Group Report
How Are Locomotor Systems Integrated and How Have Evolutionary Innovations Been Introduced?

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INTRODUCTION

There is little doubt that the maneuverability of a sprinting cheetah, the grace of a falcon as it descends upon its prey, and the rapid transition from undulating locomotion to propulsion by four limbs observed during the development of many amphibians, depend on complex systems which are highly integrated for locomotor performance. What are complex systems and how do they become integrated? Our discussions of the terms "complex systems" and "integration" resulted in general, broadly applicable definitions useful for subsequent analyses. Complex systems represent the specific arrangement of a number of structural or functional elements which facilitate the performance of a specific functional role for the organism. Integration results from those evolutionary processes that enable a number of these complex systems to function collectively. As complex systems are evolutionarily reconfigured, new levels of integration or functional expression may emerge.

Our group, dominated by empiricists, spent little time debating the structuralist/functionalist dichotomy; we are in agreement that developmental and phylogenetic histories each are important contributions to patterns of integration among locomotor systems. The focus of our discussions was twofold: (*a*) to identify and explore specific trends and problems in the evolution of vertebrate locomotion, and (*b*) to suggest fruitful areas for future study.

Approaches to the Study of Integration

Our consensus is that an understanding of the structural components of any locomotor system (to include the neuromuscular, musculoskeletal, respiratory, and cardiovascular components) is essential for clarification of evolutionary pathways and an understanding of levels of integration. In addition, we must strive to broaden the context of locomotor studies to include the fields of ecology and behavior. Finally, studies of extant species can be instructive for the interpretation of fossil forms.

The ecological framework within which locomotion occurs must dictate to some extent energy expenditure, range of limb movement, structure of the distal elements, and gait selection. As a result, the innovations necessary for the transition from aquatic to terrestrial and from terrestrial to aerial locomotion cannot be fully appreciated without consideration of the physical environment. Since water is a dense and viscous fluid, the effect of gravity on an aquatic organism is minimized. Water does, however, produce drag forces which relate to surface configuration, velocity of travel, and general body profile. Energy is required to overcome drag in an aquatic medium and should be incorporated in any analysis. For terrestrial locomotion, drag is not a primary concern but the force of gravity is. In the absence of elastic storage mechanisms, the mass-specific energy cost of locomotion varies as a regular function of body size (Taylor 1977; Taylor et al. 1970). For flight, both gravitational and drag forces are substantial, and the few published studies reveal that the relation between performance and energy cost for flying vertebrates is not simple (cf. Thomas 1975; Tucker 1973; Videler et al. 1988).

An animal's behavioral repertoire may be far greater than that predicted from morphology alone and can provide clues about evolutionary patterns. Székely (this volume), for example, reviews studies of amphibian larvae which show that the control of axial locomotion by the spinal neuraxis is determined quite early. Apparently the control system for subsequently developing limbs is "superimposed" upon the axial system even though the two are integrated to some degree (Székely, this volume; van Mier 1986). The sequence of events was demonstrated by van Mier (1986) for *Xenopus* in studies of the ontogeny of activity patterns of the primary motoneurons (to the axial musculature) and secondary motoneurons (to the limbs). Early in development, both types of motoneurons possess bursting on-off activity: a pattern which sustains in the primary motoneurons. In contrast, the secondary motoneurons begin a new and different pattern coincident with the development of limb musculature.

Hypotheses about locomotor adaptation and evolution are particularly useful when formulated in a testable framework. Bennett (this volume) provides guidelines and approaches which are useful in setting up such

frameworks and for gaining insight into the relationship of an organism's locomotor performance and fitness. Most animals have a large repertoire of potential locomotor movements. One way to establish a framework within which performance can be tested is to define and measure the various factors that limit locomotor performance. An animal's maximum speed, for example, undoubtedly reflects information about the contractile properties of muscle as well as the limits of neuromuscular control and/or musculoskeletal design. The approach may also be useful to assess locomotor performance in populations that possess variant locomotor characteristics or in individual animals after experimental manipulation of the locomotor apparatus.

PATTERNS WITHIN THE TETRAPOD LIMB

The origin of the tetrapod limb, simultaneously capable of supporting body weight and generating propulsive thrust on land, represents only one aspect of a major transition in vertebrate history. In the fish–amphibian transition, the four relatively simple "paddles" of the rhipidistians, initially suited as flexible props capable of aiding balance and support, were eventually converted to distinctly configured limb pairs. Nonetheless, little is known concerning the structural and functional stages between fins and limbs, and about the relation that this novel form of locomotion bore to other aspects of early tetrapod adaptations to land (for review, see Edwards 1989).

