INTEG. AND COMP. BIOL., 42:183–189 (2002)

A Brief History of Vertebrate Functional Morphology[1]

MIRIAM A. ASHLEY-ROSS[2,]* AND GARY B. GILLIS†

*Department of Biology, Box 7325, Wake Forest University, Winston-Salem, North Carolina 27109
†Department of Organismic and Evolutionary Biology, Harvard University, Concord Field Station, Old Causeway Road, Bedford, Massachusetts 01730

SYNOPSIS. The discipline of functional morphology grew out of a comparative anatomical tradition, its transformation into a modern experimental science facilitated largely by technological advances. Early morphologists, such as Cuvier, felt that function was predictable from organismal form, to the extent that animals and plants represented perfect adaptations to their habits. However, anatomy alone could not reveal how organisms actually performed their activities. Recording techniques capable of capturing fast motion were first required to begin to understand animal movement. Muybridge is most famous for his pioneering work in fast photography in the late 19th century, enabling him to ''freeze'' images of even the fastest horse at a full gallop. In fact, contemporary kinematic analysis grew directly out of the techniques Muybridge developed. Marey made perhaps an even greater contribution to experimental science through his invention of automatic apparati for recording events of animal motion. Over the first half of the 20th century, scientists developed practical methods to record activity patterns from muscles of a living, behaving human or animal. The technique of electromyography, initially used in clinical applications, was co-opted as a tool of organismal biologists in the late 1960s. Comparative anatomy, kinematic analysis and electromyography have for many years been the mainstay of vertebrate functional morphology; however, those interested in animal form and function have recently begun branching out to incorporate approaches from experimental biomechanics and other disciplines (see accompanying symposium papers), and functional morphology now stands at the threshold of becoming a truly integrative, central field in organismal biology.

INTRODUCTION

Humans have a history of being fascinated with how animals are constructed, and how they function in their environment. Two of the four things that defeated the wisdom of Solomon reflect this preoccupation with animal form and function: ''the way of an eagle in the air,'' and ''the way of a serpent upon a rock'' (Proverbs, 30:19). The discipline of functional morphology attempts to describe and quantify the relationship between organismal form and function. The primary tools of the contemporary functional morphologist include (1) comparative anatomical investigation of the system of interest, (2) quantitative analysis of kinematics to determine the ways in which the anatomical system moves, and (3) electromyography to determine the patterns of muscle activity driving these movements. While these tools have traditionally formed the core of research in functional morphology, many workers are broadening their repertoire by embracing the techniques of other disciplines (see the following papers from this symposium). In so doing, they are gaining the ability to address previously unanswerable questions, and forging new links with other fields to help establish functional morphology as a truly integrative discipline. Our paper will set the stage for the subsequent contributions of the symposium authors by briefly tracing the history of the field of vertebrate functional morphology, outlining the development of each of the primary tools mentioned above, and reviewing a variety of more recently co-opted experimental methods. In doing so, we emphasize selected figures and their contributions to the study of vertebrate form and function. By nature of the limited space available, we acknowledge that many important scientists will be left out of our discussion. Nevertheless, we hope to highlight many of the workers most instrumental to the development of our field.

THE DEVELOPMENT OF COMPARATIVE ANATOMY

What we now refer to as functional morphology grew out of a comparative anatomical tradition. Lacking the means by which to manipulate experimentally or measure animal movements, early natural philosophers were limited to inferring function from their observations of the structure and behavior of animals (Russell, 1982). Aristotle (384–322 B.C.) is the first comparative anatomist whose writings are well known, and he attempted to explain the relationships among different groups of animals by reference to their behavior and ecology as well as their anatomy (Aristotle, 1984; Russell, 1982). Aristotle made a philosophical break with his predecessors, particularly Plato, which was significant for science. Plato (428–347 B.C.) held that the world of ideas was the only reality, and that, therefore, contemplation was the only path to understanding Truth (Nash, 1963; Nigg and Herzog, 1999). The physical-material world was imperfect; hence, study of it was counterproductive. Any discrepancies between Perfect Ideas and evidence from the physical-material world reflected the imperfect nature of physical existence, and, thus, had to be discarded. Aristotle rejected this view, holding instead that the world re-

---

[1] From the Symposium *Molecules, Muscles, and Macroevolution: Integrative Functional Morphology* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 3–7 January 2001, at Chicago, Illinois.

