# Locomotor System

## Introduction

Primates use a very wide range of methods for travelling around their environments. Among mammalian orders only rodents could be considered to have a greater range of locomotion types (and you could probably argue the point even there depending on how you choose to define your locomotor types). Primates do not fly – Chiroptera is the only mammalian order that can do that, although the two suborders (Microchiroptera and Megachiroptera) may have evolved this ability independently [Nowak 1991]. They do not burrow or glide to any great extent but they leap, walk, run, swim and climb in a wide variety of manners and generally with a great deal of enthusiasm.

## Locomotor Types

As in many areas of biology, a classification system is useful. The scheme given in Figure 1 is widely used as a starting point for the investigation of primate locomotion. Its main difficulty is that it rather over emphasises the locomotor diversity among the anthropoids at the expense of the locomotor diversity among the prosimians. This imbalance has been addressed by subdividing the various forms of prosimian leaping into four different categories as shown in Figure 2.

| Category | Sub-type | Activity | Example |
|---|---|---|---|
| Vertical clinging and leaping | | Vertical leaping in and between trees, hopping on the ground | *Tarsier* |
| Quadrupedalism | Slow climbing | Cautious clambering and climbing | *Loris* |
| | Branch running and walking | Climbing, springing, branch-running and jumping | *Cheirogaleus* |
| | Ground running and walking | Tree climbing, rock climbing, ground running and walking | *Papio* |
| | New World semi-brachaition | Arm-swinging with the use of prehensile tail | *Ateles* |
| | Old-World semi-brachiation | Leaping and some arm-swinging | *Colobus* |
| Brachiation | True brachiation | Arm-swinging, bipedal branch running | *Hylobates* |

| | | | |
|---|---|---|---|
| | Modified brachiation: | | |
| | (1) Orang type | Climbing and swinging using all four limbs | *Pongo* |
| | (2) Chimp type | Occasional arm-swinging, knuckle-walking on ground | *Pan* |
| | (3) Gorilla type | No arm-swinging in adults, knuckle-walking | *Gorilla* |
| Bipedalism | | Standing, striding, running | *Homo* |

**Figure 1. A classification of locomotor types [Napier and Napier 1985]**

| Leaping Type | Description |
|---|---|
| Ricochetal leap | A continuous series of leaps or hops with no pause between each individual leap |
| Crouching leap | Single leap where the animal stops and crouches before takeoff |
| Falling leap | Animal drops itself from a higher substrate to a lower one |
| Running leap | Animal leaps whilst running with no pause before takeoff |

**Figure 2. Subdivisions of prosimian leaping [Oxnard et al. 1990]**

These categories classify the major locomotor activities performed by a species. Most primates can produce most locomotor performances although they only choose to display a limited locomotor repertoire in the wild. Thus macaques can be trained to walk bipedally and computer simulation has shown that lorises should be able to leap. Despite this disparity between observed and potential locomotor activity there are a number of anatomical features that can be associated with the prevalent locomotor mode and this is useful when trying to reconstruct the behaviour of fossil forms.

## Anatomical Adaptations

There are a number of descriptive anatomical features that can be linked to the locomotor type. Thus animals that leap tend to have long hindlimbs; animals that move quadrupedally tend to have hindlimbs that are the same length as their forelimbs and brachiators tend to have long forelimbs. We need to produce a more objective way of describing the length of limbs in much the same way as we did for describing brain size. However, in this case we can correct for body size by the simple approach of dividing one linear measurement by another.

The commonest index calculated in this way is the *intermembral index* which is effectively the (*forelimb length* × 100% / *hindlimb length*) (Figure 3).

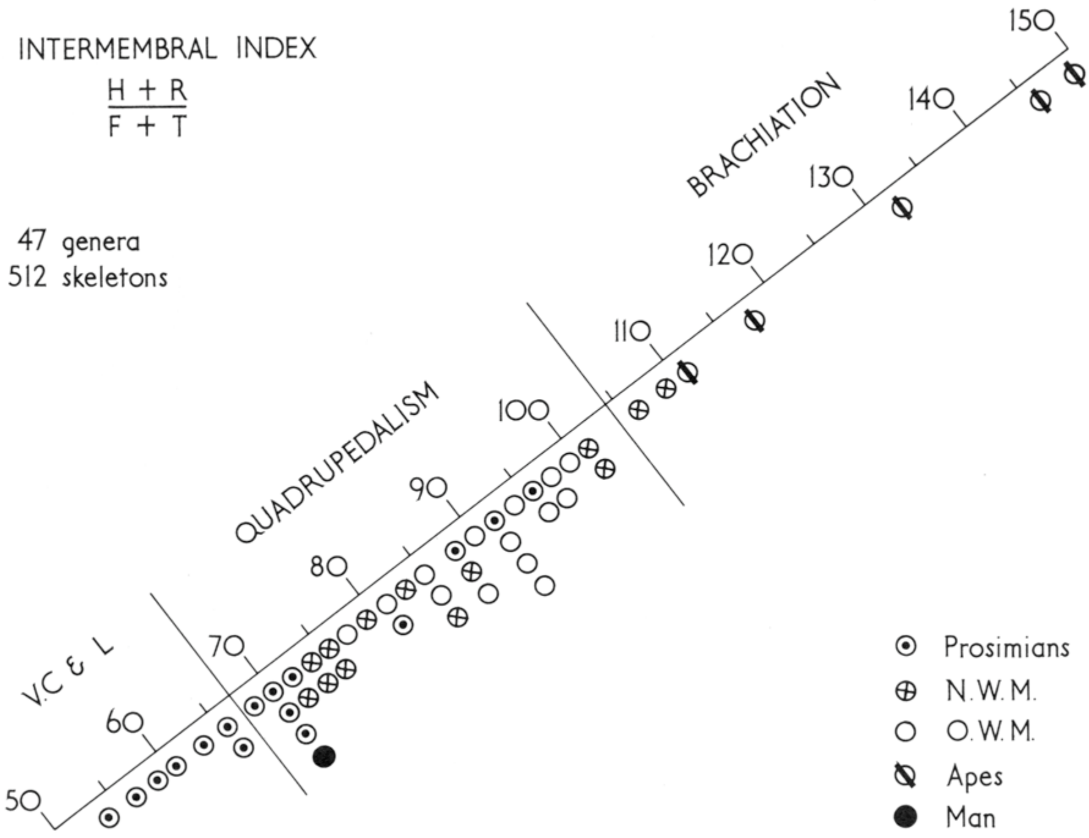
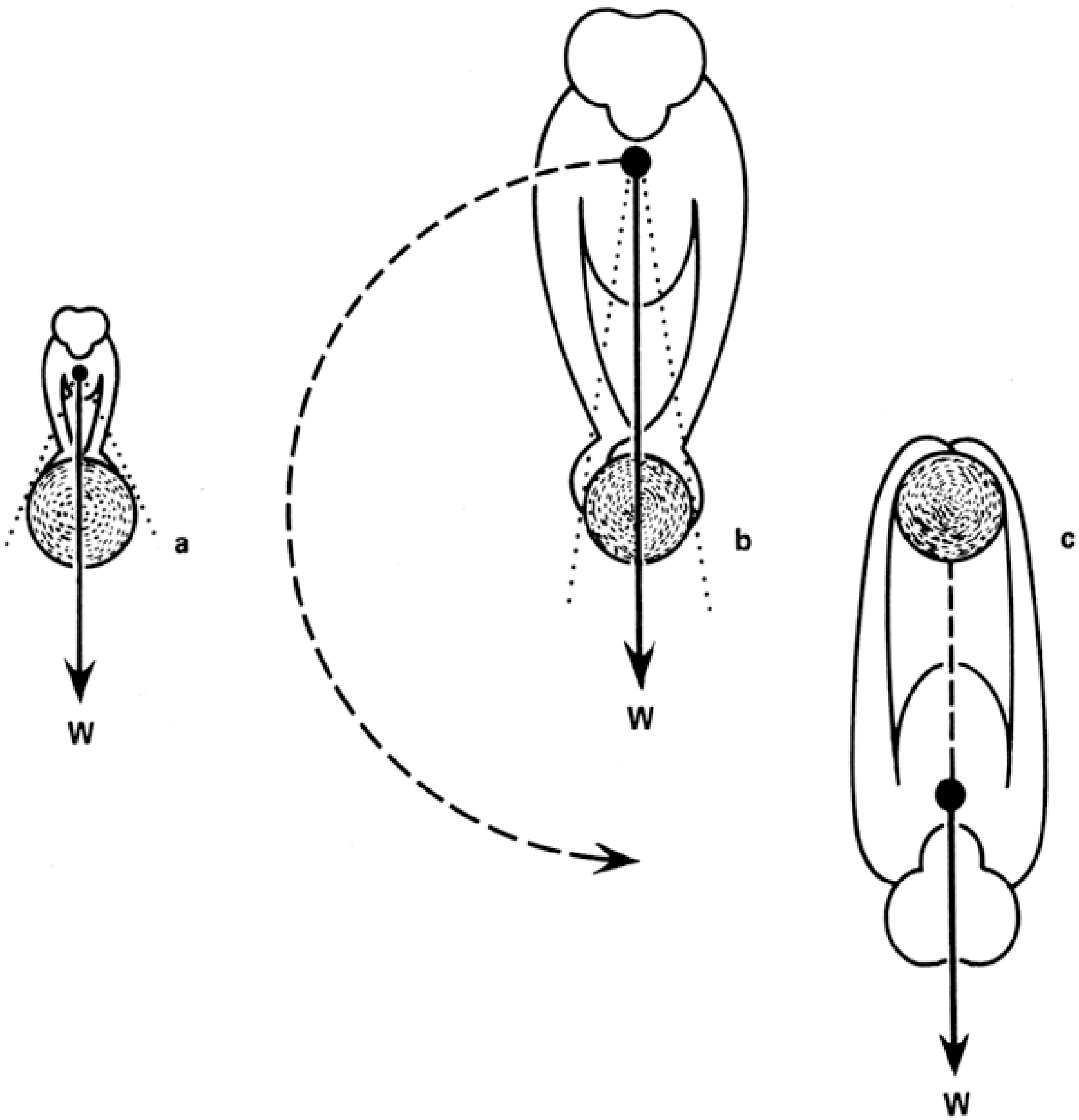



*Diagram of intermembral indices of 512 primate skeletons showing continuous range of variation from low index (long legged) to high index (long armed) forms.*

**Figure 3. Intermembral indices [Napier & Napier 1985]**

Locomotor behaviour has also been linked to body weight. It is suggested that the prevalence of suspensory locomotion in large bodied primates is related to the need to maintain postural stability (Figure 4).