We discussed two major patterns of integration in the evolution of tetrapod limbs and girdles. The first is an apparent proximodistal gradient of variation in the ontogeny and phylogeny of the limb. Related to this is the issue of polydactyly and hyperphalangy. Second, significant temporal asymmetries seem to characterize the evolution of shoulder and pelvic girdles in both the reptilian-mammalian and reptilian-avian transitions. Each is reviewed within the context of limb development.

Limb Elements

Studies of the tetrapod limb suggest a degree of developmental uniformity (although caution must be exercised whenever developmental events are compared to phylogenetic transitions), which is useful for our understanding of limb homology (Hinchliffe, this volume). Observational and experimental studies of a variety of developing tetrapod limbs reveal that the homology of limb elements has, as its fundamental basis, a common morphogenetic pattern that involves segmentation and asymmetric branching.

The musculoskeletal system of a developing limb is integrated by a relationship of two components. Kieny et al. (1986) have demonstrated the general capacity of connective tissue to impose pattern on migrating muscle cells during limb development, though the precise molecular factors of the

extracellular matrix are still being investigated. At a local level, individual cartilage elements play a role in the organization of their muscles. This was clearly demonstrated by Stopak and Harris (1982) who showed that chondrogenic elements, when co-cultured with myogenic cells, organize these into "tracts" that resemble embryonic muscles in their spatial arrangement. Conversely, in the absence of the chondrogenic elements, the myogenic developmental organization does not proceed. These observations underscore the importance of the subtle interactions between developing tissues.

Proximodistal gradient. One striking feature of the tetrapod limb is that in both evolution and development proximal elements have remained relatively conservative in comparison to distal elements. Evidence that variation is greater distally than proximally comes from several sources. First, among Paleozoic lobe-finned fishes which are possible tetrapod ancestors, the fin shows proximal elements which can easily be homologized to the humerus, radius, and ulna of the tetrapod limb; homologies of the numerous distal elements cannot easily be drawn. Within tetrapods, variation is much greater at the distal than the proximal level (Hinchliffe, this volume). Second, in the chick when polarizing cones are grafted preaxially onto a second developing limb bud, it is much more difficult to disturb and duplicate the development of the humerus than the distal elements. Third, in snakes and limbless lizards, where limbs are secondarily reduced, the most proximal elements are the last to be lost (e.g., femur in the python). Finally, in wild populations of salamanders, Hanken (1983) has shown marked variation in the distal elements of the feet, particularly in the carpus.

The evolutionary significance of the conservation of proximal elements relative to distal ones requires an assessment of (*a*) any proximodistal gradient of structural variation that exists in the developing limb or (*b*) the intensity of selection on developmental processes at the cell-cell or tissue-tissue levels. One reason for this proximal stabilization may well be selection for a high degree of developmental stability. Animals in which proximal limb elements develop abnormally are unlikely to survive, while the loss of a digit or a single element of the carpus or manus may have only minor effects on individual survival. Moreover, the developmental processes of proximal-to-distal sequential differentiation and postaxial branching in the developing limb (Hinchliffe, this volume) may predispose changes to occur distally and preaxially upon alterations in limb bud size.

Tests of the theory of proximal stabilization might be performed by experimentally perturbing any of the segments to cause either retarded or accelerated growth. Subsequently, the animals could be allowed to reach adulthood and then be evaluated in terms of locomotor performance. The various limits to locomotor performance might be measured and compared

to values for a normal population. A further and less invasive test of the influence of variation in distal limb configuration would be to examine locomotor performance in populations polymorphic for digital reduction.