[2] E-mail: rossma@wfu.edu

vealed by the senses was Reality, and that ideas were artificial abstractions. Understanding of the world could only be achieved by careful observation of Nature itself. The contributions that Aristotle made to comparative anatomy include his extensive treatises on the anatomical design of various animal groups (*Historia Animalium, De Partibus Animalium*; Aristotle, 1984). In them he recognized the unity of body plan within the major groups of animals, and emphasized the function of animal parts and the correlations between features (Russell, 1982). Aristotle's exploration of animal function was limited by the lack of technology for experimentation, typical of his time. As a result, he explained various animal functions, including movement, as being the result of ''*pneuma*,'' a spiritual breath (literally) that was carried to the various organs to activate them, and that caused the limbs to move. In addition to his careful records of observation, Aristotle and his peers left to subsequent generations the revolutionary viewpoint that the natural world was intelligible by man, and that mechanisms driving natural events could be identified and understood (Nash, 1963).

Galen (129–201 A.D.) made the first comprehensive descriptions of human anatomy and function (Galen, 1821, 1968), which, due to the lack of human cadavers for dissection, he based on animal anatomy (with consequent inaccuracies). Galen recognized that muscles were responsible for movement in both humans and animals (Galen, 1821, 1968), though he adhered to Aristotle's *pneuma* theory of their activation (Sarton, 1954). He also made some of the earliest forays into experimental physiology, with studies of phenomena as diverse as the mechanism of voice production and the course of digestion in pigs (Sarton, 1954). Galen is widely regarded as one of the most important figures in the history of medicine, and his anatomical treatises were treated as unassailable dogma for over 800 yr.

Late in the 15th century, Leonardo da Vinci (1452–1519) revived interest in the study of the relationship between form and function with his masterful illustrations of anatomy and his (often unsuccessful) inventions, some of which he hoped would allow humans to fly like birds (Gray, 1968). Leonardo made the first accurate dissections and illustrations of human anatomy (Mathé, 1978), and also rigorously applied mechanical principles to human anatomical structures. He described the parallelogram of forces, and applied this concept to the movements of human limbs. Further, Leonardo discarded Aristotle's *pneuma* theory of motive force; he clearly understood that muscles were activated by nerves that ramified through them and caused them to contract, pulling the tendons and attached bones (MacCurdy, 1954). Leonardo recognized that the muscles themselves were driving animal movement, that it was their intrinsic properties that were responsible for contraction.

Galileo Galilei (1564–1642) is known to the general public primarily as an astronomer, but he made substantial contributions to the study of form and function on several fronts. First, Galileo recognized that changing the scale of a structure, whether it be a building or an animal, necessitated changes to the proportions of its supporting elements to prevent collapse under its own weight (Galilei, 1991; Nigg and Herzog, 1999). He is thus considered to have founded the study of allometry. Second, he was the first to analyze systematically the strengths of various materials and of structures (beams, hollow cylinders), leading to the development of many of the principles of structural engineering (Gordon, 1988). Third, Galileo popularized experimentation as the way to discover scientific truth. Galileo had the gift of explaining his experiments and their results so clearly as to win over his contemporaries and convince them to embrace the experimental method. Finally, Galileo pioneered the use of inductive reasoning, still used today as an integral part of the scientific process.

Giovanni Borelli (1608–1679), a follower of Galileo, applied strictly mechanical principles to the study of animal motion and is now acknowledged as the ''father of biomechanics.'' In his treatise on animal movement, *De Motu Animalium* (1680), Borelli used geometry to describe the movements of limbs in complex motions (*e.g.*, jumping), and compared the action of muscles on bones to simple lever systems (Nigg and Herzog, 1999). Most importantly, Borelli firmly established that muscle contraction and movement could be explained and understood on a purely mechanistic basis, without the need to invoke spiritual forces (Borelli, 1989). The application of mathematical and mechanical principles to the study of animal function by Borelli and his contemporaries greatly influenced the subsequent development of experimental biology.

A century later, the great French comparative anatomist Georges Cuvier (1769–1832) set the stage for the development of the field of comparative functional morphology with his famous doctrine of the ''correspondence of parts,'' in which he stated that by examining an animal's structure (even isolated parts), he could infer the functioning of the entire organism (Russell, 1982; Appel, 1987). Cuvier left an extensive body of work on the comparative anatomy of all of the major groups of animals, providing an important resource for future experimentalists.

