Physiological Aspects of Legged Terrestrial Locomotion

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The Motor and the Machine

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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 μs. 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
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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

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