Polydactyly and hyperphalangy.   The subject of polydactyly and hyperphalangy offers an opportunity to explore the question of integration and its evolutionary consequences on multiple levels. The tetrapod pattern of five digits was established very early in their history and has persisted with few exceptions (e.g., urodeles, caecilians, snakes, ungulates) in terrestrial forms. Phalangeal formulas are more variable, but patterns *within* groups are more or less stable. Nonetheless, many mutations are known to produce either supernumerary digits or phalanges (Hinchliffe and Ede 1967; Hinchliffe and Johnson 1980). Despite the developmental capacity of tetrapod limbs to produce readily such variants there are, however, relatively few instances in which either polydactyly or hyperphalangy have become fixed as a normal phenotype. Moreover, the distribution of known cases is extraordinarily biased; virtually all examples are confined to secondarily aquatic tetrapods (Romer 1966). Polydactyly occurs in some ichthyosaurs while hyperphalangy has arisen on multiple occasions among a diverse cast of specialized marine tetrapods (e.g., ichthyosaurs, plesiosaurs, mosasaurs, cetaceans). How might these observations be interpreted?

The overall scarcity of polydactyly and hyperphalangy suggests that these departures from customary limb configuration are normally deleterious. At the same time, the biased distribution of these phenotypes among terrestrial and aquatic vertebrates indicates that the aquatic environment is somehow more permissive. On this point, two observations seem relevant. First, among secondarily aquatic tetrapods polydactyly and hyperphalangy are normally associated with specialized, paddle-like limbs in which intracarpal/ tarsal and intradigital movement is limited. Accordingly, major limb movements and their control are largely confined to muscles operating about the articulation between humerus/femur and the associated girdle. Second, these same specialized limbs are characterized by developmental retardation (= paedomorphosis), particularly with respect to ossification and joint formation.

It is easy to appreciate how certain alterations of embryonic limb structure (e.g., dorsoventral flattening, anteroposterior elongation, limited internal mobility, digital webbing) might prove "preadaptive" with respect to the evolutionary derivation of paddle-like limbs. To the extent that supernumerary digits or phalanges contribute to more appropriate limb shape and mechanical performance, these developmental variants might be favored. Although it is more difficult to identify a context in which such simplified limbs would prove beneficial in a terrestrial setting, it is not hard to imagine locomotor behaviors in which extra digits or phalanges might well be

advantageous (e.g., some kinds of digging, climbing). In fact, the presence of a falciform bone in the hand of moles and well-developed paradigital structures in geckos (Russell and Bauer 1988) may confirm some of the potential functional advantages of extra digits without abandoning the basic pentadactyl motif.

These observations suggest that the major constraint on the appearance of polydactyly and hyperphalangy resides with performance requirements. It is likely that these two phenotypic variants introduce new structural and functional complexity, particularly in the total number of movable elements within the distal limb. The critical limitation may not be the increased structural/mechanical complexity per se but rather the effective neural control of new peripheral elements. Whereas developmental mutations may produce extra digits or digital segments through relatively simple epigenetic influences on limb-bud growth (Hinchliffe and Johnson 1980), there is no a priori reason to believe that these mutations will also yield modifications of the central nervous system necessary for the effective functional integration of new peripheral limb structures. Without complementary adjustments in neural organization, peripheral additions could prove relatively useless from a functional standpoint and might also act to reduce the performance of the normal components as well. For example, peripheral somatosensory feedback from the "new digits" of a hyperdactylous individual could potentially interfere with the proper central modulation of motor output to the "old digits."

The emphasis on performance and especially those aspects of performance related to the neural control of distal limb movements would seem to fit the historical ecomorphologic expression of polydactyly and hyperphalangy. Inasmuch as the aquatic environment is less demanding in terms of gravitational support, simple, rigid limbs may be fully effective, and peripheral additions in the absence of coordinated central modifications need not be limiting. This would be especially so if peripheral additions arose *after* the limbs had already been substantially modified toward a rigid paddle. In most terrestrial locomotion the performance requirements for the distal limb will be more precise. It may be no coincidence that specialized locomotor behaviors requiring particularly high levels of performance (i.e., fast running, flying) are often associated with various forms of structural simplification of the distal limb. Included are digital reduction, bone fusions, and other passive means of reducing the range of movement of individual structural elements. Energetic considerations have been the primary explanation for such peripheral simplification (especially in cursorial forms but see Taylor et al. 1974) but neural control may be an additional factor deserving equal consideration (Gambaryan et al. 1971).

The preceding discussion leads to the following open questions. Is there evidence that polydactyly and hyperphalangy are accompanied by corresponding modifications in the neural control pathways serving these

limbs? What is known about the neural control of supernumerary digits and its anatomical and physiological basis? How does the level of motor control compare with that of adjacent "normal digits"? Does polydactyly or hyperphalangy have a measurable influence on locomotor performance in terrestrial tetrapods? If so, what locomotor behaviors are most affected? Does it matter whether the extra digits are pre- or postaxial? Is there evidence that polydactyly and hyperphalangy are introduced later rather than earlier in the evolution of paddle-like limbs in marine tetrapods?

