Aspects of skeletal muscle modelling

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The modelling of skeletal muscle raises a number of philosophical questions, particularly in the realm of the relationship between different possible levels of representation and explanation. After a brief incursion into this area, a list of desiderata is proposed as a guiding principle for the construction of a viable model, including: comprehensiveness, soundness, experimental consistency, predictive ability and refinability. Each of these principles is illustrated by means of simple examples. The presence of internal constraints, such as incompressibility, may lead to counterintuitive results. A one-panel example is exploited to advocate the use of the principle of virtual work as the ideal tool to deal with these situations. The question of stability in the descending limb of the force-length relation is addressed and a purely mechanical analogue is suggested. New experimental results confirm the assumption that fibre stiffness is positive even in the descending limb. The indeterminacy of the force-sharing problem is traditionally resolved by optimizing a, presumably, physically meaningful target function. After presenting some new results in this area, based on a separation theorem, it is suggested that a more fundamental approach to the problem is the abandoning of optimization criteria in favour of an explicit implementation of activation criteria.

Keywords: skeletal muscle; constraints; force-sharing; stability

1. INTRODUCTION

There is not a small dose of impatience, sometimes even sarcasm, whenever a scientist who has devoted, or is planning to devote, a lifetime to experimental science contemplates the idea of listening to a theoretician ('a modeller', as it is often called). The former, it would appear, deals with the 'real' world of phenomena, while the latter is nothing but a symbol juggler. The former is a soldier in the never-ending war of humanity as it tries to understand the material world and the secrets of life. The latter, meantime, is merely a conscientious objector comfortably playing chess at home. Nevertheless, models are not only just a necessary evil, but also the very goal of science. The noted Canadian philosopher of science Mario Bunge rightly emphasizes the problem of the interrelationship between levels and its implications on the question of the nature of scientific explanation.¹ What do we mean when we say that Newton explained or described the motions of the planets by means of three letters combined in a 'simple' formula ($f=ma$)? Without entering into a discussion of these fine points of epistemology, it might prove useful to explore briefly a more mundane example. Let us consider a metal or wooden beam supported, say, at its ends or, more poignantly, projecting out of a mossy wall, as Galileo wanted (figure 1) in one of the first attempts ever at tackling this problem in a serious manner (Galileo Galilei 1638), and what *is* the problem? Let us start by confessing that even this matter is not entirely clear. Is the problem one of safety? Namely, do we want to make sure

that the beam does not break under its service load? Or is it that we wish to predict the deformations of the beam? Or, perhaps, do we want to calculate the internal forces that tend to change the average distance between molecules? Molecules, did we say? What about atoms and beyond? Is there any hope of having a theory that would work for steel, aluminium, wood and rubber? Starting with Galileo, Hooke, Euler, Bernoulli, St-Venant, Cauchy and ending with quantum mechanics and solid-state physics, many questions have been answered. The beam is still projecting out of the wall. Free-body diagrams are true, and so are bending-moment diagrams, aren't they? Phase-equilibrium diagrams used by material scientists are also true, and so are lattice mechanics considerations, each atom somehow sharing the burden of load transmission with its neighbours. Or, perhaps, in rubber-like materials, it is the uncoiling of long molecules that explains the development of internal stress. These different levels of explanation all have a degree of truth, the truth of one level being, as it were, confirmed when a model at the next lower level is able to justify it as an approximation. Does this inductive chain lead us eventually to the truth of the object itself?

Were we to start a course in, say, structural mechanics with the formulation of these questions, the students would immediately report us to the Dean, who would eventually have us booked for psychiatric observation. But in biomechanics, these questions are quite sensible. In our experience, many people working in this field expect engineering to deliver models of the behaviour of living tissue, such as muscle, with a degree of comprehensiveness and detail that does not even exist for more mundane inert materials. Also, no matter what model is proposed, one can hear questions pertaining to a level that

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Figure 1. The celebrated cantilever beam from Galileo's treatise on the Two New Sciences (1638).

the model did not intend to explain. Questions such as 'what about force enhancement?' or 'are you aware of the experiments conducted last week by Professor So-and-so in Japan? Your model does not seem to be able to predict such effects!' It would be like asking Cauchy, say, after the publication in the 1820s of his seminal papers (Cauchy 1823, 1829) on the mechanics of deformable media (in which he established a paradigm for many of the scientific theories that would follow in the nineteenth and twentieth centuries), the question: 'All this is fine and well. But what would happen to your elastic steel structure if it were placed in a corrosive environment?' Having made this general point we proceed to skeletal muscle.

