectories and efficient representations of them, which would be partly dictated by evolutionary/homeostatic and neuroanatomical/biomechanical constraints. On a timescale of hours, it seems that motor learning is constrained by the existence of pre-coded/habitual solutions and that humans are not very good at finding global optima for new (never experienced) tasks (Ganesh et al., 2010; Mistry et al., 2013; de Ruyg et al., 2012). It must however be noted here that recent studies actually undermine this temporal limitation (Cluff and Scott, 2015; Selinger et al., 2015; Gaveau et al., 2016; Farshchiansadegh et al., 2016). Yet, at least over long learning periods, a process of re-optimization may occur (Izawa et al., 2008), possibly requiring the creation of new primitives, which would take a long time to acquire (d'Avella and Pai, 2010; Berger et al., 2013). In summary, modularity and optimality might be intertwined processes that develop concurrently.

## 1.5 Conclusion and overall perspectives

Hierarchical motor control, in particular grounded on the concepts of optimality and modularity, is an appealing theory to explain the formation of muscle patterns from task specification. Although it has been challenged that global optimality, in a strict sense, is always the immediate and primary goal of the human motor system when adapting to a new task on a short-time scale, daily life behaviors (such as reaching for a cup of coffee) undeniably display optimal-like signatures. Inverse OC offers a normative framework to formalize action selection and give the rationale for choosing one limb trajectory over another. The difficulties that the CNS faces in order to discover a global optimum when coping with a certain new motor task may be related to the way action planning is implemented; what is stored or learned versus what is specified on-the-fly. How the CNS seamlessly generates adequate motor commands in a fraction of a second might rely on modularity, i.e. the storage of muscle synergies that can be recalled and combined in a task-dependent manner to build genuine motor inputs. If muscle activity conforms in some sense to higher-level optimality principles, it is not surprising that low-dimensional structures can be found in EMG-based studies. Classical empirical studies of muscle activity are undoubtedly useful for providing ensemble descriptions of muscle patterns, yet their implementation in neural networks (third Marr's level of

analysis) remains putative despite remarkable efforts (Hart and Giszter, 2010; Overduin et al., 2015). At the same time we remain quite ignorant of what the (neural) nature of a motor building block (should it be called primitive, module or muscle synergy) is. The nature of the modules extracted from matrix factorization techniques applied to EMG data is often guided by the limitations of the method itself. For instance, NMF-based methods will only give rise to feedforward synergies. If synergies are posture-dependent as suggested in (Razavian et al., 2015), this would mean that more advanced machine learning methods should be used. Towards effective applications in fields where dealing with human-like movement is required but also to gain fundamental knowledge in movement neuroscience, there is still room for the proposal of new frameworks. The development of such a novel framework requires interdisciplinarity and will require advanced musculoskeletal models, neurophysiological data, psychophysical experiments and mathematics.

Arguably, having a generic framework capturing the essence of both optimality and modularity at once could be useful to advance our understanding of human movement control. Importantly, the mathematical formalism should be suited to port the main findings to robotics and engineering in order to improve the production of efficient movements in artificial systems in a rapid, robust and adaptive way. The idea of hierarchy being central and ubiquitous in motor control, it may be the cornerstone of such a framework. Based on previous experimental and computational results, a model relying on a cascade of OCPs could be envisioned. The problems could be solved recursively by the CNS: each problem could integrate a nominal trajectory coming from the previous problem and serving as a reference trajectory to the current level. An example of such a hierarchical framework connecting task-level to muscle level via skeleton level, could be as follows:

$$\begin{aligned}
 & \mathbf{x}_{ref}(\cdot) \text{ built from task} && \text{(task level)} \\
 & \quad \downarrow \mathbf{x}_{ref} \\
 & \min_{\boldsymbol{\tau}(\cdot)} \int_0^T [h(\mathbf{q}, \boldsymbol{\tau}, t) + r(\mathbf{q}, \mathbf{x}_{ref})] dt && \text{(skeleton level)} \\
 & \quad \downarrow \boldsymbol{\tau}_{ref} \\
 & \min_{\mathbf{u}(\cdot)} \int_0^T [H(\boldsymbol{\eta}, \mathbf{u}, t) + R(\boldsymbol{\eta}, \boldsymbol{\tau}_{ref})] dt && \text{(muscle level)} \\
 & \quad \downarrow \mathbf{u}_{ref} \text{ (motoneurons)}
 \end{aligned} \tag{1.1}$$

In Equation 1.1,  $\mathbf{x}$  would be the position/orientation of the end-effector in Cartesian space,  $\mathbf{x}_{ref}$  would be a reference trajectory (either a fixed target location, a geometric path such as a geodesic or a full trajectory potentially coming from a least action principle or imposed by the task with a metronome). At the skeleton level,  $\mathbf{q}$  would be the joint angles,  $\boldsymbol{\tau}$  the joint torques. A reference torque profile could be predicted by optimal control principles. At the muscle level,  $\boldsymbol{\eta}$  would be the muscle forces and  $\mathbf{u}$  the motoneuron inputs. An optimization problem could even be solved at this level if the spatiotemporal characteristics of the torque profiles are already set up. The core

piece would be that each level would lead to a reference trajectory that could be tracked in the subsequent level. The tracking is implemented via the tracking costs  $r(\mathbf{q}, \mathbf{x}_{ref})$  and  $R(\boldsymbol{\eta}, \boldsymbol{\tau}_{ref})$ , for instance by choosing at the skeleton level  $r(\mathbf{q}, \mathbf{x}_{ref}) = r(\|\varphi(\mathbf{q}) - \mathbf{x}_{ref}\|)$  where  $\mathbf{x} = \varphi(\mathbf{q})$  is the forward kinematics (and something similar at the muscle level). Because of the existence of reference trajectories, the resolution of each OCP may turn out to be faster and simplified by a local search (e.g. linearization or reduction of the search space). In this framework, we might insert other levels, introduce stochastic models and so on, but the structure is rich enough to incorporate a number of practical motor control problems.

Synergies may contribute to resolve each of these problems more efficiently if adequate motor building blocks can be stored, which could by the way justify why researchers have talked about modularity at various levels (kinematic, dynamic, muscular or even neural). Such a cascade of OCPs could be able to explain several of the experimental observations we have reviewed above but this would need to be investigated. This formulation may be reminiscent of an alternative formulation of hierarchical optimal control which has been proposed recently and in which a first OCP giving rise to an infinity of solutions is solved before a subsequent OCP is solved within the subspace of the optimal solutions of the previous level and so on (Romano et al., 2015; Geisert et al., 2017). The present hierarchical framework may be more flexible although it relies on the weighting of complementary objectives, thereby contrasting with the advantages offered by the concept of a “stack of tasks”. Furthermore, this framework could account for the observation of kinematic persistence observed in some motor tasks, especially when controlling a visual cursor on a screen or adapting to microgravity, which may reflect the influence of task-space high-level goals in certain contexts (Mistry et al., 2013; Danziger and Mussa-Ivaldi, 2012; Gaveau et al., 2011, 2016).



## Chapter 2

# 2 Research project

---

**T**HIS chapter presents my research project. In the coming years, I plan to work on a project that could be entitled “computational principles underlying self-paced human movement: motion vigor and the cost of time hypothesis”. This project will likely constitute my main research activity for the next 5 years or more. As already said, this is largely inspired from a project I proposed to the Institut Universitaire de France (IUF) (see Chapter 3).

### 2.1 Scientific positioning

This project builds on my previous research and will continue to investigate how the human brain plans voluntary movements. Imagine that, while reading these lines, you decide to put your cup of coffee on the desk in front of you. Although the task is ill-posed in the sense that plenty of motor strategies are compatible with its goal, your central nervous system (CNS) would find a strategy in a few hundred milliseconds. According to what rules has your brain selected where to put the cup, chosen the hand trajectory or even decided the overall speed of the movement? Understanding the principles underlying such motoric decisions has been the overall purpose of my research, which lies in the broad field of human neuroscience (Haggard, 2008). Here I will mainly focus on one aspect of our motor decisions that is referred to as “**movement vigor**” (Mazzoni et al., 2007; Dudman and Krakauer, 2016), i.e. the relations between amplitude, duration and speed, or put more simply, the overall pace of motion. A multidisciplinary approach is envisioned because movement vigor can intuitively be affected by various factors, from biomechanical to psychological ones, and can be relevant to various domains such as human-robot interaction. The work will be primarily grounded on a computational approach in order to build normative models that explain/predict why humans decide certain speeds over others. This will again be formalized within the framework of

optimal control (OC) theory (Todorov, 2004; Engelbrecht, 2001). Movement vigor will be assumed to arise from optimality principles that need to be better apprehended. The “cost of time” hypothesis mentioned in Chapter 1 will be the starting point of this work, which basically assumes that the effort associated with any movement is composed of a temporal part (the CoT) and a physical part (energy, smoothness etc.). This research will thus take place at the higher level of Marr’s tri-level description of computational neuroscience (Marr and Poggio, 1976), that is, it attempts to establish theories and mathematical models accounting for movement vigor and critically test them via experiments. The importance of addressing this level of analysis in movement neuroscience has been acknowledged by several authors and recently by Krakauer et al. (2017) and the current project shares this view.

## 2.2 Research objectives

The global objective of my research is to improve our understanding about how volitional movement is planned by the CNS by developing mathematical models and finding principles explaining some of the main motoric decisions. One such critical decision concerns the pace of movement. Understanding the origin and formation of self-paced movement will be the leitmotiv of the proposed research project and is currently a hot topic in motor neuroscience (Shadmehr et al., 2016; Berret and Jean, 2016; Dudman and Krakauer, 2016; Huh and Sejnowski, 2016; Wang et al., 2016). This is because one critical feature of humans or animals is the ability to regulate their overall movement speed according to the context of the action (Wilson et al., 2015). Day-to-day movements are spontaneously performed at a pace that one could qualify of comfortable or natural but what generic principles are guiding the selection of movement vigor is still unclear. However, theories have been recently proposed based on the concept of a “cost of time” (CoT) (Choi et al., 2014; Berret and Jean, 2016; Jean and Berret, 2017). As any scientific theory, they still require falsification testing from both mathematical and experimental viewpoints. While pursuing fundamental objectives, this research is also motivated by real applications (see next section). The development of novel technologies and methods to assist, replace or emulate human motor control is rapid. Yet, at some point, most projects face difficulties when one comes to real tests such as a high rejection rate for exoskeletons or the feeling of “robotized” motion perception for humanoids. A better fundamental knowledge regarding what the human motor system wants to achieve and why it does so may eventually improve the situation and contribute to designing more efficient high-level control laws for artificial systems like exoskeletons. In this respect, pace is one crucial yet often neglected motion feature. Of course, there are several aspects of motor control that deserve attention but, in this research project, the main objectives are specified as follows:

**Objective 1** Test the cost of time hypothesis in motor control and decision making.

**Objective 2** Develop general mathematical models accounting for speed choices.

As it will be detailed below, addressing this topic is inherently multidisciplinary. The idea of a CoT may be important in all the fields of research that interact with human motion at physical and/or cognitive levels.

## 2.3 Research significance

Historically, most studies about motor control have been interested with the geometrical/spatial aspect of human movement trajectories when movement time (MT) constraints were supposed to be given. Average speed and duration are yet movement variables that must be chosen by the sensorimotor system in most real-life situations. The present project aims at improving our knowledge about the underlying principles, be they computational or neural, which drive the formation of human movement vigor. To predict and account for self-paced motion is also critical to other fields of research and, interestingly, addressing this issue reveals itself to be multidisciplinary in essence. The rationale for developing a comprehensive theory of movement vigor using optimality principles is presented hereafter in a human-centered perspective but it is worth noting that this speed-choice issue is also a hot topic in animal studies (Wilson et al., 2015). Therefore, the impact of this research about human movement vigor will be of interest for a broader audience since optimality principles are also being used when questioning the speed of animals in ecological contexts. Investigating how motion vigor is elaborated by the CNS is an important question not only in neuroscience but also in connected fields such as humanoid robotics (Kajita et al., 2014), robot-assisted neuro-rehabilitation (Huang and Krakauer, 2009), brain-machine interfaces (Golub et al., 2014), computer animation (Roberts, 2012) or neuro-prosthetics (Shenoy et al., 2003). Arguably, anticipating and complying with human movement speed (and the associated spatial displacements) will be necessary to enhance natural interaction between a biological system and an artificial one, and the acceptance or usage of the latter, including when interaction is not physical but cognitive.

In neuroscience, understanding the underpinnings of movement vigor formation is important with regards to neuromotor disorders affecting the speed and amplitude of actions such as Parkinson's disease (Marsden, 1989; Berardelli et al., 2001). Bradykinesia is known to have a central origin, thought to originate from a dysfunction of a deep brain region called the Basal Ganglia (BG). The role of BG has remained mysterious for a long time (Turner and Desmurget, 2010) but it has been made clear that abnormal activity in BG leads to an overall reduction of movement vigor. Strikingly, this motion slowness can be removed by instructing verbally Parkinsonians to speed up their movement; in other words, their movement kinematics may become again normal

(Mazzoni et al., 2007), thereby proving that slowness was not a peripheral limitation. These results demonstrate that BG is involved, directly or indirectly, in movement vigor specification. Such findings are also confirmed by deep brain stimulation studies (mainly in the subthalamic nucleus or globus pallidus internus, the principal output nucleus for the BG, projecting to the motor cortex) (Montgomery et al., 2011; Vaillancourt et al., 2004; Moran and Schwartz, 1999). Interestingly, activity in premotor, supplementary and primary motor areas has also been shown to encode speed-related information about the upcoming movement speed and/or extent and their covariate variables (Churchland et al., 2006; Johnson et al., 1999; Tankus et al., 2009; Turner et al., 2003). However, speed/distance motion characteristics seem to be encoded in the motor cortex to a lesser extent than spatial ones such as direction (Churchland et al., 2006; Georgopoulos et al., 1986). It is noteworthy that these studies varied motion speed via external triggers (color code or verbal instruction): the changes of movement vigor were not self-generated. Above all, neural studies suggest that complex BG-cortical loops affect the vigor of movement and that nominal movement pace is not the mere expression of feedback mechanisms during motor execution or biomechanical artifacts. Motion duration is largely a planned quantity that may be tuned contextually. In particular, the extent to which movement vigor in ordinary daily life tasks represents an individual's trait or the current state of his/her sensorimotor system is an open question (cf. question **Q1** below).

In humanoid robotics, the objective is to build artificial systems behaving in a human-like manner in order to have autonomous robots able to behave in a human environment and with humans. In fields where a human physically interacts with a robot such as an exoskeleton (cf. applied projects **AP1** and **AP2** below), the goal is to enable efficient interaction between the user and the robot. The problem is often to predict/anticipate the user's intention and improve the "transparency" of the robot such that it can assist but not perturb the movement of the user. Movement pace is probably one of the most significant features that should be monitored in this regard as overly slow or rapid moves may conceivably cause uncomfortable sensations to the user and lead to a rejection of the technology. However, most research efforts have been spent on the control of spatial positions while the time required to perform an action was either preset by the experimenter or simply minimized (mainly for industrial applications). Actually, robotic studies often rely upon relatively rigid procedures to reliably drive a robot to some desired spatial target in an adjustable amount of time (e.g. assuming an exponential decay of the distance left to the target, in Fitts's law spirit, Mansard et al., 2009). This is typically achieved by tuning a parameter that the modeler must set by hand. A similar tuning of parameters is required to vary MT when using proportional–integral–derivative controllers and even more involved feedback schemes (Pattacini et al., 2010). Therefore, task duration is often hardcoded by fixing a desired MT at the planning stage or merely results from the application of a feedback gain at the execution stage via fine-tuning heuristics. Hence there is a lack of principled approach to generically establish nominal movement pace in sensorimotor systems,

likely because we still have a poor knowledge about the reasons leading the CNS to move at a certain pace. When interacting with humans, such artificial systems must however move their body in a realistic, human-like manner, which is neither too slow nor too fast. The field of social robotics has also been growing recently and attempts to evaluate how the actions of humanoid robots are perceived by humans and the extent to which their intention can be figured out (Sciutti et al., 2012a). Because of the action/perception coupling, the speed of the other may likely resonate in the self, which may justify the need for a proper match between the pace of human and artificial systems. It is worth noting that, in computer animation, generating characters behaving with common paces is desired for similar reasons. In neuro-prosthetics, how to actuate robotic devices such as an artificial arm with correct speeds is one of the ultimate goals to achieve but it remains quite challenging, not only for technical reasons but also because of a lack of knowledge about what the correct MT should be for a given goal-directed motion. In that field, intended motion plans are typically decoded from neural recordings and then used to actuate an artificial limb. Such investigations interestingly proved that neurons in motor and premotor cortices encode the speed of the upcoming movement, although this encoding may not be as strong as the encoding of spatial parameters such as movement direction as already said (Golub et al., 2014; Moran and Schwartz, 1999). Practically, not only direction but also speed seems to be coded by cortical cells. Since neurons or population of neurons code the speed of upcoming movements in some way, it might be possible to exploit this knowledge in neurorehabilitation protocols as well. This would suggest that motor recovery should also aim at converging back to an acceptable motion vigor. Having computational models to complement these findings could enhance the efficiency and robustness of the associated methods. Furthermore, after a neuromotor disease (e.g. stroke), speed is often drastically reduced due to both peripheral and central issues. Rehabilitation methods often consist of assisting patients in realizing an action with the aim to both guide and stimulate them (Huang and Krakauer, 2009). What should be the characteristics of the reference movements used to guide/teach the subjects? This question has often been posed in the context of their spatial characteristics (e.g. shape of hand trajectories) but studies rarely asked whether the speed of the accompanying movement was satisfactory. If time has a cost or long-duration movements are perceived as effortful by subjects (Morel et al., 2017) (and thus potentially disagreeable), this could affect the effectiveness of the rehabilitation process. Arguably, having high-level principles predicting the desired speed of a subject (and explaining why he/she would make such a choice) could contribute to get better predictions or recommendations depending on the application.

