

Physiological Aspects of Legged Terrestrial Locomotion

Giovanni Cavagna

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The Motor and the Machine

 Springer

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To My Students

Foreword

“Physiological Aspects of Legged Terrestrial Locomotion: The Motor and the Machine” is part textbook, part laboratory manual, and part biography. Cavagna takes the reader on his personal journey of discovery through muscular time and space. *Time* starting in the late 1960s with experiments performed on muscle heat production, and using Levin–Wyman ergometers (an instrument using floor-to-ceiling springs, pneumatic cylinders and mechanical catches) to control tiny levers imparting length changes on isolated frog muscles, all the way up to today. *Space* encompassing all the levels of muscle integration from proteins (myosin heads) to whole animals.

The first part of the book concerns muscle *in vitro*. Cavagna performed all of his muscle experiments in his laboratory at the Istituto di Fisiologia Umana at the Università di Milano. He built his own experimental apparatuses, starting with the aforementioned Levin–Wyman ergometer making measurements on whole frog muscles, and culminating in a home-made voice-coil lever system capable of performing controlled length changes of up to 0.2 mm in 100 μ s. This lever system was for making measurements on a small segment of an isolated frog muscle fibre (i.e. an individual muscle cell) which was delimited by two laser-illuminated ‘windows’ \sim 1 mm apart on the fibre. An optical and electronic system was capable of counting, up or down, the number of striations that passed by each window during a contraction. If the count was the same in the two windows, then the fibre segment between the two windows was isometric; if the count was greater in one window then the segment was lengthening, or if the count was less then the segment was shortening. A custom computer controlled the lever system in either length or force feedback to deliver precise isometric or isotonic conditions to the fibre segment. The results of these experiments are explained in Chap. 4.

The second part of the book concerns muscles *in vivo*. Cavagna pioneered the use of force platforms for the measurement of ground reaction forces during one or more complete locomotory cycles (step, stride, hop). In the mid-1970s Cavagna went to C. Richard (Dick) Taylor’s Concord Field Station at Harvard to pass the technique on and to do external work measurements on small animals. Taylor returned the favour, going to Milano to measure the external work on medium-sized

animals. More recently Cavagna went to Thailand to measure the external work on very large animals, Asian elephants, using a 2 m by 8 m platform. The database built up by these force platform experiments have continued to serve Cavagna right up to this day (Chaps. 6–8 and 10).

Only Cavagna has the breadth of personal experience, accumulated over many decades of hands-on experimentation involving proteins to pachyderms, to put everything together into one conceptual scheme. This book will appeal to advanced undergraduates, graduate students and professionals alike. The references at the end of each chapter not only illustrate Cavagna's contribution but also provide key papers for starting further in-depth research.

Brussels, Belgium
December 2016

Norman Heglund

Preface

Looking backward over more than fifty years of experimental work on muscle and locomotion made on the same line of thought, I felt the need to join in a logical sequence otherwise scattered results whose common link was lost. I thought that if this was what I needed, it could also be useful for others interested in the field. This connection is made in this book where *Physiological Aspects of Legged Terrestrial Locomotion* are treated in the view of the two ingredients involved in locomotion: *The Motor and the Machine*, i.e. the muscle and the lever system of the limbs.

Muscular function has been classically described mainly by its capacity to convert the energy set free by chemical reactions into positive mechanical work and heat, i.e. its motor function. Furthermore, muscular function is usually treated separately from the function of the locomotor system. I hope that this book will show the limits of this approach, how the braking function of muscle is fundamental as its motor function during exercise and how the knowledge of both these functions, and particularly of their interaction, naturally blends with the study of the motion of the body as a whole.

In the two parts of this book, “Muscle: The Motor” and “Locomotion: Motor–Machine Interaction”, I attempted to put evidence on the one side the relationship between the fundamental properties of muscle and their manifestation in muscular exercise and, on the other side, the role that the mechanics of the exercise has in modifying the mechanism of muscle operation: This last effect resulted in the subdivision of the exposition of muscle physiology in two distinct sections of the first part of this book. In both sections, muscle physiology is treated almost exclusively from a mechanical point of view: The chemical processes that fuel muscular contraction are considered solely in their thermodynamic balance, not in their identification and kinetics.

The second part of this book shows how the operation of the machine is affected during locomotion by the limits set by the functional characteristics of muscle. The two basic mechanisms used to minimize energy expenditure, the pendular mechanism of walking and the bouncing mechanism of running, trotting and hopping, are treated in two different sections. In both cases locomotion is described in different experimental conditions: Speed of progression, step frequency, age, body

mass and gravity by measuring the motion of the body as a whole, without a description of the movement of the individual body segments that cause it.

I hope that this book may help physiology, biology and physical education teachers and graduate students to get a synthetic, but comprehensive description of the mechanics of muscle contraction and of legged terrestrial locomotion. The several questions left unanswered may provide a stimulus to researchers for further experimental and analytical work. For this reason, particular attention is given to the description of the methods used in the experiments on isolated muscle specimens and on the whole body. Elementary knowledge of mathematics and physics is sufficient to understand this book.