Ideally, a model of skeletal muscle should have at least some of the following features: (i) it should be comprehensive; (ii) it should be based on sound scientific principles; (iii) it should be consistent with experimental evidence; (iv) it should have predictive value; and (v) it should be amenable to improvement and refinement. We are particularly interested in the first two aspects. By comprehensive, we mean that it should incorporate (again, ideally) the thermo-mechanical response, the thermodynamic and energetic aspects emanating from the chemistry at play, and, finally, the control mechanism responsible for neural activation. The use of computers goes some way towards the possibility of incorporating several levels in a single model and of letting the complexity of the system speak for itself once the basic building blocks have been well understood and interconnected.

Although the development of such a comprehensive model is underway in our Calgary group, our intention here is more modest: we would like to discuss a few aspects of this model at an elementary level. Following the philosophy stated above, the first item on the agenda is to clearly spell out the lowest level of description to be included in the model. For our purposes here, that lowest level will be the muscle fibre (or, perhaps, the fibre bundle). This is clearly an intermediate level (figure 2), not as low as the sarcomere or as high as a whole muscle, as predicted by some global rheological models. It permits a fuller implementation of the muscle architecture and of the behaviour arising from its complexity. It also permits

Figure 2. Levels of description of skeletal muscle. (a) The muscle is shown in its *in situ* location (here, for example, the upper arm and shoulder); (b) fibre bundle, or fascicle, isolated from the muscle; (c) an isolated fibre; (d) represents a myofibril with its typical dark-light striation pattern; (e) shows a schematic representation of a sarcomere bordered by its Z-lines, and further shows the two contractile proteins actin and myosin; (f-i) show cross-sectional cuts through the sarcomere at the locations indicated by the dashed lines; (j) shows G-actin molecules that form the actin filament. (Adapted from A. C. Guyton and J. E. Hall 2000, *Textbook of medical physiology*, 10th edn, p. 68. W. B. Saunders Company, Philadelphia, with permission.)

the application of a variety of constitutive and activation/recruitment relations, from cross-bridge theories to rheological models with memory at the fibre level. Finally, it allows for the implementation of geometrical constraints (such as incompressibility) in an exact fashion. The results of such a model may seem to contradict 'intuition', if by that word we merely mean the naive use of reasoning based on simple free-body diagrams. A muscle is, from the structural mechanics point of view, a highly statically indeterminate structure. The addition of geometrical constraints results, moreover, in the introduction of 'forces' whose nature is sometimes difficult to visualize or to include in free-body diagrams. As an elementary example, we will consider the solution of a panel consisting of four links and subjected to a constant-area constraint. The results, even in this elementary example, are not what one could expect after a cursory inspection.

2. CONTINUUM MECHANICS AND THE PRINCIPLE OF VIRTUAL WORK

Since the time of Cauchy, we have learned to conceive of any problem in continuum mechanics as consisting of