THE DEVELOPMENT OF KINEMATIC ANALYSIS

The emergence of functional morphology as a quantitative, experimental discipline was sparked by technical developments in the second half of the 19th century. Working independently, Etienne-Jules Marey and Eadweard Muybridge developed equipment and procedures for high-speed photographic investigations of animal movement. These two men are so central to the historical development of the study of animal motion that their lives and contributions will be explored in some detail.

Muybridge (1830–1904) approached the field of animal locomotion from a photographic, rather than scientific, background. His life is marked by interesting twists and turns and, if not for an accident, he might not have made his famous study of animal motion, and the history of functional morphology might have turned out quite differently. Muybridge was born in 1830 in Great Britain, and he immigrated to the United States in 1852. He was initially employed as a book-purchasing agent for several years on the East Coast before moving to San Francisco and establishing himself as a book dealer. In 1860, while on a book-buying trip to New York, he was involved in a near-fatal stagecoach accident. He recuperated for several years in his native England, and took up photography during this time, apparently as part of the ‘‘natural therapy’’ prescribed by his physician (Mozley, 1979).

Upon returning to San Francisco in 1866, Muybridge established himself as a scenic photographer. His first important work, a series of photos entitled *Scenery of the Yosemite Valley*, was received by the national press as a triumph of photographic technique (Mozley, 1979). In the 1860s, photography was a demanding process that entailed an elaborate series of physically challenging tasks (See Mozley, 1979 for a description of the wet collodion process, the most advanced photographic method of the time). Muybridge showed the tenacity that would serve him well in his later work on animal movement, as he managed to take excellent photos using the difficult wet-collodion method in the wilderness of Yosemite Valley (Mozley, 1979).

Muybridge’s Yosemite photographs brought him to the attention of former California governor Leland Stanford, also the owner of a famous fast trotting horse named Occident. In 1872, Stanford challenged Muybridge to produce a photo of Occident at full speed to discover whether Stanford was correct in his belief that there was a phase in the trotting stride in which all four hooves were off the ground. An essay that Muybridge later published anonymously described the meeting between the men, and also shows his flair for the dramatic:

> ‘‘Mr. Stanford startled the photographer by stating that what Mr. Stanford desired was a photograph of his horse, Occident, and taken while the horse was at full speed. No wonder even the skilled Government photographer was startled, for at that date, the only attempts that had ever been made to photograph objects in motion had been made only in London and in Paris, only by the most conspicuous masters of the art, and only of the most practicable street scenes. . . .
> . . . Mr. Muybridge therefore plainly told Mr. Stanford that such a thing had never been heard of; that photography had not yet arrived at any such wonderful perfection as would enable it to depict a trotting horse at speed. The firm, quiet man who had, over mountains and deserts and through the malignant jeers of the world, built the railroad declared impossible, simply said: ‘I think if you will give your attention to the subject, you will be able to do it, and I want you to try.’’’ (Muybridge, 1881)

Muybridge succeeded in producing a shadowy picture of Occident in 1874, and it convinced his patron that the project was worth pursuing further. Unfortunately, the photo was retouched before it was released to the press, and many believed that the entire thing was fake (MacDonnell, 1972). Muybridge and Stanford resolved to produce better proof, and assured by Stanford that money was no object, Muybridge procured 12 cameras with the finest lenses then made, arranging them in a series along a track to capture successive phases of the horse’s motion (Mozley, 1979). In June of 1878, Stanford invited members of the local press to his estate in Palo Alto to witness a demonstration of the photographic technique in capturing the motion of his horses trotting and galloping. An excerpt from an issue of *Pacific Life* dated June 22, 1878 describes the event:

> ‘‘The most important experiments ever made in connection with electrophotography were brought to a successful conclusion on Saturday last, in the presence of Governor Stanford and a few invited guests at his race track at Palo Alto. The experiment in question was to reproduce the action of a horse at every point in his stride when trotting at a 2:20 gait, and as already mentioned the result was so successful as to be beyond the cavillings of a few skeptics whose admirably propounded axioms in this respect are thoroughly put to nought. To Governor Stanford must be accorded the merit of first broaching to Mr. Muybridge the feasibility of the plan, and to his liberality in furnishing the funds for a series of costly experiments must be ascribed the present success; but to Mr. Muybridge great praise is due for the skill shown in the succession of experiments made that step by step have resulted in such a grand impulsion in the history of the photographic art.’’ (MacDonnell, 1972, p. 23)

Even after the first horse had been trotted past the battery of cameras, apparently some of the more cynical members of the press were unconvinced. However, when a second horse galloped past the camera, breaking threads that had been stretched across the track to trigger the shutters, the press was convinced; the mare startled and broke her saddle girth in the middle of the trackway, and the entire incident was captured in the photo sequence, thus erasing any doubts regarding authenticity (MacDonnell, 1972).