I wish to thank Andrea Cavagna for several useful suggestions and Mario Legramandi for his careful revision of the final draft of this book.

Milan, Italy

Giovanni Cavagna

Contents

Part I Muscle: The Motor

1	Experimental Procedures in the Study of Muscle Mechanics	9
1.1	Muscle Chamber and Stimulation	9
1.2	Isometric Contraction	10
1.3	Isotonic Contraction	11
1.4	Isovelocity Contraction	14
1.5	Single Muscle Fiber and Fiber Segment	15
1.6	Response of a System to an Action	18
	References	23
2	Functional Anatomy of Muscle	25
2.1	Structures in Series and in Parallel	25
2.2	Localization of the “Motor” and of the Undamped Elastic Elements	29
2.3	Elastic Elements Having the Function of Containing and Centering the Contractile Component	32
	References	34
3	Measurements Made During or Starting from a State of Isometric Contraction	35
3.1	Phases of Muscular Contraction Determined on the Whole Muscle	35
3.2	Stress-Strain Diagram of the Apparent Elastic Elements Determined on the Whole Muscle	36
3.3	Twitch, Clonus and Tetanus	39
3.4	Force-Length Relation (Isometric Contraction)	43
3.5	Functional Consequences of the Force-Length Relation	46
3.5.1	Equilibrium Conditions	46
3.5.2	Limitation of the Movement Created by the Sarcomeres	48

- 3.6 Force-Velocity Relation (Isotonic and Isovelocity Contractions) 49
 - 3.6.1 Experimental Procedure. 49
 - 3.6.2 Description of the Force-Velocity Diagram 50
 - 3.6.3 Effect of Muscle Length 51
 - 3.6.4 Force-Velocity of Shortening Relation at Different Times Since the Beginning of Stimulation 52
 - 3.6.5 General Meaning of the Force-Velocity of Shortening Relation. 52
 - 3.6.6 Theoretical Interpretation of the Force-Velocity of Shortening Relation. 54
- 3.7 Functional Consequences of the Force-Velocity Relation 58
 - 3.7.1 Power 58
 - 3.7.2 Cost of Positive and Negative Work 59
- 3.8 Dynamic Force-Length Diagram (Iso-velocity Contraction) 59
- 3.9 Phases of Muscular Contraction Determined on the Single Muscle Fiber. 61
 - 3.9.1 Force-Length Diagram of the Undamped Structure Within the Sarcomere 63
 - 3.9.2 Force-Length Diagram of the Damped Structure Within the Sarcomere 65
- References. 66
- 4 Measurements Made After Stretching the Contracting Muscle 69**
 - 4.1 Evidence of an Enhancement of Positive Work Production by a Previously Stretched Muscle. 69
 - 4.2 What is the Origin of the Extra Work Done by a Previously Stretched Muscle?. 72
 - 4.3 Experiments Made on the Whole Muscle 73
 - 4.3.1 Mechanical Work and Efficiency in Isolated Frog and Rat Muscle 73
 - 4.3.2 The Apparent Enhancement of the Contractile Component 74
 - 4.3.3 Modification of the Apparent Elastic Characteristics of Muscle 78
 - 4.3.4 Physiological Meaning of the Modification of the Apparent Elastic Characteristics of Muscle 83
 - 4.3.5 Effect of Temperature on the Kinetics of the Fall in Force After Stretching (Stress-Relaxation). 83
 - 4.3.6 Effect of a Time Interval Between Stretching and Shortening 85

- 4.4 Experiments Made on the Single Muscular Fiber 86
 - 4.4.1 Effect of Temperature and of the Velocity of Lengthening on the Kinetics of the Fall in Force After Stretching 86
 - 4.4.2 The Four Phases of Shortening Against the Maximal Isometric Force Taking Place After a Ramp Stretch . . . 88
 - 4.4.3 Effect of a Time Interval Between End of Stretching and Release to the Maximal Isometric Force 90
- 4.5 Experiments Made on a Tendon-Free Segment of the Muscular Fiber 91
 - 4.5.1 Transient Shortening Against the Maximal Isometric Force Is not Due to Stress-Relaxation of Tendons 91
 - 4.5.2 Transient Shortening Against the Maximal Isometric Force Is Independent of the Velocity of Stretching 93
 - 4.5.3 Transient Shortening Against the Maximal Isometric Force Is Independent of Sarcomere Stiffness 95
 - 4.5.4 Transient Shortening Against the Maximal Isometric Force also Occurs When the Ramp Stretch Takes Place on the Ascending Limb of the Force-Length Relation 96
 - 4.5.5 Energy Transfer During Stress Relaxation Following Sarcomere Stretch 98
- 4.6 Interpretation of the Experimental Results: Conclusive Remarks 103
- 4.7 Differences Between In Vitro and In Vivo Conditions 105
 - 4.7.1 Characteristics of the Movement Imposed to the Muscle 106
 - 4.7.2 Effect of a Sub Maximal Stimulation 106
- References 107
- 5 Muscle Thermodynamics 109**
 - 5.1 Interpretation of the Heat Exchanges Between Muscle and Environment 110
 - 5.2 Methods of Heat Measurement 114
 - 5.3 Resting Heat 115
 - 5.4 Initial Heat 115
 - 5.4.1 Activation and Maintenance Heat 115
 - 5.4.2 Shortening Heat 117
 - 5.4.3 Fenn Effect: A Connection Between Heat Production and the Force-Velocity of Shortening Relation? 117
 - 5.4.4 Heat Production During Forcible Stretching a Contracting Muscle 119
 - 5.4.5 Relaxation Heat 120