*Providing ratio of branch to body size and weight (W) is high, balance is maintained; b. with increase in body size the ratio becomes critical and overbalancing can occur; c. suspension provides one solution.*

**Figure 4. Postural stability [Napier & Napier 1985]**

### How do we study locomotion?

There are a whole host of ways of studying locomotion and I am only going to give a few examples here. This will be grouped by the use that the data is being put to.

Behavioural monitoring

Locomotion is primarily a behaviour so many of the general behavioural monitoring techniques can be applied to the study of locomotion. So an ecologists interested in time and energy budgets will record locomotor behaviour as one of the classes of activity that an animal performs. At the simplest level this will involve noting down what locomotion activity an animal is doing at regular intervals throughout the observation period.

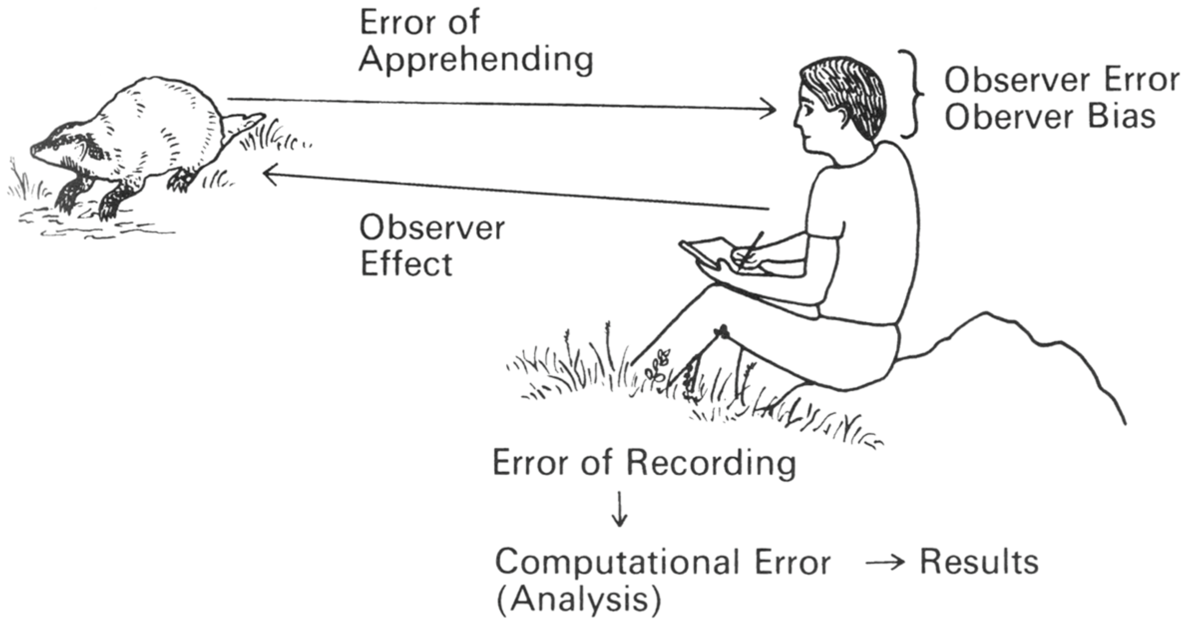



**Figure 5. Simple behavioural monitoring and sources of error [Lehner 1996]**

**Figure 6. Senegal bushbaby (*Galago senegalensis*) [Alexander 1992]**

This information will eventually enable us to build up an ethogram of the behaviour of a particular animal. This is an indication of the amount of time an animal spends doing various behaviours of interest. For an arboreal primate this will include information of the supports that the animal prefers to move along, the height in the forest that it was seen, and the types of locomotion that were observed.

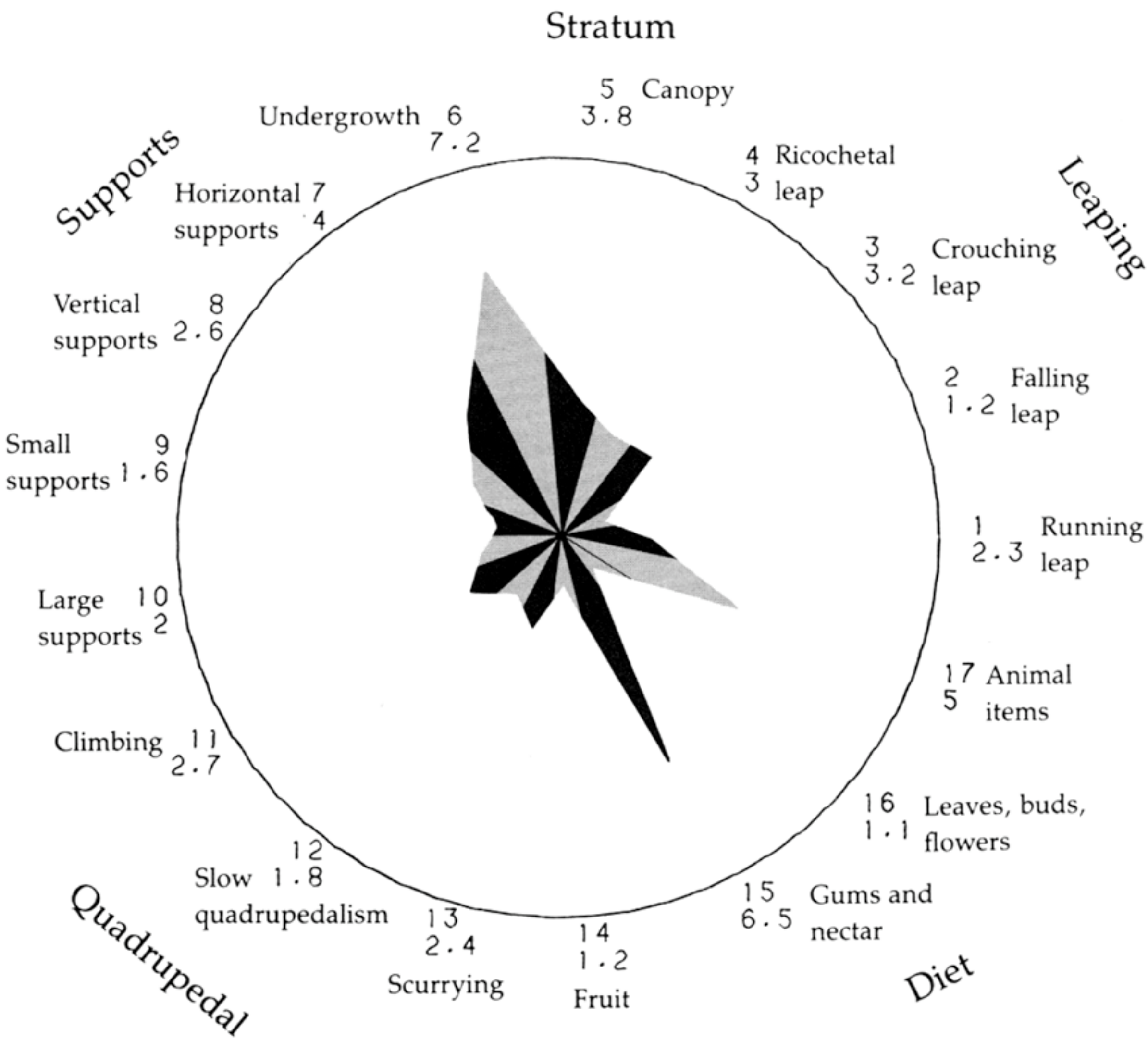



**Figure 7. Polar plot of the activity profile of the Senegal bushbaby (Galago senegalensis) [Oxnard et al 1990]**

To increase the amount of information, the observer can estimate the quantitative nature of the movement: slow quadrupedalism; fast quadrupedalism; 2 metre leap etc. Often we are interested in how far an animal moves in a given period and this can be done by mapping the animal's position at regular intervals. Spatial position can be measured in a rather more sophisticated by various types of radio tracking. Triangulation using two or more directional receivers can be used to define the position or for very large scale studies (migration of marine mammals for example), the animal can be fitted with a data logging system connected to a GPS satellite receiver. Flocking of birds or the population dynamics of marine algae can be picked up directly from satellite images.

