

Modelling approaches in biomechanics

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Conceptual, physical and mathematical models have all proved useful in biomechanics. Conceptual models, which have been used only occasionally, clarify a point without having to be constructed physically or analysed mathematically. Some physical models are designed to demonstrate a proposed mechanism, for example the folding mechanisms of insect wings. Others have been used to check the conclusions of mathematical modelling. However, others facilitate observations that would be difficult to make on real organisms, for example on the flow of air around the wings of small insects. Mathematical models have been used more often than physical ones. Some of them are predictive, designed for example to calculate the effects of anatomical changes on jumping performance, or the pattern of flow in a 3D assembly of semicircular canals. Others seek an optimum, for example the best possible technique for a high jump. A few have been used in inverse optimization studies, which search for variables that are optimized by observed patterns of behaviour. Mathematical models range from the extreme simplicity of some models of walking and running, to the complexity of models that represent numerous body segments and muscles, or elaborate bone shapes. The simpler the model, the clearer it is which of its features is essential to the calculated effect.

Keywords: model; mathematical model; optimization; biomechanics

1. INTRODUCTION

This paper presents a wide-ranging review of the kinds of models that have been used in biomechanics, and aims to show how they have been useful. Physical models and mathematical models are clearly different in nature, and I will discuss them in separate sections of this paper. I also think it useful to distinguish a third category, conceptual models, which clarify a point without having to be constructed physically or analysed mathematically. Mathematical models have been by far the most numerous category in biomechanics. Some of them are very simple, while others attempt to imitate as much as possible of the relevant parts of the human or animal body. I will compare simple models with complex ones and discuss the merits of both.

2. CONCEPTUAL MODELS

Conceptual models that make their point without mathematical analysis have been used only rarely in biomechanics, and I will offer just one example. Margaria (1976) compared human walking to an egg rolling end over end on a level surface. As it rolls, the egg's centre of mass rises and falls, so its gravitational potential energy increases and decreases. Whenever its gravitational energy falls, its kinetic energy rises (it speeds up), and vice versa. Thus energy is swapped back and forth between the gravitational and kinetic forms, as also happens in walking. Margaria wrote no equations for this model. It is difficult or impossible to roll an egg as he described, because the

egg is unstable, and it seems unlikely that he expected his readers to attempt the feat. However, even without either mathematics or experiment, the model may aid understanding.

3. PHYSICAL MODELS

Physical models have proved effective for several different functions in biomechanics. First, a physical model may show that a proposed mechanism actually works. Sir James Gray (1953) used simple models to explain some of the basic principles of fish swimming, of snake crawling, and of the balance of terrestrial mammals. He designed these models to illustrate lectures to an audience of schoolchildren at the Royal Institution. Haas & Wootton (1996) described paper models of insect wings in a paper designed for professional scientists rather than for students. The hind wings of beetles provide the aerodynamic forces for flight. They are very much longer than the elytra (modified fore wings) which protect them when the insect is resting. However, as the wings are furled after a bout of flight, they fold so as to fit under the elytra. Haas & Wootton (1996) explained two mechanisms of folding that are used by different groups of beetles, and by some other insects. They published diagrams showing how sheets of paper should be creased to make models that fold like the insect wings, and encouraged readers to make and try out the models. I find that the mechanisms are very much easier to understand when I have a model in my hands, than if I rely solely on the text and illustrations of the paper.

Second, physical models have sometimes been used for observations that would be difficult to make on real animals or plants. Photoelastic models have been used to investigate patterns of stress in irregularly shaped bones;

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for example, the Achilles tendon inserts on an epiphysis on the heel. Smith (1962) used a photoelastic model of the human heel to argue that the epiphysal plate is shaped in such a way as to minimize the danger that it will be sheared off by tension in the tendon. This method has been superseded by finite element analysis (discussed in § 4b), and seems unlikely to be used again.