Without being exhaustive, the above considerations motivate fundamental research to uncover the underpinnings of movement pace formation within the CNS. Importantly, due to the different nature of artificial and human systems, developing mathematical models of movement pace is likely a crucial step to port findings from human neuroscience to connected fields such as humanoid

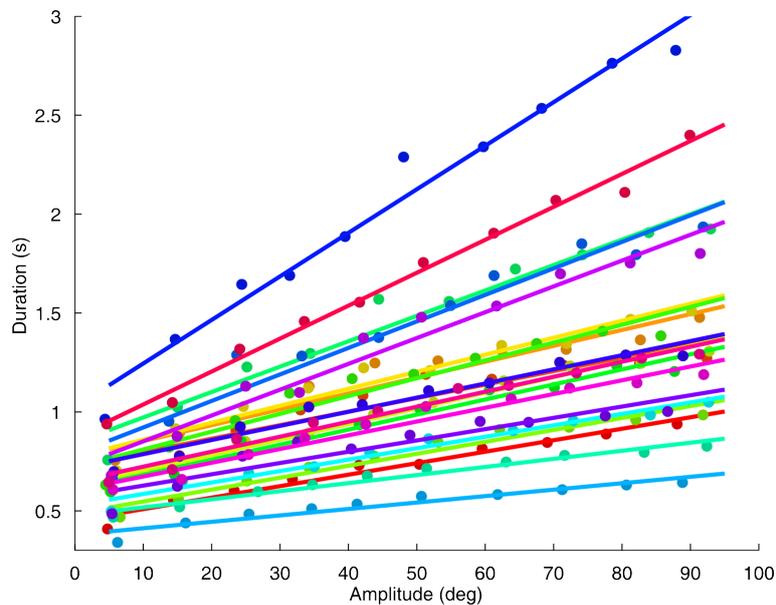


Figure 2.1: Amplitude-duration relationship for self-paced planar single-joint arm movements in a pointing task. Colours stand for individuals. Note the large inter-individual variability despite the simplicity of the motor task. For example, a 50-degree reaching movement may last from about 0.5 s to 1.5 s across individuals.

robotics, robot-assisted rehabilitation or character animation (see applied projects below **AP1** and **AP2**). In this respect, OC theory is an appealing and adequate tool because it reaches a level of abstraction that is high enough to be directly exploited in engineering control techniques. This is by the way the essence of the Institute for Control and Decision (iCODE) I am part of (see Chapter 3).

Thus far, no consensus has been reached as to why the human brain does select a preferred MT or nominal overall-speed as it does for any given task. An intriguing fact is the great variability of MT that can be observed across individuals even for very basic movement tasks: movement vigor may vary as much as 100% between people during very simple arm pointing movements (see Figure 2.1).

This is also true for individuals sharing very similar anthropometric characteristics. Interestingly, such large inter-individual differences have been observed in other behaviors like ocular saccades (Choi et al., 2014) (up to 50% of speed variation across individuals) or walking (Knoblauch et al., 1996). While metabolic energy consumption may predict an optimal movement speed, this is not sufficient in general as humans clearly regulate speed in a context-dependent manner (Shadmehr et al., 2016). For example, saccades have been shown to be faster when directed to targets with

a larger expected reward (Xu-Wilson et al., 2009) or directed to faces compared to other random pixel images (Takikawa et al., 2002). Walking speed has been shown to be greater in cities with larger populations where the environment is more stressful (Bornstein and Bornstein, 1976) or to depart from metabolic optima in many situations (Yandell and Zelik, 2016). To account for these observations, the CoT theory, presented in more details below, is a promising concept that still requires further investigations and developments.

## 2.4 Research program

### 2.4.1 Fundamental research

#### **Cost of time theory.**

Making a voluntary movement typically aims at fulfilling a certain goal that has some utility for the CNS (e.g. grasping for a glass of water because one is thirsty). It has been proposed that the goal of any voluntary movement is thus to put the system in a more rewarding state (Shadmehr, 2010). However, performing such a goal-directed movement requires time (and generally physical effort) before a “reward” can be obtained. Hence MT can be seen as a delay before reward acquisition. Because our brain tends to discount the actual value of future reward (Myerson and Green, 1995), slower movements may result in smaller reward, which may be internally represented in the brain via dopamine or serotonin signals (Cohen, 2015). This logical reasoning led to the assertion that the time elapsed until action completion may entail a cost in the brain, thereby making slow moves non-optimal. Because reward and cost are mathematically related (maximizing a reward is equivalent to minimizing a cost), Shadmehr and colleagues advanced the idea that the vigor of biological movement could be driven by a “cost of time” (Shadmehr, 2010; Shadmehr et al., 2010). Slow movements would be undesirable in this context because the passage of time incurs a cost: it is “better” to achieve a task sooner than later. This makes sense as to want something “now” rather than “later” is a common attitude in humans. This would result from the functioning of the central reward system (temporal discounting of reward) via the cortico-BG loop since movement vigor seems to originate from this neural circuitry. Hence the CoT is an appealing concept to explain why humans are so reluctant to move slowly (van der Wel et al., 2010) but also why they might be embarrassed by the slowness of other individuals or systems (e.g. everyone has experienced how annoying it can be to walk alongside someone slow). Moreover, long-duration movements have been shown to be perceived as more effortful than short-duration movements of the same size (Morel et al., 2017). In motor control, time may be costly for other reasons than just a temporal discounting of reward (Wolpert and Landy, 2012); decay of working memory, cost of attentional

resources or neural energy expenditure may be further reasons that may prevent humans from moving too slow. More philosophically, according to an adage from the ancient Greek Antiphon, time is the most costly outlay in life.

If one hypothesizes that time carries a cost in motor control, then one must understand how the brain penalizes the passage of time during action planning, i.e. according to what function? This question was analyzed in depth for saccades by Shadmehr's group where the authors concluded at the end of one of their articles (Shadmehr et al., 2010): "If we could develop robust techniques to measure [parameters] in the reward function of individuals, it would be possible to test for within-subject correlations between the reward function and movement kinematics". By saying that, these authors stressed two key points: (1) there is a need for robust methods to infer the CoT or at least some of its parameters; (2) reliable identification could then be used to predict and investigate the variability of overall-speed across different individuals and tasks.

In this vein, we developed a complete methodology allowing to identify the CoT in motor control, in the framework of OC, and without making prior assumptions about its hypothetical shape (Berret and Jean, 2016). This inverse OC result, allowed us to robustly infer its shape for saccades and reaching by sampling values of the CoT from experimental data. Equipped with that methodology, several questions can be better resolved but the assumptions and predictions made by the theory should also be further tested. Before presenting my research program, it is worth recalling briefly the mathematical foundation of the theory and how it is possible to uncover the shape of the time cost using OC modeling.

### Identification of the CoT.

Let

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mathbf{u}) \tag{2.1}$$

represent the dynamics of the biological system under consideration (e.g. an eye, an arm, legs or the whole body), which depends on the system state  $\mathbf{x} \in \mathbb{R}^n$  and the motor command  $\mathbf{u} \in \mathbb{R}^m$ . A dot above a variable stands for its time derivative. According to optimal control (OC) theory, a cost is associated with any movement strategy via an integral cost  $\int_0^{T_{\mathbf{u}}} h(\mathbf{x}, \mathbf{u}, t) dt$  that depends on the duration  $T_{\mathbf{u}}$  which itself depends on  $\mathbf{u}$ . Here the problem is formulated in *free time* such that movement duration emerges automatically from the optimality criterion. In contrast, most existing OC models have actually been formulated in *fixed time* where MT is chosen *a priori*, which explains why the vigor of our movements has been largely neglected in seminal studies (Flash and Hogan, 1985; Uno et al., 1989). Importantly, OC theory assumes that humans make motoric decisions that reflect the minimization of a certain cost function, in the "least action" principle spirit

except that the biological analog of the Lagrangian,  $h(\mathbf{x}, \mathbf{u}, t)$ , is unknown in motor control and is sought for. This ability to choose minimal trajectories could originate from evolution and learning during development. In any case, it is an appealing tool to describe compactly infinity of biological movements and hypothesize about their benefit compared to other motor strategies. Addressing Marr's higher level (cf. scientific positioning) leads actually to an inverse optimal control problem: from presumably optimal trajectories the aim is to recover the cost function, i.e.  $h(\mathbf{x}, \mathbf{u}, t)$ . In general this is an ill-posed, difficult problem which must be restricted and structured to be tractable. Assume that can be decomposed into a term that depends on the time  $t$  only (i.e. the CoT) and another term that is independent of  $t$  in an additive manner. This additive separability can be seen as a first-order approximation of a more general problem and makes the framework compatible with earlier works in fixed time. Namely, we assume:

$$h(\mathbf{x}, \mathbf{u}, t) = g(t) + l(\mathbf{x}, \mathbf{u}) \quad (2.2)$$

Under this hypothesis, it can be shown that by solving an OCP joining an initial state  $\mathbf{x}_0$  to a final state  $\mathbf{x}_f$  in **fixed time**  $t$  with the cost function  $\int_0^t l(\mathbf{x}(\tau), \mathbf{u}(\tau)) d\tau$ , we can recover the value of  $g(t)$  (see Berret and Jean, 2016; Jean and Berret, 2017). This value is exactly equal to the value taken by the (optimized) Hamiltonian  $\mathcal{H}_0$  along the optimal trajectory for this associated fixed time OCP (cf. Pontryagin's maximum principle, Pontryagin et al., 1964; Kirk, 1970), that is:

$$g(t) = -\mathcal{H}_0(\mathbf{u}^*, \mathbf{x}, \mathbf{p}), \quad (2.3)$$

where  $\mathbf{u}^*$ ,  $\mathbf{x}$ ,  $\mathbf{p}$  are respectively the optimal state, co-state and control of the OCP in fixed time  $t$  (note that the Hamiltonian  $\mathcal{H}_0$  is indeed constant along the optimal trajectory for this time-invariant OCP). The key point is that a transversality condition states that the Hamiltonian vanishes at the final state for the free-time OCP with running cost  $g(t) + l(\mathbf{x}, \mathbf{u})$  and the Hamiltonian in both problems defines the same state/costate equations such that the optimal trajectories coincide for the same durations (predicted in the free-time case and preset in the other case).

According to Hamilton-Jacobi-Bellman theory,  $g(t)$  can also be computed from the value function  $V_{\mathbf{x}_f}$  of the associated (possibly stochastic this time!) OC problem in fixed time  $t$ , as follows:

$$g(t) = -\frac{\partial V_{\mathbf{x}_f}}{\partial t}(t, \mathbf{x}_0) \quad (2.4)$$

where  $V_{\mathbf{x}_f}(t, \mathbf{x}_0)$  is the infimum of costs taken over all  $\mathbf{u}(\cdot)$  joining  $\mathbf{x}_0$  to  $\mathbf{x}_f$  in fixed time  $t$ . Therefore, solutions can be obtained accurately for the class of LQG problems (e.g. Todorov, 2006; Kappen, 2011).

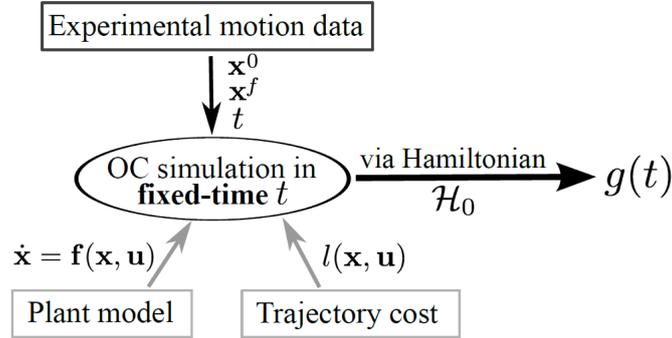


Figure 2.2: Illustration of the methodology to sample values of the CoT from experimental data. It is only necessary to solve an OCP in fixed time and evaluate the constant value of Hamiltonian along the optimal trajectory. The subscript 0 is used to mark the difference with the Hamiltonian of the associated free-time OCP, including the term  $g(t)$  into the cost function.

Note that this is somewhat similar to the concept of “Drive” introduced recently (Huh and Sejnowski, 2016), but instead of assuming that  $g(\cdot)$  is the same (constant) function for all movements, the present methodology allows to sample its actual values right from basic experimental motion data, namely initial/final states and duration. A flowchart of the methodology is illustrated in Figure 2.2.

To better clarify how we can compute  $g(t)$  for some time  $t$ , a detailed procedure in a simple linear-quadratic setting is provided in Appendix. This simple framework is enough to model simple arm or eye movements with one DOF. The rationale for providing the details of the solution in such a case is that it accounts for a variety of tasks and problems that are envisioned in this project. Hence it can serve as the computational basis for the investigation of the CoT hypothesis in all one-dimensional tasks where the end-effector path is imposed and only time-related or speed-related choices are made by participants.

This methodology is easily extendable to nonlinear dynamics and arbitrary costs using numerical techniques (e.g. pseudospectral methods, Rao et al., 2010). The optimal Hamiltonian value of certain fixed-time OCPs just needs to be estimated. Using this methodology, the time costs underlying horizontal saccades and planar arm reaching were previously identified with success (Berret and Jean, 2016). These costs were different. The CoT was compatible with a hyperbolic discounting of reward for saccades, thereby confirming previous results (Haith et al., 2012), and it was sigmoidal for reaching (which was hardly predictable *a priori*). Note that they were defined on different time scales (<300 ms for saccades, >300 ms for reaching), posing questions about the

existence of a single or multiple time costs within the CNS.

While the methodology proved to be effective and robust to measure the CoT for different sensorimotor systems, several hypotheses were made to derive these results (e.g. the very existence of a CoT or the additive separability of the temporal and trajectory costs). The goal of this project is to better understand the origin (e.g. neural metabolic cost or temporal reward discounting) and versatility of the CoT (are there several time costs? If so, are they consistent across sensorimotor systems, days, tasks, individuals? etc.). Intuitively, speed-choices are expected to be influenced by biomechanical, physiological, neurological, psychological, or social factors, which places the topic at the frontier of several disciplines. This inherent multidisciplinary nature requires setting up collaborations with experts in various fields. The scientific cluster offered by the Université Paris-Saclay constitutes an ideal framework as most of the required competencies can be found locally. Keeping in mind all the potential applications, resolving questions related to the existence of a CoT represented by the CNS should contribute to making fundamental breakthroughs regarding speed choices for intelligent agents. In particular, my program is to address the following more precise questions related to the time cost, in order to test and develop the theory:

- Q1.** How versatile is the time cost across time (e.g. sessions, days) and individuals? Does it reflect a trait of an individual or rather the state of the system at the time it is measured?
- Q2.** What is the consistency of the time cost across different systems and tasks such as an eye, leg, arm, or the whole body? Do individuals who move their eyes more quickly than others also move their arms more quickly? This would indicate the extent to which the time cost is shared among different sensorimotor systems. In particular, I plan to compare the vigor of individuals during saccades, reaching and walking.
- Q3.** What is the consistency of the time cost across different tasks such as discrete or cyclical tasks (e.g. curve-drawing vs pointing). Considering cyclical drawing task may allow sampling the time cost for larger durations (e.g. circular drawing) while so far it is just extrapolated for large durations. What are the links with alternative theories that have considered similar rhythmic curve-drawing tasks (Bennequin et al., 2009; Huh and Sejnowski, 2016)?
- Q4.** What is the interplay between effort (cost of trajectory depending on muscular energy expenditure, work or heat energy loss) and time costs? Can the time cost explain behavior when the physical cost is manipulated by the experimenter? What is the time cost during an isometric reaching task? What happens if the task can be realized without physical/muscular effort? Can it allow disentangling the neural/mental and muscular parts of the time cost? The same questions can be approached using an upper-arm exoskeleton (link with **AP2** below)?
- Q5.** Is there a way to isolate the CoT in non-motoric decision-making tasks (e.g. simulating

the decision behavior of waiting in a queue in order to get a unitary reward)? Does this “cognitive” CoT relate to its motoric expression (e.g. in motor tasks such as arm pointing)?

- Q6.** Can we account for a preferred walking speed using the CoT hypothesis, although the metabolic cost of walking already explains the preferred speed because it has a “U” shape with respect to walking speed? (link with **AP1** below). This also requires understanding how to model such rhythmical task (link with **Q3**)
- Q7.** Can we find perceptive correlates of the time cost during action observation? Do we judge the vigor of someone else based on our own time cost? This can be done by building psychometric functions using some well-designed experiment of the perception of biological movement speeds of various amplitudes.
- Q8.** Can we propose and test other formulations of the problem (with a multiplicative time cost or with a discounted trajectory cost, Shadmehr et al., 2016)? Can the predictions of the proposed model(s) be falsified using experiments designed on purpose?

