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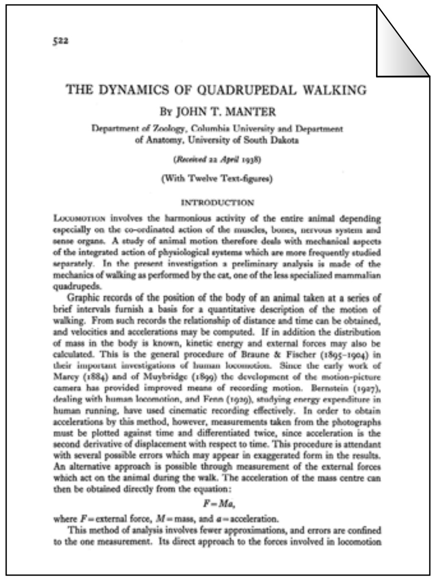
JEB Classics

A STEP FORWARD FOR LOCOMOTOR MECHANICS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THE DYNAMICS OF QUADRUPEDAL WALKING

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(With Twelve Text-figures)

INTRODUCTION

Locomotion involves the harmonious activity of the entire animal depending especially on the co-ordinated action of the muscles, bones, nervous system and sense organs. A study of animal motion therefore deals with mechanical aspects of the integrated action of physiological systems which are more frequently studied separately. In the present investigation a preliminary analysis is made of the mechanics of walking as performed by the cat, one of the less specialized mammalian quadrupeds.

Graphic records of the position of the body of an animal taken at a series of brief intervals furnish a basis for a quantitative description of the motion of walking. From such records the relationship of distance and time can be obtained, and velocities and accelerations may be computed. If in addition the distribution of mass in the body is known, kinetic energy and external forces may also be calculated. This is the general procedure of Braune & Fischer (1895–1904) in their important investigations of human locomotion. Since the early work of Marey (1884) and of Muybridge (1899) the development of the motion-picture camera has provided improved means of recording motion. Bernstein (1927), dealing with human locomotion, and Fenn (1929), studying energy expenditure in human running, have used cinematic recording effectively. In order to obtain accelerations by this method, however, measurements taken from the photographs must be plotted against time and differentiated twice, since acceleration is the second derivative of displacement with respect to time. This procedure is attendant with several possible errors which may appear in exaggerated form in the results. An alternative approach is possible through measurement of the external forces which act on the animal during the walk. The acceleration of the mass centre can then be obtained directly from the equation:

$$F = Ma,$$

where F = external force, M = mass, and a = acceleration.

This method of analysis involves fewer approximations, and errors are confined to the one measurement. Its direct approach to the forces involved in locomotion

Thomas Roberts writes about J. T. Manter's classic 1938 study of the dynamics of quadrupedal walking.

Truth be told, more than a few biologists owe their original fascination with animal locomotion to their aesthetic, rather than analytic, sensibilities. Perhaps this appeal results from the fact that the flow of energy that is central to all of biology is so readily visualized in animal motion. Our current understanding of animal movement relies on the ability not just to appreciate the flow of energy during movement, but to measure it. In his classic 1938 study of the mechanics of walking in cats, J. T. Manter employed critical analytical approaches for measuring mechanical energy changes during walking and running that are still used by biomechanics researchers today. His paper also presented some glimpses into ideas that are now central paradigms in locomotor mechanics.

Manter's study was built on a novel experimental tool, ingeniously applied. From the earliest studies, researchers recognized that an accurate measurement of forces produced by a runner or walker against the ground might yield insight into how muscles power movement (Marey, 1874; Fenn, 1930; Elftman, 1939). Marey's clever pneumatic devices were the first force platforms, followed by Fenn's spring-based device and arrays of deformable rubber pyramids used by H. O. Elftman. Working with Elftman, Manter designed and built a spring-based platform, with a lever system to magnify small deflections as the platform was loaded by an animal's weight. They visualized and measured the displacement of these levers in the same high-speed film images used to record the positions of the animal's limbs. Manter's elegant force plate design stands out from others because it was the first to record forces in three axes – vertical, fore–aft and lateral – and therefore is the prototype of the modern force plate used in biomechanics research as well as clinical orthopedics. It is only recently that an analogous tool has become available for those interested in forces produced by swimming and flying animals. Particle image velocimetry is currently providing the same kind of fundamental insights into movement in fluid media that force plates have provided into terrestrial locomotion over the past century (Lauder and Drucker, 2004; Tobalske et al., 2005).