Physical models have proved especially useful in biological hydrodynamics. It is often convenient to use models that differ in size from the living system. In such cases, compensating changes must be made in the speed of the flow or in the properties of the fluid, to match the Reynolds number of the model system to that of the natural one. If this is not done, the pattern of flow may be altered, making it impossible to draw useful conclusions about the natural system.

Koehl (1996) measured the forces on models of seaweed, in a tank in which water flowed alternately forward and back, simulating waves. She used models of various lengths, made of several materials that differed in stiffness. Her results indicated that the hydrodynamic forces on a long flexible weed on a wave-swept shore could be remarkably low. If the weed is long and flexible enough, a limited further increase in length may actually reduce the hydrodynamic force. Ellerby & Ennos (1998) used greatly enlarged models of xylem vessels to investigate the effect of perforation plates on resistance to the flow of sap. Their results would not have been applicable to flow in real plants if the Reynolds numbers had been different, but they matched the Reynolds numbers in their wide models to those in slender xylem vessels by using glycerol to represent the sap.

Harris (1936) made remarkably sophisticated use of a rigid cast of a dogfish, in his early experiments on the stability of fish swimming. He mounted the model on an aerodynamic balance in a wind tunnel, and made air flow past it at a speed that gave a Reynolds number within the range that would have applied when the fish was swimming in water. He fixed it at different angles to the flow, with and without fins, and measured the aerodynamic moments that acted on it. He showed that the fish would be stable in yaw when its anterior dorsal fin was limp, but neutrally stable when this fin was stiffened by contraction of its muscles. He suggested that the fish may exploit these properties in turning.

Sixty years later, Ellington *et al.* (1996) used a robotic model to investigate airflow over the wings of a hovering hawkmoth. They made some of their observations on real moths, but needed the larger model (with 10 times the wingspan) to show some of the detail. By driving the model at 1/100 of the natural wingbeat frequency they satisfied the conditions for aerodynamic similarity between model and moth. (Because the wings flapped, it was not enough to get the Reynolds number right; another dimensionless number known as the Strouhal number had to be right as well.) The wings were driven through a complex gearbox, which made them imitate the 3D motion of the real wings. Ellington and his colleagues released smoke through holes in the model's wings and discovered that the leading edge vortex spiralled out towards the wing tip. This unexpected phenomenon provided an explanation of the ability of insect wings to generate more lift than conventional aerodynamics predicted.

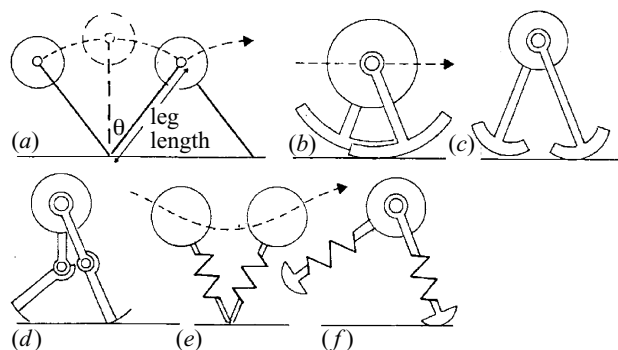


Figure 1. Some simple mathematical models of bipedal walking and running. (a) Alexander's (1976) model of walking; (b) to (d) McGeer's (1990a) models of walking; (e) the model of running analysed by Blickhan (1989) and by McMahon & Cheng (1990); and (f) McGeer's (1990b) model of running. (From Alexander 1995a.)

Ellington *et al.* (1996) made some measurements of velocity in the vortex, but the main result of that particular paper was qualitative. In experiments with a different robot, Dickinson *et al.* (1999) measured forces as well as observing patterns of flow. Their robot represented a fruitfly, a very much smaller insect than the hawkmoth. It moved in mineral oil instead of water; this made it possible to match the Reynolds number to the real insect, and still get forces large enough to measure conveniently. Using it, they demonstrated force peaks due to rotation of the wing about its long axis at the end of each wing stroke, and due to the wing moving back into its own wake at the beginning of the next stroke. They varied the timing of the rotation of the wing at stroke reversal, and showed that this strongly affected the forces. This illustrates an important advantage of working with models: they can be used to find out what the consequences would be if the structure of an animal, or its pattern of movement, were changed.