**Figure 8. Radio collared coyote (*Canis latrans*) [Lehner 1996]**

**Figure 9. Mobile radio-tracking tower [White & Garrott 1990]**

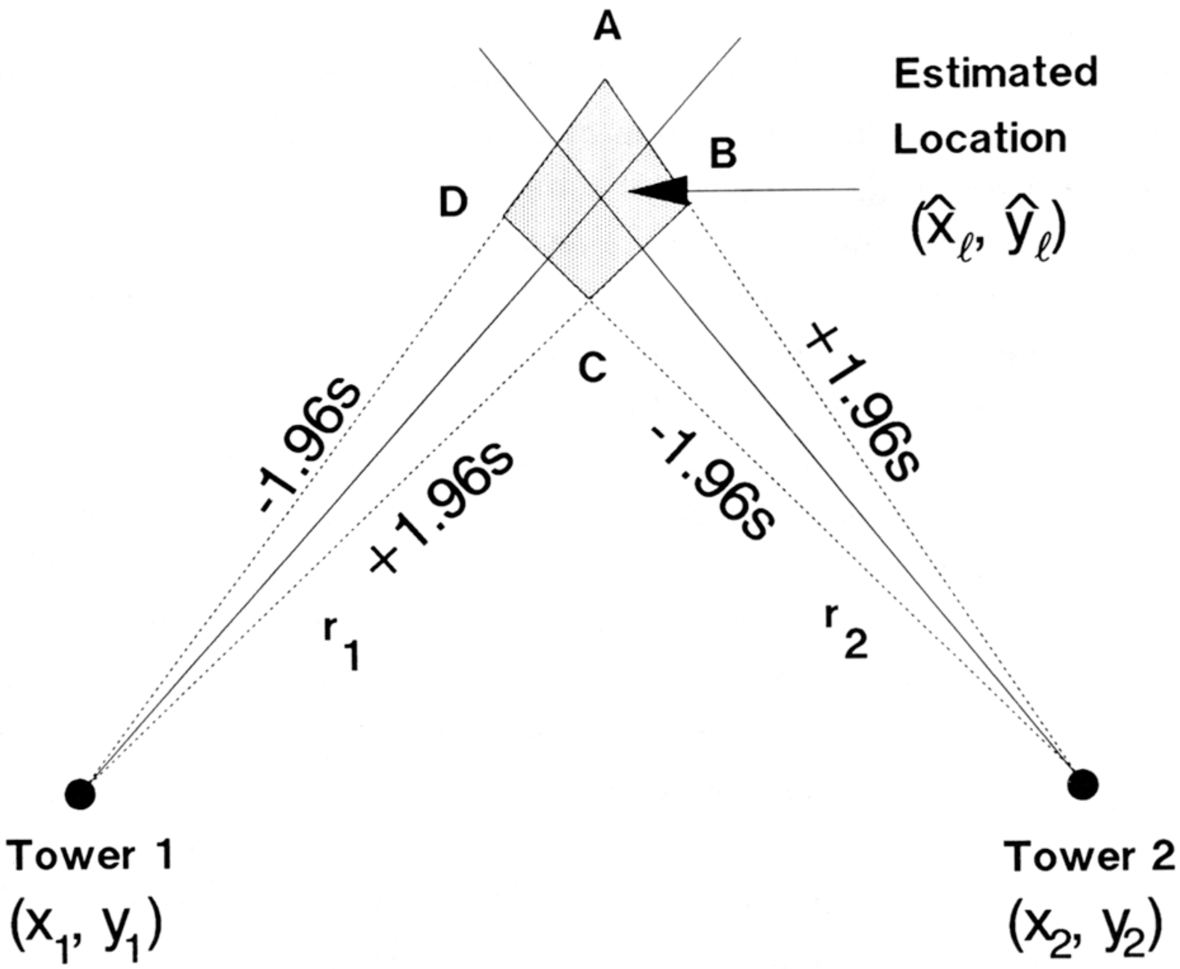



**Figure 10. Estimation of location by triangulation [White & Garrott 1990]**

We also use radio collars to measure other parameters that directly reflect the locomotor state of the animal. Acceleration is a useful measure with apparatus varying from a mercury switch that pulses the transmitter signal on and off as the animal moves to integrated circuits (the sort used to trigger car air-bags or measure the acceleration experienced by pilots) that directly measure acceleration which can be used to calculate leap distances and the duration of strenuous bursts of activity.

**Figure 11. Accelerometer collar on a mongoose lemur (*Eulemur mongoz*)**

One of the more direct approaches that was used to measure maximum speeds of various savannah ungulates was to chase them around with a landrover and see how fast you had to drive to overtake the subjects.

## Motion analysis

Those of us interested in biomechanics and functional anatomy often use motion analysis to look at the details of what is going on. In its simplest form this involves filming the animal in question and looking at the individual frames of film to see how the animal moves from frame to frame. This technique was pioneered in the late 19th century by Eadward Muybridge who used a number of fixed cameras which were triggered by trip wires that were activated when the subject broke them. He was the first person to solve the problem of what galloping horses looked like in mid-stride (something that had troubled artists wanting to paint galloping horses for the previous few centuries).