three parts: (i) a geometric theory of deformation (or *kinematics*); (ii) a set of universal physical laws (*dynamics*, *thermodynamics*, etc.); and (iii) a description of material properties (*constitutive formulation*). The weakest link (and therefore, the most interesting one and the one providing an exciting relationship between experimentalist and modeller) is obviously the last. Nevertheless, the first two are not without challenges and pitfalls of their own. In the end, it is the correct combination of these three ingredients that produces a consistent model. Rather than presenting the whole picture, however, we choose to concentrate on the PVW because it is through its application that the aforementioned combination can be best mediated. In some form or another, this principle was already known to Archimedes and Hero of Alexandria. Even Aristotle is thought to have understood it to some degree. By 1200, Jordanus de Nemore was able to apply it (in his book *De ratione ponderis*) to the laws of the lever and to the correct decomposition of forces in an inclined-plane situation. This pioneering work was available to Galileo, who made further progress on this topic. Contrary to the idea of a free-body diagram, the PVW in the realm of rigid-body statics advocates not to free the body completely from its surrounding, but rather use the fact that it is at least partly constrained to eliminate the need for dealing with the corresponding reactions. For example, let us assume that we wanted to calculate the right-end reaction of a simply supported beam subjected to an external force, as shown in figure 3. The PVW asserts that if this support is removed so that the corresponding reaction manifests itself, then at equilibrium the total (virtual) work done by the forces on any small (virtual) displacement compatible with the remaining supports must vanish. Notice that this is a *scalar*, not a *vector*, identity.

Consider now a deformable bar, and let us assume that we want to calculate its deflection. The PVW asserts that the correct deflected shape has the following property: if it is slightly disturbed in a manner compatible with the supports, the (virtual) work of the external forces is exactly balanced by that of the internal stresses. In this way, as shown in figure 4, we are able to obtain the correct differential equation governing the deflected shape. Notice that the reactions play no direct role in this derivation, since they perform no work. The PVW delivers the equations of equilibrium in a neat, almost automatic way. It is, indeed, equivalent to a complete static (or dynamic, if inertia forces are included) formulation. The constitutive equations have not yet entered the picture.

As previously demonstrated, the PVW has the great advantage, over the conventional (Newtonian) formulation, of not incorporating the forces of constraint, since the virtual deformations are, by definition, compatible with the supports. But Lagrange noticed that even if this requirement is eliminated one is still allowed to use the PVW by means of an ingenious device known today as the Lagrange Multiplier technique. This technique is particularly fruitful in the case of geometric constraints of a complicated nature, such as the constraint of incompressibility, which plays a role in muscle modelling. To illustrate these ideas, we will present an artificial example and will show that a reasoning based on a seemingly correct free-body diagram yields completely incorrect and misleading results. This example is shown in figure 5. To

Figure 3. The PVW for a rigid simply supported beam. To determine the reaction R at the right-end support, this support is removed and a small arbitrary (virtual) rotation $\delta\theta$ is applied to the system. The total virtual work done by all forces is easily calculated as $Pa\delta\theta - RL\delta\theta$. The PVW asserts that, for equilibrium, this work must vanish identically, whence we obtain $R = Pa/L$.

Figure 4. The PVW for a deformable system. The PVW can be used to obtain the governing differential equations of equilibrium of a deformable system. A deformable statically indeterminate beam is acted upon by a uniformly distributed load q over its whole length L . The deformability of the system allows for a virtual deformation function $\delta v(x)$ compatible with the support conditions, as shown. The work of the external load over this deformation is given by the integral $EVW = -\int q\delta v dx$. During this deformation, the internal bending moment $M(x)$ performs the internal virtual work $IVW = \int M(\delta v)'' dx$, where primes denote x -derivatives. Note that the second derivative of the virtual deformation yields the virtual curvature. According to the PVW, we must have $EVW = IVW$ identically for all virtual deformations. Integrating the IVW by parts twice (to eliminate the second derivative) one obtains $M'' = -q$, which is the correct differential equation of equilibrium for a beam.