Birch & Dickinson (2001) observed flow in the oil around the same model, by particle image velocimetry. They showed that the pattern of flow was strikingly different from the pattern that Ellington *et al.* (1996) had observed for the hawkmoth (which works at very much higher Reynolds numbers). In an experiment that would have been prohibitively difficult with a real fly, they attached baffles to the model wing, to prevent flow towards the wing tip. This change did not affect the stability of the leading edge vortex, nor did it change the pattern of forces on the wing. It appears that different aerodynamic effects are important in the flight of large moths and of small flies.

Finally, a physical model may serve to check the results of mathematical modelling. McGeer (1990a) investigated the stability of bipedal walking by analysing the motion of the model shown in figure 1c, walking passively down a slope. I will discuss his mathematical model in § 4. In addition to the mathematical model, he built and tested a physical model with the same structure. He showed that when he set it moving on a slope, it settled into a steady and stable gait after a few strides, as the mathematics predicted it should do. Its stride frequency was slightly lower than the mathematics had predicted, but this could be

accounted for by friction that had not been incorporated in the initial mathematical model.

McGeer's bipedal walker is a good illustration of the point that a physical model can be informative without closely imitating the structure or movements of real organisms. Another example is provided by the experiments of Vogel & Bretz (1972). They used a simple plastic model to demonstrate the principle of viscous entrainment, whereby currents in the surrounding water drive the flow of water through the pores of sponges.

4. MATHEMATICAL MODELS

It will be convenient to review mathematical models under four headings, although some models could be described under more than one of them.

(a) *Simple models*

Very simple mathematical models have been found useful in discussions of human walking. Figure 1*a* shows the simplest of them all (Alexander 1976). It consists of a point mass moving on rigid legs of negligible mass. As it walks, its centre of mass travels forward along a series of arcs of circles of radius l equal to the length of the legs. The velocity of the centre of mass fluctuates a little in the course of each step as kinetic energy is converted to gravitational potential energy, and vice versa. Let this velocity be v_0 at the stage when the supporting leg is vertical. At this stage, the body is travelling with velocity v_0 along an arc of radius l , so it has an acceleration v_0^2/l towards the centre of the circular arc (that is, vertically downwards). This acceleration is driven by gravity, so cannot be greater than the gravitational acceleration g . Hence v_0 cannot be greater than \sqrt{gl} . This is 3 m s^{-1} for a typical man with legs 0.9 m long. Thus the model suggests that it should be impossible to walk faster than 3 m s^{-1} . Athletes achieve speeds over 4 m s^{-1} in walking races, only by violating the assumptions of the model (Alexander 1984). They make the centre of mass of the body travel along flatter arcs, with a larger radius of curvature, by a peculiar movement of the pelvis.

McGeer (1990*a*) used a series of mathematical models (figure 1*a-d*) in his discussion of walking. The one shown in figure 1*c* corresponds to the physical model discussed in § 3, and is particularly interesting. It is a little more complex than the model of figure 1*a*, in that the legs as well as the trunk have mass, and the feet are arcs of circles. In the course of each step, it rolls forward on the supporting foot, simulating the action of a human walker who strikes the ground with the heel and rolls forward onto the ball of the foot.

Though this model was simple in structure, sophisticated mathematics was needed to analyse its motion. McGeer (1990*a*) was able to show that with reasonable values for the parameters, its motion was stable; after a small disturbance, the model returned automatically to its original pattern of movement. However, this model was 2D. Kuo (1999) extended the analysis to a 3D version of the model that was capable of rocking from side to side, and showed that it was unstable in roll.