### 2.4.2 Applied projects

Besides the fundamental questions related to the CoT in motor control described above, I plan to work on two projects involving exoskeletons: one for the lower limbs and one for the upper limb. Here as well, speed-choices are central with respect to the interaction between the human and the robot. The CoT may thus play an important role for enhancing the collaboration between an artificial system and a human user. These projects are called “applied” because the ultimate goal is related to rehabilitation or physical ergonomics and is developed with expert partners whose objectives are not directly related to better understanding how the brain controls movement.

#### **AP1. Infant-size exoskeleton and development of walking**

Over 68 million people worldwide are in wheelchair. However, unfortunately, teenagers and infants constitute a considerable fraction of this whole population, with important social difficulties such as going to school. In order to improve their quality of life and allow them to interact better with their environment, the wheelchair might be ideally replaced by an exoskeleton system (Figure 2.3).

The development of exoskeletons having scalability properties to adapt to growth is under active development in the team of Dr. Samer Alfayad. However, the development of appropriate high-level controllers ensuring the walk stability and its effectiveness remains challenging. Unlike

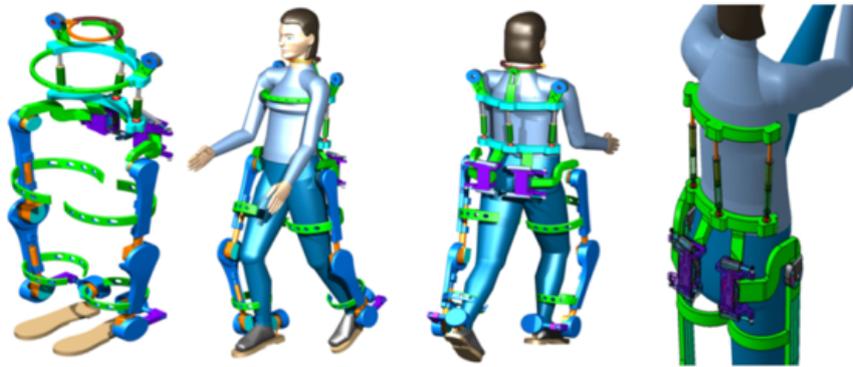


Figure 2.3: Lower-limb exoskeleton illustration (credit to S. Alfayad)

humanoid robots, an exoskeleton is in continuous interaction with the user's body. Therefore, the capability of the exoskeleton to ensure safe interaction with the individual and cooperate with him constitutes a critical feature of high-level control. While safe interaction will be warranted by the low-level compliant joints, the powered exoskeleton should be able to reproduce a teenager's walk. Bio-inspired neural control will play a very important role in emulating this walk. This biological control loop, envisioned within the optimal control theory framework, will allow the user to separately trigger walking from other reaching/grasping actions, thereby preventing from involuntary stepping during tasks like opening a door. This will require developing adaptive and subject-specific algorithms to refine the high-level control of the exoskeleton in order to match the reference teenager's walking pattern. The reference pattern will be primarily characterized via the step frequency, the step length or the walking speed as these variables should reflect the capacity of the exoskeleton to produce an effective motor coordination during walking. Indeed, walking speed will likely be a critical indicator of action efficiency and may give relevant insights about the exoskeleton usability and utility. Patients will be recruited thanks to an ongoing collaboration with Dr. Didier Pradon (Raymond Poincaré Hospital in Garches, gait analysis lab) and experimental research will be carried out with Dr. Caroline Teulier (CIAMS) who is an expert of the development of walking in infants. It is noteworthy that this project is part of a larger project taking place within the iCODE (financed by IDEX Paris-Saclay and supported by additional funds in order to build and upgrade the exoskeleton, cf. Chapter 3, research grants paragraph). PhD students and post-docs may eventually be involved in this project, which is just starting.

## AP2. Upper-limb exoskeleton during arm reaching

Musculoskeletal disorders (MSDs) can arise from making the same motions repeatedly or when lifting a large load suddenly. MSDs affect millions of workers and have a cost of about 800M€ per



Figure 2.4: Photo of the exoskeleton ABLE worn by P. Garrec (credit to CEA-LIST) (Garrec, 2010)

year in France for the industries. Wearable exoskeletons have been proposed as a possible solution to reduce physical load at work and reduce the number of MSDs. Yet, a lot of research efforts remain to be done to understand how to improve the transparency of the exoskeleton (i.e. let the users move effortlessly and with no discomfort when wearing the exoskeleton). Few systematic assessments have been done to check how the users adapt to the exoskeleton but promising recent works exist (Pirondini et al., 2016; Proietti et al., 2017). Moreover, understanding how to let the exoskeleton anticipate movements from the user and comply with them remains to be investigated more in depth. Thus far, exoskeletons can rarely be used in real situations because the interaction between the user and the exoskeleton is not efficient enough. In particular, how humans modify the speed of the motion when wearing the exoskeleton or how they react when the exoskeleton is autonomously driving the user's arm must be investigated. Part of this work will be developed with Dr. Franck Geffard, CEA-LIST researcher, who is an expert of the exoskeleton (cf. ABLE, Figure 2.4) and its control, and with Dr. Nicolas Vignais (CIAMS) who is an expert in biomechanics and physical ergonomics. Master and PhD students will be involved in this part of the project (students from the newly created "Ingénierie et Sciences du Mouvement Humain" Master program of Université Paris-Saclay where I teach). In particular, a PhD thesis is starting on this topic in October 2017 (see Chapter 3).

N.B.: Data collected from exoskeleton studies in the two projects presented above (**AP1** and **AP2**) can be used to answer fundamental questions related to the speed of human movements. Therefore,

exoskeletons can be used both as a tool to advance fundamental research related to how the brain control movement and as a research topic *per se* that can be boosted by the integration of motor control scientists into the loop.

## 2.5 Complementary research projects

Besides this main research proposal, I expect to continue working on other ongoing projects. In particular, I am interested in upper-limb control during French sign language (with A. Braffort, CNRS), co-contraction control in humans and humanoids for which it would be interesting to develop open-loop stochastic optimal control methods able to replicate how the CNS modulates co-contraction according to the instability of the task (Burdet et al., 2001; Gribble et al., 2003; Mitrovic et al., 2010; Missenard and Fernandez, 2011) (joint work with F. Nori, IIT, e.g. Berret et al., 2011c, 2013), and motor synergies in gait control (pathological, with D. Pradon, N. Roche, Garches; developmental, with C. Teulier, Univ. Paris-Sud). I also plan to better investigate the action selection processes using eye-hand coordination especially in tasks with an infinity of compatible end points (“manifold reaching paradigm”) (Berret et al., 2014). We need to extend previous experiments to more reliable eye tracking and to EEG signals in order to better understand the cortical processes involved in such a type of motoric decisions for which the “where to go?” issue is central.



# 3 Chapter 3

---

## Curriculum vitae

**T**HIS chapter gives a summary of my educational and academic activities in link with my research. In brief, I did a PhD in mathematics and computational motor control at the Univ. Bourgogne (Dijon, FR), about gravity integration in human movement and co-funded by the CNES, whose highlights were a cover of the Journal of Neuroscience (2009) and a press release following a publication in PLoS Computational Biology (2008). Between 2009 and 2012, I was a postdoctoral researcher at the Italian Institute of Technology of Genoa within the Robotics, Brain and Cognitive Sciences department. There, I conducted multidisciplinary research about humanoid robotics and human motor control, which gave rise to publications in neuroscience journals and IEEE proceedings. Since September 2012, I am Maître de Conférences (~ tenured assistant professor) at the Univ. Paris-Sud (Orsay, FR) where I obtained some grants to develop my multidisciplinary work with mathematicians, roboticists and psychologists within the Université Paris-Saclay cluster. In 2015, I was awarded with the PEDR (national PhD supervision & research bonus). Since October 2017, I am a junior member of the "Institut Universitaire de France" (IUF).

### 3.1 General information

**BERRET Bastien**

**Date of birth:** July 31, 1981

**Family situation:** marital relationship (2 children)

**Professional situation:** Maître de Conférences (~ tenured assistant professor), UFR STAPS, Univ. Paris-Sud, Université Paris-Saclay, "Complexité, Innovation, Activités Motrices et Sportives" (CIAMS) laboratory, EA4532

**Nationality:** French

**Address:** Université Paris-Sud, Bâtiment 335, Bureau 32, 91405 Orsay cedex

**Telephone:** +33 1 69 15 78 82 (office)

**Email:** bastien.berret@u-psud.fr

**Home Page:** <http://hebergement.u-psud.fr/berret/>

## 3.2 Scientific education

**From May 2009 to Aug. 2012** Postdoctoral researcher at the Italian Institute of Technology (IIT, Genoa, Italy), Robotics, Brain and Cognitive Sciences (RBCS) department, dir. Prof. G. Sandini, collaborations with Dr. F. Nori and Dr. S. Panzeri.

**From Dec. 2005 to Dec. 2008** PhD in computational neurosciences and mathematics, supported by the CNES (Centre National d'Etudes Spatiales) and the Regional Council of Bourgogne, at INSERM U887 laboratory (Univ. Bourgogne, Dijon, France), entitled: "The integration of gravity during the planning and control of human arm or whole-body movements". Advisors: Pr. T. Pozzo (Neurophysiologist) and Pr. J-P. Gauthier (Mathematician).

**Jury** (defense on Dec. 15th 2008, in french/english):

|                            |   |                    |
|----------------------------|---|--------------------|
| Mme Tamar Flash            | Professeur, Weizmann Institute of Science, Israël | Rapporteur         |
| M. Philippe Souères        | Directeur CNRS, LAAS-CNRS, Toulouse               | Rapporteur         |
| M. Rémi Langevin           | Professeur, Université de Bourgogne               | Examineur          |
| M. Charalambos Papaxanthis | Professeur, Université de Bourgogne               | Examineur          |
| M. Thierry Pozzo           | Professeur, Université de Bourgogne               | Directeur de thèse |
| M. Jean-Paul Gauthier      | Professeur, Université de Toulon                  | Directeur de thèse |

**From 2004 to 2005** Master in Computer Sciences, Image processing and Medical Imaging, at Univ. Bourgogne.

**From 2003 to 2004** Preparation and admissibility to the "agrégation de mathématique" ('admissibilité'), national competitive examination in mathematics, at Univ. Bourgogne.

**From 2001 to 2003** BSc & MSc in Mathematics, at Univ. Bourgogne.

**From 1999 to 2001** Post-secondary preparatory school / classes preparing for entrance examinations to the French "Grandes Ecoles" (CPGE) – Dijon. Speciality: Maths, Physics and Informatics. Admissibility to competitive exams.

## 3.3 Career

### *Curriculum*

**From 2017 to 2022** Institut Universitaire de France (IUF), junior member

**From 2015 to 2019** “Prime d’encadrement doctoral et de recherche” (PEDR) (national doctoral supervision and research award) from CNU 74 (top 20% of applicants).

**Since Sept. 2012** Assistant Professor (« Maître de Conférences ») in CIAMS laboratory, UFR STAPS, Univ. Paris-Sud, Université Paris-Saclay, Orsay, France.

**2009** Qualification in CNU 74 (STAPS), 69 (Neurosciences) and 26 (Applied Maths)

### *Highlights*

- Journal cover for a Journal of Neuroscience article in 2009 (<http://hebergement.u-psud.fr/berret/papers/coverJN2009.png>)
- Press release for a PLoS Comp Biol article in 2008 ([http://www.eurekalert.org/pub\\_releases/2008-10/plos-thb102108.php](http://www.eurekalert.org/pub_releases/2008-10/plos-thb102108.php))

**Metrics (as of September 2017)** h-index (according to Google Scholar): 16

Number of citations (according to Google Scholar): 651

## 3.4 Supervision work

**Master student (1st year) – duration of internship ~7 weeks** I supervise 1st year Master students on a regular basis to initiate them to research. For illustrative purposes, since I am in Univ. Paris-Sud, I supervised two students in 2013-2014 (in co-supervision with Dr. C. Teulier (Univ. Paris-Sud) and Dr. D. Pradon (Garches-UVSQ), on muscle synergies and three students in 2015-2016 (in co-supervision with Dr. E. Yiou, P. Fourcade (n=1) and T. Deroche and C. Castanier (n=2), on the integration of gravity in the postural control during vertical arm raising and the investigation about the cost of time (cf. research project), respectively. In 2016-2017, I co-supervised 3 students on to continue those projects.

**Master student (2nd year) – duration of internship ~4-6 months**

|                       |  |
|-----------------------|--|
| <b>I Yung</b>         |  |
| Date:                 | from Jan. 2012 to Sept. 2012   |
| Location:             | Italian Institute of Technology (Genoa) and University of Genoa  |
| Title:                | « Comparison of Open-Loop Stochastic Optimal Control Algorithms of Variable Impedance Manipulator for Unstable Tasks » |
| Role:                 | Main supervisor (100%)   |
| Last known position:  | PhD student at Umea University (Sweden)  |
| Related Publications: | 1 publication from the supervision (IEEE proceedings - IROS)   |

|                       |  |
|-----------------------|--|
| <b>Anthony Supiot</b> |  |
| Date:                 | from Jan. 2015 to June 2015  |
| Location:             | Univ Paris-Sud & Hôpital Raymond Poincaré (Garches)  |
| Title:                | « Effect of speed on muscle synergies during walking in healthy subjects »   |
| Role:                 | Co-Supervisor 50% (with Dr. Didier Pradon)   |
| Last known position:  | PhD student at UVSQ (I now co-supervise his work still on muscle synergies during walking in post-stroke or spinal cord injury patients) |

|                      |   |
|----------------------|---|
| <b>Florian Vidal</b> |   |
| Date:                | from Jan. 2016 to June 2016   |
| Location:            | LIMSI CNRS  |
| Title:               | « Perception of French sign language: comparison between avatars and real signers » |
| Role:                | Co-Supervisor 33% (with Dr. Annelies Braffort & Dr. Elise Prigent)                  |

|                         |   |
|-------------------------|---|
| <b>Elodie Hinnekens</b> |   |
| Date:                   | from Jan. 2016 to Sept. 2016  |
| Location:               | Univ Paris-Sud, CIAMS   |
| Title:                  | « Effect of cognitive constraints and dual tasks on muscle synergies during healthy walking » |
| Role:                   | Co-Supervisor 50% (with Dr. Caroline Teulier)   |
| Last known position:    | PhD student with Dr. Caroline Teulier at CIAMS laboratory (I now co-supervise her work)       |

|                      |   |
|----------------------|---|
| <b>Simon Bastide</b> |   |
| Date:                | from Feb. 2017 to June 2017   |
| Location:            | Univ Paris-Sud, CIAMS and CEA-LIST  |
| Title:               | « Impact of wearing an exoskeleton on upper-limb human motricity »        |
| Role:                | Co-Supervisor 50% (with Dr. Nicolas Vignais and Dr. Franck Geffard)       |
| Last known position: | PhD student with me (50%), Nicolas Vignais (30%) and Franck Geffard (20%) |
| Related publication  | 1 paper in Computer Methods in Biomechanics and Biomedical Engineering    |

|                           |  |
|---------------------------|--|
| <b>Malala Vonjiniaina</b> |  |
| Date:                     | from Feb. 2017 to June 2017  |
| Location:                 | Univ Paris-Sud, LIMSI  |
| Title:                    | « Perception of French Sign Language: influence of the level of degradation of the virtual signer and of the level of the FSL observer » |
| Role:                     | Co-Supervisor 33% (with Dr. Annelies Braffort & Dr. Elise Prigent)   |

### **PhD Student supervision**

|                       |  |
|-----------------------|--|
| <b>Ioannis Delis</b>  |  |
| Date:                 | Jan. 2010 – Apr. 2013 (completed)  |
| Location:             | Italian Institute of Technology (Genoa, Italy)   |
| Title:                | « Novel single-trial computational approaches to the identification of modular muscle activation patterns and their evaluation in task space » |
| Role:                 | Co-supervisor (33% with Prof. Stefano Panzeri and Prof. Thierry Pozzo) - <u>unofficial</u>   |
| Last known position:  | post-doctoral fellow at Columbia University, New York  |
| Related Publications: | 6 publications from PhD work (J. Neuroscience, J. Neurophysiology, Front. Comp. Neurosc. x3 in a Research Topic, x1 Front. Human Neurosc.)     |

|                       |  |
|-----------------------|--|
| <b>Pauline Hilt</b>   |  |
| Date:                 | from Sept. 2012 to Dec. 2015 (completed)   |
| Location:             | Université de Bourgogne, Laboratoire INSERM U1093 Cognition, Action et Plasticité Sensorimotrice |
| Title:                | « Motor decision and modular control of a hyper-redundant system »                               |
| Role:                 | Co-director (50% with Prof. Thierry Pozzo, Université de Bourgogne) - <u>official</u>            |
| Last known position:  | post-doctoral fellow at Italian Institute of Technology, Ferrara                                 |
| Related Publications: | 1 publication from PhD work (Scientific Reports) – 1 article submitted                           |

### 3 Curriculum vitae

---

|                       |   |
|-----------------------|---|
| <b>Vu Van Hoan</b>    |   |
| Date:                 | from Sept. 2012 to Dec. 2016 ( <u>completed</u> )   |
| Location:             | Univ. Paris-Sud, CIAMS, Orsay   |
| Title:                | « Identification and simulation of motor command in 3D multijoint and unconstrained movements » |
| Role:                 | Co-director - 50% with Prof. Brice Isableu (Univ. Aix-Marseille) - <u>official</u>              |
| Last known position:  | post-doctoral fellow at the Institut des Sciences du Mouvement, Marseille                       |
| Related Publications: | 2 publications from PhD work (in Neuroscience and Scientific Reports)                           |

|                          |  |
|--------------------------|--|
| <b>Mohamed Benchiheb</b> |  |
| Date:                    | from Sept. 2013 to Apr. 2017 ( <u>PhD defense in Nov. 2017</u> )                       |
| Location:                | LIMSI-CNRS   |
| Title:                   | « Analysis and modeling of movements in French Sign Language »                         |
| Role:                    | Co-director - 50% with Dr. Annelies Braffort (LIMSI-CNRS, DR1 CNRS) - <u>official</u>  |
| Last known position:     | ATER, Department of Informatics, Univ. Paris-Sud                                       |
| Related Publications:    | 2 publications in peer-reviewed conference proceedings (ACM), 1 article in preparation |

|                      |   |
|----------------------|---|
| <b>Simon Bastide</b> |   |
| Date:                | started in Oct. 2017  |
| Location:            | Univ. Paris-Sud, CIAMS, CEA-LIST  |
| Title:               | « Adaptation of Humans to the interaction with an upper-limb exoskeleton: analysis and modeling of control laws » |
| Role:                | Co-director - 50% with Dr. Nicolas Vignais (30%) and Franck Geffard (20%) - <u>official</u>                       |

Finally, I am involved as a collaborator/co-supervisor in two PhD theses of previous Master students (see above, E. Hinnekens and A. Supiot).