Figure 5. (a) The PVW for a deformable system in the presence of geometrical constraints. The panel shown is assumed to preserve its area throughout the deformation process, while the surrounding pin-jointed bars experience elongations governed by the five displacements shown. The PVW now states that the difference between the internal and the external virtual works is no longer zero but rather equal to an unknown multiplier times the (differential) variation of a function whose vanishing expresses the preservation of the area. (b) Incorrect free-body diagram for the constrained system of (a). What is missing is the force necessary to maintain the constraint.

facilitate the exposition, we have conducted the formulation under the assumption of small displacements, but the conclusions are the same for a more general case. The panel shown is bounded by two pairs of pin-jointed parallel bars of lengths a and b at angles α and β , respectively, with the horizontal. The leftmost corner is fixed while the rightmost corner is allowed to move horizontally under the action of a force F , as shown. As described so far, this system is unstable, since the application of the slightest force would result in the collapse of all the bars onto the horizontal line. To stabilize the system, we will assume that the area of the panel is preserved throughout the deformation process. The initial area of the panel is Dh , and the final area is given by $0.5(D + u_3)(h + v_1 + h - v_2)$, where u and v represent, respectively, the horizontal and vertical displacements of subscripted nodes. Assuming, moreover, small displacements (which is the case, for example, if the force is relatively small or the bars relatively stiff), the products of displacements can be neglected and the preservation-of-area constraint is expressed as the vanishing of the function $\phi = 0.5D(v_1 - v_2) + hu_3$. In other words, the geometrical constraint is represented by the vanishing of a function ϕ of the degrees of freedom of the structure. In the presence of a geometrical constraint of this kind, the PVW must be modified to read $IVW - EVW = \lambda \delta \phi$. Here λ , a so-called Lagrange multiplier, becomes a new variable of the problem with the physical meaning of a 'force' necessary to maintain the constraint (in our case, λ may be interpreted as a kind of internal pressure). The term $\delta \phi$ represents a variation (or differential) of the constraint function, and it will therefore be given by a linear expression in the virtual displacements,

with coefficients given by the corresponding partial derivatives, namely

$$\delta \phi = (\delta \phi / \delta u_1) \delta u_1 + (\delta \phi / \delta v_1) \delta v_1 + \dots$$

In our example we obtain $\delta \phi = D(\delta v_1 - \delta v_2) + h \delta u_3$. The external virtual work is $EVW = F \delta u_3$, and the internal virtual work is $IVW = 2(N_a \delta a + N_b \delta b)$, where N_a and N_b are, respectively, the internal axial forces in the bars with lengths a and b . The variations δa and δb of these lengths can be evaluated as (linear) expressions in terms of the variations of the nodal displacements. Once all this is done, equating the coefficients of the corresponding displacement variations yields the following results: $N_a = 0.5F \cos \beta / \cos(\alpha + \beta)$ and $N_b = 0.5F \cos \alpha / \cos(\alpha + \beta)$. These results should be sharply contrasted with the simplistic free-body resolution of the external force F into the directions of the two concurrent bars (figure 5; lower panel), which would yield $N_a = F \sin \beta / \sin(\alpha + \beta)$ and $N_b = F \sin \alpha / \sin(\alpha + \beta)$. What is wrong with this 'intuitive' free-body diagram is the omission of the (unknown) force of constraint. In particular, the usual concept of projecting the fibre force on the direction of the external force is, at least in this example, meaningless. A complete treatment of this case has been published previously (Epstein & Herzog 1998).

3. A QUESTION OF STABILITY

Beyond the issue of inclusion of geometrical constraints, another baffling question in muscle modelling arises from the existence of the so-called 'descending limb' of the force-length relationship. If this relationship were to be interpreted as the constitutive equation of an elastic material, there is no doubt that the negative slope of the descending limb would imply a 'softening' and, therefore, unstable behaviour. Since some muscles operate perfectly well in the descending limb, we must conclude that either this interpretation is wrong or that there exist additional elastic elements accounting for the desired stability. We opt for the first alternative, namely, that the force-length relationship is not to be interpreted as the constitutive equation of an elastic material. Indeed, to obtain the force-length curve experimentally one proceeds schematically as follows: (i) a muscle fibre is passively elongated to a desired length and then fixed at its ends to provide the so-called isometric conditions; (ii) the fibre is then tetanized by application of an electric potential; (iii) the force applied by the tetanized isometric fibre to the supporting device is measured. This triple process provides a single point in the force-length curve and, therefore, has to be repeated afresh for each point. This last observation should be contrasted with an experiment to determine the constitutive equation of an elastic material, whereby the length can be gradually increased as the corresponding force is successively measured. In other words, there is no need to unload (or 'deactivate') the specimen before the next measurement. The stability of a structural member, on the other hand, depends on its response to an infinitesimal perturbation from the position of equilibrium. Thus, to know if a spring is stable at a given configuration all we need to do is to investigate whether a further infinitesimal elongation necessitates an increase in the force. Translated to the muscle fibre experiment, this