Very simple models have been used to model running as well as walking. The simplest, analysed by Blickhan (1989) and McMahon & Cheng (1990), is a mass bounc-

ing along on springs (figure 1*e*). McGeer's (1990*b*) model is slightly more complicated (figure 1*f*). McMahon & Cheng (1990) used their model to show that runners' legs behave like springs of constant stiffness, independent of the speed of running. This was a surprising result because legs are not passive springs; the movements of their joints depend partly on the inelastic length changes of muscle fibres, and only partly on the passive elastic properties of tendons. McGeer (1990*b*) showed that his model of running was unstable except at very high stride frequencies.

The results from analysis of these simple models could not have been obtained by experiments on human subjects. Humans cannot be trained to walk passively, without reflexes or other active control mechanisms.

These models had no more than two legs, but Kubow & Full's (1999) model of insect walking necessarily had six. It was nevertheless very simple; it was a horizontal planar model, with each leg represented as a force acting between the body and a point of contact with the ground. Using it, Kubow and Full obtained the remarkable result that insect-like running is dynamically stable to perturbations of speed and direction.

Very simple mathematical models have been applied to jumping as well as to running. Hubbard & Trinkle (1985) threw useful light on the mechanics of high jumping by treating the human body as a straight rigid rod. Alexander (1995*b*) devised a model of standing jumps that was sufficiently general to be applied (with different values for the parameters) to jumpers ranging in size and structure from fleas to humans. It jumped by extending its knees, whose muscles had elastic tendons and realistic physiological properties. I used the model to investigate the relative merits of different jumping techniques, showing for example that a countermovement (the knees bend immediately before extending) can increase the height of the jump substantially for large (human sized) jumpers, but is less effective for small (flea sized) ones. I also used it to explore the effects of changing the properties of the tendons or muscles, and even of changing the number of joints in the leg. Plainly, these investigations could not have been made by experiments on real animals.

The long bones in the legs of mammals and lizards generally have epiphyses, which ossify separately from the main shaft of the bone. Birds, dinosaurs and amphibians, however, tend not to form epiphyses. In mammals and lizards, perichondral and endochondral ossification proceed more or less simultaneously, whereas in the other vertebrates perichondral ossification is dominant in the early stages of development. Carter *et al.* (1998) used a computer model to show that this difference in timing could explain the formation or not of epiphyses. They started with very simple models of a long bone at an early stage of development. These models were composed of a large number of tiny blocks, so that different parts of the model could be given different mechanical properties (representing bone, cartilage or marrow), and the calculations could be performed by finite element analysis. The models were identical in shape, but differed in the distribution of perichondral bone. Carter and his colleagues simulated the development of the bone under the influence of intermittent loading by muscles. They assumed that intermittent shear stresses accelerate ossification of cartilage, while intermittent compressive stresses inhibit it.

The mammal-like model developed epiphyses and the bird-like one did not.

Muller *et al.* (1982) used a very different mathematical model to elucidate the principles of suction feeding by fishes. Teleost fishes suck food in by a rapid enlargement of the mouth cavity, which involves expansion of the whole head. The head is a very complex structure with more than 100 bones, most of them movable relative to their neighbours. Muller *et al.* (1982) nevertheless represented it very simply, as a hollow truncated cone with the mouth at the narrow end. At the start of a feeding movement, the wide end of the cone was closed. The cone expanded rapidly in diameter, and at a chosen instant its posterior end opened, representing opening of the opercular valves. Muller and his colleagues used classical hydrodynamics to calculate the distributions and time courses of pressures and velocities of flow, both in the water surrounding the fish and in the mouth cavity. The rotational symmetry of the model made the computing less onerous than it would have been if the mouth opening and mouth cavity had been given more realistic shapes. Unlike its predecessors, this analysis of suction feeding took full account of the inertia of the water. It showed how steep pressure gradients could develop within the mouth cavity; that water could be expected to flow against the pressure gradient at times; and that it could be expected to continue to flow into the mouth (and out of the opercular slits) after the mouth and opercular cavities had ceased to expand.

