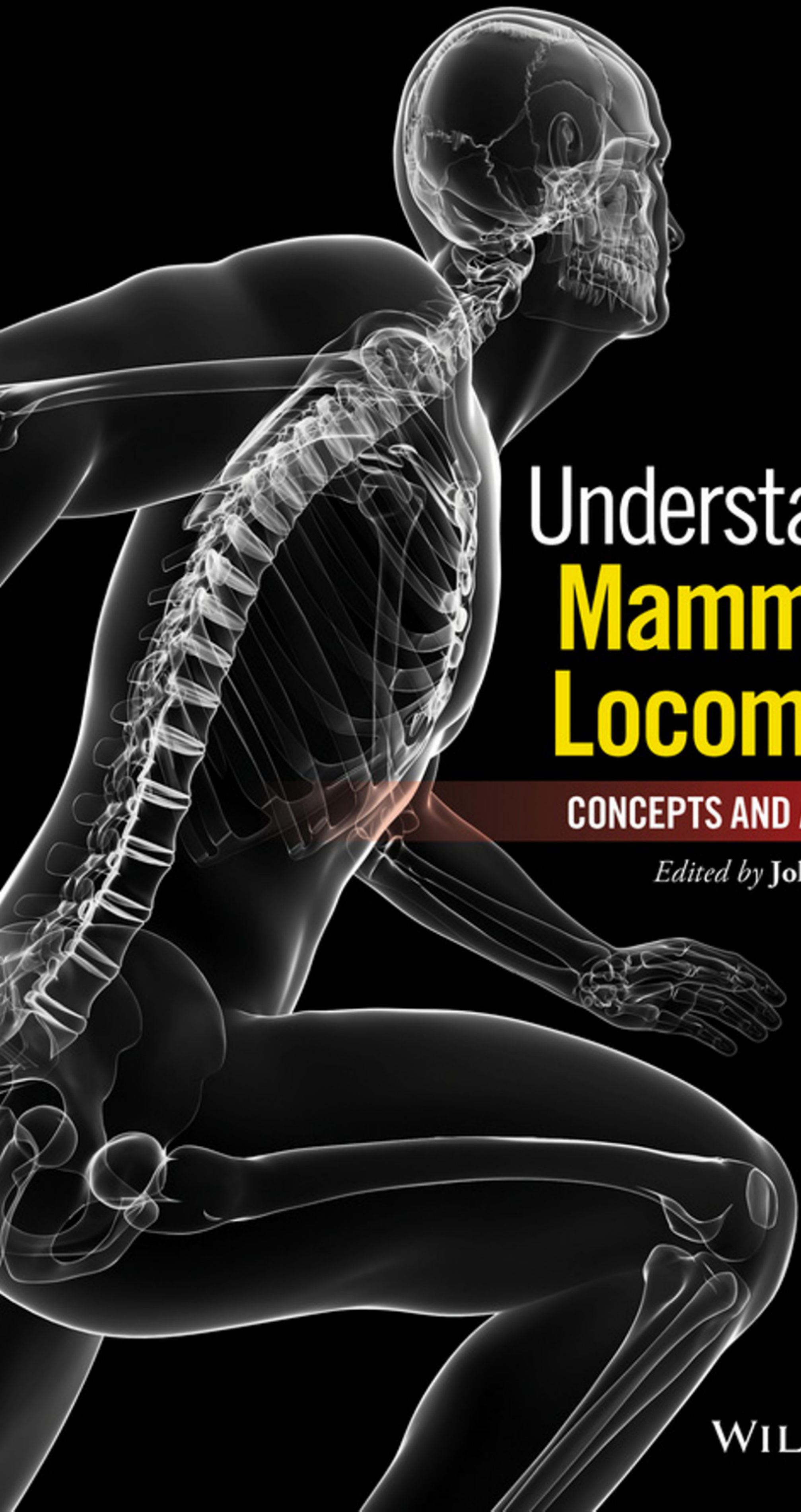

Understanding Mammalian Locomotion

CONCEPTS AND APPLICATIONS

Edited by **John E.A. Bertram**

WILEY Blackwell

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Published by John Wiley & Sons, Inc., Hoboken, New Jersey