means that to assess stability we must leave the activation constant while slightly elongating the fibre (thus violating the isometric boundary condition of the original experiment). There is no *a priori* reason why the force necessary to maintain this extra elongation should lie on the force-length curve! Indeed, this curve was obtained under different experimental conditions. What needs to be done, therefore, is to replicate experimentally the conditions required by the definition of stability, namely, to add the following step to the previous experimental protocol: (iv) keeping constant tetanized conditions, the supports are slightly pulled apart and the new force is recorded.

Before proceeding to presenting the results of such experiments, it is interesting to consider a purely mechanical analogy that we already presented elsewhere (Epstein & Herzog 1998) to at least envision the possibility of an apparently softening but stable behaviour. Consider a pair of (two-dimensional) identical toothbrushes placed opposite to each other with their handles parallel but pointing in opposite directions, and with their bristles partly penetrating each other. Depending on the initial penetration depth, the bristles will be in contact until a sufficiently large relative displacement d is applied parallel to the handles. To produce such displacement a force needs to be applied whose magnitude depends on the (positive) bending stiffness of the bristles and on the number of bristles engaged. Thus, for a while at least, the behaviour of the system is perfectly stable. As the critical displacement d is reached, the bristles will momentarily lose contact and will immediately engage the next neighbour. When this happens, however, some of the bristles will not find a match, since the toothbrushes are now displaced partially beyond each other's reach. The result of this observation is that the total force necessary to achieve the next further displacement d is smaller than before. If the force applied versus the total relative displacement were plotted, one would obtain a jagged diagram made of small segments with positive slope (corresponding to each of the extra displacements d), each segment being positioned slightly lower than the preceding one (owing to the progressive loss in the number of pairs of engaged bristles). In other words, although the instantaneous stiffness is always positive, the overall appearance is one of a softening behaviour. If only a finite number of experiments are carried out with the toothbrushes placed inside a black box and only the handles sticking out of the box, one would be led to think that what is inside the box is a system with negative stiffness! The analogy with a finite number of isometric experiments in a muscle is obvious.

Having thus introduced the possibility of a softening but stable behaviour in an inert mechanical system, we proceed to examine the experimental evidence in the case of skeletal muscle. The first experiments in this direction were conducted by Edman *et al.* (1982). They demonstrated, in single fibres from frog (*Rana temporaria*) tibialis anterior, that stretching of the activated fibre caused an increase in force, as expected based on the force-velocity property of Hill (1938). More importantly, though, they also found that when the stretch was finished and the fibre was kept activated at the final (constant) length, the steady-state isometric force achieved after several seconds often remained greater than either the purely isometric

Figure 6. Relationship between active force (stress) and sarcomere lengths. Circles and the corresponding straight lines represent the active isometric force-length relationship for single fibres from the tibialis anterior of *Rana temporaria*. Triangles, squares and diamonds represent the steady-state forces at 4.2 s after the completion of stretches of 0.112, 0.197 and 0.274 μm per sarcomere. The dashed lines connecting the isometric force-length curve with the steady-state force values following stretch show the origin and the end of the stretch. Note that the dashed lines do not show the actual force-length trace followed during the stretch. Note further that the active forces were obtained from the total force by subtracting the passive forces obtained in a passive experiment. Therefore, it was assumed that the passive forces at a given fibre length were the same for the active and passive fibre. Temperature: 0.8–3.8 $^{\circ}\text{C}$, cross-sectional area of fibre: $7.2 \times 10^{-3} \text{ mm}^2$. (Redrawn from fig. 3a of Edman *et al.* (1982), with permission.)

force at the corresponding length, or the isometric force at the length from which the stretch was initiated (figure 6). These results would indicate that stretching of a muscle fibre will cause a positive stiffness, and not the negative slope associated with the descending limb of the force-length relationship. Similar results to those found by Edman *et al.* (1982) have also been observed in whole muscle preparations (e.g. Herzog & Leonard 2002).