(b) *More realistic models*

Very simple models are often the best for establishing general principles, but there are some problems that demand more complex models. Yeadon (1990) set out to explain how divers and trampolinists execute twisting somersaults. He could not have thrown much light on the problem by modelling the body as a single rigid rod, as Hubbard & Trinkle (1985) had done in their discussion of high jumping. Instead, he treated it as an assembly of 11 rigid segments connected by 10 joints (at the neck, lumbar region and two each of shoulders, elbows, hips and knees). This was still greatly simplified compared with the real body, but it generated a formidable array of equations. Six equations of motion are needed for a rigid body moving in three dimensions, so 66 were needed for this model.

Some other models have represented only a single limb with only three or four joints, but have represented a large number of muscles, or have given the muscles complex properties. Seireg & Arvikar's (1973) model of human standing had 29 muscles in each leg. The model of human jumping analysed by Pandy *et al.* (1990) was restricted to two dimensions and had only eight muscles in the leg, but each muscle consisted of a contractile component with realistic force-length-velocity properties, series elastic and parallel elastic elements and an elastic tendon.

Complex models are also needed for calculations of stresses in elaborately shaped bones. Finite element analysis is generally used. In what seems to be the most complex finite element model used so far in biology, Rayfield *et al.* (2001) used 146 398 tiny tetrahedra to build their mathematical model of the skull of *Allosaurus*. They used the model to calculate the distribution of stresses in the skull, in strong biting. Even with this degree of elaboration, many details that might have affected the results

significantly were omitted. No account was taken of the anisotropy of the bone, of variations in bone properties between one part of the skull and another, or of the mechanical properties of sutures. Inevitably (because the model was based on a fossil) there was uncertainty about the dimensions of the jaw muscles and the arrangement of their fibres. However, the results were sufficiently clear to show that the skull was many times stronger than would be needed to withstand the forces that the jaw muscles could have exerted.

Models may be more realistic than their predecessors, without closely imitating the structure of particular species. Van Leeuwen & Spoor's (1992) models of pennate muscles are good examples. Previously, pennate muscles had been modelled as parallelepipeds in which the muscle fibres remained straight. Van Leeuwen and Spoor pointed out that this architecture would be unstable, and formulated a model in which the fibres were free to bend. They showed that when it developed tension, this model would adopt a fusiform shape similar to the shapes of real muscles. Another example is provided by Muller & Verhagen's (1988) model of semicircular canal systems, which allows the dimensions of the canals and their orientation in space to be varied, without imitating details of the structure of particular species. Previous models had considered the canals separately, but this one predicted endolymph flow in the entire system of interconnected canals. It showed patterns of flow that the previous models could not predict.

(c) *Optimization models*

Mathematical models have often been used to calculate the structure or pattern of movement that is (according to some theory) the best possible. For example, Mattheck & Bethge (1998) used computer aided optimization to calculate how trees should be shaped at branching points, to avoid stress concentrations.

Other models predict optimum patterns of movement instead of optimal structure. For example, Alexander (1990) formulated a very simple model of human jumping (figure 2a). The trunk was represented as a rigid body and the leg consisted of two segments of negligible mass. The only muscle was a knee extensor, which was given realistic force-velocity properties (figure 2b) and a compliant tendon. The model ran up at a chosen speed and set down its leg at a chosen angle, with the knee almost straight. The muscle was activated and the knee bent and re-extended, throwing the model into the air. In figure 2c, contours show the length of the jump for different combinations of initial speed and leg angle. They show that the longest jumps are achieved by running up as fast as possible and setting down the leg at *ca.* 65°. The contours in figure 2d show that for high jumping it is better to run up more slowly. The greatest height is achieved with a speed of 7 m s⁻¹ and an angle of 45–50°. This simple model predicts the techniques of successful athletes remarkably accurately, but the accuracy must be to some extent fortuitous. The significance of the result was not its accuracy, but its demonstration of a principle that could account for a relatively slow run-up being more effective than a faster one. Seyfarth *et al.* (2000) refined the model, giving the muscle and its tendon more realistic properties.