The real power of Manter's work resulted not from the design of his force plate, but from its application as a tool for measuring mechanical work. From the early 20th century, oxygen consumption measurements quantified the metabolic energy used by muscles during walking and running. A better understanding of running and walking mechanics promised to reveal, as H. O. Elftman summarized, '*the use to which this energy is put*' (Elftman, 1940). Early studies of the mechanical work of running relied on high-speed film measurements of the movements of the body and limbs. Each step a runner takes involves cyclic fluctuations in the kinetic and potential energy of the body and limbs, and these energy changes can be calculated from known limb dimensions and movements. Film-based measurements, however, suffer from the fact that the body's center of mass cannot be identified by an obvious anatomical landmark, and its location varies with changes in posture.

Manter recognized that his force plate could provide an alternative to film as a method for measuring body movement. The forces on the body are related to its acceleration according to Newton's second law (force=mass×acceleration), and velocities and positions can be determined by integrating accelerations. From body position and velocity, changes in potential and kinetic energy can be calculated. Manter applied this approach to walking cats, and concluded that it was superior to film-based methods. This approach was ultimately developed rigorously and dubbed 'force-plate ergometry' by Cavagna and coworkers (Cavagna et al., 1964; Cavagna, 1975). This method has been an essential tool for investigating how the mechanical work of walking and running relates to metabolic energy consumed, a topic that continues to motivate locomotor research today (e.g. Taylor, 1994; Marsh et al., 2004; Griffin et al., 2003).

It turns out that relating the mechanical work of walking and running to the metabolic energy muscles consume is not so easy, primarily because much of the work is done not by muscles but by passive mechanisms. Manter recognized one of the most important of these when he observed that not all of the increases in the body's kinetic energy in each step had to be supplied by muscle work, but could instead result from a transfer of energy from potential to kinetic. This kind of exchange explains how a pendulum maintains a lot of motion without much energy input. Since walkers vault over the limb with each step, the cyclic exchange of the body's potential and kinetic energy has been termed the 'inverted pendulum' mechanism (Cavagna et al., 1977). Studies including a diverse assemblage of animals, from rams and turkeys (Cavagna et al., 1977) to crabs (Full, 1989) and frogs (Ahn et al., 2004), have demonstrated that this mechanism is nearly universal among walkers. Recent studies of slightly unusual walkers provide exceptions that prove the rule: penguins pendulum in a side-to-side waddle (Griffin and Kram, 2000), and Galapagos tortoises are the first documented examples of animals that walk without any pendulum mechanism at all (Zani et al., 2005). Our understanding of the inverted pendulum mechanism has not only informed biologists. A pendulum-like mechanism has been incorporated into many robots that walk. Robot designers have found that mimicking nature's walkers simplifies control and improves energy efficiency (McGeer, 1990; Collins et al., 2004).

Manter's study appears to be the first to combine simultaneous measurements of individual foot forces and film to use the modern inverse dynamics approach to estimate the muscle forces acting at individual joints. This non-invasive method of determining muscle function is still used in clinical gait analysis. As a research tool, it has provided a wide range of insights into locomotor function, including the change in limb posture with size in mammals (Biewener, 1990), the mechanical role of biarticular muscles (van Ingen Schenau, 1992; Jacobs et al., 1996), and the motor coordination of movement (Zajac et al., 1981; Winter, 1990). Manter's inverse dynamics analysis of cat walking led him to conclude that some muscles may act isometrically to effectively produce high forces, an idea that has recently received renewed interest (Taylor et al., 1994; Roberts et al., 1997; Fukunaga et al., 2001).

Manter's study includes elegant diagrams and a clear description of the force-plate-based inverse dynamics calculations. It is unclear why Elftman's paper published the following year is usually cited as the definitive inverse dynamics paper (Elftman, 1939). Elftman's subjects were human rather than feline, but adapting the approach from cats to humans requires only a change in the constants used for the mass and dimensions of the limbs.

Is Manter's paper a forgotten classic? A survey of modern citations of Manter's paper suggests that his work has been cited extensively in some fields but left behind in others. Citations to this paper are well-represented in the physical anthropology literature, spotty in the comparative locomotor mechanics literature, and almost completely absent from the extensive literature on human locomotor mechanics and inverse dynamics. For both its technical prowess and its insights into questions still under debate today, this JEB classic is worth a second look.

A PDF file of the original paper can be accessed online: http://jeb.biologists.org/cgi/content/full/208/22/4191/DC1

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