Muybridge’s most famous, and lasting, contribution is his exhaustive photographic investigations of human and animal locomotion carried out at the University of Pennsylvania from 1883–1886 (Muybridge, 1979). Over 20,000 individual photographs were taken of human and animal subjects walking, running, turning, and (in the humans) performing various tasks, such as swinging a pick, throwing a ball, shoeing a horse, or emptying a pail of water. Muybridge’s sequences are widely used in teaching, and are still valuable for researchers. His sequential photographic technique was the forerunner of the high-speed video technique widely used today in kinematic analysis. Further, Muybridge is justly regarded as the ‘‘father of the motion picture’’ (MacDonnell, 1972), having invented the first device (his ‘‘zoopraxiscope’’) that showed sequences of pictures through a projection apparatus.

The Frenchman Etienne-Jules Marey (1830–1904) is less well known than Eadweard Muybridge. However, Marey made perhaps even more significant contributions to the development of the experimental analysis of human and animal function. Marey invented the graphical method of recording events over time. Indeed, the numerous machines he designed and built to record physiological events are the basis upon which nearly all modern recording instrumentation (*e.g.,* oscilloscopes, electrocardiographs, electroencephalographs) are designed (Braun, 1992). Several of his devices were specifically designed to generate a graphical record (what Marey termed ‘‘chronography’’) of kinematic events. For example, he constructed special shoes connected to a recorder that would generate a trace corresponding to the footfalls and pressure exerted by the feet during the stride in humans or other animals (Marey, 1895; Braun, 1992). However, Marey eventually grew dissatisfied with his graphical method, believing that he needed to see the actual motion he was studying in order to understand it (Braun, 1992). Working independently of Muybridge, Marey turned his attention to developing photographic methods that would allow him to freeze fast motion as well as capture successive phases of movement. He developed the ‘‘photographic rifle,’’ a forerunner of the modern film camera and camcorder, and also a method for making multiple exposures on a single photographic plate (Braun, 1992). Together, Muybridge and Marey set the stage for the quantitative analysis of animal motion and, ultimately, laid the foundation for what has come to be considered ‘‘modern kinematics.’’

Another series of advances in the field occurred in Britain in the middle of the 20th century. Sir James Gray (1968), Sir James Lighthill (1969) and R. McNeill Alexander (1968), and their colleagues, added rigorous mathematical analysis to help describe and understand the anatomical structures and movements involved in various modes of animal locomotion. In addition, these scientists calculated forces acting upon appendages and/or bodies, power requirements for swimming, running, and flying, and energetic costs associated with locomotion. These analyses were drawn from the established field of mechanics in the physical sciences, and included the first formal integration of physical principles into the field of functional morphology.

THE DEVELOPMENT OF ELECTROMYOGRAPHY

By the late 19th century, biologists had been accurately describing organismal structural design for centuries and now were also capable of quantifying the dynamic capacities of these structural features in living animals. However, linking the anatomical design to the dynamic behaviors of animals required an understanding of the contributions of the actuators themselves, the muscles, to the different movements underlying each behavior. The technique of electromyography, the recording of electrical activity in active muscles, provided this link and remains an integral component of the contemporary functional morphologist’s toolbox.