5.5 Recovery Heat 121
 5.6 Efficiency 122
 References. 123

Part II Locomotion: Motor–Machine Interaction

6 External, Internal and Total Mechanical Work Done During Locomotion 129
 6.1 External Work 129
 6.1.1 Mechanical Energy Changes of the Center of Mass During Locomotion 131
 6.1.2 Assumptions Made in Calculating External Work from the Force Exerted on the Ground 134
 6.2 Internal Work 135
 6.3 Total Work. 137
 References. 138

7 Walking 139
 7.1 The Pendular Mechanism of Walking: A Way to Reduce External Work 139
 7.2 Assessment of the Exchange Between Potential and Kinetic Energy. 140
 7.3 Phase Shift Between Kinetic and Potential Energy. 146
 7.4 Within the Step Pendular Energy Transduction in Human Walking 147
 7.5 The Mechanism of Walking During Growth. 148
 7.6 Optimal and Freely Chosen Walking Speed 150
 7.7 The Mechanism of Walking in Different Animal Species. 151
 7.8 Effect of Step Frequency on the Mechanical Power Output in Human Walking 151
 7.9 Role of Gravity in Human Walking 156
 7.10 Mechanics of Competition Walking 158
 7.11 Ergometric Evaluation of Pathological Gait 161
 References. 164

8 Bouncing Gaits: Running, Trotting and Hopping. 167
 8.1 Transition from the Mechanism of Walking to the Mechanism of Running 167
 8.2 The Bouncing Mechanism of Progression. 168
 8.3 Vertical Oscillation of the Center of Mass 173
 8.4 Physical Division of the Vertical Oscillation of the Center of Mass. 175
 8.5 The On-Off-Ground Symmetry and Asymmetry of the Rebound. 177

- 8.6 The Landing-Takeoff Symmetry and Asymmetry of the Rebound 180
 - 8.6.1 Height of the Center of Mass at Touch Down and Takeoff 181
 - 8.6.2 The Four Phases of the Bounce and the Transduction of Mechanical Energy During the Running Step 182
 - 8.6.3 Positive and Negative Work Durations 185
- 8.7 Landing-Takeoff Asymmetry of the Bouncing Step: Asymmetric Motor or Asymmetric Machine? 186
 - 8.7.1 Different Machines with the Same Motor 187
 - 8.7.2 Running Backwards: Soft Landing—Hard Takeoff 191
- References. 200
- 9 Effect of Speed, Step Frequency and Age on the Bouncing Step 203**
 - 9.1 Effect of the Running Speed on the On-Off-Ground Asymmetry and the Landing-Takeoff Asymmetry. 203
 - 9.2 Effect of the Step Frequency on the Mechanical Power Output in Human Running 206
 - 9.3 The Resonant Step Frequency in Human Running 210
 - 9.4 Effect of Age 212
 - 9.4.1 On-Off-Ground Symmetry and Asymmetry 212
 - 9.4.2 Landing-Takeoff Asymmetry During Growth 212
 - 9.4.3 Landing-Takeoff Asymmetry in Old Age 216
 - References. 220
- 10 Work, Efficiency and Elastic Recovery 223**
 - 10.1 Mechanical Work Done by Adult Humans as a Function of Speed 223
 - 10.1.1 External Work 223
 - 10.1.2 Internal Work 225
 - 10.1.3 Total Work and Efficiency. 227
 - 10.2 Running Children 230
 - 10.2.1 External Work 230
 - 10.2.2 Internal Work, Total Work and Efficiency. 237
 - 10.3 Old Men Running. 239
 - 10.4 Effect of Body Mass on Elastic Recovery. 244
 - 10.5 Effect of Gravity in Human Running 253
 - 10.6 Sprint Running 257
 - 10.7 Vertical Jump 264
 - 10.7.1 Effect of Stretch Amplitude. 266
 - 10.7.2 Jumping at Different Simulated Gravities 268
 - 10.7.3 Metabolic Energy Expenditure 271
 - References. 271