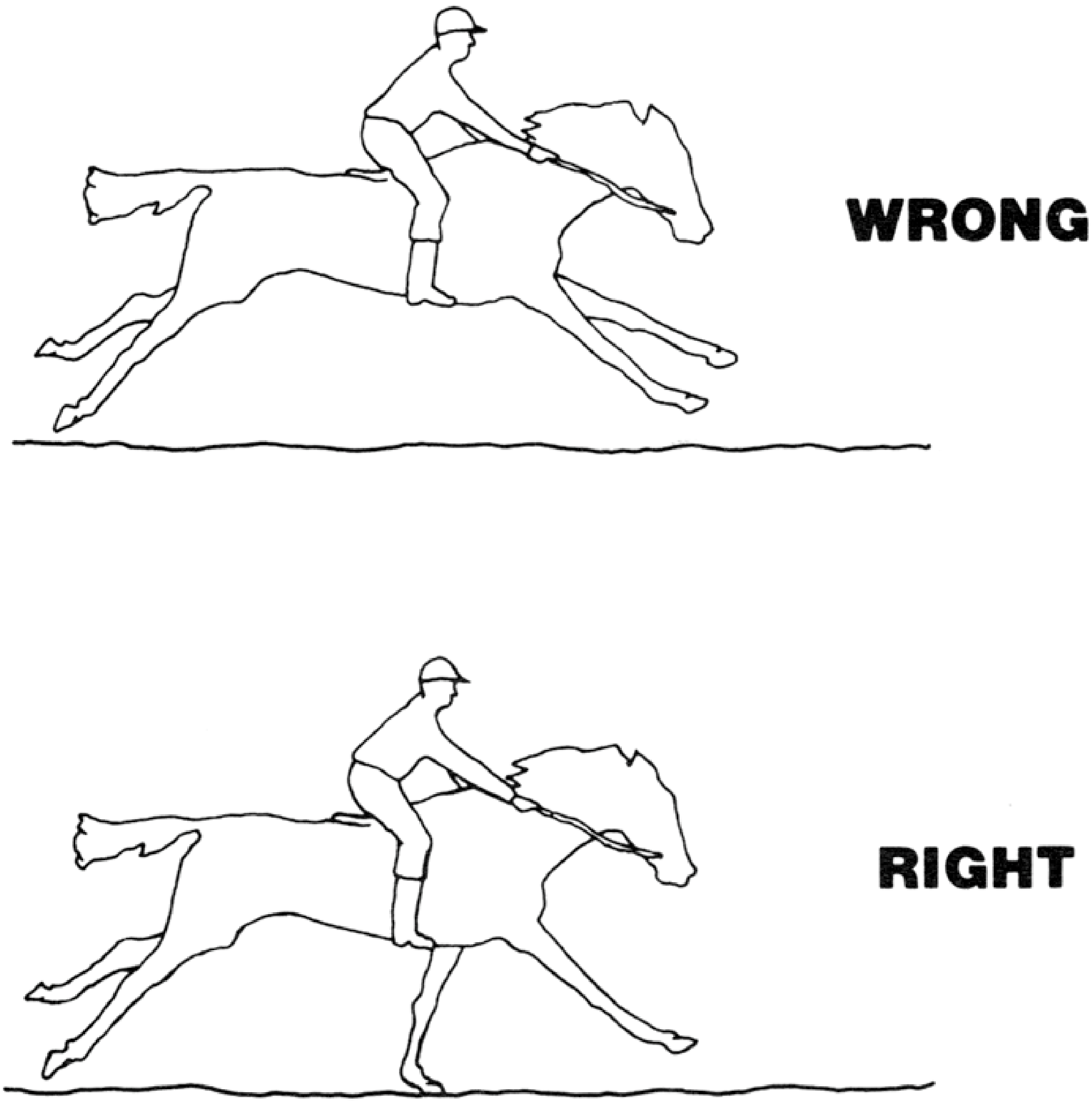



**Figure 12. Drawing Horses [Martin & Bateson 1986]**

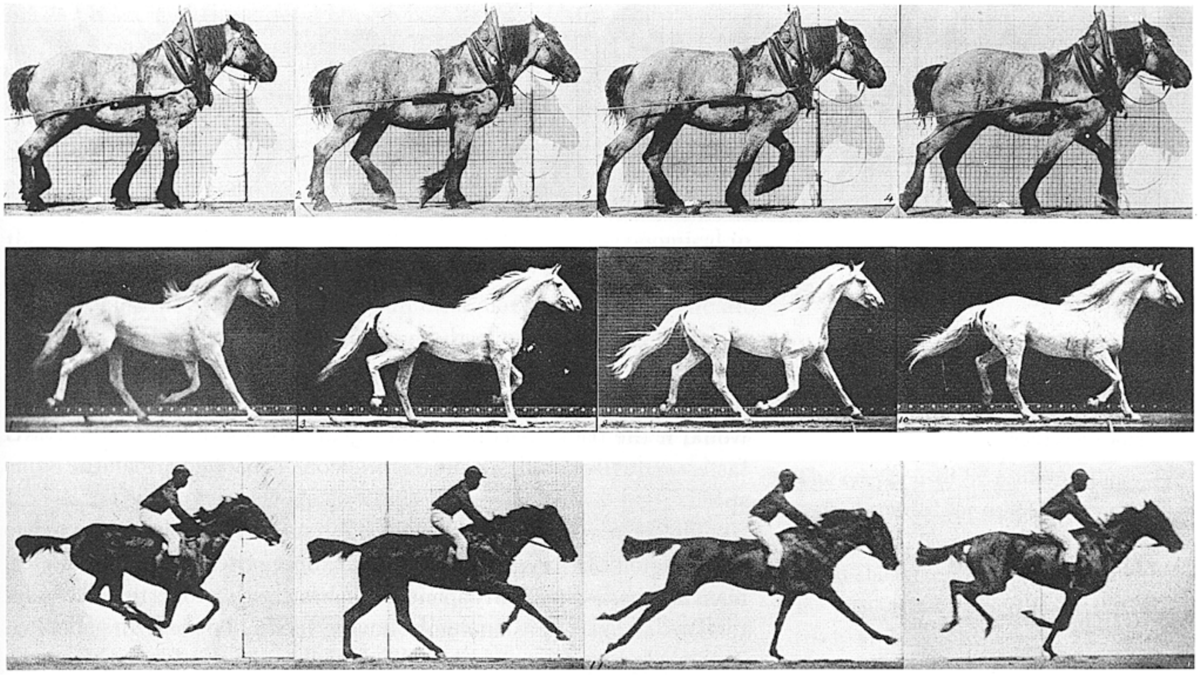


**Figure 13. Eadward Muybridge's horses [Alexander 1992]**

Modern studies have looked at much faster animal movements such as the flapping wings of a humming bird or a lacewing. The humming bird diagram is a single high-speed photograph, but the lacewing picture has been taken using a triple flash. By knowing the time between flashes we can calculate a number of important parameters such as the wingbeat frequency and the velocity of the animal.

**Figure 14. Antillean crested Hummingbird (*Orthorhynchus cristatus*) [Alexander 1992]**

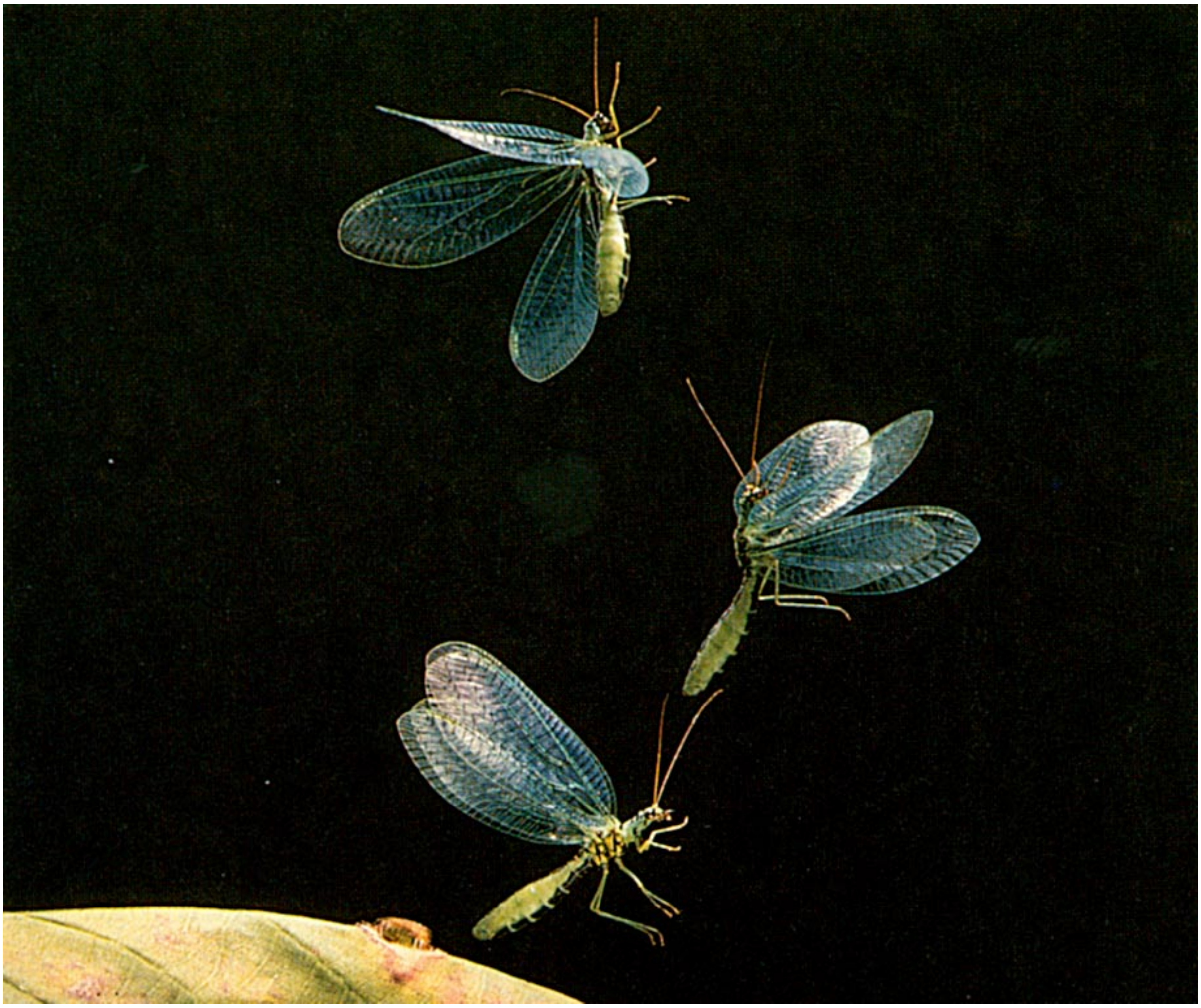


**Figure 15. Triple flash photograph of a lacewing (*Chrysopa carnea*) [Alexander 1992]**

Using high-speed video equipment we can sample movements up to several thousand times a second and if you have enough patience you can look through the still images and measure the animal's position, frame by frame. Once you have position data you can differentiate with respect to time to find velocities and again to find accelerations. If you then apply Newton's Laws of motion you can calculate the forces that are involved and hence the forces that need to be generated by the animal and the stresses that the skeleton needs to accommodate.

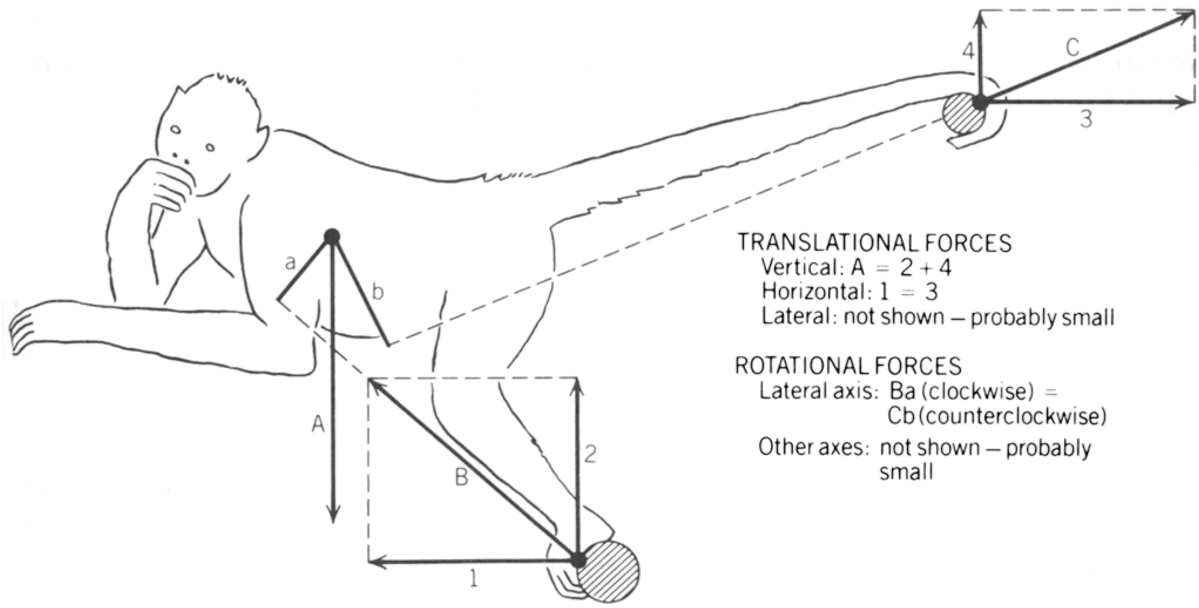



**Figure 16. Free-body diagram of a spider monkey (*Ateles* sp.) [Hildebrand 1995]**

We can directly measure other parameters associated with movement. Muscle activation can be monitored by electrodes attached to the skin of the animal (or needles inserted into the muscle body). Stresses can be measure by strain gauges attached to the bones and tendons of interest. X-ray films can be taken which allow you to see the movements of the bones inside the animal rather than just the externally visible movement.