Published simultaneously in Canada

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Library of Congress Cataloging-in-Publication data applied for

ISBN: 9780470454640 (Hardback)
9781119113737 (EPDF)
9781119113720 (epub)
9781119113713 (oBook)

Cover image: Runner Skeleton
Credit: Eraxion

Caption: 3D rendered illustration – runner anatomy
Collection: iStock / Getty Image Plus

Set in 10/12pt ITC Garamond by SPi Global, Pondicherry, India

1 2016

To my mentors, colleagues and students – all of whom have been responsible for guiding me to see a wonderful world I had previously been unaware of.

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Preface

Locomotion is one of the three key functional capacities of mammals, along with feeding and reproduction. An understanding of locomotion is imperative to understanding how adaptive evolution has allowed an organism and its ancestors to exploit the environmental opportunities and deal with the constraints and obstacles encountered in daily activity. Comparative analysis of terrestrial locomotion is an area of widespread interest, but the diversity of forms, as well as physiological and behavioral differences, make a comprehensive analysis of all animal forms a challenge to either produce or assimilate.

In this volume, the main focus is on a single group of specific interest – in this case, my colleagues and I have (largely) chosen the terrestrial mammals (I say largely, because some of the concepts are mentioned in the context of other clades, where these species serve as particularly good examples of the ideas being discussed, or where a discussion of the generality of the concept(s) is of value). The book presents a collection of chapters that will give the reader insight into some important factors that influence how mammals move using legs to travel in the terrestrial environment, and how we can use this understanding to interpret form and performance. Although each chapter should stand on its own, the collected pieces are intended to sum to a good introduction to the field of terrestrial locomotion and the concepts that are useful (imperative?) when delving into these issues.

As the title indicates, there are two main objectives of this volume. One is to identify some important concepts that should be understood by those with an interest in investigating terrestrial locomotion. These are meant to serve as a starting-point for discussions of the issues involved in investigating the "how and why" of terrestrial locomotion. Even though detailed analysis is important in order to verify precisely how a system works, it is conceptual understanding that allows the perception of patterns and the interpretation of meaning that will not be evident based on observation alone, regardless of how detailed or precise that observation (measurement) is. Concepts allow the interpretation of the patterns that exist in nature, and provide the insight into why the patterns exist as they do. As Aristotle stated; "*We have to examine the reasons for all these facts, and others cognate to them; that the facts are such is clear from our Natural History, we have now to ask the reasons for the facts*." (Aristotle, *On the gaits of Animals*, ASL Farquharson, trans.).

Sometimes, the most important concepts are evident only in highly obscured behaviors, hidden as apparently smaller features of more impressive aspects of mammalian movement. These "little things" are sometimes very difficult to observe, indeed, but can actually be the determining features of an important functional behavior, such as locomotion. I learned this early in my career, when I was investigating arboreal locomotion in gibbons. Following many others, I was able to describe how gibbons moved across a series of handholds but, no matter how closely I observed and analyzed these motions, discovering the reasons why these animals chose the movement paths they did was elusive. As often happens when delving into the natural world, some aspects of the motions were trivial to interpret, while other features did not fit into any obvious category.

However, once I had established a collaboration with a colleague who knew very little about gibbons, but knew a great deal about the dynamics of objects physically interacting with each other, it was possible to realize that our current perspective on gibbon locomotion lacked a critical feature – the recognition that energetic loss occurs when the path of the mass of the organism changes abruptly (see Chapters 5 and 6 for a specific discussion of this). Ironically, avoiding this energetic loss is so important to successful brachiation that it is, for all intents and purposes, eliminated from the locomotion of gibbons (at least when brachiating). The implication of this, of course, is that the most important dynamic feature of this animal's locomotion is not directly observable!