Asynchrony of Forelimb and Hindlimb Evolution

The transitions from reptiles to therian mammals on the one hand and to birds on the other are characterized by asynchronies in the appearance of structures and functions of the shoulder and pelvis. Within the mammalian line, for example, a "typical" mammalian pelvis occurs in the earliest known mammals, but the shoulder remains at a cynodont level of organization throughout much of the Mesozoic (Bramble and Jenkins, this volume). *Archaeopteryx* may be characterized as having a "typical" reptilian pelvis whereas the elements of its shoulder and wing are distinctly avian (Ostrom 1976). We recognize a priori that the reptilian pelvis consists of fewer elements than the shoulder. Nevertheless, the relative conservation of the pelvis may relate to (*a*) the demands placed upon it by the hindlimbs, the primary providers of support and propulsion in terrestrial locomotion, and/ or (*b*) the facilitation of live birth (mammals) or the passage of hard-shelled eggs (birds).

Despite a marked reduction in the number of bones and muscles of the shoulder, the repertoire of shoulder movement has increased greatly in mammals; in birds, forelimb use foregoes the alternate pattern of reptiles and adopts synchronous strokes for flight. In addition to locomotion, the mammalian forelimbs may be used for a variety of functions, including food manipulation, grooming, prey capture, and intraspecific interactions. These complex behaviors reflect integration of the neural control and musculoskeletal elements at several levels. Are the levels of integration different for forelimbs and hindlimbs? Is behavioral modification likely to precede structural change? If so, how might we recognize it?

A current thrust in neurobiology is to identify the components of the peripheral and central nervous system responsible for behavior. Studies of invertebrates have provided insight by employing a "top down" approach, wherein individual neuron activity is correlated to specific locomotor behaviors (Kandel 1976). An alternative approach, commonly used in studies of tetrapods, is to perturb elements of the nervous system and subsequently note the associated behavioral response. Such experiments reveal that neuronal networks are "plastic" to some degree and that this plasticity relates to modifications in behavior. Investigations that center around the

recovery of function following injury, for example, suggest that a high degree of redundancy of function is present in the vertebrate central nervous system and that this plasticity facilitates recovery (see Goldberger 1980). Whether recovery requires activation of a previously unused in-parallel nervous pathway, the functional reorganization of undamaged tissue, or some combination, is the focus of ongoing studies. What role, if any, does the capacity for plasticity play in the evolution of locomotor systems in general and the differential use of fore- and hindlimbs in reptiles, birds, and mammals specifically? In monkeys (and presumably other mammals) visual guidance is important for forelimb use in addition to central and segmental afferent input (Bossom and Ommaya 1968). To what extent has vision influenced forelimb evolution in mammals?

Living monotremes possess a shoulder girdle that closely resembles that of mammal-like reptiles. Detailed studies of the shoulder of these primitive mammals might reveal features present in the organization of early mammalian neural control and/or neuromuscular systems. Only a limited number of comparisons of limb kinematics, muscle architecture, muscle mechanics, and neuromuscular organization of the shoulder and pelvis among tetrapods have been made. The data are still too few to formulate general principles, but following studies of the limb kinematics and electromyographic patterns of shoulder muscles in one species of reptile and several species of mammals, one hypothesis that relates to the neural control of the shoulder in tetrapods has emerged (for a review, see Goslow et al. 1989): important innovations in tetrapod locomotor evolution might arise via alterations in peripheral musculoskeletal organization, with little or no corresponding change in the central commands. Although reptiles and mammals have distinctly different shoulder morphologies, substantial similarities in the motor control program were found. The electrical activity patterns of presumed homologous muscles retain their basic timing within the step cycle even though, in some cases, their peripheral connections and apparent actions are distinctly different. Similar conclusions about conservatism in the neural control mechanisms for feeding among tetrapods are reviewed by Roth and Wake (this volume). The general hypothesis of motor program conservatism and peripheral plasticity as it relates to tetrapod locomotion needs rigorous experimental testing. If substantiated, however, this model would be of major conceptual value in further efforts to understand patterns of vertebrate locomotor (and feeding) evolution.