### 3.5 Teaching, pedagogic and administrative duties

Since I am “Maître de Conférences” at Univ. Paris-Sud, I have been involved in the following teaching activities:

### 3.5 Teaching, pedagogic and administrative duties

| Topic   | Degree        | Nature | Annual hours (~TD) |
|---|---------------|--------|--------------------|
| “Pré-requis Scientifiques”                                  | L1            | TD     | 20h                |
| “Planification & contrôle du geste et de la posture”        | L3 APA&S      | CM     | 4h                 |
|   |               | TD     | 4h                 |
| “Biomécanique”  | L1            | CM     | 13.5h              |
|   |               | TD     | 13.5h              |
| “Statistiques”  | L3 Management | TD     | 15h                |
| “Analyse de données et statistiques<br>« niveau 2 » Matlab” | M2 PCMPS      | TD     | 10h                |
| “Traitement du Signal - Matlab”                             | M2 ISMH       | TD     | 30h                |
| “Maths pour le mouvement humain”                            | M1 ISMH       | CM     | 30h                |
|   |               | TD     | 30h                |
| “Théories du Contrôle Moteur”                               | M1 PCMPS/ISMH | CM     | 7.5h               |
|   |               | TD     | 5h                 |

Legend: CM = lecture, TD = tutorial classes, PCMPS=“Psychologie, Contrôle Moteur et Performance Sportive”, ISMH=“Ingénierie et Sciences du Mouvement Humain”

#### Total service per year

**2012-2013** : 150h ~TD (“décharge néo-MCF” from Univ. Paris-Sud)

**2013-2014** : 150h ~TD (“décharge néo-MCF” from Univ. Paris-Sud)

**2014-2015** : 192h ~TD

**2015-2016**: 192h ~TD

**2016-2017**: 202.25h ~TD

N.B. : within UFR STAPS at Univ. Paris-Sud, pedagogic duties can be equivalent to a fixed amount of practical tutorials hours (~TD hours) (e.g. 20h/year are counted for the Master program responsibility)

#### Pedagogic duties

- In charge of an e-learning project – AAP CEVU 2014 – budget 27 k€ (2014-2015)

Creation of online courses for the teaching of movement biomechanics for undergraduate students (L1 STAPS). It consisted in creating 11 webcasts (~10 minutes each), interactive

animations in 3D powered by Unity (e.g. basketball game to let student better apprehend a ball's trajectory in the gravity field), multiple-choice questionnaires to check the student's understanding after watching the webcast etc.

Online lessons were followed by ~500 students

Tutorial classes were also created to resolve sport biomechanics exercises in small groups (~30 students / group, TD)

- In charge of Master program (M1 « Psychologie, Contrôle Moteur et Performance Sportive » (PCMPS) - mention STAPS) for 2 full years (2015-2017)

With the newly created Université Paris-Saclay, new Masters were developed and ported by several Universities and Engineer Schools to reinforce collaborations and reduce costs.

The Master Program PCMPS is part of the "Sport and Human Movement Science School" (<http://www.universite-paris-saclay.fr/en/education/school/sports-sciences-and-human-movement>).

It opened in September 2015 but the work started in 2014 by anticipation.

My role was to recruit the teachers, select the students/candidates, organize the exams, create the schedule, supervise internships, organize oral examinations, maintain the website of the formation (<http://universite-paris-saclay.fr/en/education/master/human-movement-sport-sciences>), invite professional speakers and interaction with companies and sport federations, and manage any other issue related to the Master program.

- In charge of the teaching of Biomechanics for the Bachelor (« Licence Staps », L1, L2 to L3 levels at Univ. Paris-Sud).

Biomechanics is taught at several levels in the department and by several teachers for undergraduates. My role is to supervise and coordinate the teaching of biomechanics at UFR STAPS at Univ. Paris-Sud (~700 undergraduates involved and more than 10 teachers + teachers who are external to the institution/university and must be recruited specifically to teach those lessons).

#### **Administrative duties**

- Creation and maintenance of a specific website to handle exams for the whole UFR STAPS (~90 teachers concerned and all the formations, Bachelors & Masters). The website allows teachers to select exams to supervise in real time and automatically, and it counts their hours

up. The aim was to simplify the life of secretaries and teachers of UFR STAPS. Programmed in Python.

## 3.6 Scientific activity

### *Invited talks (lab seminars and workshops)*

- « The Cost of Time in Motor Control and its relation to the idiosyncrasy of movement vigor and individual traits », Third PACE Thematic Workshop “Robotics”, Italian Institute of Technology, Genoa (Italy), October, 2017
- « Why don't we move slower: the cost of time in the neural control of movement », LSIS Semirar, Université Toulon-Var, Toulon (France), May, 2016
- « Why don't we move slower: the cost of time in the neural control of movement », iCODE final congress, Gif-sur-Yvette (France), May, 2016
- « Direct and inverse optimal control for arm movement planning in humans », M2H Euromov Semirar, Montpellier (France), February, 2014
- « Why do humans move the way they do? Direct and inverse optimal control approaches », Journées de l'Université de Toulon, Toulon (France), April, 2013
- « Why do we move the way we do? An inverse optimal control approach », Séminaire d'Automatique du Plateau de Saclay, Laboratoire L2S-Supélec, Gif-Sur-Yvette (France), January, 2012
- « Integration of gravity during the motor planning of human movements », LAAS-CNRS, Toulouse (France), Feb., 2009
- « Integration of gravity during the motor planning of human movements », LSIS, Toulon (France), March, 2009
- « Integration of gravity during the motor planning of human movements », Italian Institute of Technology, Genoa (Italy), September, 2008

### *Co-organization of a workshop*

Conference: IROS 2012

Title: « Optimality principles and adaptation in humanoid robotic control »

Location: Vila Moura, Portugal

### 3 Curriculum vitae

---

Date: October, 7th, 2012

Co-organizers: S. Ivaldi (ISIR-UPMC), B. Berret (IIT/Univ. Paris-Sud), O. Sigaud (ISIR-UPMC), F. Nori (IIT)

Main speakers: Stephen Scott (Queen's university, Canada), Etienne Burdet (Imperial College, UK), David Franklin (Cambridge, UK), Jean-Paul Laumond (LAAS-CNRS, FR)

#### **Scientific collaborations (currently active)**

##### National

- Univ. Bourgogne (Prof. Thierry Pozzo, Prof. Charalambos Papaxanthis & Dr. Jérémie Gaveau), Dijon  
Topic: study of whole-body movements and muscle synergy organization, role of gravity in motor planning, eye/hand coordination in free endpoint reaching tasks
- ENSTA-ParisTech (Prof. Frédéric Jean, Palaiseau)  
Topic: study and modeling of human movement pace from the optimal control viewpoint and inverse optimal control
- Univ. Versailles Saint-Quentin – Raymond Poincaré Hospital (Dr. Didier Pradon, Garches), laboratory “Handicap Technological and Clinical Research Group (GRCTH)  
Topic: study of muscle organization during healthy and pathological gait using the space-by-time modularity
- LIMSI-CNRS (Dr. Annelies Braffort, CNRS, Orsay)  
Topic: study of French sign language from the motor control viewpoint using 3D motion capture techniques, with a modeling perspective

##### International

- Italian Institute of Technology of Genoa (Dr. Francesco Nori, Italy)  
Topic: Variable impedance actuators mimicking the co-contraction properties of human muscles and modeling in the open-loop stochastic optimal control framework
- Italian Institute of Technology of Genoa (Dr. Gabriel Baud-Bovy, Italy)  
Topic: Investigating the cost of time using haptic interfaces and an isometric reaching task
- Columbia University (Dr. Ioannis Delis, US, soon lecturer in Leeds University)  
Topic: design and development of new muscle synergy extraction methods to improve existing models: towards synergy extraction without time normalization and capturing the role of sensorimotor feedback

### **Diffusion of scientific work**

- Creation of a personal academic webpage (<http://hebergement.u-psud.fr/berret/>) including software and codes related to publications
- Member of the “experimentarium” (organism of scientific popularization) from 2006 to 2008 [http://experimentarium.u-bourgogne.fr/spip.php?page=article\\_a&id\\_rubrique=16&id\\_auteur=132](http://experimentarium.u-bourgogne.fr/spip.php?page=article_a&id_rubrique=16&id_auteur=132)

### **Research Grants**

**2014** Co-PI for an « AAP Attractivité Paris-Sud » project : « Development of motor primitives during the first year of life: sensorimotor study and modeling approach » with Dr. C. Teulier (50%) – budget 23 k€

**2014-2016** PI of a project within iCODE (Institute for Control and Decision) (IDEX Paris-Saclay) – budget 15.6k€: ‘Theoretical foundation of inverse optimal control and application to the identification of a time cost in human movements’. Collaborators: F. Jean (ENSTA), T. Deroche (CIAMS). Link: <http://www.icode-institute.fr/>

**2012 and 2013** PhD grants from Univ. Paris-Sud and the doctoral school « École Doctorale 566, Sciences du Sport, de la Motricité et du Mouvement Humain », ~100k€ twice

**2016-2019** Member of the steering committee (CoPil) of iCODE (Institute for Control and Decision) coordinated by Prof. Yacine Chitour (“AAP Institut de Recherche Stratégique” within Paris-Saclay). Involved in the “Exo” Research Initiative coordinated by Samer Alfayad (~300 k€ for the challenge “Exo” for building and developing an adjustable size whole-body exoskeleton).

**2017-2022** Junior member of IUF (75 k€)

**2017** PhD grant from IDEX Paris-Saclay for investigating motor control with upper-limb exoskeletons (~100 k€)

**2017** ERM grant (“Équipement de Recherche Mutualisé”) from Univ. Paris-Sud to create a research platform including an upper-limb exoskeleton with human motion capture devices (55 k€)

### **Professor Invitation**

- Dr. Francesco Nori (June, 2015 - 1 month)  
Invitation of Dr. Francesco Nori at Univ. Paris-Sud (CIAMS) in the framework of a research

project related to inverse optimal control approaches to human and humanoid movements, and application to their duration (cf. iCODE grant)

### **Referee for international journals**

- PLoS Computational Biology, PLoS One, Experimental Brain Research, Frontiers in Computational Neuroscience, Frontiers in Human Neuroscience, Journal of Neurophysiology, IEEE transactions on Industrial Electronics, IEEE transactions on Control Systems Technology, IEEE proceedings (IROS, Humanoids, BioRob...), International Journal of Social Robotics, Journal of Neuroscience Methods, Journal of NeuroEngineering and Rehabilitation
- “Outstanding Elsevier reviewer” award in 2014
- Review Editor for Frontiers in Computational Neuroscience

### **Project and thesis expertise**

- Expertise of an INSEP (« Institut national du sport, de l’expertise et de la performance ») project in 2013
- Member of PhD thesis committee (April 2017) at University of Genoa and IIT of Genoa
- Member of scientific committee for the ACAPS meeting (Dijon, 2017)

## **3.7 List of publications**

### **International Journal Publications (peer-reviewed)**

- 29.** P. M. Hilt, I. Delis, T. Pozzo and B. Berret, Spatiotemporal organization of whole-body muscle activity during upright reaching movements in various directions: modularity or not modularity?, *Biorxiv*, 2017
- 28.** V. H. Vu, B. Isableu and B. Berret, Adaptive use of interaction torque during arm reaching movement from the optimal control viewpoint, *Scientific Reports*, 2016.
- 27.** J. Gaveau, B. Berret, D. Angelaki, and C. Papaxanthis. Direction-dependent arm kinematics reveal optimal integration of gravity cues, *eLife*, 2016, 10.7554/eLife.16394.
- 26.** B. Berret and F. Jean, Why don’t we move slower? The value of time in the neural control of action, *The Journal of Neuroscience*, 36(4):1056-1070, 2016

25. V. H. Vu, B. Isableu and B. Berret, On the nature of motor planning variables during arm pointing movement: compositeness and speed dependence, 328:127–146, *Neuroscience*, 2016
24. P. Hilt, B. Berret, C. Papaxanthis, P. Stapley, and T. Pozzo, Evidence for subjective values guiding posture and movement coordination in a free-endpoint whole-body reaching task, *Scientific Reports*, 6, Article number:23868, 2016
23. I. Delis, S. Panzeri, T. Pozzo, and B. Berret, Task-discriminative space-by-time factorization of muscle activity, *Front. Hum. Neurosci.*, 9:399, 2015
22. B. Berret, A. Bisio, M. Jacono, and T. Pozzo, Reach Endpoint Formation during the Visuomotor Planning of Free Arm Pointing, *European Journal of Neuroscience*, 40(10):3491-3503, 2014
21. J. Gaveau, B. Berret, L. Demougeot, L. Fadiga, T. Pozzo, and C. Papaxanthis, Energy-related optimal control accounts for gravitational load: comparing shoulder, elbow and wrist rotations, *Journal of Neurophysiology*, 111(1):4-16, 2014
20. I. Delis, S. Panzeri, T. Pozzo, and B. Berret, A unifying model of concurrent spatial and temporal modularity in muscle activity, *Journal of Neurophysiology*, 111(3):675-693, 2014
19. I. Delis, B. Berret, T. Pozzo, and S. Panzeri, A methodology for assessing the effect of correlations among muscle synergy activations on task-discriminating information, *Front. Comput. Neurosci.*, 7:54 2013
18. I. Delis, B. Berret, T. Pozzo, and S. Panzeri, Quantitative evaluation of muscle synergy models: a single-trial task decoding approach, *Front. Comput. Neurosci.*, 7:8, 2013
17. E. Chiovetto, B. Berret, I. Delis, S. Panzeri, and T. Pozzo, Investigating reduction of dimensionality during single-joint elbow movements: a case study on muscle synergies, *Front. Comput. Neurosci.*, 7:11, 2013
16. C. Alessandro, I. Delis, F. Nori, S. Panzeri, and B. Berret, Muscle synergies in neuroscience and robotics: from input-space to task-space perspectives, *Front. Comput. Neurosci.*, 7:43, 2013 (Review)
15. S. Ivaldi, O. Sigaud, B. Berret, and F. Nori, From Humans to Humanoids: the Optimal Control Framework, *Paladyn Journal of Behavioral Robotics*, 3(2):75-91, 2012 (Review)
14. A. Sciutti, L. Demougeot, B. Berret, S. Toma, G. Sandini, C. Papaxanthis, and T. Pozzo, Visual gravity influences arm movement planning, *Journal of Neurophysiology*, 106(4):2086-102, 2012

13. B. Berret, E. Chiovetto, F. Nori, and T. Pozzo, Evidence for Composite Cost Functions in Arm Movement Planning: An Inverse Optimal Control Approach, *PLoS Comput Biol*, 7(10):e1002183, 2011
12. B. Berret, E. Chiovetto, F. Nori, and T. Pozzo, Manifold reaching paradigm: how do we handle target redundancy?, *Journal of Neurophysiology*, 106(4):2086-102, 2011
11. A. Tolambiya, E. Thomas, E. Chiovetto, B. Berret, and T. Pozzo, An Ensemble Analysis of Electromyographic Activity During Whole Body Pointing with the use of Support Vector Machines, *PLoS One*, 6(7):e20732, 2011
10. J. Gaveau, C. Paizis, B. Berret, T. Pozzo, and C. Papaxanthis, Sensorimotor adaptation of point-to-point arm movements after space-flight: the role of the internal representation of gravity force in trajectory planning, *Journal of Neurophysiology*, 106(2):620-9, 2011
9. E. Chiovetto, B. Berret, and T. Pozzo, Tri-dimensional and triphasic muscle organization of whole-body pointing movements, *Neuroscience*, 170(4):1223-1238, 2010
8. L. Fautrelle, C. Prablanc, B. Berret, Y. Ballay, and F. Bonnetblanc, Pointing to double-step visual stimuli from a standing position: very short latency (express) corrections are observed in upper and lower limbs and may not require cortical involvement, *Neuroscience*, 169(2):697-705, 2010
7. I. Delis, E. Chiovetto, and B. Berret, On the Origins of Modularity in Motor Control, *The Journal of Neuroscience*, 30(22):7451-7452, 2010 (journal club)
6. J-P. Gauthier, B. Berret, and F. Jean, A Biomechanical Inactivation Principle, *Proceedings of the Steklov Institute of Mathematics*, 268:93-116, 2010
5. L. Fautrelle, B. Berret, E. Chiovetto, T. Pozzo, and F. Bonnetblanc, Equilibrium constraints do not affect the timing of muscular synergies during the initiation of a whole body reaching movement, *Experimental Brain Research*, 203(1):147-58, 2010
4. B. Berret, F. Bonnetblanc, C. Papaxanthis, and T. Pozzo, Modular control of pointing beyond arm's length, *The Journal of Neuroscience*, 29(1):191-205, 2009
3. B. Berret, C. Darlot, F. Jean, T. Pozzo, C. Papaxanthis, and J-P. Gauthier, The Inactivation Principle: Mathematical Solutions minimizing the Absolute Work and Biological Implications for the Planning of Arm movements, *PLoS Comput Biol*, 4(10):e1000194, 2008
2. B. Berret, J-P. Gauthier, and C. Papaxanthis, How humans control arm movements, *Proceedings of the Steklov Institute of Mathematics*, 261:44-58, 2008