Edman *et al.* (1982) stated that although the steady-state force enhancement following fibre stretching could be quite considerable, it seemed impossible that it could exceed the purely isometric forces at the optimum fibre length (Gordon *et al.* 1966). This observation was explained by some with the idea that force enhancement was caused by the development of non-uniformities in sarcomere lengths when a fibre (or muscle) was stretched on the descending limb of the force-length relationship. The steady-state forces following such stretching were associated with the active, contractile force of the 'shortest' sarcomeres, while force equilibrium with the 'longest' sarcomeres was achieved by means of passive forces that supported the vastly elongated sarcomeres (figure 7). If this mechanism causes force enhancement, the peak steady-state forces following fibre stretching cannot exceed the purely isometric forces at optimum fibre length, since this length represents the limit of sarcomere force production.

Recently, we discovered that force enhancement is caused by an unknown, but presumably active, component and by a directly observable passive component

Figure 7. Illustration of force enhancement on the descending limb of the force-length relationship according to the sarcomere length non-uniformity theory. Imagine that the muscle is at a short length (open circle) and is stretched such that the average sarcomere length becomes that shown by the filled square. According to the sarcomere length non-uniformity theory, some sarcomeres will be stretched more than average and will fall onto the passive force curve (right filled circle), while other sarcomeres will be stretched less than average and will remain on the descending limb of the force-length relationship (left filled circle). At force equilibrium (horizontal dashed line), the force is greater (enhanced) than what one would expect based on the average sarcomere length (filled square).

Figure 8. Illustration of passive force enhancement (ΔP). Shown are the force-time histories of an isometric contraction at the final reference length (middle, steady trace), an active stretch contraction (top trace), and a passive stretch (bottom trace). After stretching, the active and passive muscles are at the final reference length. Observe the steady-state, isometric force enhancement following the active stretch (ΔF), and the passive force that remains considerably greater following the deactivation of the muscle after the active stretch (passive force enhancement, ΔP) compared with the passive force following the active isometric contraction and the passive stretch.

(figure 8). Furthermore, we found steady-state force enhancement values that clearly exceeded the purely isometric forces at optimum length in single fibres of frog (*Rana pipiens*) tibialis anterior and flexor digitorum brevis (figure 9). This result appears to eliminate the sarcomere length non-uniformity theory as the single mechanism for force enhancement.

Typically cross-bridge models of muscle contraction (Huxley 1957, 1969; Huxley & Simmons 1971) do not account for history dependence. Similarly, many models of sarcomere interactions in muscles do not account for

Figure 9. Mean force-length relationship and mean (± 1 s.d.) steady-state force enhancement following stretch tests in single fibres of frog (*Rana pipiens*) flexor digitorum brevis ($n = 22$). Forces were normalized with respect to the maximal isometric force for comparison across fibres. Fibre lengths were normalized relative to the optimum fibre length, i.e. the length at which the active isometric force was greatest. Note that the mean force enhancement always exceeded the isometric force at the initial fibre length, and that force enhancement for several conditions exceeded the maximal isometric forces. Note further that force enhancement was directly related to the stretch magnitude for all initial lengths.

the contractile history; thus, the descending limb of the force-length relationship is unstable, sarcomere length non-uniformities develop, and force enhancement is predicted as a consequence of this structural non-uniformity (e.g. Morgan 1990; Zahalak 1997). In view of the experimental evidence, these theoretical models should be re-evaluated and their predictions should be considered with caution.