That model was specific to human athletics, but some

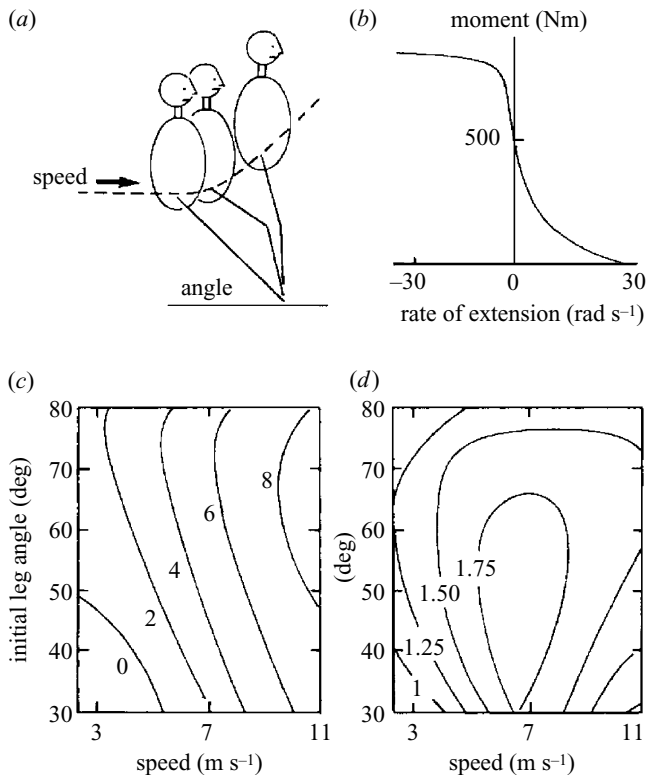


Figure 2. A mathematical model of human jumping. (a) Successive positions of the model during take-off. (b) The moments that the knee extensor muscle was assumed to be capable of exerting, at different rates of knee extension. (c) and (d) The predicted lengths and heights of the jump, respectively, in metres. These are shown as contours on plots of initial leg angle against run-up speed. (From Alexander 1990.)

other optimization models are much more general. One example is Alexander's (1997b) model of oscillatory movements, which can be applied to systems as different as a swimming dolphin, a hovering bee and a galloping horse. It predicts the optimum properties for muscles and their tendons, to minimize the metabolic energy costs of the movements. The method of calculating energy costs was questionable, because metabolic measurements on muscles shortening under constant load were used to estimate the energy costs of cycles of lengthening and shortening against fluctuating loads, but the model will nevertheless serve as an example of a potentially useful approach.

Niklas & Kerchner (1984) used simple geometric rules to generate computer models of plants with different branching patterns. They generated patterns from all parts of the range that their rules allowed, and calculated for each the amount of light it would intercept in the course of a day, and the bending moments exerted by the weights of its branches. They looked for patterns of branching that maximized light interception and minimized bending moments. Rather than a single optimum pattern, they found several alternative patterns that were more or less equally good, and better than any others.

(d) *Inverse optimization*

The models we have been considering sought the best possible structure or pattern of movement, in particular

circumstances. There is another approach that reverses that one. Instead of seeking the best possible solution to a problem, it asks: if this structure or pattern of movement is the best possible solution to a problem, what was the problem?