It is only through an analysis of alternative movement strategies (that are not used by the organism, because they are so disadvantageous) that the key determinant can be identified. Sometimes, the most obvious aspects of movement are not the most important, and some factors that appear diminishingly small can be far more influential than expected. Hopefully, this volume will provide a number of such "insights" that will build toward a sophisticated perspective on mammalian locomotion.

The second objective of this volume is to introduce and discuss how these concepts can be applied. Thus, many of the chapters provide specific examples of how fundamental concepts are applied to locomotion research to interpret the meaning of the form and function of locomotion. However, it is fully acknowledged that the interpretation of observations through the formulation and application of concepts continues to generate controversy now, just as it has done in the past. When dealing with systems as complex as those occurring in the natural world, working to a final and unambiguous conclusion on a system is a hard-forged and iterative process. As with our personal progress in learning, however, the objective of our exploration of the natural world is not so much to rid ourselves of all questions, but to replace simple questions with ones that are more and more sophisticated.

George Bernard Shaw proposed that "*All great truths begin as blasphemies*". Following from that, I might contend that all lesser truths begin as controversies. And, as much as we might eventually be interested in great truths, most of us spend our day-to-day research lives working on lesser truths (where the practical potential to document progress is much more achievable). The scientific method has many complexities, but one view of scientific progress is the systematic identification and resolution of controversies. With regard to the locomotion of terrestrial mammals, this book is intended to assist with that process.

There is no intention here to produce an authoritative compendium of answers but, instead, the volume should be viewed as a guide to some important questions currently present in locomotion studies – an attempt to lead the reader to the edge of the "envelope", as it were. The exploration of concepts and their application, with the inevitable revelation (and not necessarily immediate resolution) of controversies is the scientific process – a much broader and intellectually rich endeavor than is the simple application of the scientific method.

Rather than try to provide proof to resolve controversies, an important objective of this volume is to expose these controversies within the context of the concepts on which they are based. Identifying and discussing these controversies serves the purpose of stimulating the next generation of researchers to embrace the discussion and to work to expand our understanding of this important aspect of mammalian biology, to solve those particular controversies and to replace them with the next set, as thought radiates into currently unoccupied "logical space". It is really for the next generation of researchers in locomotion biomechanics that this volume was assembled.

This is a particularly interesting time to be studying locomotion. We are the beneficiaries of a suite of new technical tools that allow the measurement and analysis of a wide range of animal movements and novel concepts. These promise to provide new insights into both the "how" and "why" of the movements we observe, and the morphological specializations they are dependent on.

Of even greater importance, however, is my contention that the field of locomotion mechanics is currently undergoing a revolution of perspective of such substance that it borders on a complete paradigm shift. Mammalian terrestrial locomotion has been of academic interest since academic interest originated (see the Aristotle reference above, for instance, or Chapter 1), yet substantial questions remain, in spite of sophisticated investigative tools currently at our disposal. For instance, the fastest quadrupedal gait – the gallop – demonstrates a number of apparently ambiguous mechanical features that have defied the understanding of the mechanical function of this gait (although it remains extremely well-described). That such a roadblock to understanding the meaning of the gait exists, in the face of highly technical advances in analysis techniques, indicates that it is not a technical limitation that prevents our full understanding of this important locomotion strategy, but a conceptual one.

The general approach of the volume is to explore the dynamics of locomotion in terrestrial legged mammals, with some consideration of the mechanics behind these motions. In the process, we are particularly searching for some general principles that can be used to understand and explain how morphology (form) and behavior (action) influence locomotory performance, broadly defined.

Often, locomotion is considered in terms of the neural control responsible for the active motions that can be observed. It will be noticed that there is not much mention of neural control in this volume. This is not because neural control is not acknowledged to be of critical importance in locomotion, but because the focus of the discussions move toward understanding how the biological entity, the organism, interacts and is influenced by its physical environment. The brain is, indeed, the driver of the locomotory system and, just like the driver of an automobile, it is ultimately in charge and directs the motion of the vehicle. However, like any good driver, an individual operating a vehicle must find his/her way between the boundaries of the specific roadway and obey the traffic regulations.