1. C. Paizis, C. Papaxanthis, B. Berret, and T. Pozzo, Reaching beyond arm length in normal aging: adaptation of hand trajectory and dynamic equilibrium, *Behavioral Neuroscience*, 122(6):1361-70, 2008

#### **International Conference Publications (peer-reviewed)**

11. M. Benchiheb, B. Berret, and A. Braffort. Collecting and Analysing a Motion-Capture Corpus of French Sign Language, Proceedings of the 7th Workshop on the Representation and Processing of Sign Languages: Corpus Mining, *10th edition of the Language Resources and Evaluation Conference (LREC)*, 2016.
10. A. Braffort, M. Benchiheb, and B. Berret, APLUS: A 3D Corpus of French Sign Language, *Proceedings of the 17th International ACM SIGACCESS Conference on Computers & Accessibility (ASSETS)*, 381-382, 2015.
9. V.H. Vu, B. Isableu, and B. Berret, Velocity-dependent tuning of motor strategy during 3D arm movement and its relationship to composite cost functions, *33rd International Conference on Sport Biomechanics (ISBS)*, sciencesconf.org:isbs2015:58612, 2015
8. B. Berret, I Yung, and F. Nori, Open-loop stochastic optimal control of a passive noise-rejection variable stiffness actuator: application to unstable tasks, *IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS)*, 2013
7. B. Berret, G. Sandini, and F. Nori, Design principles for muscle-like variable impedance actuators with noise rejection property via co-contraction, *IEEE-RAS International Conference on Humanoid Robots (HUMANOIDS)*, 2012
6. L. Fiorio, A. Parmiggiani, B. Berret, G. Sandini, and F. Nori, pnrVSA: human-like actuator with non-linear springs in agonist-antagonist configuration, *IEEE-RAS International Conference on Humanoid Robots (HUMANOIDS)*, 2012
5. L. Patanè, A. Sciutti, B. Berret, V. Squeri, L. Masia, G. Sandini, and F. Nori, Modeling Kinematic Forward Model Adaptation by Modular Decomposition, *Fourth IEEE RAS/EMBS International Conference on Biomedical Robotics and Biomechanics (BIOROB)*, 2012
4. F. Nori, B. Berret, L.Fiorio, A.Parmiggiani, and G.Sandini, Control of a single degree of freedom noise-rejecting variable impedance, *Proceedings of the 10th international IFAC symposium on Robot Control (SYROCO)*, 2012
3. B. Berret, S. Ivaldi, F. Nori, and G. Sandini, Stochastic optimal control with variable impedance manipulators in presence of uncertainties and delayed feedback, *IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS)*, 2011

### 3 Curriculum vitae

---

2. B. Berret, F. Jean, and J.P. Gauthier, A biomechanical theory of inactivation, *Computer Methods in Biomechanics and Biomedical Engineering*, 12(1):41-42, 2009
1. B. Berret, J-P. Gauthier, and V. Zakalyukin, Nonholonomic Interpolation: a general methodology for motion planning in robotics, *17th International Symposium on Mathematical Theory of Networks and Systems*, 2006

N.B.: posters and abstracts are not included for simplicity.

#### **Book chapters (peer-reviewed)**

1. F. Jean and B. Berret, On the duration of human movement: from self-paced to slow/fast reaches up to Fitts's law, *Springer Star Series « Geometric and Numerical Foundations of Movements »*, 2017

#### **Patent**

| Application           | Filing Date           | Publication       | Publication Date     | Title   | Inventors   |
|-----------------------|-----------------------|-------------------|----------------------|---|---|
| PCT/IB2013<br>/056834 | August<br>23,<br>2013 | WO<br>2014/033603 | February<br>28, 2014 | Variable-Stiffness<br>Actuator With<br>Passive Disturbance<br>Rejection | Francesco NORI,<br>Bastien BERRET,<br>Luca FIORIO,<br>Alberto<br>PARMIGGIANI,<br>Giulio SANDINI |

Patent's description: This patent describes a novel type of Variable Stiffness Actuator (VSA) for actuating a robot joint. The actuator possesses a fundamental feature, nominally the ability to augment passive disturbance rejection. In this context, the adjective passive refers to the fact rejection is not obtained with active control loops but derive from the intrinsic (i.e. passive) properties of the system. The set of actuators possessing this feature will be nominated "noise rejecting passive VSA" (nrpVSA). At first, in order for the patent to include multiple design solutions, we mathematically characterize a wide set of nrpVSA actuators, by pointing out different mechanical configurations leading to the desired joint-level noise rejection capability. Then, among multiple design solutions, one specific design is chosen and characterized. The proposed design is based on an agonist-antagonist configuration of two electric motors. Stiffness regulation is obtained by non-linear springs, which can be stiffened up via motors co-activation. Feedback-free

joint-level noise rejection is finally the result of increasing the stiffness of all the elastic elements that connect the joint to the world frame. A proof-of-concept example shows how the proposed actuator deals with instabilities and disturbances exploiting co-activation and without resorting to position feedback.

See also: <https://encrypted.google.com/patents/EP2890527A1?cl=tr>

### 3.8 Five most relevant publications

|           |  |
|-----------|--|
| #1 Title  | Why don't we move slower? The value of time in the neural control of action  |
| Authors   | B. Berret and F. Jean  |
| Reference | The Journal of Neuroscience, 36(4):1056-1070, 2016   |
| Abstract  | <p>To want something now rather than later is a common attitude that reflects the brain's tendency to value the passage of time. Because the time taken to accomplish an action inevitably delays task achievement and reward acquisition, this idea was ported to neural movement control within the "cost of time" theory. This theory provides a normative framework to account for the underpinnings of movement time formation within the brain and the origin of a self-selected pace in human and animal motion. Then, how does the brain exactly value time in the control of action? To tackle this issue, we used an inverse optimal control approach and developed a general methodology allowing to squarely sample infinitesimal values of the time cost from experimental motion data. The cost of time underlying saccades was found to have a concave growth, thereby confirming previous results on hyperbolic reward discounting, yet without making any prior assumption about this hypothetical nature. For self-paced reaching, however, movement time was primarily valued according to a striking sigmoidal shape; its rate of change consistently presented a steep rise before a maximum was reached and a slower decay was observed. Theoretical properties of uniqueness and robustness of the inferred time cost were established for the class of problems under investigation, thus reinforcing the significance of the present findings. These results may offer a unique opportunity to uncover how the brain values the passage of time in healthy and pathological motor control and shed new light on the processes underlying action invigoration.</p> |

|           |  |
|-----------|--|
| #2 Title  | The Inactivation Principle: Mathematical Solutions minimizing the Absolute Work and Biological Implications for the Planning of Arm movements  |
| Authors   | B. Berret, C. Darlot, F. Jean, T. Pozzo, C. Papaxanthis, and J-P. Gauthier   |
| Reference | PLoS Comput Biol, 4(10):e1000194, 2008   |
| Abstract  | <p>An important question in the literature focusing on motor control is to determine which laws drive biological limb movements. This question has prompted numerous investigations analyzing arm movements in both humans and monkeys. Many theories assume that among all possible movements the one actually performed satisfies an optimality criterion. In the framework of optimal control theory, a first approach is to choose a cost function and test whether the proposed model fits with experimental data. A second approach (generally considered as the more difficult) is to infer the cost function from behavioral data. The cost proposed here includes a term called the absolute work of forces, reflecting the mechanical energy expenditure. Contrary to most investigations studying optimality principles of arm movements, this model has the particularity of using a cost function that is not smooth. First, a mathematical theory related to both direct and inverse optimal control approaches is presented. The first theoretical result is the Inactivation Principle, according to which minimizing a term similar to the absolute work implies simultaneous inactivation of agonistic and antagonistic muscles acting on a single joint, near the time of peak velocity. The second theoretical result is that, conversely, the presence of non-smoothness in the cost function is a necessary condition for the existence of such inactivation. Second, during an experimental study, participants were asked to perform fast vertical arm movements with one, two, and three degrees of freedom. Observed trajectories, velocity profiles, and final postures were accurately simulated by the model. In accordance, electromyographic signals showed brief simultaneous inactivation of opposing muscles during movements. Thus, assuming that human movements are optimal with respect to a certain integral cost, the minimization of an absolute-work-like cost is supported by experimental observations. Such types of optimality criteria may be applied to a large range of biological movements.</p> |

### 3.8 Five most relevant publications

|           |   |
|-----------|---|
| #3 Title  | Modular control of pointing beyond arm's length   |
| Authors   | B. Berret, F. Bonnetblanc, C. Papaxanthis, and T. Pozzo   |
| Reference | Journal of Neuroscience, 29(1) :191-205, 2009   |
| Abstract  | <p>Hand reaching and bipedal equilibrium are two important functions of the human motor behavior. However, how the brain plans goal-oriented actions combining target reaching with equilibrium regulation is not yet clearly understood. An important question is whether postural control and reaching are integrated in one single module or controlled separately. Here, we show that postural control and reaching motor commands are processed by means of a modular and flexible organization. Principal component and correlation analyses between pairs of angles were used to extract global and local coupling during a whole-body pointing beyond arm's length. A low-dimensional organization of the redundant kinematic chain allowing simultaneous target reaching and regulation of the center of mass (CoM) displacement in extrinsic space emerged from the first analysis. In follow-up experiments, both the CoM and finger trajectories were constrained by asking participants to reach from a reduced base of support with or without knee flexion, or by moving the endpoint along a predefined trajectory (straight or semicircular trajectories). Whereas joint covaried during free conditions and under equilibrium restrictions, it was decomposed in two task-dependent and task-independent modules, corresponding to a dissociation of arm versus legs, trunk, and head coordination, respectively, under imposed finger path conditions. A numerical simulation supported the idea that both postural and focal subtasks are basically integrated into the same motor command and that the CNS is able to combine or to separate the movement into autonomous functional synergies according to the task requirements.</p> |

|           |  |
|-----------|--|
| #4 Title  | Evidence for Composite Cost Functions in Arm Movement Planning: An Inverse Optimal Control Approach  |
| Authors   | B. Berret, E. Chiovetto, F. Nori, and T. Pozzo   |
| Reference | PLoS Comput Biol, 7(10):e1002183, 2011   |
| Abstract  | <p>An important issue in motor control is understanding the basic principles underlying the accomplishment of natural movements. According to optimal control theory, the problem can be stated in these terms: what cost function do we optimize to coordinate the many more degrees of freedom than necessary to fulfill a specific motor goal? This question has not received a final answer yet, since what is optimized partly depends on the requirements of the task. Many cost functions were proposed in the past, and most of them were found to be in agreement with experimental data. Therefore, the actual principles on which the brain relies to achieve a certain motor behavior are still unclear. Existing results might suggest that movements are not the results of the minimization of single but rather of composite cost functions. In order to better clarify this last point, we consider an innovative experimental paradigm characterized by arm reaching with target redundancy. Within this framework, we make use of an inverse optimal control technique to automatically infer the (combination of) optimality criteria that best fit the experimental data. Results show that the subjects exhibited a consistent behavior during each experimental condition, even though the target point was not prescribed in advance. Inverse and direct optimal control together reveal that the average arm trajectories were best replicated when optimizing the combination of two cost functions, nominally a mix between the absolute work of torques and the integrated squared joint acceleration. Our results thus support the cost combination hypothesis and demonstrate that the recorded movements were closely linked to the combination of two complementary functions related to mechanical energy expenditure and joint-level smoothness.</p> |

|           |   |
|-----------|---|
| #5 Title  | A unifying model of concurrent spatial and temporal modularity in muscle activity   |
| Authors   | I. Delis, S. Panzeri, T. Pozzo, and B. Berret   |
| Reference | Journal of Neurophysiology, 111(3):675-693, 2014  |
| Abstract  | <p>Modularity in the central nervous system (CNS), i.e. the brain capability to generate a wide repertoire of movements by combining a small number of building blocks ("modules"), is thought to underlie the control of movement. Numerous studies reported evidence for such a modular organization by identifying invariant muscle activation patterns across various tasks. However, previous studies relied on decompositions differing in both the nature and dimensionality of the identified modules. Here, we derive a single framework that encompasses all influential models of muscle activation modularity. We introduce a new model (named space-by-time decomposition) that factorizes muscle activations into concurrent spatial and temporal modules. To infer these modules, we develop an algorithm, referred to as sample-based non-negative matrix tri-factorization (sNM3F). We test the space-by-time decomposition on a comprehensive electromyographic dataset recorded during execution of arm pointing movements and show that it provides a low-dimensional yet accurate, highly flexible and task-relevant representation of muscle patterns. The extracted modules have a well-characterized functional meaning and implement an efficient trade-off between replication of the original muscle patterns and task discriminability. Furthermore, they are compatible with the modules extracted from existing models such as synchronous synergies and temporal primitives, and generalize time-varying synergies. Our results indicate the effectiveness of a simultaneous but separate condensation of spatial and temporal dimensions of muscle patterns. The space-by-time decomposition accommodates a unified view of the hierarchical mapping from task parameters to coordinated muscle activations, which could be employed as a reference framework for studying compositional motor control.</p> |

# Appendix

## Cost of time computation in a simple setting.

The value  $g(t)$  (see Eq. 2.2) can be computed for linear-quadratic problems with a one-dimensional control as follows.

Consider a linear system dynamics of the form

$$\frac{d\mathbf{x}}{d\tau} = \dot{\mathbf{x}} = A\mathbf{x} + Bu \quad (4.1)$$

where  $\mathbf{x}$  is the system state and  $u$  the 1-D control (time-varying quantities, i.e. functions of time  $\tau$ ).

Next consider a fixed time OCP whose aim is to find the optimal control  $u(\tau)$  and the corresponding trajectory  $\mathbf{x}(\tau)$  for  $\tau \in [0, t]$ , joining a given initial state  $\mathbf{x}(0) = \mathbf{x}_0$  to a given final state  $\mathbf{x}(t) = \mathbf{x}_f$ , that minimize the following integral cost (called “effort” in general):

$$C(u) = \int_0^t |u(\tau)|^2 d\tau. \quad (4.2)$$

To solve this OCP, we can use Pontryagin Maximum Principle (Pontryagin et al., 1964; Kirk, 1970), which gives necessary conditions of optimality, and define the Hamiltonian associated with this problem as follows:

$$\mathcal{H}_0(u, \mathbf{x}, \mathbf{p}) = u^2 + \mathbf{p}^\top (A\mathbf{x} + Bu) \quad (4.3)$$

where  $\mathbf{p}$  is the co-state (or adjoint) vector.

We now compute the optimal control that minimizes the Hamiltonian with respect to  $u$  and get:

$$u^* = -\frac{1}{2}B^\top \mathbf{p}. \quad (4.4)$$

The co-state equation is given by:

$$\dot{\mathbf{p}} = -\frac{\partial \mathcal{H}}{\partial \mathbf{x}} = -A^\top \mathbf{p} \quad (4.5)$$

and thus the optimally controlled dynamics writes:

$$\dot{\mathbf{x}} = A\mathbf{x} - \frac{1}{2}BB^\top \mathbf{p} \quad (4.6)$$

Furthermore, we know that for this time-invariant problem the minimized Hamiltonian will be constant along the optimal trajectory:

$$\mathcal{H}_0(u^*, \mathbf{x}, \mathbf{p}) = -\frac{1}{4}\mathbf{p}^\top BB^\top \mathbf{p} + \mathbf{p}^\top A\mathbf{x} = \mathcal{H}_0^* = \text{constant}. \quad (4.7)$$

Let us define the matrix:

$$H = \begin{pmatrix} A & -\frac{1}{2}BB^\top \\ 0 & -A^\top \end{pmatrix}. \quad (4.8)$$

Defining  $\xi = \begin{pmatrix} \mathbf{x} \\ \mathbf{p} \end{pmatrix}$ , we get the Hamiltonian system

$$\dot{\xi} = H\xi \quad (4.9)$$

whose solution writes as follows:

$$\xi(\tau) = \Phi(\tau)\xi_0 \quad (4.10)$$

where  $\Phi(\tau)$  is the state-transition matrix from  $\tau = 0$ , defined as  $\Phi(\tau) = \exp(H\tau)$  and  $\xi_0 = \begin{pmatrix} \mathbf{x}_0 \\ \mathbf{p}_0 \end{pmatrix}$ .