4. FORCE SHARING

Most skeletal joints are endowed with more muscles than are strictly needed to perform the basic movements. Whatever the physiological reasons for this superabundance of muscles, from the structural mechanics point of view it results in a static indeterminacy of the problem. In other words, the equations of statics alone are not sufficient to determine the force in each muscle under given geometrical and external force conditions. This is known as the force-sharing problem. Certainly, most engineering elastic structures, such as high-rise buildings and bridges, are statically indeterminate and no one considers this as a problematic issue. Why? Because the knowledge of the constitutive equations (stress-strain relations) of the materials used permits the expression of geometric compatibility conditions in terms of internal forces, thus rendering the problem determinate. A simple example is provided by a weight suspended from a roof beam by means of two hinged bars in a vertical plane. This problem is statically determinate and (assuming a small deflection regime) solvable by a simple free-body diagram. If a third bar were added in the same vertical plane, however, the problem would become statically indeterminate and the solution would depend not only on the geometry but also on the relative stiffness of the bars. This is not a difficult problem to solve, since the 'missing' equation is provided by conditions of compatibility at the point of suspension, namely: the bars must elongate in such a way that at the end of the process they still converge at one point. Using the known constitutive equations of the bars, this kinem-

atic compatibility condition can be expressed in terms of forces, thus rendering the problem determinate. What is then the problem in muscle mechanics? The answer is clear: the force-length relationship is not a fully fledged constitutive equation. A more appropriate description for such an equation should be a 'force-length-velocity-activation-memory' relation. Let us only consider the activation, and let us naively assume that whatever this activation is it manifests itself through a single scalar parameter varying between zero and one, and that the force-length relation is to simply be scaled down by this parameter. The problem is that this parameter becomes an extra variable in the formulation, a variable for which there is no physical constitutive modelling. There are, therefore, essentially two policies to adopt. The first one consists of ignoring this parameter altogether and resolving the statical indeterminacy by resorting to some optimization criterion. The most frequently used optimization criteria are based on maximizing or minimizing some physiological variable: maximization of muscle endurance, minimization of stress, or minimization of the metabolic cost of movement are examples. The corresponding cost functions can often be written in the form

$$\text{Min } \Phi; \Phi = \sum (f_i/w_i)^\alpha, \quad (4.1)$$

where f_i represents the individual muscle forces, w_i is some weighting factor (e.g. the physiological cross-sectional area of muscles; Crowninshield & Brand 1981), and the exponent α is a number greater than 1.0. Note that, for the special case of $\alpha = 2$, the problem can be solved explicitly (Ait-Haddou *et al.* 2002a). The corresponding constraint functions include that muscle forces can only be tensile, typically defined as positive ($f_i \geq 0$), and that the resultant joint moments are satisfied by the moments arising from the muscle forces, namely

$$A\mathbf{f} = \mathbf{b}, \quad (4.2)$$

where A is a matrix representing the moment arms of each muscle about each joint, $\mathbf{f}$ is the vector of unknown muscle forces, and $\mathbf{b}$ is the vector of moments the muscles are required to produce.

There is an extensive bibliography on this approach that has produced a fair amount of controversy and confusion, primarily because solutions of numerical approaches or small-scale analytical models have been generalized incorrectly. We determined a general solution of the optimization approach shown in equations (4.1) and (4.2) with the force constraint $f_i \geq 0$. One of the more remarkable results was that we proved the existence of a hyperplane through the origin of the moment arm vector space of the muscles that separates active ($f_i > 0$) from silent ($f_i = 0$) muscles (Ait-Haddou *et al.* 2002b). This result immediately allows for generalization of the agonistic and antagonistic behaviour of muscles that is independent of the system's geometry. For example, it had been stated that antagonistic muscles could not be predicted to co-contract using the above optimization approach (Hughes & Chaffin 1988; Zajac & Gordon 1989). This statement can be proven incorrect by using the hyperplane theorem. In fact, it can be shown that any two antagonistic muscles can always co-contract, independently of the system's geometry, provided they are not collinear. Other force-

sharing problems that had eluded general description involved those with three-dimensional system geometries. These, in fact, can be shown to behave identically to equivalent planar systems that can be found in a straightforward manner for each three-dimensional system. Therefore, any three-dimensional problem can be solved using an equivalent two-dimensional system.