In one sense, this book can be considered an exploration of the "road map" that locomotion navigates, and the "highway regulations" governing how the brain must operate the system in order to be a successful "driver" of locomotion. No matter how much the brain would like it otherwise, in locomotion "F" (force) always equals "ma" (the product of mass and acceleration), and the influence of gravity cannot be avoided (no matter how fast an animal runs, it still weighs the same). Often, control of locomotion is approached from the perspective that "anything is possible", and the specific control patterns selected are analyzed with respect to the internal patterns and relationships between signals. Activity of the neural system, of course, results in activity of the limbs, trunk and other components of the organism. It is those patterns of motion that interact with the external world, and that interaction has consequences, both positive and negative, that we need to be aware of if we are to interpret locomotion effectively (even the central nervous system's role in that process).

One crucial aspect of observing and deciphering the interaction of the organism with its physical environment during the dynamic movements of locomotion is distinguishing the "phenomenon" of locomotion from the "mechanisms" of locomotion. Not much consideration is usually given to this, because the focus is more often on meticulously measuring (often under adverse circumstances, working with uncooperative animals) the dizzying array of movements that occur at all levels of system organization. It is the contention here, however, that the "dizzying array" of motions can only really be interpreted if what they accomplish for the organism can be identified. What is accomplished for the organism is the phenomenon of locomotion, while most of the readily observable motions constitute the mechanism(s) through which the phenomenon is achieved. The chapters in this work try to identify features of the phenomenon of locomotion, and the structural form of mammals organized to achieve locomotion, and to describe its relationship to the mechanisms responsible for making it happen. In so doing, the discussions direct attention to a new and, hopefully, insightful perspective on mammal locomotion.

A range of authors appear in this volume. They were selected on two criteria: that they had something interesting to contribute, and had demonstrated expertise. It will be noted that many of these individuals are not at the end of their careers, unlike we see in many summary texts designed to exploit the perspectives of those with extensive experience in the field. Rather, in keeping with my prediction that the field is moving through an important change of perspective, I have invited individuals to participate with me in this volume who are contributing to those changes.

Some of the chapters were invited because they provide a description of the important concepts, but most were invited because they described the application of those concepts, so they could relay some of the important controversies. All chapters were evaluated by one, or more, independent reviewers. Some of these reviewers came from within the ranks of the contributors to this volume, while others were solicited externally, because of their particular expertise. For their contributions in this regard, I would like to particularly thank R. McNeill Alexander, University of Leeds, J. Max Donelan, Simon Fraser University, Brock Fenton, University of Western Ontario, and Colin Pennycuick, University of Bristol. As always, however, the views portrayed in the chapters of this book are those of the authors, with whom the responsibility for producing and approving each contribution lies.

John E. A. Bertram

CHAPTER ONE

Concepts Through Time: Historical Perspectives on Mammalian Locomotion

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1.1 INTRODUCTION

This chapter is meant only as a subjective description of some important landmarks along the route that has brought the field of terrestrial (primarily) mammalian locomotion to its current position. I have not been particularly interested in documenting the sequence of specific events, but have instead tried to follow the often circuitous path of ideas as they originate, are modified and are passed along to influence others.

In evaluating the current status of the field of terrestrial locomotion, I find that those of us working in this area are part of a long, and often very illustrious, community of individuals who seek out novel and creative methods of divining the constraints and opportunities exploited by animals in attaining movement within the physical world. The motivation for the development of this volume is to focus attention on the role of mechanics in understanding animal locomotion and, particularly, that of terrestrial mammals. The field is currently undergoing a substantive change in perspective, as new

Understanding Mammalian Locomotion: Concepts and Applications, First Edition.
Edited by John E. A. Bertram.
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technologies allow the critical evaluation of dynamic features of gait, and novel conceptual approaches are being assessed (although as we will see, few ideas in a field with such a long history can be considered truly novel). Overall, this volume is designed to stimulate the discussion of these newly arising opportunities, and this chapter is designed to "set the stage" for such a discussion.