Many human tasks involve moving a hand from one point to another, for example lifting a cup onto a shelf. Often, a wide range of trajectories could be used: the hand could be moved along a straight line or a curve, and many variations of speed would be possible in the course of the movement. However, experiments have shown that for any particular task, the chosen trajectory is highly predictable. For some tasks, it is almost straight. For others in which a straight path would be equally possible, the preferred path of the hand is markedly curved. Several attempts have been made to find a rule that might govern the choice of trajectory. Flash & Hogan (1985) tested the hypothesis that trajectories are chosen to minimize jerk (rate of change of acceleration). They found that this hypothesis successfully predicted the time-course of the speed of the hand, but it did not predict curved paths. In any case, it is not evident why this principle should be a good one except for tasks such as moving a cup of coffee without spilling. Uno *et al.* (1989) postulated that rates of change of joint torques are minimized, but this hypothesis explains some movements less well, and again it is not obvious why this principle would be a good one. Alexander (1997a) suggested that trajectories might be chosen to minimize metabolic energy costs, and also had some success in explaining observed movements. However, the energy costs of many arm movements must be trivial. So far, these investigations of hand movements have not produced a clear conclusion.

An inverse optimization approach has also been adopted in investigations of load sharing between muscles. The numbers of muscles in the bodies of humans and vertebrate animals are many times greater than the numbers of degrees of freedom of movement allowed by the joints. Consequently, it is generally impossible to calculate the forces in individual muscles unambiguously, from measurements of the accelerations of body parts and of the forces exerted on the environment. Seireg & Arvikar (1973) postulated that loads were shared between cooperating muscles according to some optimizing principle. They attempted to find optimization criteria that could explain load sharing between muscles in human standing, but I will use a more recent study as an example of the approach.

The ankles of cats have three extensor muscles, the gastrocnemius, the plantaris and the soleus. The same moment can be exerted at the ankle by different combinations of forces in the three muscles. Herzog & Leonard (1991) used a mathematical model to calculate how much force each muscle should contribute at successive stages of walking and trotting strides, if the load were shared according to each of several optimization principles. They calculated what the forces would be if they were adjusted to minimize the total of the forces in the individual muscles, or the total of the stresses. They also calculated what the forces would be if the squares or cubes of these quantities were minimized. They compared these predictions with actual muscle forces, measured by means of transducers attached to the tendons of the three muscles.

They found that none of the optimization criteria predicted the forces consistently well.

5. CONCLUSIONS

The examples given in previous sections illustrate the wide variety of models that have proved useful in biomechanics. They also show that models can serve a variety of functions. Conceptual models may aid understanding. Physical models may be used to demonstrate a mechanism, to test the conclusion of a mathematical model, or to facilitate observations that would be difficult or impossible to make on real organisms. Mathematical models may be used to predict effects, to find optimal structures or patterns of behaviour, or to identify variables that organisms seem to optimize. In this section, I will discuss some of the characteristics that may make a model a good one.

Niklas (1992) has argued provocatively that the only good model is one that fails. He points out that when a model yields results that conflict with reality, we gain the useful information that our assumptions about how reality works are either inadequate or incorrect. If, however, the model's predictions match reality, we are left uncertain whether we have understood reality correctly, or whether the agreement is fortuitous. That argument does not alter the fact that biomechanists are generally best pleased when the predictions of their models conform to reality, admitting the possibility that their understanding may be sound.

A good model must be well designed for a defined function, whether that is to demonstrate a principle, to answer a question or to test a hypothesis. This point seems so obvious that it seems unnecessary to discuss it further.

Even the most complex of the models that I have discussed are simplified representations of reality. There is a strong advantage in making them as simple as possible, because the simpler the model, the clearer it is which of its characteristics are essential to the observed effect. However, a model may fail because it is too simple for its purpose. For example, a model of human jumping which ignored the mass of the legs seemed to show that no advantage was to be gained by activating muscles sequentially (Alexander 1989). A more complex model that took account of leg mass predicted an optimum sequence of contraction for the leg muscles, which agreed well with the pattern of activation used by athletes (Pandy *et al.* 1990).

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