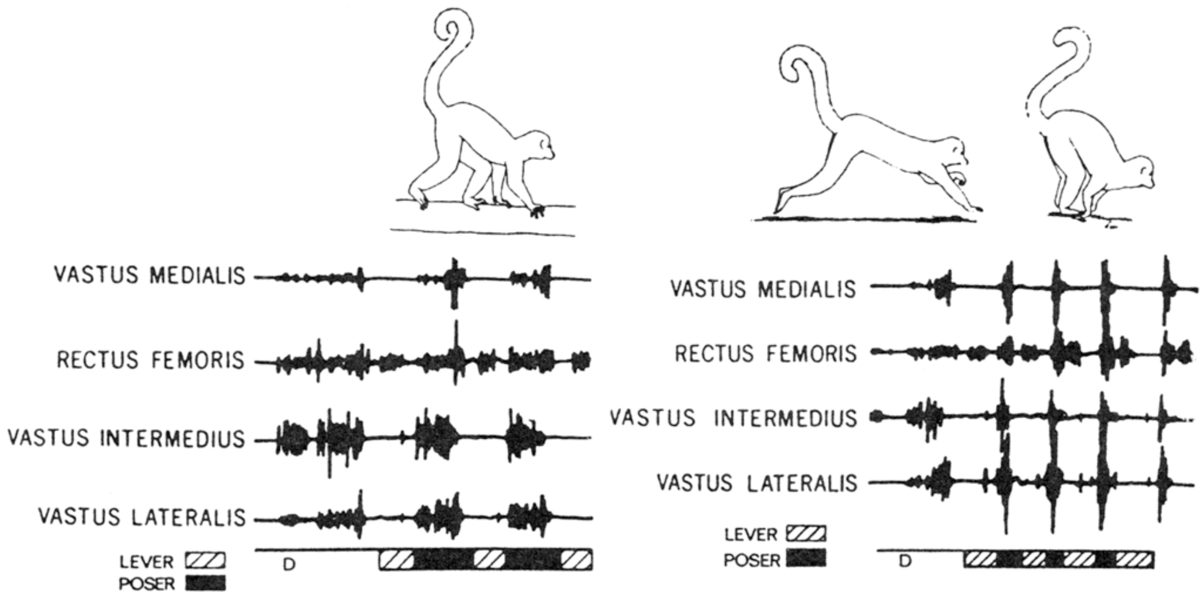



**Figure 17. Electromyographic recordings from a brown lemur (*Eulemur fulvus*) [Ferembach *et al.* 1986]**

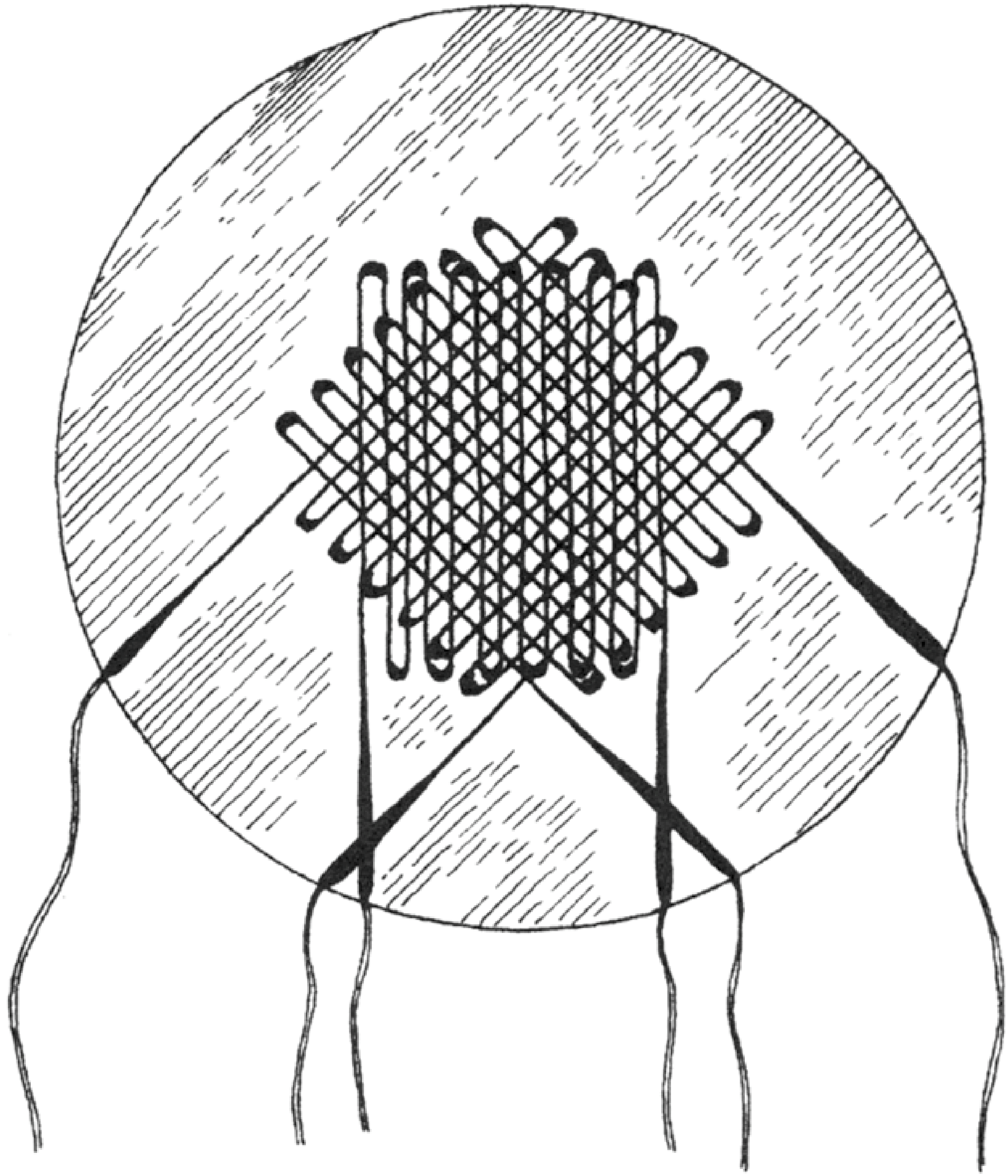


**Figure 18. Rosette strain gauge [McGowan 1999]**

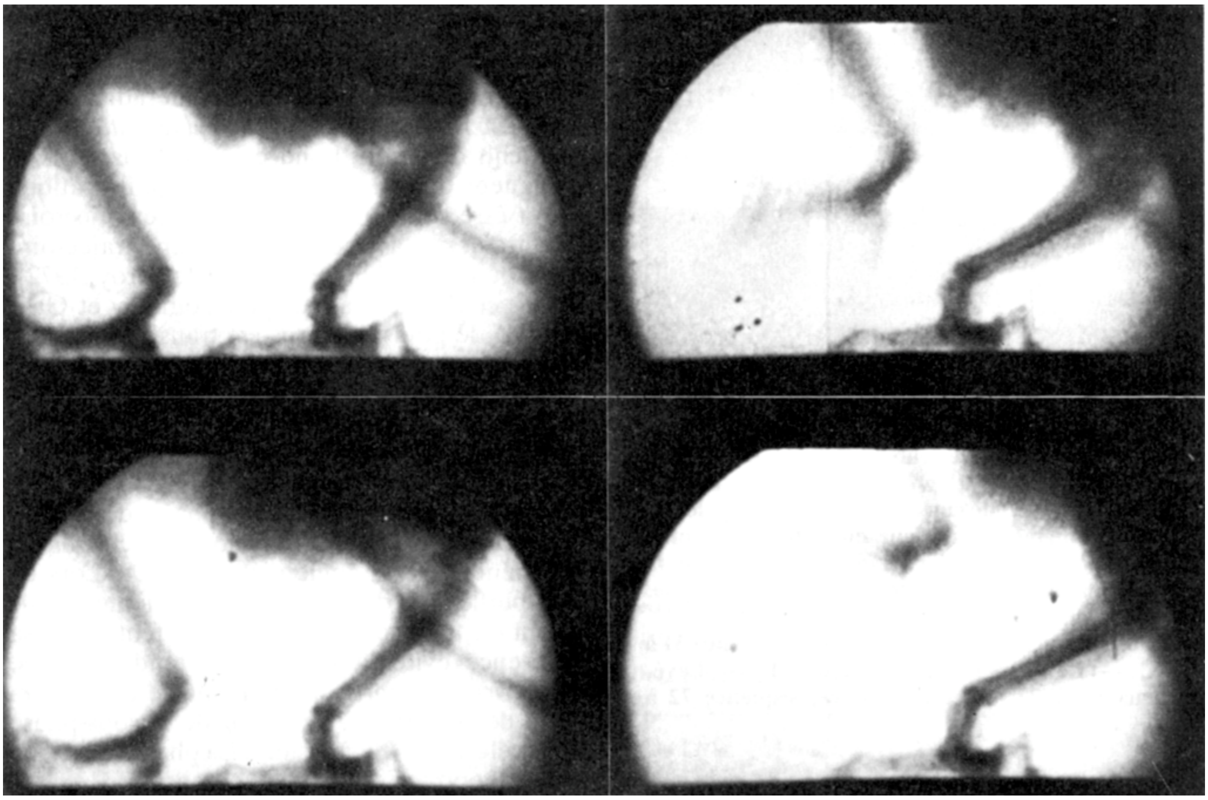


**Figure 19. X-ray film of an asymmetric leap of Allen's bushbaby (*Galago alleni*) [Ferembach *et al.* 1986]**

## Functional anatomy

In order to understand movement you need to know the mechanics of the underlying structure. This takes us into the realms of functional anatomy. People have been dissecting animals for centuries – millennia in fact. Bony skeletons can tell us a lot about the mechanical engineering underlying a structure since the physical principles are exactly the same. Trusses are a way of minimising the weight of a structure by separating the compressive and tensile elements of the beam. Figure 20 shows how this is used in the necks of quadrupedal mammals.