The initial demonstration of ‘‘bioelectricity’’ was made by Luigi Galvani (1737–1798) in the late eighteenth century. By showing first that frog muscle contracts when exposed to a variety of external electrical sources, and then demonstrating that muscle also contracts when exposed to the nerve of another frog, Galvani was able to establish the presence of electrical currents in living tissue (Geddes and Hoff, 1971). In the mid-nineteenth century, Emil DuBois Reymond (1818–1896) confirmed that both nerves and muscles generate and conduct electrical currents. More importantly, he was one of the first not only to detect, but also to measure precisely bioelectric currents. By using over five kilometers of copper wire coiled nearly 24,000 times around a magnet, DuBois Reymond constructed a galvanometer capable of measuring electrical potential differences on a scale of millivolts (Sabbatini, 1998). Using this device he was able to show that the currents traveling through nerves and muscles were in the form of small, brief electrical impulses (Katz, 1966; Basmajian and de Luca, 1985) that we now call action potentials. In addition, DuBois Reymond is acknowledged for being the first to measure electrical signals from voluntary muscular contractions (Basmajian and de Luca, 1985).

Because of the technical difficulties associated with measuring and recording bioelectric events in the latter half of the nineteenth century, the bulk of the important work performed during this time involved using stimulation experiments to study muscle action. However, instead of simply demonstrating muscular contraction upon exposure to electrical current (like Galvani), workers were now systematically assessing the function of individual muscles by observing their mechanical actions *in vivo* in response to electrical stimulation. G. B. Duchenne (1959), in his *Physiologie des Mouvements,* (1867) exemplified this approach and began to piece together the sequential contributions of the actions of different muscles to normal movements (Granit, 1981).

In the early twentieth century, the invention of several devices led to dramatic progress in the development of electromyography as an experimental technique. The invention of the cathode ray tube oscilloscope and vacuum tube amplifier allowed for very small voltage differences to be readily and accurately measured and recorded with respect to time (Katz, 1966; Basmajian and de Luca, 1985). The development of the hypodermic needle electrode by Adrian and Bronk (1929) permitted electrophysiologists a straightforward means for recording regionalized electrical activity in individual muscles (in contrast to earlier surface recordings that summed potentials from more extensive regions, possibly including adjacent muscles). To this day, modern analogs of these early oscilloscopes, amplifiers and needle-electrodes are still in regular use by scientists employing electromyography to study muscle activation patterns.

During the 1940s, 1950s and 1960s, electromyography flourished, largely in a clinical setting, and the development and use of fine-wire electrodes by John Basmajian and others (*e.g.*, Basmajian and Stecko, 1962) reduced the pain associated with implantation and permitted long-term in-dwelling experiments and recordings to be performed (Geddes, 1972). By 1965 nearly every human skeletal muscle had been studied with respect to its patterns of activity during stasis as well as in a variety of activities (see Basmajian and de Luca, 1985 for a thorough review). Despite this seemingly exhaustive work of Basmajian and colleagues, a current Medline search using the key word electromyography will attest to the continuing importance of this technique in teasing apart the intricacies of the neural control of muscle actions in humans.

Between 1940 and 1960, experiments that were performed on other mammals, such as cats, dogs, rabbits and monkeys contributed to the understanding of homologous muscle function in humans and added important insights into the basic properties of skeletal muscle more generally. It was not until the mid-to-late 1960s that workers outside of the biomedical field began applying the technique of electromyography to a much wider variety of vertebrates. For example, Henson (1965) recorded activity from the middle ear muscles of bats to try to understand their roles in echolocation. Bone (1966) used recordings from shark muscle during swimming to begin differentiating between red and white muscle fiber recruitment during locomotion, while Osse (1969) explored the muscular basis of feeding in bony fishes. As the techniques became easier and more practical to apply (see Basmajian and de Luca, 1985 and Loeb and Gans, 1986 for current technical aspects of electromyography), their use spread rapidly among the growing body of workers interested in understanding organismal structure and function from a comparative or evolutionary perspective.

The comparative studies mentioned above were influenced heavily by a re-thinking of the approach to vertebrate morphology that occurred in the early 1960s, engineered by Milton Hildebrand, Carl Gans, and Dwight Davis, among others. These scientists laid out a clear research plan for functional morphology that emphasized investigation into the functioning of anatomical systems both within the context of immediate use by the animal, and also with reference to the evolutionary history of the system under study (Liem, 1989). In the early 1970s, functional morphologists with an interest in vertebrate locomotion were brought together with neurophysiologists, biomechanists, and exercise scientists in two international conferences (Stein *et al.*, 1973; Herman *et al.*, 1976) that heavily influenced subsequent research directions on vertebrate locomotion, its neuromuscular control, and functional morphology in general.