Historical evaluations relevant to the field of locomotion science appear with some regularity, either as a contribution designed to put the field in historical context (Cappozzo *et al.*, 1992; Medved, 2001; Ashley-Ross and Gillis, 2002) or integrated within a discussion of the state of the field at the time of writing a more comprehensive assemblage of knowledge on the topic (Howell, 1944; Gambaryan, 1974; Walker, 1972). My interest is in emphasizing the origin of unifying (or dividing?) concepts, rather than exhaustively mapping the history of the field. To this end, I will trace my personal impression of key conceptual breakthroughs, whether in the fields of animal or human biomechanics and physiology or, indeed, even if it strays into robotics or the fundamental mechanics that ultimately underlies our field. I will liberally add my "interpretation" of events and the stimulus that led to them. When doing so, I will provide the evidence as I see it, but in few cases will this be conclusive, so all such descriptions should be evaluated as only the personal opinion of an interested observer.

1.2 THE ANCIENTS AND THE CONTEMPLATION OF MOTION

Undoubtedly, prehistoric man observed and wondered at the remarkable abilities of animals to move, likely largely motivated by the elusiveness of the prey they pursued, but also by wonderment at the fleetness of some terrestrial runners. The cave paintings from Lascaux, France (approximately 15,000 BC) demonstrate that our distant ancestors were, indeed, keen observers of the form and movement of mammals, indicating a fundamental interest in understanding and interpreting animal motion (Figure 1.1).

The movement of animals and their relationship to the locomotion of humans also holds an inherent interest for those trying to understand the world they observe. Such was the case with Aristotle (384–322 BC), an individual who has had a great influence on philosophical thought and the foundations of modern science. Among Aristotle's influential writings was *De motu Animalia* (On the Gait of Animals). Aristotle's interest in locomotion derived from the fundamental question of the difference between passive matter and the activity of living things, placing questions of locomotion at the foundation of major philosophical issues regarding the makeup and function of the physical world.

Among other surprising observations listed in *De motu Animalia*, Aristotle noted vertical motion of the human when walking, by observing the "zig-zag" movement of the shadow against a flat wall (as translated by Farquharson, 2007). This was particularly in reference to how the swing limb must flex in order to pass under the individual, but the observation was astute and important in recognizing the complexity of motions required to produce effective locomotion, and that locomotion involved multidimensional movement of the body as well as the limbs.

FIGURE 1.1

The cave painting from Lascaux, France, known as the "Third Chinese Horse". This painting depicts a galloping horse with arrows approaching its back, taken from the series referred to as the "Chinese horses". The cave was discovered by adventurous boys in 1940. The painting likely dates from 15,000 BC.

Aristotle also described the limb motions of quadrupeds as they walked, but these "observations" seem to have come more from theoretical analyses than from direct observation. As will be described below, some two millennia later, Borelli revised some of these descriptions to reflect more accurately the actual movements of walking quadrupeds as a means to explain some of the reasons that motions occur as they do.

1.3 THE EUROPEAN RENAISSANCE AND FOUNDATIONS OF THE AGE OF DISCOVERY

Although it is well known that Leonardo da Vinci (1452–1519) studied fish swimming and bird flight, it is not so well known that he also studied human and animal terrestrial locomotion. His approach to the investigation of structure, including meticulous anatomical studies, paved the way for considering the mechanisms of movement. Indeed, his work, in many ways, heralded the beginning of the European Renaissance. He performed many artistic studies on the form of animals and people in motion. For many of these studies, it is difficult to tell whether the objective of the work was to understand the function of the system, or to observe the natural motions in order to improve his art – in many cases, for da Vinci, these seem to have been one and the same.

Of particular note are his drawings of individuals walking up and down stairs, standing from a seated position and stopping from a run, all of which represent the mechanical realities of each of these circumstances. His pen and ink studies of individuals and animals laboring, demonstrating a variety of positions, are reminiscent of Muybridge's photographic studies that followed nearly 500 years later. Da Vinci's notebooks indicate that he was collecting material for a never-completed work on mechanics, a work that would have given us a complete view of his understanding of motion, including that of animals and people.