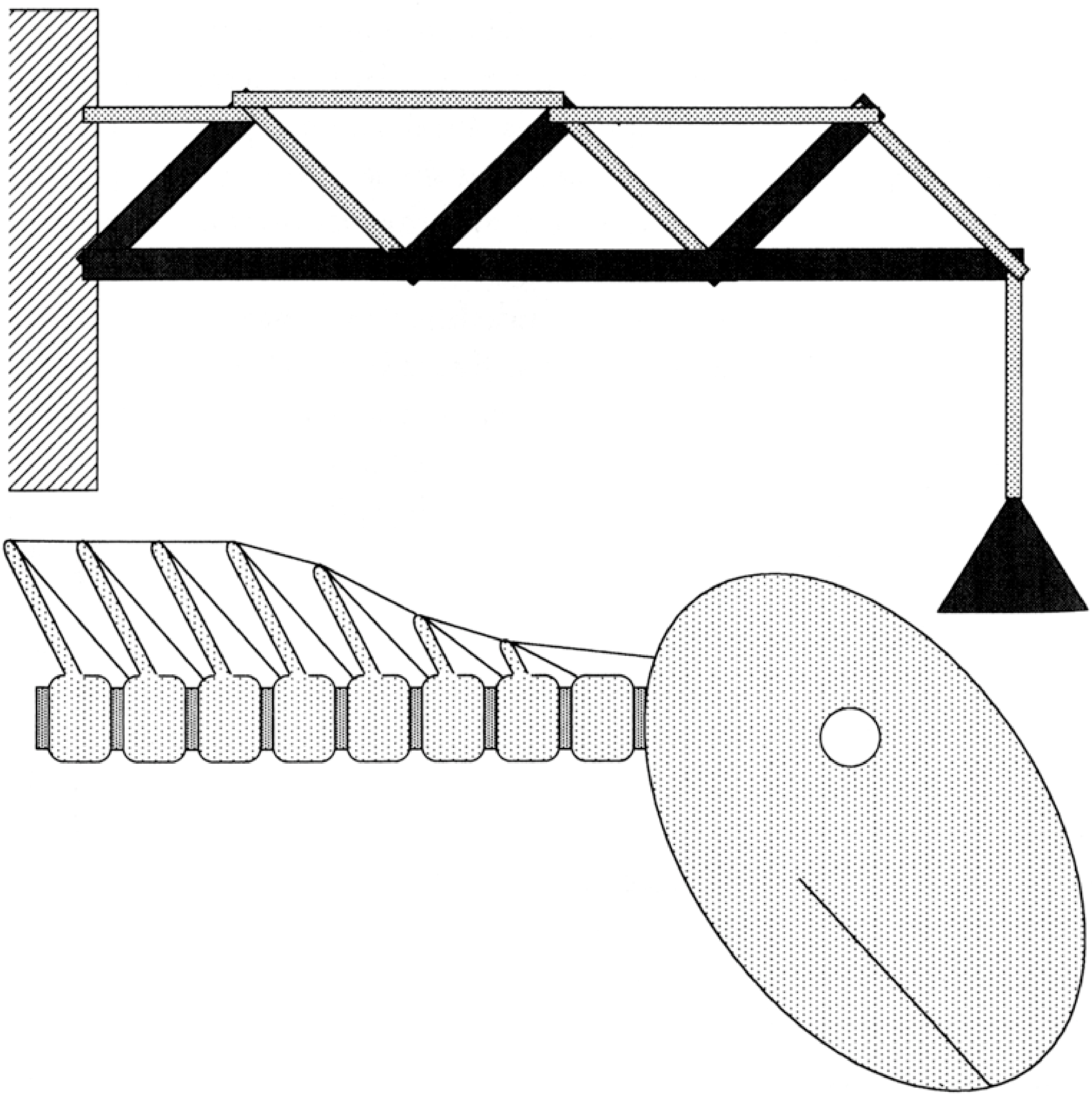


**Figure 20. Protruding trusses [Vogel 1998]**

Similarly joints and muscles can be treated as lever systems with the joint restricting the movement at the joint and the muscles applying forces (Figure 21). The actions of muscles can be measured *in situ* using electromyography as illustrated in Figure 17.

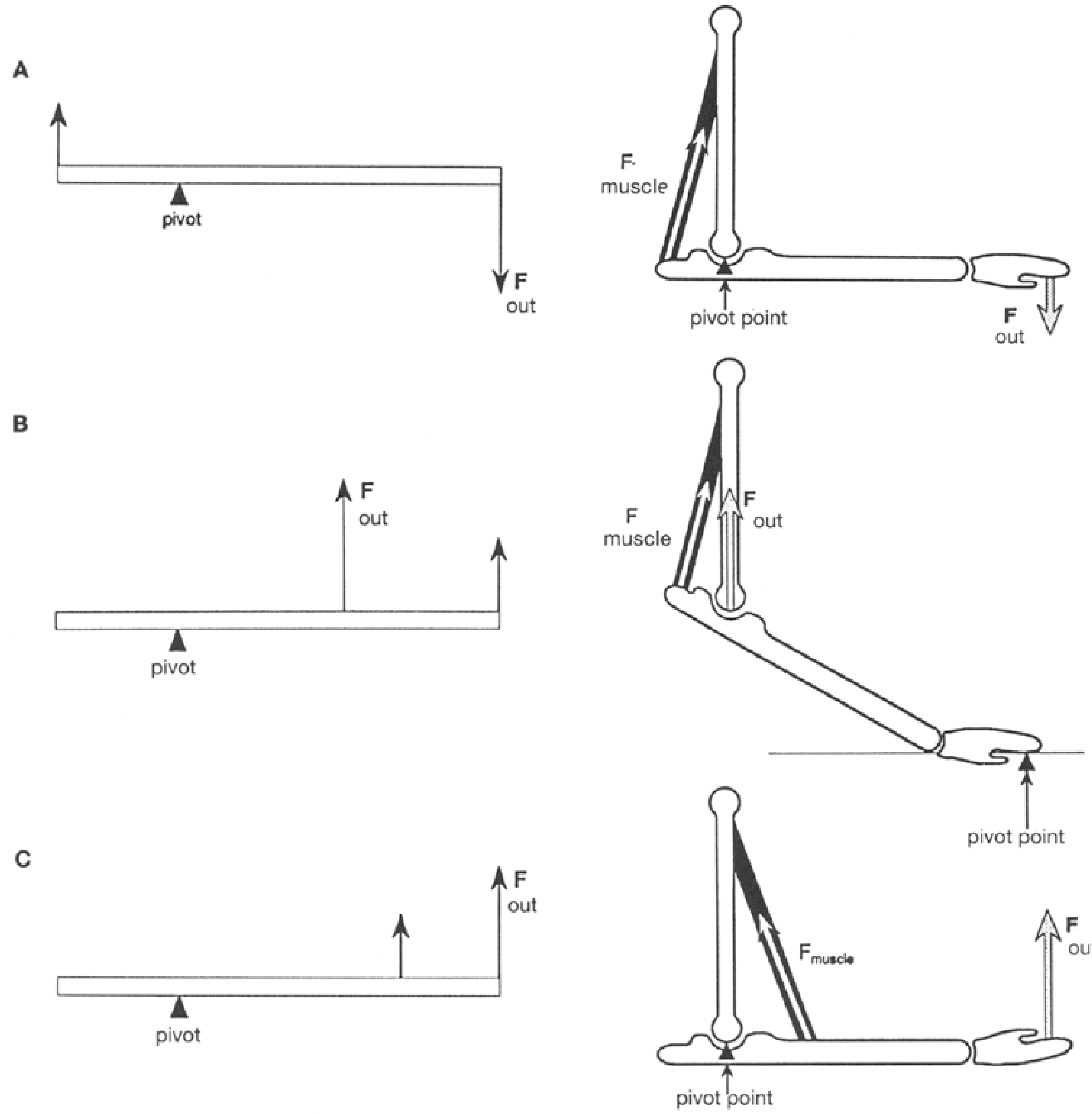



**Figure 21. Lever analysis of forces acting at joints [Swartz 1993]**

Functional anatomy is often essential when trying to find out how an animal moves the way it does. Jumping spiders use hydraulic pressure to extend their hind legs. Kinkajous have specialised ankle morphology that allow the animal to rotate its foot through 180° so that it hang by its claws with its head downwards.