The second line of attack consists of adding to the mechanical model an activation/recruitment criterion that effectively completes the constitutive picture. In terms of Bunge's terminology, the first approach is merely subsumptive, while the second has at least the hope of becoming interpretive. Indeed, in the second approach one may be able to invoke facts coming from a lower level, such as the neural proprioceptors. Mathematically, control theory may now enter the picture, but this is a price that one should be willing to pay if the final goal is a deeper understanding of muscle control and function.

5. ENERGETICS

A final remark we would like to make pertains to the basic function of skeletal muscle as a motor, namely, as a physical device whose main purpose is to transform chemical energy into mechanical work. The chemical reactions involved in the hydrolysis of ATP are fairly well understood, but the overall description of the muscle as a motor is not yet a standard part of global muscle models. An intriguing attempt at obtaining the force-velocity relation as a result of a criterion of minimal consumption of metabolic energy has been presented by Hardt (1978) in his doctoral dissertation, but this approach has not received the attention that it probably deserves. Nevertheless, it is important to realize that even the most elementary models incorporating energy consumption should take into consideration the fact that a muscle expends metabolic energy even if it is not producing mechanical work. For example, holding a weight by the outstretched arm necessitates energy supply. The situation can be described by the following analogy that, in the same vein as the brush model suggested for the explanation of stability, it should not be considered as the description of the actual phenomenon, but merely as a heuristic tool for thought.

Consider a material that can be somehow alternatively activated or deactivated to produce a change in mechanical response. A simple instance is given by an electromagnet, namely, an iron bar of a finite length surrounded by a solenoid made of a wire whose ends are attached to a battery that can be connected or disconnected. This wire has a certain electrical resistance, so that when the circuit is closed a definite consumption of power results. We note that this power is independent of the relative position of the iron bar within the solenoid. If the bar is only partly inserted, however, its magnetization will be less than when it is fully inserted. Thus, the force of attraction exerted on an external piece of iron depends on the amount of this insertion. The analogy with the force-length relation is clear. What is also clear is that to sustain a force under isometric conditions (such as when holding a weight) a definite amount of power needs to be supplied. This type of consideration needs to be included in a model to give

precise definitions of energetic concepts, such as efficiency.

6. CONCLUSIONS

In this brief paper we have attempted to touch upon a number of issues that preoccupy the muscle modelling community. No definitive answers have been given, but a certain epistemological position has been advocated. It can be summarized as follows. (i) Whenever available, sound physical principles should be preferred to intuitive considerations. An example of this position has been provided by means of a simple mechanism subjected to a geometrical constraint. We hope that, in spite or because of its simplicity, this example has driven the point home. (ii) Whenever possible, interpretive models should be preferred to subsumptive models. In other words, one should attempt to use the lowest possible level compatible with the computing power available. Thus, the mist and myth of the force-sharing conundrum should be dispelled by the search and incorporation of a good model of activation/recruitment, while *ad hoc* optimization functions should be eventually abandoned. In the meantime, one should not despair. It is indeed this lack of precise knowledge that makes biomechanics one of the most exciting fields of research today.

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ENDNOTE

¹In recent work, Bunge (1998) distinguishes between subsumptive and interpretive explanations. 'Subsumptive explanation', he says, 'i.e. the subsumption of a singular under a generalization, smacks of *explicatio obscurum per obscurius* it does not assuage our thirst for intellection.' 'A phenomenological theory, one not representing any "mechanism", will provide subsumptive explanations; but only representational theories, i.e. theories purporting to represent the *modus operandi* of their referents, can give deeper explanations. These shall be called *interpretive explanations*.' 'The reason that interpretive explanation is deeper than subsumptive explanation, is that the former involves a *deeper analysis*, one often involving a reference to levels of reality other (usually deeper) than the level to which the explanation belongs. Subsumptive explanation, by contrast, involves relations among items standing on the same level.'

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GLOSSARY

EVW: external virtual work
 IVW: internal virtual work
 PVW: principle of virtual work