LOCOMOTION AND RESPIRATION: AN EMERGENT LEVEL OF INTEGRATION

Recent studies suggest that mechanical and possibly neurophysiological couplings exist between the locomotor and respiratory systems of mammals

(see review in Bramble and Jenkins, this volume). If so, its presence in mammals illustrates a level of integration between these two systems which has not been observed in fishes or other groups of tetrapods.

Mechanical coupling of respiration and locomotion in mammals might relate to their capacity for rapid and sustained locomotor behaviors (Bennett 1985; Bennett and Ruben 1979). Any animal's ability to sustain a given speed for any extended period of time is related to its aerobic capacity. That is, when the demands for movement are such that muscles must depend on anaerobic as opposed to aerobic metabolism, fatigue is imminent. The cost of locomotion (measured as energy required per unit body mass per unit distance) is substantially lower for animals swimming in water than for animals walking on land. Terrestrial amphibians and reptiles do not possess a greater capacity for aerobic energy processing than do fishes. Thus, the capacity of these ectotherms for aerobically supported (i.e., sustainable) locomotion is severely limited to a slow walk or a relatively short dash.

Vertebrates in general are capable of moving over a wide range of velocities, ranging from slow sustainable movements to maximal nonsustainable speeds. At various points along this range, various physiological or morphological factors will differentially limit performance and others will be permissive or even irrelevant to their performance at a particular speed (Bennett, this volume). For instance, the ability to transport oxygen limits endurance capacity at intermediate speeds. However, limb structure (in amniotes) at these speeds is permissive and not limiting, and anaerobic capacity is irrelevant as it is not activated. At bursts of high speeds, limb structure or function (e.g., muscle contraction speed, limb biomechanics) or anaerobic capacity may be limiting, but aerobic capacity is irrelevant. No single factor or set of factors may thus be necessarily related to or linked with changes in locomotor performance during evolution. If selection operates on endurance capacity, for example, changes might be anticipated in the pulmonary and cardiovascular systems but not necessarily in limb morphology. Strong coupling, either in a functional or an evolutionary sense, between different systems is thus not always anticipated.

The respiratory system of most fishes depends upon the gills stationed in the head, whereas the locomotory system is associated with the trunk. There is no coupling between respiration and locomotion (exceptions are those fishes which rely on "ram ventilation" of the gills while swimming). With the advent of true lungs located within the trunk, the potential for both conflicting and synergistic interactions of locomotor and respiratory mechanics arises. The basic ventilatory mechanisms are understood for some amphibians and various species of reptiles including snakes, turtles, and one species of crocodile, but there are few studies of lung ventilation during locomotor activity. A recent study by Carrier (1987a) revealed no consistent correlation between respiratory and locomotor movements in four species of lizards.

During overground locomotion, lung ventilation and especially tidal volume
declined at speeds exceeding a fast walk. Carrier (1987b) proposed that the
absence of effective lung ventilation in running lizards is the result of a
mechanical constraint stemming from the marked lateral bending of the
trunk. Why lung ventilation is apparently interrupted during the faster gaits
requires further study, but the absence of effective locomotor-respiratory
coupling is significant.

As a consequence of their different evolutionary histories, the gas exchange
requirements of birds and mammals are satisfied by respiratory systems of
very different design. Studies suggest that the effectiveness of gas exchange
is less in the mammalian lung than in the through-flow avian air-sac/lung
system (cf. Bernstein and Schmidt-Nielson 1974; Tucker 1968). However,
the rates of oxygen consumption of flying bats and birds of comparable size
are about the same; these rates are 2–3 times greater than the highest rates
which similar-sized mammals appear to be capable of during heavy exercise
(see Thomas et al. 1984). The shoulder girdle of birds, designed to support
synchronously flapping wings, is free from the duties of terrestrial locomotion.
In addition, the synchronous movements of the forelimbs of birds are in
marked contrast to the alternating movements of these limbs in mammals.
Surely, a reorganization of the neural control system during the transition
from reptiles to birds has occurred, but its structural and/or functional basis
has yet to be discovered. Comparative studies to date, in fact, suggest
remarkable similarities in the descending motor pathways in birds and
mammals (Webster and Steeves 1988).