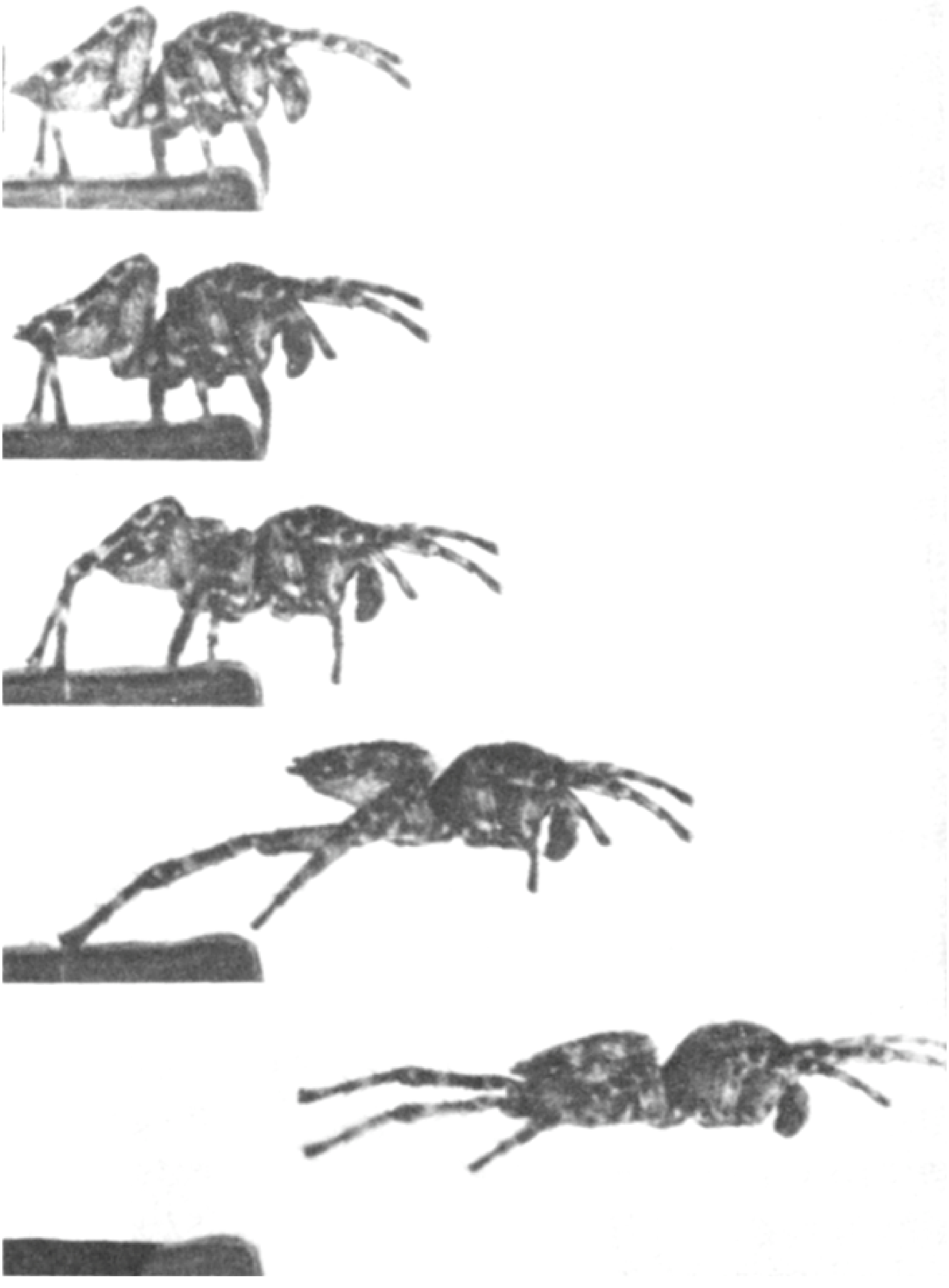


**Figure 22. Leaping jumping spider (*Sitticus pubescens*) [Schmidt-Nielsen 1983]**

**Figure 23. Kinkajou (*Potos flavus*) hanging by its hind feet [Alexander 1992]**

## Modelling and Simulation

Many modern studies of animal movement use some sort of modelling technique. This includes simple predictions of movement from forces acting about joints to full-blown 3D computer simulations. It is particularly useful for studying movements that cannot be observed. If you are interested in how dinosaurs move then you can base your model on how large terrestrial mammals move and extrapolate to the dinosaur you are interested in. You can even feed in information from fossilised footprints to produce a more accurate (or perhaps I should say a more believable) estimate.

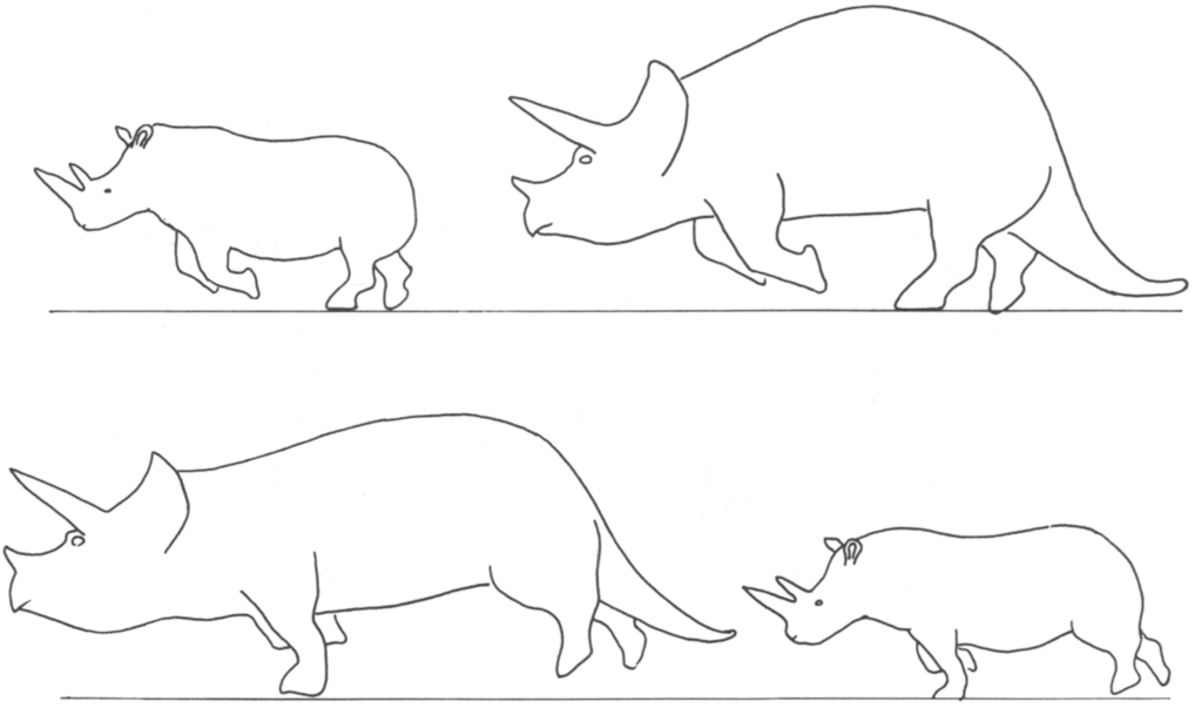


**Figure 24. How a Triceratops might have galloped based on a white rhinoceros (*Ceratotherium simum*) [Alexander 1989a]**

| | ESTIMATED LEG LENGTH | ESTIMATED SPEED | | GAIT |
|---|---|---|---|---|
| | *Meters* | *Meters Per Second* | *Miles Per Hour* | |
| data from Davenport Ranch (fig. 3.4) | | | | |
| large theropod | 2.0 | 2.2 | (4.9) | walk |
| small theropod | 1.0 | 3.6 | (8.1) | run |
| large sauropod | 3.0 | 1.0 | (2.2) | walk |
| small sauropod | 1.5 | 1.1 | (2.5) | walk |
| data from Winton (fig. 3.1) | | | | |
| large theropod | 2.6 | 2.0 | (4.5) | walk |
| small theropods | 0.13–0.22 | 3.0–3.5 | (6.7–7.8) | run |
| ornithopods | 0.14–1.6 | 4.3–4.8 | (9.6–10.7) | run |

**Figure 25. Estimated speeds of dinosaurs [Alexander 1989a]**

Similarly modelling can be used to generate theories behind the mechanics of human locomotion. Figure 26 illustrates the inverted pendulum model that suggest bipedal locomotion can be thought of as an upside-down pendulum and its mechanics modelled accordingly.

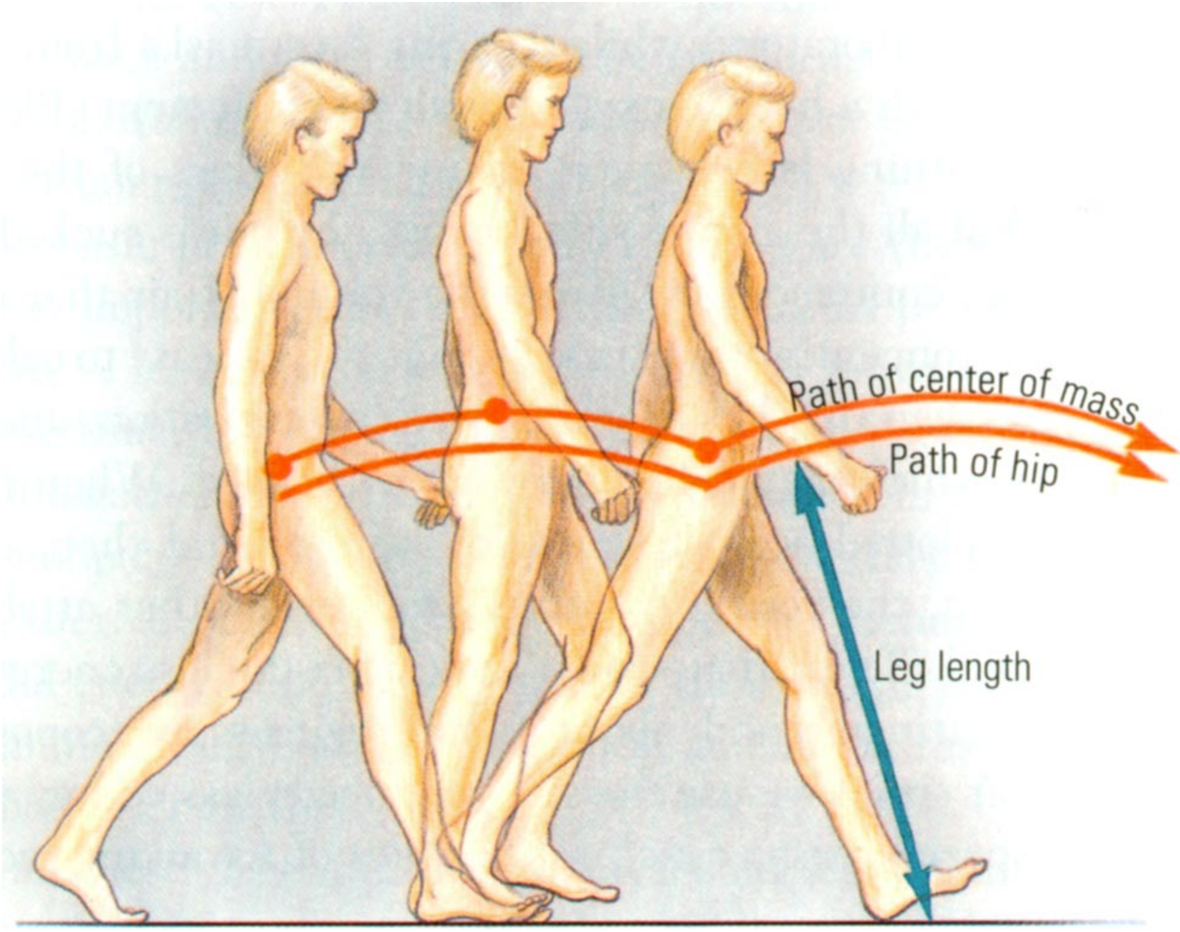



**Figure 26. Diagram illustrating the inverted pendulum model of walking [Alexander 1992]**

Some ongoing work I am involved in concerns the specialised locomotor form of gibbons which is called brachiation. I am trying to find out whether this form of locomotion is particularly suited to arboreal animals of a particular body size since gibbons live sympatrically with other primates that do not use this form of locomotion.