We can partition the matrix  $\Phi(\tau)$  in four blocks as follows:

$$\Phi(\tau) = \begin{pmatrix} \Phi_{11}(\tau) & \Phi_{12}(\tau) \\ 0 & \Phi_{22}(\tau) \end{pmatrix}, \quad (4.11)$$

where  $\Phi_{11}(\tau) = \exp(A\tau)$ ,  $\Phi_{22}(\tau) = \exp(-A^\top\tau)$  and  $\Phi_{12}(\tau) = -\frac{1}{2}\int_0^\tau \exp(A(\tau-s))BB^\top \exp(-A^\top s)ds$ .

From this block matrix and  $\xi(\tau) = \Phi(\tau)\xi_0$ , we conclude in particular that

$$\mathbf{x}_f = \mathbf{x}(t) = \Phi_{11}(t)\mathbf{x}_0 + \Phi_{12}(t)\mathbf{p}_0. \quad (4.12)$$

Therefore, if  $\Phi_{12}^{-1}(t)$  exists (which is the case if the system is fully controllable), we get:

$$\mathbf{p}_0 = \Phi_{12}^{-1}(t)(\mathbf{x}_f - \Phi_{11}(t)\mathbf{x}_0). \quad (4.13)$$

Since the Hamiltonian is constant along the optimal trajectory we get:

$$\mathcal{H}_0^* = -\frac{1}{4}\mathbf{p}_0^\top BB^\top \mathbf{p}_0 + \mathbf{p}_0^\top A\mathbf{x}_0. \quad (4.14)$$

Finally, the infinitesimal cost of time at time  $t$  is, according to Eq. 2.3:

$$g(t) = -\mathcal{H}_0^* = \frac{1}{4}\mathbf{p}_0^\top BB^\top \mathbf{p}_0 - \mathbf{p}_0^\top A\mathbf{x}_0. \quad (4.15)$$

Eventually, only one matrix exponential, i.e.  $\exp(Ht)$ , has to be computed in order to obtain the value of  $g(t)$ . If we repeat this procedure for different durations  $t$  we can get different values  $g(t)$  and, therefore, we can infer the shape of  $g(\cdot)$  on some time interval and integrate it to recover the actual cost of time  $G(T) = \int_0^T g(t)dt$  (up to a constant though due to the integration).

See also Berret and Jean (2016) and Jean and Berret (2017) for further details.

# Bibliography

- Ajami, A., Gauthier, J.-P., Maillot, T., and Serres, U. (2013). How humans fly. *ESAIM: COCV*, 19(4):1030–1054.
- Ajemian, R. and Hogan, N. (2010). Experimenting with theoretical motor neuroscience.
- Alessandro, C., Carbajal, J. P., and d’Avella, A. (2013a). A computational analysis of motor synergies by dynamic response decomposition. *Front. Comput. Neurosci.*, 7.
- Alessandro, C., Delis, I., Nori, F., Panzeri, S., and Berret, B. (2013b). Muscle synergies in neuroscience and robotics: from input-space to task-space perspectives. *Front. Comput. Neurosci.*, 7:43.
- Alessandro, C. and Nori, F. (2012). Identification of synergies by optimization of trajectory tracking tasks. In *Biomedical Robotics and Biomechatronics (BioRob), 2012 4th IEEE RAS & EMBS International Conference on*, pages 924–930. IEEE.
- Allen, J. L. and Neptune, R. R. (2012). Three-dimensional modular control of human walking. *J. Biomech.*, 45(12):2157–2163.
- Atkeson, C. G. and Hollerbach, J. M. (1985). Kinematic features of unrestrained vertical arm movements. *J. Neurosci.*, 5(9):2318–2330.
- Baraduc, P., Thobois, S., Gan, J., Broussolle, E., and Desmurget, M. (2013). A common optimization principle for motor execution in healthy subjects and parkinsonian patients. *J. Neurosci.*, 33(2):665–677.
- Bellman, R. E. (1957). *Dynamic Programming*. Princeton, NJ.
- Bennequin, D., Fuchs, R., Berthoz, A., and Flash, T. (2009). Movement timing and invariance arise from several geometries. *PLoS Comput. Biol.*, 5(7):e1000426.
- Berardelli, A., Rothwell, J. C., Thompson, P. D., and Hallett, M. (2001). Pathophysiology of bradykinesia in parkinson’s disease. *Brain*, 124(Pt 11):2131–2146.
- Berger, D. J., Gentner, R., Edmunds, T., Pai, D. K., and d’Avella, A. (2013). Differences in adaptation rates after virtual surgeries provide direct evidence for modularity. *J. Neurosci.*, 33(30):12384–12394.
- Bernardin, D., Isableu, B., Fourcade, P., and Bardy, B. G. (2005). Differential exploitation of the inertia tensor in multi-joint arm reaching. *Exp. Brain Res.*, 167(4):487–495.
- Berniker, M. and Körding, K. P. (2015). Deep networks for motor control functions. *Front. Comput. Neurosci.*, 9.
- Bernstein, N. (1967). *The Coordination and Regulation of Movements*. Oxford: Pergamon Press.

## Bibliography

---

- Berret, B., Bisio, A., Jacono, M., and Pozzo, T. (2014). Reach endpoint formation during the visuomotor planning of free arm pointing. *Eur. J. Neurosci.*, 40(10):3491–3503.
- Berret, B., Bonnetblanc, F., Papaxanthis, C., and Pozzo, T. (2009). Modular control of pointing beyond arm's length. *J. Neurosci.*, 29(1):191–205.
- Berret, B., Chiovetto, E., Nori, F., and Pozzo, T. (2011a). Evidence for composite cost functions in arm movement planning: an inverse optimal control approach. *PLoS Comput. Biol.*, 7(10):e1002183.
- Berret, B., Chiovetto, E., Nori, F., and Pozzo, T. (2011b). Manifold reaching paradigm: how do we handle target redundancy? *J. Neurophysiol.*, 106(4):2086–2102.
- Berret, B., Darlot, C., Jean, F., Pozzo, T., Papaxanthis, C., and Gauthier, J. P. (2008a). The inactivation principle: mathematical solutions minimizing the absolute work and biological implications for the planning of arm movements. *PLoS Comput. Biol.*, 4(10):e1000194.
- Berret, B., Gauthier, J. P., and Papaxanthis, C. (2008b). How humans control arm movements. *Proceedings of the Steklov Institute of Mathematics*, 261:44–58.
- Berret, B., Ivaldi, S., Nori, F., and Sandini, G. (2011c). Stochastic optimal control with variable impedance manipulators in presence of uncertainties and delayed feedback. In *Proc. IEEE/RSJ Int Intelligent Robots and Systems (IROS) Conf*, pages 4354–4359.
- Berret, B. and Jean, F. (2016). Why don't we move slower? the value of time in the neural control of action. *J. Neurosci.*, 36(4):1056–1070.
- Berret, B., Yung, I., and Nori, F. (2013). Open-loop stochastic optimal control of a passive noise-rejection variable stiffness actuator: application to unstable tasks. In *IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS 2013)*, Tokyo, Japan.
- Bornstein, M. H. and Bornstein, H. G. (1976). The pace of life. *Nature*, 259(5544):557–559.
- Brochier, T., Spinks, R. L., Umiltà, M. A., and Lemon, R. N. (2004). Patterns of muscle activity underlying object-specific grasp by the macaque monkey. *J. Neurophysiol.*, 92(3):1770–1782.
- Buneo, C. A., Soechting, J. F., and Flanders, M. (1994). Muscle activation patterns for reaching: the representation of distance and time. *J. Neurophysiol.*, 71(4):1546–1558.
- Burdet, E., Osu, R., Franklin, D. W., Milner, T. E., and Kawato, M. (2001). The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature*, 414(6862):446–449.
- Cappellini, G., Ivanenko, Y. P., Poppele, R. E., and Lacquaniti, F. (2006). Motor patterns in human walking and running. *J. Neurophysiol.*, 95(6):3426–37.
- Cheung, V. C., d'Avella, A., Tresch, M. C., and Bizzi, E. (2005). Central and sensory contributions to the activation and organization of muscle synergies during natural motor behaviors. *J. Neurosci.*, 25(27):6419–34.
- Cheung, V. C., Piron, L., Agostini, M., Silvoni, S., Turolla, A., and Bizzi, E. (2009). Stability of muscle synergies for voluntary actions after cortical stroke in humans. *Proc. Natl. Acad. Sci. U.S.A.*, 106(46):19563–8.

- Cheung, V. C. K., Turolla, A., Agostini, M., Silvoni, S., Bennis, C., Kasi, P., Paganoni, S., Bonato, P., and Bizzi, E. (2012). Muscle synergy patterns as physiological markers of motor cortical damage. *Proc. Natl. Acad. Sci. U.S.A.*, 109(36):14652–14656.
- Chhabra, M. and Jacobs, R. A. (2006). Properties of synergies arising from a theory of optimal motor behavior. *Neural Comput.*, 18(10):2320–2342.
- Chiovetto, E., Berret, B., Delis, I., Panzeri, S., and Pozzo, T. (2013). Investigating reduction of dimensionality during single-joint elbow movements: a case study on muscle synergies. *Front. Comput. Neurosci.*, 7:11.
- Chiovetto, E., Berret, B., and Pozzo, T. (2010). Tri-dimensional and triphasic muscle organization of whole-body pointing movements. *Neuroscience*, 170(4):1223–1238.
- Chittaro, F., Jean, F., and Mason, P. (2013). On the inverse optimal control problems of the human locomotion: stability and robustness of the minimizers. *Journal of Mathematical Sciences*, 195(3):269–287.
- Choi, J. E. S., Vaswani, P. A., and Shadmehr, R. (2014). Vigor of Movements and the Cost of Time in Decision Making. *The Journal of Neuroscience*, 34(4):1212–1223.
- Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Foster, J. D., Nuyujukian, P., Ryu, S. I., and Shenoy, K. V. (2012). Neural population dynamics during reaching. *Nature*, 487(7405):51–56.
- Churchland, M. M., Santhanam, G., and Shenoy, K. V. (2006). Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach. *J. Neurophysiol.*, 96(6):3130–3146.
- Chvatal, S. A., Torres-Oviedo, G., Safavynia, S. A., and Ting, L. H. (2011). Common muscle synergies for control of center of mass and force in nonstepping and stepping postural behaviors. *J. Neurophysiol.*, 106(2):999–1015.
- Clark, D. J., Ting, L. H., Zajac, F. E., Neptune, R. R., and Kautz, S. A. (2010). Merging of healthy motor modules predicts reduced locomotor performance and muscle coordination complexity post-stroke. *J. Neurophysiol.*, 103(2):844–857.
- Cluff, T. and Scott, S. H. (2015). Apparent and actual trajectory control depend on the behavioral context in upper limb motor tasks. *J. Neurosci.*, 35(36):12465–12476.
- Cohen, J. Y. (2015). Dopamine and serotonin signals for reward across time scales. *Science*, 350(6256):47–48.
- Crevecoeur, F., McIntyre, J., Thonnard, J.-L., and Lefèvre, P. (2010). Movement stability under uncertain internal models of dynamics. *J. Neurophysiol.*, 104(3):1301–1313.
- Crevecoeur, F., Thonnard, J. L., and Lefèvre, P. (2009). Optimal integration of gravity in trajectory planning of vertical pointing movements. *J. Neurophysiol.*, 102(2):786–796.
- Danziger, Z. and Mussa-Ivaldi, F. A. (2012). The influence of visual motion on motor learning. *J. Neurosci.*, 32(29):9859–9869.
- d’Avella, A. and Bizzi, E. (2005). Shared and specific muscle synergies in natural motor behaviors. *Proc. Natl. Acad. Sci. U.S.A.*, 102(8):3076–3081.

## Bibliography

---

- d'Avella, A., Fernandez, L., Portone, A., and Lacquaniti, F. (2008). Modulation of phasic and tonic muscle synergies with reaching direction and speed. *J. Neurophysiol.*, 100(3):1433–1454.
- d'Avella, A. and Pai, D. K. (2010). Modularity for sensorimotor control: evidence and a new prediction. *Journal of motor behavior*, 42(6):361–369.
- d'Avella, A., Portone, A., Fernandez, L., and Lacquaniti, F. (2006). Control of fast-reaching movements by muscle synergy combinations. *J. Neurosci.*, 26(30):7791–7810.
- d'Avella, A., Saltiel, P., and Bizzi, E. (2003). Combinations of muscle synergies in the construction of a natural motor behavior. *Nat. Neurosci.*, 6(3):300–308.
- d'Avella, A. and Tresch, M. C. (2001). Modularity in the motor system: decomposition of muscle patterns as combinations of time-varying synergies. In Dietterich, T. G., Becker, S., and Ghahramani, Z., editors, *NIPS*, pages 141–148. MIT Press.
- de Rugy, A., Loeb, G. E., and Carroll, T. J. (2012). Muscle coordination is habitual rather than optimal. *J. Neurosci.*, 32(21):7384–7391.
- de Rugy, A., Loeb, G. E., and Carroll, T. J. (2013). Are muscle synergies useful for neural control? *Front. Comput. Neurosci.*, 7:19.
- Delis, I., Berret, B., Pozzo, T., and Panzeri, S. (2013a). A methodology for assessing the effect of correlations among muscle synergy activations on task-discriminating information. *Front. Comput. Neurosci.*, 7:54.
- Delis, I., Berret, B., Pozzo, T., and Panzeri, S. (2013b). Quantitative evaluation of muscle synergy models: a single-trial task decoding approach. *Front. Comput. Neurosci.*, 7:8.
- Delis, I., Panzeri, S., Pozzo, T., and Berret, B. (2014). A unifying model of concurrent spatial and temporal modularity in muscle activity. *J. Neurophysiol.*, 111(3):675–693.
- Delis, I., Panzeri, S., Pozzo, T., and Berret, B. (2015). Task-discriminative space-by-time factorization of muscle activity. *Front. Hum. Neurosci.*, 9:399.
- Desmurget, M., Péliſson, D., Rossetti, Y., and Prablanc, C. (1998). From eye to hand: planning goal-directed movements. *Neurosci. Biobehav. Rev.*, 22(6):761–788.
- Desmurget, M., Richard, N., Harquel, S., Baraduc, P., Szathmari, A., Mottolese, C., and Sirigu, A. (2014). Neural representations of ethologically relevant hand/mouth synergies in the human precentral gyrus. *Proc. Natl. Acad. Sci. U.S.A.*, 111(15):5718–5722.
- Diedrichsen, J., Shadmehr, R., and Ivry, R. B. (2009). The coordination of movement: optimal feedback control and beyond. *Trends Cogn Sci.*
- Dominici, N., Ivanenko, Y. P., Cappellini, G., d'Avella, A., Mondīŕœ, V., Cicchese, M., Fabiano, A., Silei, T., Di Paolo, A., Giannini, C., Poppele, R. E., and Lacquaniti, F. (2011). Locomotor primitives in newborn babies and their development. *Science*, 334(6058):997–999.
- Douglas, J. (1941). Solution of the inverse problem of the calculus of variations. *Transactions of the American Mathematical Society*, 50(1):71–128.

- Dudman, J. T. and Krakauer, J. W. (2016). The basal ganglia: from motor commands to the control of vigor. *Curr. Opin. Neurobiol.*, 37:158–166.
- Engelbrecht, S. (2001). Minimum principles in motor control. *J. Math. Psychol.*, 45(3):497–542.
- Farshchiansadegh, A., Melendez-Calderon, A., Ranganathan, R., Murphey, T. D., and Mussa-Ivaldi, F. A. (2016). Sensory agreement guides kinetic energy optimization of arm movements during object manipulation. *PLoS Comput. Biol.*, 12(4):e1004861.
- Flanders, M., Pellegrini, J. J., and Geisler, S. D. (1996). Basic features of phasic activation for reaching in vertical planes. *Exp. Brain Res.*, 110(1):67–79.
- Flash, T. and Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *J. Neurosci.*, 5(7):1688–1703.
- Friston, K. (2011). What is optimal about motor control? *Neuron*, 72:488–498.
- Ganesh, G., Haruno, M., Kawato, M., and Burdet, E. (2010). Motor memory and local minimization of error and effort, not global optimization, determine motor behavior. *J. Neurophysiol.*, 104(1):382–390.
- Gao, P. and Ganguli, S. (2015). On simplicity and complexity in the brave new world of large-scale neuroscience. *Curr. Opin. Neurobiol.*, 32:148–155.
- Garrec, P. (2010). Screw and cable actuators (scs) and their applications to force feedback teleoperation, exoskeleton and anthropomorphic robotics. In *Robotics 2010 Current and Future Challenges*. InTech.
- Gauthier, J. P., Berret, B., and Jean, F. (2010). A biomechanical inactivation principle. *Proceedings of the Steklov Institute of Mathematics*, 268:93–116.
- Gaveau, J., Berret, B., Angelaki, D. E., and Papaxanthis, C. (2016). Direction-dependent arm kinematics reveal optimal integration of gravity cues. *eLife*, 5:e16394.
- Gaveau, J., Berret, B., Demougeot, L., Fadiga, L., Pozzo, T., and Papaxanthis, C. (2014). Energy-related optimal control accounts for gravitational load: comparing shoulder, elbow, and wrist rotations. *J. Neurophysiol.*, 111(1):4–16.
- Gaveau, J., Paizis, C., Berret, B., Pozzo, T., and Papaxanthis, C. (2011). Sensorimotor adaptation of point-to-point arm movements after space-flight: the role of the internal representation of gravity force in trajectory planning. *J. Neurophysiol.*
- Gaveau, J. and Papaxanthis, C. (2011). The temporal structure of vertical arm movements. *PLoS One*, 6(7):e22045.
- Geisert, M., Del Prete, A., Mansard, N., Romano, F., and Nori, F. (2017). Regularized hierarchical differential dynamic programming. *IEEE Trans. Rob.*
- Gentili, R., Cahouet, V., and Papaxanthis, C. (2007). Motor planning of arm movements is direction-dependent in the gravity field. *Neuroscience*, 145(1):20–32.
- Georgopoulos, A. P., Schwartz, A. B., and Kettner, R. E. (1986). Neuronal population coding of movement direction. *Science*, 233(4771):1416–1419.