As keen an observer as he was, however, he did make some errors. He clearly believed, as all of us do as children, that heavier objects fall more rapidly than lighter ones. Our modern perspective of the world benefits from the luxury of the accumulated understanding that we call knowledge, served to us in the form of education.

The extensive notebooks of da Vinci hold numerous examples of his understanding of locomotion mechanics, some of which have proven correct, while others were not so successful. Leonardo (more or less) correctly observed that, "*Man and every animal undergoes more fatigue in going upwards than downwards, for as he ascends he bears his weight with him and as he descends he simply lets it go*." However, he profoundly misunderstood the role of impulse, and suggested, "*A man, in running, throws less of his weight on his legs than when he is standing still. In like manner the horse, when running, is less conscious of the weight of the man whom it is carrying; consequently many consider it marvelous that a horse in a race can support itself on one foot only. Therefore we may say regarding weight in transverse movement that the swifter the movement, the less the weight towards the centre of the earth*." (p. 150, Richter and Wells, 2008).

It is now eminently clear that, provided we remain in the Newtonian realm, we weigh the same regardless of how fast we run. It is the subtle strategies employed to deal with this fact that make the understanding of running gaits, in people and other mammals, a challenge to understand.

A substantial influence on the origins of biomechanics were the works of Galileo Galilei (1564–1642), particularly *Discourses on Two New Sciences*. One of these "New Sciences" was the formal western origin of mechanics. The principles outlined formulated the basis of understanding the mechanics of biological movement. Indeed, many examples described in the *Discourses* are biological, indicating that, in Galileo's mind, there was no definitive difference between the mechanics of the organic world and that constructed by humans. TA McMahon (1975) referred to Galileo's analysis of scaling issues, noting ironically that a woodcut from *Discourses* (Drake, 1989, p. 127 and 128) differed somewhat from Galileo's own discussion and analysis of scaling mechanics, and appeared to represent a scaling relationship intermediate between constant shape geometric "isometry" and the changing proportions of "static stress similarity", which Galileo suggested was necessary to preserve mechanical support function over large size changes. From more thorough analyses, McMahon described the consequences of this alternative scaling model, which he termed "Elastic Similarity" (1973, 1975; see also Chapter 8).

Giovanni Borelli (1608–1679) is noted for applying Galileo's principles of mechanics to the action of the musculoskeletal system – "*Borelli then shows what the forces of various muscles must be: for example, the force exerted by the biceps when a weight of 28 lbs is being held by the hand with the arm extended horizontally is 560 lbs*"

(Des Chene, 2005). Borelli's major contribution, *De Motu Animalium* (On the movement of animals, published posthumously in two parts in 1680 and 1681), is full of examples that would not be out of place in a modern introductory university course on musculoskeletal mechanics. Borelli worked on numerous problems in parallel with Newton, whose career and influence was rising toward the end of Borelli's life.

Although he studied planetary movement and pendular motion, Borelli never arrived at the conceptual formulation of gravity or the laws of motion that were some of Newton's greatest contributions. One of his most profound errors was to assert that, in some cases, forces were not "equal and opposite" but that, within the body, they could be unequal. However, he was extremely influential in describing the function of muscles, and also in his description of locomotion, particularly quadrupedal walking. With meticulous illustrations and well-founded arguments, Borelli was able to dispense with Aristotle's contention of diagonal-only foot contacts in quadrupedal walking, and was able to describe the features of balance associated with a stability tripod, as later championed by Sir James Gray (1944, 1968). The arguments were apparently convincing enough that the depiction of animal walking in sculpture and painting began to change following the publication of Borelli's book.

Another 17th century luminary was Claude Perrault (1613–1688). Like Borelli, he was instrumental in applying mechanical concepts to the action and organization of the musculoskeletal system. He introduced some important concepts, such as the spring-like capacity of muscles and joint position, representing the equilibrium between protagonist and antagonist muscles. Perrault also astutely observed that muscles function through "introduction of the spirituous substance brought by the nerves from the brain" (Des Chene, 2005).