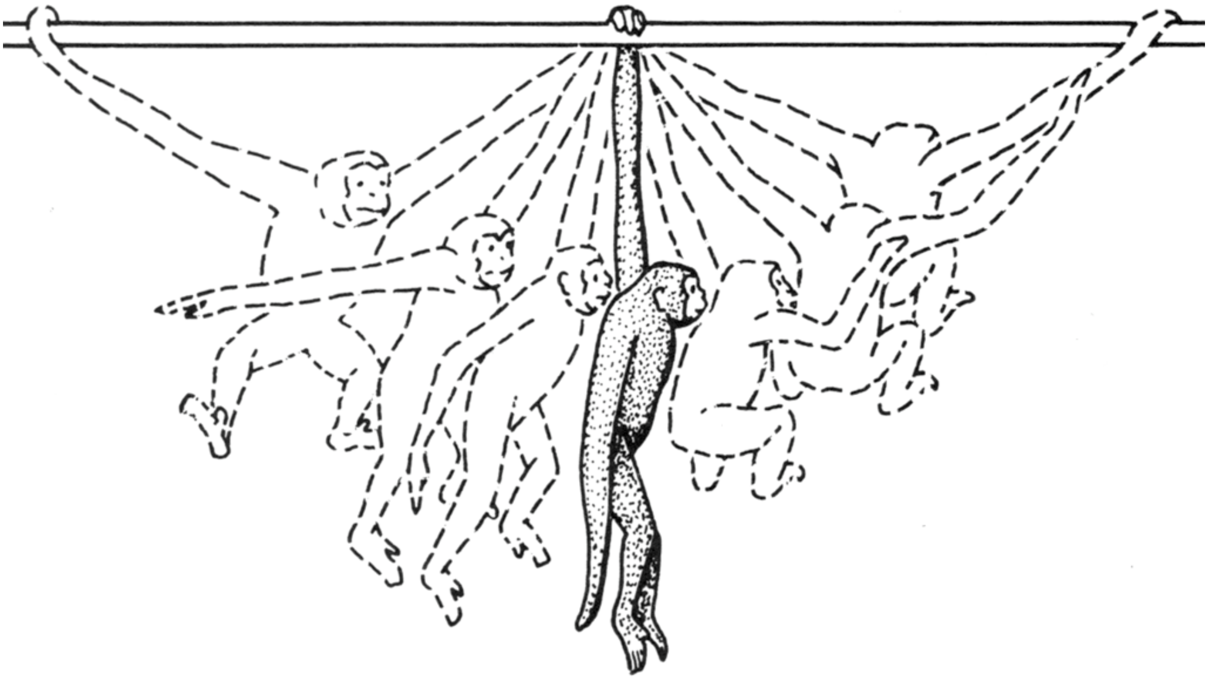
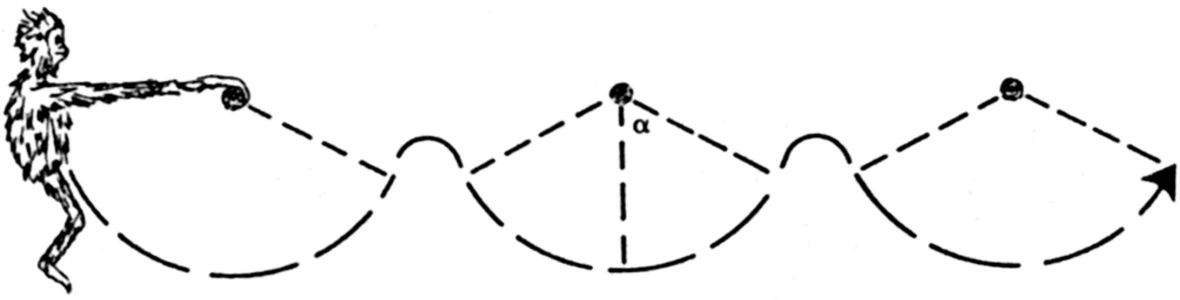


**Figure 27. Illustration of a siamang (Hylobates syndactylus) brachiating [Napier & Napier 1985]**

This is ongoing work but we are using a multi-way approach including video motion analysis of captive gibbons at Edinburgh Zoo, human motion analysis of people pretending to be gibbons (only for the more athletic) and computer simulation.

**Figure 28. Video footage of a siamang (*Hylobates syndactylus*) at Edinburgh Zoo**

This form of locomotion is a much more obvious pendulum as illustrated in Figure 29. This approach allows us to estimate the top speed and swing frequency that should be chosen by the animal.




For $\alpha = 90°$; $$v = 0.5\sqrt{\frac{g}{l}}$$

As $\alpha$ gets smaller; $$v = 1.4\sqrt{\frac{g}{l}}$$

**Figure 29. Diagram illustrating brachiation theory [Alexander 1989b]**

Figure 30 shows a computer simulation of this form of locomotion that can be used to explore the mechanics further and to see the effects of changes in limb dimensions and body size.

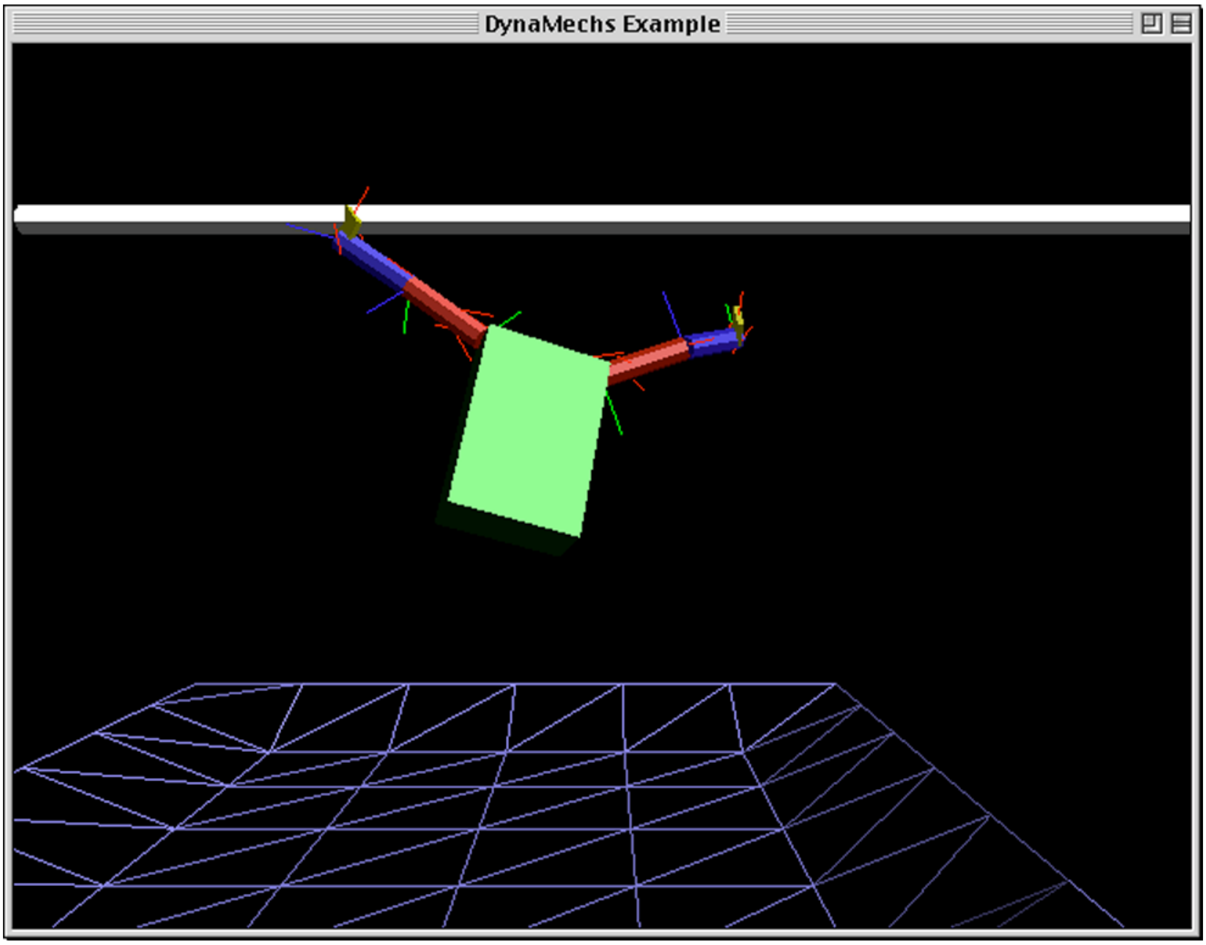



**Figure 30. Computer simulation of a gibbon brachiating**

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