OTHER TOOLS OF THE CONTEMPORARY FUNCTIONAL MORPHOLOGIST

While anatomical description, kinematic analysis, and electromyographic recordings provide the technical foundations of the modern functional morphologist, a variety of other techniques are now being exploited by biologists interested in anatomical form and function. Many of these techniques provide direct insight into the mechanical behavior of bones and muscles during dynamic activities.

The development of strain gauge technology in the latter half of the 20th century led to the development of a number of methods for transducing the forces applied to or generated by the musculoskeletal system of living organisms. Following the example first set by Marey in the late 19th century and continued by Fenn (1930) and others a number of decades later, various workers developed and honed techniques for using strain gauges to construct platforms for recording forces exerted by animals against the ground during locomotion (Cavagna 1975; Gola, 1980; Heglund, 1981; Biewener and Full, 1992). Strain gauges can also be used for direct measurements of force and strain in diverse anatomical elements including skulls (*e.g.*, Weijs and de Jongh, 1977), limb bones (*e.g.*, Lanyon and Smith, 1970), and muscle/tendon units (*e.g.*, Walmsley *et al.*, 1978). Moreover, gauges can also be affixed to mechanical models designed to mimic biological systems. Such models are often constructed in order to elucidate the forces acting on structures too small, or the mechanics of activities inconvenient to study directly (*e.g.*, *Drosophila* wings during flight; Dickinson *et al.*, 1999).

In addition to tools designed for force transduction, a variety of techniques have also now been developed to transduce length or shape changes in biological tissues such as muscle and tendon. Sonomicrometry, a technique originally developed for measuring length and shape changes in cardiac muscle, was co-opted in the 1980s by organismal biologists (*e.g.*, Griffiths, 1987) for measuring skeletal muscle length changes *in vivo* during dynamic activities such as locomotion. Briefly, sonomicrometry relies on the transmission of ultrasonic pulses between piezoelectric crystals implanted into the muscle of interest. Based on the transit time of the pulses between crystals, and the speed of sound through the tissue, a direct measurement of inter-crystal distance can be recorded. Because the pulses are emitted at a high frequency, an accurate assessment of length changes during the activity of choice can be transduced with good temporal resolution. To date, this technique has been used for measuring muscle length changes in a variety of invertebrate and vertebrate systems, and has provided important insights into the length-change trajectories of muscles important for aquatic, terrestrial, and aerial locomotion. In addition, sonomicrometry has also been used to measure the kinematics of internal anatomical structures not easily assessed using more traditional movement analyses (*e.g.,* Summers and Ferry-Graham, 2001). In a similar vein, ultrasonographic techniques are also beginning to be used to transduce three-dimensional shape changes in tendon and muscle during assorted dynamic activities (*e.g.,* Fukunaga *et al.*, 2001).

Finally, the explicit recognition that functioning morphological systems have a history and been shaped over time by evolutionary forces (*e.g.,* Lauder, 1982) has led to the development and application of numerous methodological techniques for understanding and taking into account the role of phylogenetic history in the structural and functional design of organisms. Today, numerous statistical methods and experimental designs that explicitly take phylogeny into account are available to the functional morphologist interested in the evolution of complex anatomical systems.

CONCLUSIONS

Even today, functional morphologists rely heavily on a trio of analytical techniques: (1) detailed analysis of anatomical structure and design; (2) high-speed imaging and kinematics; and (3) electromyography. Despite the utility of these techniques, their prevalence may have limited the development and use of other methods to study functional properties of organisms. Further, the heavy reliance on these techniques has sometimes led to the creation of research programs based almost exclusively on experiments during which organisms are placed in a controlled laboratory environment and manipulated in ways that are convenient for the scientists, but may not represent ecologically relevant conditions. The challenge for functional morphologists is to build bridges with those working in other fields of inquiry to enhance our understanding of organismal design and establish functional morphology as a fully integrated discipline in biology. To this end, inroads have already been made with the relatively recent incorporation of various techniques traditionally associated with fields such as biomechanics (*e.g.,* muscle force and length transduction, material properties testing) and evolutionary biology (*e.g.,* modern phylogenetic and comparative analyses). The following papers from this symposium will identify and discuss, in more detail, additional disciplines with which functional morphologists are now establishing connections. The continuing growth and development of functional morphology can be summed up nicely by Knut Schmidt-Nielsen's (1972) observation that, ''A simple biological problem may arouse our interests, but as we gain more knowledge the questions . . . appear to grow in complexity. This may take us to new and seemingly unrelated problems, but in retrospect, they are all related to the desire to find out how things work.''