## Bibliography

---

- Giszter, S. F. and Hart, C. B. (2013). Motor primitives and synergies in the spinal cord and after injury– the current state of play. *Ann. N.Y. Acad. Sci.*, 1279(1):114–126.
- Gizzi, L., Nielsen, J. F., Felici, F., Ivanenko, Y. P., and Farina, D. (2011). Impulses of activation but not motor modules are preserved in the locomotion of subacute stroke patients. *J. Neurophysiol.*, 106(1):202–10.
- Golub, M. D., Yu, B. M., Schwartz, A. B., and Chase, S. M. (2014). Motor cortical control of movement speed with implications for brain-machine interface control. *J. Neurophysiol.*, 112(2):411–429.
- Gordon, J., Ghilardi, M. F., Cooper, S. E., and Ghez, C. (1994). Accuracy of planar reaching movements. ii. systematic extent errors resulting from inertial anisotropy. *Exp. Brain Res.*, 99(1):112–130.
- Gribble, P. L., Mullin, L. I., Cothros, N., and Mattar, A. (2003). Role of cocontraction in arm movement accuracy. *J. Neurophysiol.*, 89(5):2396–2405.
- Guigon, E., Baraduc, P., and Desmurget, M. (2007). Computational motor control: redundancy and invariance. *J. Neurophysiol.*, 97(1):331–347.
- Haggard, P. (2008). Human volition: towards a neuroscience of will. *Nat. Rev. Neurosci.*, 9(12):934–946.
- Haith, A. M., Reppert, T. R., and Shadmehr, R. (2012). Evidence for hyperbolic temporal discounting of reward in control of movements. *J. Neurosci.*, 32(34):11727–11736.
- Harris, C. M. and Wolpert, D. M. (1998). Signal-dependent noise determines motor planning. *Nature*, 394(6695):780–784.
- Hart, C. B. and Giszter, S. F. (2004). Modular premotor drives and unit bursts as primitives for frog motor behaviors. *J. Neurosci.*, 24(22):5269–5282.
- Hart, C. B. and Giszter, S. F. (2010). A neural basis for motor primitives in the spinal cord. *J. Neurosci.*, 30(4):1322–1336.
- Hilt, P. M., Berret, B., Papaxanthis, C., Stapley, P. J., and Pozzo, T. (2016). Evidence for subjective values guiding posture and movement coordination in a free-endpoint whole-body reaching task. *Sci. Rep.*, 6:23868.
- Hilt, P. M., Delis, I., Pozzo, T., and Berret, B. (2017). Spatiotemporal organization of whole-body muscle activity during upright reaching movements in various directions: modularity or not modularity? *bioRxiv*, page 155085.
- Hirashima, M. and Oya, T. (2016). How does the brain solve muscle redundancy? filling the gap between optimization and muscle synergy hypotheses. *Neurosci. Res.*, 104:80–87.
- Hoff, B. (1994). A model of duration in normal and perturbed reaching movement. *Biol. Cybern.*, pages 481–488.
- Holdefer, R. N. and Miller, L. E. (2002). Primary motor cortical neurons encode functional muscle synergies. *Exp. Brain Res.*, 146(2):233–43.
- Hollerbach, J. M. and Flash, T. (1982). Dynamic interactions between limb segments during planar arm movement. *Biol. Cybern.*, 44(1):67–77.

- Hondzinski, J. M., Soebbing, C. M., French, A. E., and Winges, S. A. (2016). Different damping responses explain vertical endpoint error differences between visual conditions. *Exp. Brain Res.*, 234(6):1575–1587.
- Huang, V. S. and Krakauer, J. W. (2009). Robotic neurorehabilitation: a computational motor learning perspective. *J. NeuroEng. Rehabil.*, 6:5.
- Hug, F., Turpin, N. A., Couturier, A., and Dorel, S. (2011). Consistency of muscle synergies during pedaling across different mechanical constraints. *J. Neurophysiol.*, 106(1):91–103.
- Hug, F., Turpin, N. A., Guével, A., and Dorel, S. (2010). Is interindividual variability of emg patterns in trained cyclists related to different muscle synergies? *J. Appl. Physiol.*, 108(6):1727–1736.
- Huh, D. and Sejnowski, T. J. (2016). Conservation law for self-paced movements. *Proc. Natl. Acad. Sci. U.S.A.*, 113(31):8831–8836.
- Inouye, J. M. and Valero-Cuevas, F. J. (2016). Muscle synergies heavily influence the neural control of arm endpoint stiffness and energy consumption. *PLoS Comput. Biol.*, 12(2):e1004737.
- Isableu, B., Rezzoug, N., Mallet, G., Bernardin, D., Gorce, P., and Pagano, C. (2009). Velocity-dependent changes of rotational axes in the non-visual control of unconstrained 3d arm motions. *Neuroscience*, 164(4):1632–1647.
- Ivaldi, S., Sigaud, O., Berret, B., and Nori, F. (2012). From humans to humanoids: The optimal control framework. *Paladyn Journal of Behavioral Robotics*, 3(2):75–91.
- Ivanenko, Y. P., Cappellini, G., Dominici, N., Poppele, R. E., and Lacquaniti, F. (2005). Coordination of locomotion with voluntary movements in humans. *J. Neurosci.*, 25(31):7238–7253.
- Ivanenko, Y. P., Grasso, R., Zago, M., Molinari, M., Scivoletto, G., Castellano, V., Macellari, V., and Lacquaniti, F. (2003). Temporal components of the motor patterns expressed by the human spinal cord reflect foot kinematics. *J. Neurophysiol.*, 90(5):3555–65.
- Ivanenko, Y. P., Poppele, R. E., and Lacquaniti, F. (2004). Five basic muscle activation patterns account for muscle activity during human locomotion. *J Physiol*, 556(Pt 1):267–282.
- Izawa, J., Rane, T., Donchin, O., and Shadmehr, R. (2008). Motor adaptation as a process of reoptimization. *J. Neurosci.*, 28(11):2883–2891.
- Jean, F. and Berret, B. (2017). *On the Duration of Human Movement: From Self-paced to Slow/Fast Reaches up to Fitts's Law*, pages 43–65. Springer International Publishing, Cham.
- Johnson, M. T., Coltz, J. D., and Ebner, T. J. (1999). Encoding of target direction and speed during visual instruction and arm tracking in dorsal premotor and primary motor cortical neurons. *Eur. J. Neurosci.*, 11(12):4433–4445.
- Kajita, S., Hirukawa, H., Harada, K., and Yokoi, K. (2014). *Introduction to Humanoid Robotics*. Springer.
- Kalman, R. (1964). When is a linear control system optimal? *ASME Transactions, Journal of Basic Engineering*, 86:51–60.

- Kappen, H. J. (2011). Optimal control theory and the linear bellman equation. In Barber, D., Cemgil, A. T., and Chiappa, S., editors, *Bayesian Time Series Models*, pages 363–387. Cambridge University Press. Cambridge Books Online.
- Kargo, W. J. and Giszter, S. F. (2008). Individual premotor drive pulses, not time-varying synergies, are the units of adjustment for limb trajectories constructed in spinal cord. *J. Neurosci.*, 28(10):2409–25.
- Kargo, W. J. and Nitz, D. A. (2003). Early skill learning is expressed through selection and tuning of cortically represented muscle synergies. *J. Neurosci.*, 23(35):11255–11269.
- Kelso, J. S. (1997). *Dynamic patterns: The self-organization of brain and behavior*. MIT press.
- Kirk, D. E. (1970). *Optimal control theory: An Introduction*. Prentice-Hall, New Jersey.
- Knill, D. C., Bondada, A., and Chhabra, M. (2011). Flexible, task-dependent use of sensory feedback to control hand movements. *J. Neurosci.*, 31(4):1219–1237.
- Knoblauch, R., Pietrucha, M., and Nitzburg, M. (1996). Field studies of pedestrian walking speed and start-up time. *Transportation Research Record: Journal of the Transportation Research Board*, 1538:27–38.
- Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., and Poeppel, D. (2017). Neuroscience needs behavior: correcting a reductionist bias. *Neuron*, 93(3):480–490.
- Kutch, J. J. and Valero-Cuevas, F. J. (2012). Challenges and new approaches to proving the existence of muscle synergies of neural origin. *PLoS Comput. Biol.*, 8(5):e1002434.
- Lacquanti, F., Ivanenko, Y. P., and Zago, M. (2012). Patterned control of human locomotion. *J Physiol*, 590(Pt 10):2189–2199.
- Le Seac'h, A. B. and McIntyre, J. (2007). Multimodal reference frame for the planning of vertical arms movements. *Neurosci. Lett.*, 423(3):211–215.
- Lebedev, S., Tsui, W. H., and Van Gelder, P. (2001). Drawing movements as an outcome of the principle of least action. *J. Math. Psychol.*, 45(1):43–52.
- Li, W. and Todorov, E. (2007). Iterative linearization methods for approximately optimal control and estimation of non-linear stochastic system. *Int. J. Control*, 80(9):1439–1453.
- Loeb, E., Giszter, S., Bizzi, P. S., E, and Mussa-Ivaldi, F. (2000). Output units of motor behavior: an experimental and modeling study. *J. Cognit. Neurosci.*, 12(1):78–97.
- Loeb, G. E. (2012). Optimal isn't good enough. *Biol. Cybern.*, 106(11-12):757–765.
- Mansard, N., Stasse, O., Evrard, P., and Kheddar, A. (2009). A versatile Generalized Inverted Kinematics implementation for collaborative working humanoid robots: The Stack Of Tasks. In *International Conference on Advanced Robotics, 2009. ICAR 2009*, pages 1–6.
- Marr, D. (1983). *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. Henry Holt & Company.
- Marr, D. and Poggio, T. (1976). From understanding computation to understanding neural circuitry. Technical report, Cambridge, MA, USA.

- Marsden, C. D. (1989). Slowness of movement in Parkinson's disease. *Movement Disorders: Official Journal of the Movement Disorder Society*, 4 Suppl 1:S26–37.
- Mazzoni, P., Hristova, A., and Krakauer, J. W. (2007). Why don't we move faster? parkinson's disease, movement vigor, and implicit motivation. *J. Neurosci.*, 27(27):7105–7116.
- McKay, J. L. and Ting, L. H. (2012). Optimization of muscle activity for task-level goals predicts complex changes in limb forces across biomechanical contexts. *PLoS Comput. Biol.*, 8(4):e1002465.
- Mehrabi, N., Razavian, R. S., Ghannadi, B., and McPhee, J. (2016). Predictive simulation of reaching moving targets using nonlinear model predictive control. *Front. Comput. Neurosci.*, 10.
- Missenard, O. and Fernandez, L. (2011). Moving faster while preserving accuracy. *Neuroscience*, 197:233–241.
- Mistry, M., Theodorou, E., Schaal, S., and Kawato, M. (2013). Optimal control of reaching includes kinematic constraints. *J. Neurophysiol.*, 110(1):1–11.
- Mitrovic, D., Klanke, S., Osu, R., Kawato, M., and Vijayakumar, S. (2010). A Computational Model of Limb Impedance Control Based on Principles of Internal Model Uncertainty. *PLoS One*, 5(10):e13601.
- Mohan, V. and Morasso, P. (2011). Passive motion paradigm: an alternative to optimal control. *Front. Neurobot.*, 5:4.
- Montgomery, E. B., Huang, H., Walker, H. C., Guthrie, B. L., and Watts, R. L. (2011). High-Frequency Deep Brain Stimulation of the Putamen Improves Bradykinesia in Parkinson's Disease. *Movement disorders : official journal of the Movement Disorder Society*, 26(12):2232–2238.
- Moran, D. W. and Schwartz, A. B. (1999). Motor cortical representation of speed and direction during reaching. *J. Neurophysiol.*, 82(5):2676–2692.
- Morel, P., Ulbrich, P., and Gail, A. (2017). What makes a reach movement effortful? physical effort discounting supports common minimization principles in decision making and motor control. *PLoS Biol.*, 15(6):e2001323.
- Muceli, S., Boye, A. T., d'Avella, A., and Farina, D. (2010). Identifying representative synergy matrices for describing muscular activation patterns during multidirectional reaching in the horizontal plane. *J. Neurophysiol.*, 103(3):1532–42.
- Mussa-Ivaldi, F. A. (1997). Nonlinear force fields: a distributed system of control primitives for representing and learning movements. In *Computational Intelligence in Robotics and Automation, 1997. CIRA'97., Proceedings., 1997 IEEE International Symposium on*, pages 84–90. IEEE.
- Mussa-Ivaldi, F. A., Giszter, S. F., and Bizzi, E. (1994). Linear combinations of primitives in vertebrate motor control. *Proc. Natl. Acad. Sci. U.S.A.*, 91(16):7534–7538.
- Myerson, J. and Green, L. (1995). Discounting of delayed rewards: Models of individual choice. *J. Exp. Anal. Behav.*, 64(3):263–276.
- Nashed, J. Y., Crevecoeur, F., and Scott, S. H. (2012). Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *J. Neurophysiol.*, 108(4):999–1009.

- Nelson, W. L. (1983). Physical principles for economies of skilled movements. *Biol. Cybern.*, 46(2):135–147.
- Neptune, R. R., Clark, D. J., and Kautz, S. A. (2009). Modular control of human walking: a simulation study. *J. Biomech.*, 42(9):1282–7.
- Nori, F. and Frezza, R. (2004). Linear optimal control problems and quadratic cost functions estimation. In *12th Mediterranean Conference on Control and Automation, MED'04. Kusadasi, Aydin, Turkey.*
- Nori, F. and Frezza, R. (2005). A control theory approach to the analysis and synthesis of the experimentally observed motion primitives. *Biol. Cybern.*, 93(5):323–342.
- Overduin, S. A., d'Avella, A., Carmena, J. M., and Bizzi, E. (2012). Microstimulation activates a handful of muscle synergies. *Neuron*, 76(6):1071–1077.
- Overduin, S. A., d'Avella, A., Roh, J., and Bizzi, E. (2008). Modulation of muscle synergy recruitment in primate grasping. *J. Neurosci.*, 28(4):880–92.
- Overduin, S. A., d'Avella, A., Roh, J., Carmena, J. M., and Bizzi, E. (2015). Representation of muscle synergies in the primate brain. *J. Neurosci.*, 35(37):12615–12624.
- Papaxanthis, C., Pozzo, T., and McIntyre, J. (2005). Kinematic and dynamic processes for the control of pointing movements in humans revealed by short-term exposure to microgravity. *Neuroscience*, 135(2):371–383.
- Papaxanthis, C., Pozzo, T., and Schieppati, M. (2003). Trajectories of arm pointing movements on the sagittal plane vary with both direction and speed. *Exp. Brain Res.*, 148(4):498–503.
- Pattacini, U., Nori, F., Natale, L., Metta, G., and Sandini, G. (2010). An experimental evaluation of a novel minimum-jerk cartesian controller for humanoid robots. In *Intelligent Robots and Systems (IROS), 2010 IEEE/RSJ International Conference on*, pages 1668–1674.
- Pauwels, E., Henrion, D., and Lasserre, J.-B. (2014). Inverse optimal control with polynomial optimization. In *Decision and Control (CDC), 2014 IEEE 53rd Annual Conference on*, pages 5581–5586. IEEE.
- Perreault, E. J., Chen, K., Trumbower, R. D., and Lewis, G. (2008). Interactions with compliant loads alter stretch reflex gains but not intermuscular coordination. *J. Neurophysiol.*, 99(5):2101–2113.
- Pirondini, E., Coscia, M., Marcheschi, S., Roas, G., Salsedo, F., Frisoli, A., Bergamasco, M., and Micera, S. (2016). Evaluation of the effects of the Arm Light Exoskeleton on movement execution and muscle activities: a pilot study on healthy subjects. *J. NeuroEng. Rehabil.*, 13.
- Pontryagin, L. S., Boltyanskii, V. G., Gamkrelidze, R. V., and Mishchenko, E. F. (1964). *The Mathematical Theory of Optimal Processes*. Pergamon Press.
- Proietti, T., Guigon, E., Roby-Brami, A., and Jarrassé, N. (2017). Modifying upper-limb inter-joint coordination in healthy subjects by training with a robotic exoskeleton. *J. NeuroEng. Rehabil.*, 14(1):55.
- Qian, N., Jiang, Y., Jiang, Z.-P., and Mazzoni, P. (2013). Movement duration, fitts's law, and an infinite-horizon optimal feedback control model for biological motor systems. *Neural Comput.*, 25(3):697–724.