As da Vinci had influenced thought and helped to initiate the Renaissance, Isaac Newton's (1643–1727) formulation of the laws of mechanics and the explicit role of gravity initiated a new era of enlightened modern science. Newton provided the theoretical framework with which to evaluate the role of the organic components of animal and human function in the physical world, within which they operate and from which their motions are influenced. Newton's Laws of Mechanics form the foundation of all modern biomechanics and find their way, at least in implied assumptions, into basically all modern work in the field.

1.4 THE ERA OF TECHNOLOGICAL OBSERVATION

With the beginning of the modern era and the application of novel technological advancements came the possibility of observing and quantitatively measuring aspects of human and animal movement that had previously not been available. Goiffon and Vincent (1779) are widely acknowledged as an important early example of applying technical evaluation to gait studies. A bell system was attached to the front hooves of horses, and the difference in ring pattern for different gaits was evaluated. As da Vinci's studies of motion and Borelli's descriptions of quadrupedal walking influenced the interpretation of how motion is shown in art, one stated purpose of the Goiffon and Vincent evaluation of the equine gait was to inform artists with regard to how the gaits of horses should be depicted in order to properly represent their actual motion.

In a conceptually parallel but more sophisticated approach, Marey (1884) used pneumatic bulbs attached to the feet of horses that operated an armature recording pressure changes on a smoked drum carried by a rider. From this apparatus, fairly accurate determinations of the foot contacts were documented for all of the standard equine gaits. Marey also applied a similar approach to the study of human locomotion. His work overlapped with that of Muybridge, and in his later career, he adopted photographic approaches originated by Muybridge and added to these by developing several novel technological innovations of his own – for instance, the photographic "rifle" (1892) and the development of modern-style multiple-frame "movies" (1899).

The ability to technically observe locomotion achieved a watershed point with the work of Muybridge (1887). Through the use of a series of shuttered still cameras operated by trip wires, Muybridge was able to produce high-quality serial still image photographs through the range of motions of a wide variety of human and animal activities. The motivation for this innovative approach apparently derives from his involvement in a bet regarding whether a trotting horse has any portion of its stride without contact with the ground. Settling this bet to the satisfaction of all involved required clear demonstration of the gait cycle, with adequate time resolution to indicate how the motions were produced.

Muybridge recognized that his novel technique provided a totally new perception of (and perspective on) movement. He produced a remarkable data set of images from as wide a variety of animal and human motion as he could manage. Included in these were figures of humans doing everyday tasks that, though composed of evenly timed separate images, resemble the "snap-shot" views drawn by da Vinci centuries previously. It is likely that da Vinci would have liked to produce the series as Muybridge had, if the technology had been available to him. Muybridge's original compilation (Muybridge, 1887), ten volumes in total, has been reproduced in a variety of abridged editions that remain remarkably useful through to the current day (Hildebrand, 1962, 1989; Bertram and Gutmann, 2008).

Imaging motion yields a range of information about the process of locomotion, but the analysis of much of the mechanics is facilitated by also measuring the forces involved. Amar (1916, cited in Jarrett *et al.*, 1980) developed a mechanical force-reactive platform that had a great deal of early influence on the analysis of human locomotion, particularly in adapting technology to the needs of amputees returning from World War I. Elftmann (1934) later developed a reliable mechanical force platform system for human locomotion. Manter (1938), working with Elftmann, devised a multiple mechanical force plate system (two platforms in series) appropriate for analysis of quadrupedal locomotion, and used these to analyze the locomotion of the cat.

Gray (1944) recognized that Manter's results indicated that horizontal forces generated by the limbs of quadrupeds create turning moments around the animal's center of mass, which can ultimately influence the measured vertical forces at each foot. Due to the complications arising from redistributed forces in quadrupeds moving at non-steady speeds, in his highly influential 1968 compendium of animal locomotion mechanics, Gray advised stringent control of horizontal accelerations for quadrupedal gait analyses. Unfortunately, the difficulty in controlling animal motion meant that this advice was not always followed appropriately, and the "stringent" limits on speed