ACKNOWLEDGMENTS

We thank the organizers of this symposium, and the National Science Foundation for supporting the symposium (grant IBN-0095244 to M. Ashley-Ross, L. Ferry-Graham and A. Gibb). We would also like to acknowledge the thorough and helpful reviews made by Dominique Homberger and Ted Goslow. They are important role models in our discipline and their comments were instrumental in helping us focus and improve our original manuscript.

REFERENCES

Adrian, E. D. and D. W. Bronk. 1929. The discharge of impulses in motor nerve fibers. Part II. J. Physiol. 67:119–151.

Alexander, R. McN. 1968. *Animal mechanics.* University of Washington Press, Seattle, Washington.

Appel, T. A. 1987. *The Cuvier–Geoffrey debate: French biology in the decades before Darwin.* Oxford University Press, Oxford, UK.

Aristotle. 1984. *The complete works of Aristotle*, Vol. 1. J. Barnes ed. Princeton University Press, Princeton, New Jersey.

Basmajian, J. V. and C. J. de Luca. 1985. *Muscles alive: Their functions revealed by electromyography*. 5th ed. Williams and Wilkins, Baltimore, Maryland.

Basmajian, J. V. and G. Stecko. 1962. A new bipolar electrode for electromyography. J. Appl. Physiol. 17:849.

Biewener, A. A. and R. J. Full. 1992. Force platform and kinematic analysis. *In* A. A. Biewener (ed.), *Biomechanics structures and systems: A practical approach*, pp. 45–73. Oxford University Press, Oxford.

Bone, Q. 1966. On the function of the two types of myotomal muscle fibre in elasmobranch fish. J. Mar. Biol. Ass. U.K. 46:321–349.

Borelli, G. A. 1989. *On the movement of animals (de Motu Animalium)* [1680–81]. P. Maquet, trans. Springer-Verlag, Berlin, Germany.

Braun, M. 1992. *Picturing time: The life and work of Etienne-Jules Marey (1830–1904).* University of Chicago Press, Chicago, Illinois.

Cavagna, G. A. 1975. Force platforms as ergometers. J. Appl. Phys. 39:174–179.

Dickinson, M. H., F. O. Lehmann, and S. P. Sane. 1999. Wing rotation and the aerodynamic basis of insect flight. Science 284: 1954–1960.

Duchenne, G. B. A. 1959. *Physiology of movement (Physiologie des Mouvements)* [1867]. E. B. Kaplan, trans. W. B. Saunders, Philadelphia, Pennsylvania.

Fenn, W. O. 1930. Work against gravity and work due to velocity changes in running. Am. J. Physiol. 93:433–462.

Fukunaga, T., K. Kubo, Y. Kawakami, S. Fukashiro, H. Kanehisa, and C. N. Maganaris. 2001. *In vivo* behaviour of human muscle tendon during walking. Proc. R. Soc. London B. 268:229–233.

Galen. 1821. *Opera omnia* [ca. 1500]. C. G. Kuhn, trans. and ed. Georg Olms, Leipzig, Germany.

Galen. 1968. *On the usefulness of the parts of the body.* [ca. 1522]. M. T. May, trans. Cornell University Press, Ithaca, New York.

Galilei, G. 1991. *Dialogues concerning two new sciences* [ca. 1637]. A. de Salvio and H. Crew, trans. Prometheus Books, Amherst, New York.

Geddes, L. A. 1972. *Electrodes and the measurement of bioelectric events.* Wiley-Interscience, New York, New York.

Geddes, L. A. and H. E. Hoff. 1971. The discovery of bioelectricity and current electricity (The Galvani-Volta controversy). IEEE Spectrum 8:38–46.

Gola, M. M. 1980. Mechanical design, constructional details and calibration of a new force plate. J. Biomech. 13:113–128.

Gordon, J. E. 1988. *The science of structures and materials.* Scientific American Library, W. H. Freeman and Co., New York, New York.

Granit, R. 1981. Comments on history of motor control. In *Handbook of physiology,* Section 1, *The nervous system,* Vol. 2, *Motor control Part 1.* American Physiological Society, Bethesda Maryland.