- Rao, A. V., Benson, D. A., Darby, C. L., Patterson, M. A., Franco, C., Sanders, I., and Huntington, G. T. (2010). Algorithm 902: Gpops, a matlab software for solving multiple-phase optimal control problems using the gauss pseudospectral method. *ACM Trans. Math. Software*, 37(2):1–39.
- Razavian, R. S., Mehrabi, N., and McPhee, J. (2015). A model-based approach to predict muscle synergies using optimization: application to feedback control. *Front. Comput. Neurosci.*, 9.
- Roberts, S. (2012). *Character Animation Fundamentals: Developing Skills for 2D and 3D Character Animation*. Taylor & Francis.
- Roh, J., Cheung, V. C. K., and Bizzi, E. (2011). Modules in the brain stem and spinal cord underlying motor behaviors. *J. Neurophysiol.*, 106(3):1363–1378.
- Roh, J., Rymer, W. Z., and Beer, R. F. (2015). Evidence for altered upper extremity muscle synergies in chronic stroke survivors with mild and moderate impairment. *Front. Hum. Neurosci.*, 9:6.
- Roh, J., Rymer, W. Z., Perreault, E. J., Yoo, S. B., and Beer, R. F. (2013). Alterations in upper limb muscle synergy structure in chronic stroke survivors. *J. Neurophysiol.*, 109(3):768–781.
- Romano, F., Del Prete, A., Mansard, N., and Nori, F. (2015). Prioritized optimal control: A hierarchical differential dynamic programming approach. In *Robotics and Automation (ICRA), 2015 IEEE International Conference on*, pages 3590–3595. IEEE.
- Russo, M., D’Andola, M., Portone, A., Lacquaniti, F., and d’Avella, A. (2014). Dimensionality of joint torques and muscle patterns for reaching. *Front. Comput. Neurosci.*, 8:24.
- Saltiel, P., Wyler-Duda, K., D’Avella, A., Tresch, M. C., and Bizzi, E. (2001). Muscle synergies encoded within the spinal cord: evidence from focal intraspinal nmda iontophoresis in the frog. *J. Neurophysiol.*, 85(2):605–19.
- Santello, M., Flanders, M., and Soechting, J. F. (1998). Postural hand synergies for tool use. *J. Neurosci.*, 18(23):10105–10115.
- Schwartz, A. B. (2016). Movement: how the brain communicates with the world. *Cell*, 164(6):1122–1135.
- Sciutti, A., Bisio, A., Nori, F., Metta, G., Fadiga, L., Pozzo, T., and Sandini, G. (2012a). Measuring Human-Robot Interaction Through Motor Resonance. *International Journal of Social Robotics*, 4(3):223–234.
- Sciutti, A., Demougeot, L., Berret, B., Toma, S., Sandini, G., Papaxanthis, C., and Pozzo, T. (2012b). Visual gravity influences arm movement planning. *J. Neurophysiol.*, 107(12):3433–3445.
- Scott, S. H. (2004). Optimal feedback control and the neural basis of volitional motor control. *Nat. Rev. Neurosci.*, 5(7):532–546.
- Scott, S. H. (2012). The computational and neural basis of voluntary motor control and planning. *Trends in cognitive sciences*, 16(11):541–549.
- Selinger, J. C., O’Connor, S. M., Wong, J. D., and Donelan, J. M. (2015). Humans can continuously optimize energetic cost during walking. *Curr. Biol.*, 25(18):2452–2456.

- Shadmehr, R. (2010). Control of movements and temporal discounting of reward. *Curr. Opin. Neurobiol.*, 20(6):726–730.
- Shadmehr, R., Huang, H. J., and Ahmed, A. A. (2016). A representation of effort in decision-making and motor control. *Curr. Biol.*, 26:1929–1934.
- Shadmehr, R. and Krakauer, J. W. (2008). A computational neuroanatomy for motor control. *Exp. Brain Res.*, 185(3):359–381.
- Shadmehr, R., Orban de Xivry, J. J., Xu-Wilson, M., and Shih, T.-Y. (2010). Temporal discounting of reward and the cost of time in motor control. *J. Neurosci.*, 30(31):10507–10516.
- Shenoy, K. V., Churchland, M. M., Santhanam, G., Yu, B. M., and Ryu, S. I. (2003). Influence of movement speed on plan activity in monkey pre-motor cortex and implications for high-performance neural prosthetic system design. In *Proceedings of the 25th Annual International Conference of the IEEE Engineering in Medicine and Biology Society, 2003*, volume 2, pages 1897–1900 Vol.2.
- Sockol, M. D., Raichlen, D. A., and Pontzer, H. (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *Proceedings of the National Academy of Sciences*, 104(30):12265–12269.
- Sponberg, S., Daniel, T. L., and Fairhall, A. L. (2015). Dual dimensionality reduction reveals independent encoding of motor features in a muscle synergy for insect flight control. *PLoS Comput. Biol.*, 11:e1004168.
- Steele, K. M., Tresch, M. C., and Perreault, E. J. (2013). The number and choice of muscles impact the results of muscle synergy analyses. *Front. Comput. Neurosci.*, 7.
- Taïx, M., Tran, M. T., Souères, P., and Guigon, E. (2013). Generating human-like reaching movements with a humanoid robot: A computational approach. *Journal of Computational Science*, 4(4):269–284.
- Takikawa, Y., Kawagoe, R., Itoh, H., Nakahara, H., and Hikosaka, O. (2002). Modulation of saccadic eye movements by predicted reward outcome. *Exp. Brain Res.*, 142(2):284–291.
- Tanaka, H., Krakauer, J. W., and Qian, N. (2006). An optimization principle for determining movement duration. *J. Neurophysiol.*, 95(6):3875–3886.
- Tankus, A., Yeshurun, Y., Flash, T., and Fried, I. (2009). Encoding of speed and direction of movement in the human supplementary motor area. *J. Neurosurg.*, 110(6):1304–1316.
- Terekhov, A. V., Pesin, Y. B., Niu, X., Latash, M. L., and Zatsiorsky, V. M. (2010). An analytical approach to the problem of inverse optimization with additive objective functions: an application to human prehension. *J. Math. Biol.*, 61(3):423–453.
- Thomas, J. S., Corcos, D. M., and Hasan, Z. (2005). Kinematic and kinetic constraints on arm, trunk, and leg segments in target-reaching movements. *J. Neurophysiol.*, 93(1):352–364.
- Ting, L. H., Chiel, H. J., Trumbower, R. D., Allen, J. L., McKay, J. L., Hackney, M. E., and Kesar, T. M. (2015). Neuromechanical principles underlying movement modularity and their implications for rehabilitation. *Neuron*, 86(1):38–54.
- Ting, L. H. and Macpherson, J. M. (2005). A limited set of muscle synergies for force control during a postural task. *J. Neurophysiol.*, 93(1):609–613.

- Ting, L. H. and McKay, J. L. (2007). Neuromechanics of muscle synergies for posture and movement. *Curr. Opin. Neurobiol.*, 17(6):622–628.
- Todorov, E. (2004). Optimality principles in sensorimotor control. *Nat. Neurosci.*, 7(9):907–915.
- Todorov, E. (2005). Stochastic optimal control and estimation methods adapted to the noise characteristics of the sensorimotor system. *Neural Comput.*, 17(5):1084–1108.
- Todorov, E. (2006). *Optimal control theory*, chapter 12, pages 269–298. Bayesian Brain: Probabilistic Approaches to Neural Coding, Doya K (ed).
- Todorov, E. (2009a). Compositionality of optimal control laws. *Advances in Neural Information Processing Systems*, 22:1856–1864.
- Todorov, E. (2009b). Efficient computation of optimal actions. *Proc. Natl. Acad. Sci. U.S.A.*, 106(28):11478–11483.
- Todorov, E. and Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.*, 5(11):1226–1235.
- Todorov, E., Li, W., and Pan, X. (2005). From task parameters to motor synergies: A hierarchical framework for approximately-optimal control of redundant manipulators. *J Robot Syst*, 22(11):691–710.
- Togo, S., Yoshioka, T., and Imamizu, H. (2017). Control strategy of hand movement depends on target redundancy. *Sci. Rep.*, 7:45722.
- Toma, S., Sciutti, A., Papaxanthis, C., and Pozzo, T. (2015). Visuomotor adaptation to a visual rotation is gravity dependent. *J. Neurophysiol.*, 113(6):1885–1895.
- Torres-Oviedo, G., Macpherson, J. M., and Ting, L. H. (2006). Muscle synergy organization is robust across a variety of postural perturbations. *J. Neurophysiol.*, 96(3):1530–1546.
- Torres-Oviedo, G. and Ting, L. H. (2007). Muscle synergies characterizing human postural responses. *J. Neurophysiol.*, 98(4):2144–56.
- Torres-Oviedo, G. and Ting, L. H. (2010). Subject-specific muscle synergies in human balance control are consistent across different biomechanical contexts. *J. Neurophysiol.*, 103(6):3084–98.
- Tresch, M. C., Cheung, V. C. K., and d’Avella, A. (2006). Matrix factorization algorithms for the identification of muscle synergies: evaluation on simulated and experimental data sets. *J. Neurophysiol.*, 95(4):2199–2212.
- Tresch, M. C. and Jarc, A. (2009). The case for and against muscle synergies. *Curr. Opin. Neurobiol.*, 19(6):601–7.
- Tresch, M. C., Saltiel, P., and Bizzi, E. (1999). The construction of movement by the spinal cord. *Nat. Neurosci.*, 2(2):162–7.
- Turner, R. S. and Desmurget, M. (2010). Basal ganglia contributions to motor control: a vigorous tutor. *Curr. Opin. Neurobiol.*, 20(6):704–716.

## Bibliography

---

- Turner, R. S., Desmurget, M., Grethe, J., Crutcher, M. D., and Grafton, S. T. (2003). Motor Subcircuits Mediating the Control of Movement Extent and Speed. *J. Neurophysiol.*, 90(6):3958–3966.
- Turvey, M. T. (1990). Coordination. *Am. Psychol.*, 45(8):938.
- Uno, Y., Kawato, M., and Suzuki, R. (1989). Formation and control of optimal trajectory in human multijoint arm movement. minimum torque-change model. *Biol. Cybern.*, 61(2):89–101.
- Vaillancourt, D. E., Prodoehl, J., Verhagen Metman, L., Bakay, R. A., and Corcos, D. M. (2004). Effects of deep brain stimulation and medication on bradykinesia and muscle activation in Parkinson's disease. *Brain: A Journal of Neurology*, 127(Pt 3):491–504.
- Valero-Cuevas, F. J., Venkadesan, M., and Todorov, E. (2009). Structured variability of muscle activations supports the minimal intervention principle of motor control. *J. Neurophysiol.*, 102(1):59–68.
- van der Wel, R. P. R. D., Sternad, D., and Rosenbaum, D. A. (2010). Moving the arm at different rates: slow movements are avoided. *J Mot Behav*, 42(1):29–36.
- Viviani, P. and Flash, T. (1995). Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning. *J. Exp. Psychol. Hum. Percept. Perform.*, 21(1):32–53.
- Vu, V. H., Isableu, B., and Berret, B. (2016a). Adaptive use of interaction torque during arm reaching movement from the optimal control viewpoint. *Sci. Rep.*, 6.
- Vu, V. H., Isableu, B., and Berret, B. (2016b). On the nature of motor planning variables during arm pointing movement: Compositeness and speed dependence. *Neuroscience*, 328:127–146.
- Wang, C., Xiao, Y., Burdet, E., Gordon, J., and Schweighofer, N. (2016). The duration of reaching movement is longer than predicted by minimum variance. *J. Neurophysiol.*, 116(5):2342–2345.
- Weiss, E. J. and Flanders, M. (2004). Muscular and postural synergies of the human hand. *J. Neurophysiol.*, 92(1):523–535.
- Wilson, R. S., Husak, J. F., Halsey, L. G., and Clemente, C. J. (2015). Predicting the Movement Speeds of Animals in Natural Environments. *Integr. Comp. Biol.*, 55(6):1125–1141.
- Wolpert, D. M., Ghahramani, Z., and Jordan, M. I. (1995). Are arm trajectories planned in kinematic or dynamic coordinates? an adaptation study. *Exp. Brain Res.*, 103(3):460–470.
- Wolpert, D. M. and Landy, M. S. (2012). Motor control is decision-making. *Curr. Opin. Neurobiol.*, 22(6):996–1003.
- Xu-Wilson, M., Zee, D. S., and Shadmehr, R. (2009). The intrinsic value of visual information affects saccade velocities. *Exp. Brain Res.*, 196(4):475–481.
- Yamamoto, S. and Koshiro, K. (2014). Direction-dependent differences in temporal kinematics for vertical prehension movements. *Exp. Brain Res.*, 232(2):703–711.
- Yandell, M. B. and Zelik, K. E. (2016). Preferred barefoot step frequency is influenced by factors beyond minimizing metabolic rate. *Sci. Rep.*, 6.
- Zelik, K. E. and Kuo, A. D. (2012). Mechanical work as an indirect measure of subjective costs influencing human movement. *PLoS One*, 7(2):e31143.

## **Part II**

# **Selection of full-text articles**

---

A list of my articles can be found at <http://hebergement.u-psud.fr/berret/publications.html>.

Note that a long version of this HDR manuscript, including the original text of the five relevant articles mentioned in Section 3.8, is also available.

## Abstract

In this manuscript, I present a synthesis of my past works related to the optimal and modular control hypotheses for human movement. Optimal control theory is often thought to imply that the brain computes global optima continuously for each motor task it faces. Modular control theory typically assumes that the brain explicitly stores genuine synergies in specific neural circuits whose combined recruitment yields task-effective motor commands. Said like that, these two influential motor control theories are pushed to extreme positions. A more nuanced view is discussed in this manuscript, which is framed within Marr's tri-level computational theory applied to movement neuroscience. It is argued that optimal control is best viewed as helping to understand "why" certain movements are preferred over others but does not say much about how the brain would practically trigger optimal strategies. We also argue that dimensionality reduction found in muscle activities may be a by-product of optimality and cannot be attributed to neurally hardwired synergies *stricto sensu*, in particular when the synergies are extracted from factorization algorithms applied to electromyographic data such that their nature is strongly dictated by the methodology itself. Hence, more modeling work is required in order to critically test the modularity hypothesis and assess its potential neural origins. An adequate mathematical formulation of hierarchical motor control could help to bridge the gap between optimality and modularity, and advance our knowledge about the organization of motor control in general.

For what concerns my research project, I propose to investigate the principles underlying self-paced movement formation. This is a critical issue in neuroscience because many neural disorders like Parkinson's disease lead to a loss of motion vigor as well as in human-machine interfaces for reasons of usability/acceptability (e.g. interaction with an exoskeleton). Time is notably a key variable influencing the speed of our daily movements. Recently, a theory according to which the duration of movement might entail a cost for our central nervous system has been proposed: the cost of time (CoT) hypothesis. A methodology allowing to reliably identify this CoT, presumably playing a role in motor planning and decision-making, has been successfully developed within the optimal control framework. Yet, several questions regarding the very existence of a CoT, its assumptions, origin, nature or consistency remain unresolved. The goal of this project is to test these questions from both experimental and theoretical viewpoints.

## Résumé

Dans ce mémoire, je présente une synthèse de mes travaux antérieurs portant sur les hypothèses du contrôle optimal et du contrôle modulaire pour le mouvement humain. La théorie du contrôle optimal est souvent vue comme impliquant que le cerveau calcule continuellement des optima globaux pour chaque tâche motrice à laquelle il est confronté. La théorie du contrôle modulaire suppose, quant à elle, que le cerveau stockerait d'authentiques synergies dans ses circuits neuronaux et dont l'activation combinée donnerait lieu à des commandes motrices adéquates vis-à-vis de la tâche à réaliser. Stipulées ainsi, ces deux théories influentes du contrôle moteur sont positionnées de manière extrême. Une vue plus nuancée est discutée dans ce manuscrit, dans le cadre de la théorie computationnelle à 3 niveaux de Marr, appliquée aux neurosciences du mouvement. Il est argumenté que la réduction de dimensionnalité trouvée dans les activités musculaires pourrait être le sous-produit d'une contrainte d'optimalité de plus haut niveau et qu'elle ne peut pas être attribuée *stricto sensu* à de réelles synergies codées au niveau neural. Ceci est en particulier vrai quand les synergies sont extraites à partir d'algorithmes de factorisation appliqués à des données électromyographiques si bien que leur nature est profondément dictée par la méthodologie employée. Plus de travaux de modélisation sont donc requis pour tester de manière critique l'hypothèse de modularité et ses potentielles origines neurales. Une formulation mathématique adéquate d'un contrôle moteur hiérarchique pourrait notamment aider à combler l'écart entre optimalité et modularité, et faire avancer nos connaissances sur l'organisation du contrôle moteur en général.

En ce qui concerne mon projet de recherche, il vise à mieux comprendre d'où vient la vitesse du mouvement humain. Ceci est un enjeu crucial en neurosciences en raison des troubles neuromoteurs qui affectent la vigueur des gestes (ex : maladie de Parkinson) ainsi que pour l'acceptabilité/utilisabilité des interfaces homme-machine (ex : interaction avec un exosquelette). Le temps est de fait une variable clé influençant la vitesse de nos mouvements au quotidien. La théorie du coût du temps (CdT) selon laquelle la durée du mouvement entraînerait un coût pour le cerveau a été proposée. Ce CdT a pu être identifié dans le cadre du contrôle optimal. Cependant de nombreuses questions liées à l'existence même du CdT, ses hypothèses, sa nature ou consistance restent en suspens. Elles seront traitées dans ce projet tant d'un point de vue expérimental que théorique.