The avian shoulder is characterized by a broad sternum and strong
coracoids with specialized articulations proximally at the shoulder and distally
at the sternum. These structures, together with the furcula, serve as origin
for the two major muscles used in flight. This specialized shoulder
configuration, including its separation from the anterior thoracic cage by
air-sac diverticula (Duncker 1971), differs markedly from the relationship
of the shoulder to the thoracic cage in mammals. In contrast to mammals,
running at high speed, most birds show no obligatory coordination between
their wing-beat and respiratory cycles during flight (Berger and Hart 1974).

The general musculoskeletal dynamics of locomotor-respiratory coupling
in mammals have been described (Bramble 1989) and the basis has been
set for a variety of observational and experimental studies aimed at
identifying all of the functional components involved. In the mammalian
species thus far investigated, coupling is only employed during the faster
gaits; this makes detailed measurements difficult. Whereas the mechanical
coupling of the locomotor and respiratory system of mammals apparently
relies heavily on movements of the rib cage during locomotion, Duncker
(this volume) notes that lung ventilation in birds might best proceed within
a rigid thoracic cage. Jenkins et al. (1988) have reported that there are

substantial movements of the furcula (wishbone) coupled with small excursions of the sternum with each wingbeat of the European starling during flight. How these skeletal movements relate to the respiratory apparatus of birds remains to be elucidated.

To determine the true extent of locomotor-respiratory coupling in tetrapods and its physiological importance, additional studies are required. Rib cage kinematics, pressure records, and electromyography will provide valuable insight into the biomechanical bases for locomotor-respiratory integration.

CONCLUSIONS

We have identified some potential avenues of research that may be addressed in future studies.

1. One rewarding area of research centers around the relationship between the development of the central and peripheral nervous systems and changes in locomotor patterns during ontogeny. The bullfrog (*Rana catesbeiana*) and the clawed toad (*Xenopus laevis*), for example, use only tail locomotion until the time of metamorphosis. During metamorphosis, the tail disappears and the extremities develop, followed by a second type of locomotion in which the hindlimbs predominate (cf. Stehouwer and Farel 1985; van Mier 1986).
2. Some fishes (e.g., *Anableps*, *Clarias*) regularly use their limbs in different ways dependent upon whether they are in the water or on land. The Australian lungfish, *Neoceratodus*, uses its paired fins not only for swimming but as supporting props while resting on the bottom. Finally, a functional comparison of locomotion in sprawling tetrapods and antennarid anglerfishes reveals a high degree of convergence between these two very separate groups (Edwards 1989). Although starting with very different propulsor organs, nearly identical solutions have evolved to execute a common behavior, i.e., locomotion across a substrate. Analyses of the central and peripheral organization of the neuromuscular and musculoskeletal systems which relate to the locomotion of these forms, as well as their behavioral repertoires, should reveal underlying patterns of integration.
3. The proximodistal gradient of developmental events that occurs during limb development is not confined just to the limb. The developmental gradients of the most proximal elements, the shoulder and pelvic girdles, also should be investigated.
4. The evolution of endothermy in both birds and mammals is regarded as an "emergent" characteristic. It may be that selective forces acted to favor sustained locomotor behavior. If so, investigation of those structural

and physiological factors thought to be limiting in each line may provide insight into evolutionary mechanisms.

5. One approach to the evolution of locomotor-respiratory coupling is to study associated integrative systems in closely related forms which show varying degrees of coupling. For example, within the scombrid fishes some forms are totally dependent on "ram ventilation" for respiration, while others are not.

6. A mechanical coupling between respiration and locomotion has been investigated in only a few species, all of which are cursorial. Within mammals, groups that possess diverse locomotor styles and body size should be examined. The diaphragm of mammals represents a form/ function complex not seen in other major vertebrate groups. Did this complex provide a mechanism for an uncoupling of at least one mechanical component of respiration (i.e., inspiration) from the thoracic chestwall? If so, could this be related to conflicting mechanical demands stemming from changes in body support and propulsion associated with the reptile-mammal transition?

7. Musculoskeletal dynamics during locomotion reflect the outflow of commands of the nervous system and the mechanics of the limbs. There is much to be learned about levels of integration by analyses of muscle design and function from the fiber to whole muscle level. We should study not only such mechanical properties as contraction speed, endurance, and force in isolated motor units or whole muscles but also should document muscle behavior during normal movements. The timing of muscle contractions and/or force profiles generated may be measured by electromyography and strategically placed strain gauges. These data, coupled with rates of shortening and/or lengthening during locomotion, provide fundamental comparative information necessary to determine functional innovation and evolutionary pathways.

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