Gray, J. 1968. *Animal locomotion.* Norton and Company, New York, New York.

Griffiths, R. I. 1987. Ultrasound transit time gives direct measurement of muscle fibre length *in vivo.* J. Neurosci. Meth. 21:159–165.

Heglund, N. C. 1981. A simple design for a force-plate to measure ground reaction forces. J. Exp. Biol. 93:333–338.

Henson, O. W., Jr. 1965. The activity and function of the middle-ear muscles in echo-locating bats. J. Physiol. 180:871–887.

Herman, R. M., S. Grillner, P. S. G. Stein, and D. G. Stuart. (eds.) 1976. *Neural control of locomotion.* Plenum Press, New York, New York.

Katz, B. 1966. *Nerve, muscle, and synapse.* McGraw Hill, New York, New York.

Lanyon, L. E. and R. N. Smith. 1970. Bone strain in the tibia during normal quadrupedal locomotion. Acta Orthop. Scandinav. 41: 238–248.

Lauder, G. V. 1982. Historical biology and the problem of design. J. Theor. Biol. 97:57–67.

Liem, K. F. 1989. Milton Hildebrand: Architect of the rebirth of vertebrate morphology. Amer. Zool. 29:191–194.

Lighthill, J. 1969. Hydromechanics of aquatic animal propulsion. Ann. Rev. Fluid Mech. 1:413–446.

Loeb, G. E. and C. Gans. 1986. *Electromyography for experimentalists.* University of Chicago Press, Chicago, Illinois.

MacCurdy, E. 1954. *The notebooks of Leonardo da Vinci.* George Braziller, New York, New York.

MacDonnell, K. 1972. *Eadweard Muybridge: The man who invented the moving picture.* Little, Brown and Co., Boston, Massachusetts.

Marey, E. J. 1895. *Movement.* E. Pritchard, trans. Appleton and Co., New York, New York.

Mathé, J. 1978. *Leonardo da Vinci: Anatomical drawings.* Crown Publishers, Inc., New York, New York.

Mozley, A. V. 1979. Introduction. *In* E. Muybridge, *Muybridge's complete human and animal locomotion: All 781 plates from the 1887* Animal Locomotion, pp. vii–xxxviii. Dover Publications, Inc., New York, New York.

Muybridge, E. 1881. Leland Stanford's gift to art and science, Mr. Muybridge's inventions of instant photography and the marvelous Zoogyroscope. *San Francisco Examiner,* 6 February 1881.

Muybridge, E. 1979. *Muybridge's complete human and animal locomotion: All 781 plates from the 1887* Animal Locomotion. Dover Publications, Inc., New York, New York.

Nash, L. K. 1963. *The nature of the natural sciences.* Little, Brown and Co., Boston, Maryland.

Nigg, B. M. and W. Herzog. 1999. *Biomechanics of the musculo-skeletal system.* 2nd ed. John Wiley and Sons, New York.

Osse, J. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.): An electromyographic study. Netherlands J. Zool. 19(3):289–393.

Russell, E. S. 1982. *Form and function: A contribution to the history of animal morphology.* 2nd ed. University of Chicago Press, Chicago, Illinois.

Sabbatini, R. M. E. 1998. The discovery of bioelectricity. *Brain and mind: Electronic magazine on neuroscience* (6) http://www.epub.org.br/cm/home_i.htm.

Sarton, G. 1954. *Galen of Pergamon. (Logan Clendening lectures on the history and philosophy of medicine).* University of Kansas Press, Lawrence, Kansas.

Schmidt-Nielsen, K. 1972. *How animals work.* Cambridge University Press, Cambridge, UK.

Stein, R. B., K. G. Pearson, R. S. Smith, and J. B. Redford. (eds.) 1973. *Control of posture and locomotion.* Plenum Press, New York, New York.

Summers, A. P. and L. A. Ferry-Graham. 2001. Ventilatory modes and mechanics of the hedgehog skate (*Leucoraja erinacea*): Testing the continuous flow model. J. Exp. Biol. 204:1577–1587.

Walmsley, B., J. A. Hodgson, and R. E. Burke. 1978. Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. J. Neurophysiol. 41:1203–1216.

Weijs, W. A. and H. J. de Jongh. 1977. Strain in mandibular alveolar bone during mastication in the rabbit. Archs. Oral Biol. 22:667–675.