**Force Control with A Muscle-Activated Endoskeleton**

The MIT Faculty has made this article openly available. Please share how this access benefits you. Your story matters.

<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>As Published</td>
<td><a href="http://dx.doi.org/10.1007/978-3-540-37347-6_10">http://dx.doi.org/10.1007/978-3-540-37347-6_10</a></td>
</tr>
<tr>
<td>Publisher</td>
<td>Springer-Verlag</td>
</tr>
<tr>
<td>Version</td>
<td>Final published version</td>
</tr>
<tr>
<td>Accessed</td>
<td>Tue Dec 18 03:21:13 EST 2018</td>
</tr>
<tr>
<td>Citable Link</td>
<td><a href="http://hdl.handle.net/1721.1/70031">http://hdl.handle.net/1721.1/70031</a></td>
</tr>
<tr>
<td>Terms of Use</td>
<td>Article is made available in accordance with the publisher’s policy and may be subject to US copyright law. Please refer to the publisher’s site for terms of use.</td>
</tr>
<tr>
<td>Detailed Terms</td>
<td></td>
</tr>
</tbody>
</table>
Summary. The advantages and challenges of producing and controlling force with a mechanism like the human skeleton driven by actuators like mammalian muscles are considered. Some counter-intuitive subtleties of musculo-skeletal biomechanics are discovered: despite the energetic cost of isometric muscle activation, exerting forces that do no work may reduce metabolic energy consumption; in some circumstances, anatomical antagonist muscles may become functional synergists; and muscle tension acts to make skeletal posture statically unstable. The latter effect can be counteracted by muscle mechanical impedance, which emerges as an essential adjunct to muscle force production.

1 Introduction

Physical interaction with the world is a commonplace of life; we touch things, squeeze them, push them. Successful interaction with objects in the world depends in part on the ability to control the force we exert on them. The human body is richly endowed with muscles; they comprise about half of our body weight and they appear to be uniquely specialized for producing force. However, because of the unique properties of muscles and the way they are connected to the skeleton, force production presents some interesting challenges and opportunities. Some of them are reviewed below.

This chapter is dedicated to Professor Suguru Arimoto on the occasion of his 70th birthday. Throughout his influential career, Professor Arimoto has advocated and articulated the value of a physics-based approach to control: understanding the physics of a manipulator and the tasks it performs leads to improved designs and more effective methods for its control. In the following, that physics-based approach is applied to “reverse-engineer” force control in the mammalian biomechanical system. Some counter-intuitive observations are discovered and the possibility is raised that some of muscle’s unique properties may have evolved in response to the challenges and opportunities of force production.
Because of the molecular underpinnings of muscle contraction, exerting muscle force always consumes metabolic energy. This is true even when no mechanical work is done because muscle length remains constant or when muscle absorbs work by lengthening under load. It may therefore seem that to economize metabolic energy consumption we should avoid exerting forces that do no useful work. However, an analysis of force exertion against a kinematic constraint will show that workless forces may, in fact, be used to reduce effort and energy consumption.

Another basic fact of muscle physiology is that skeletal muscles pull but don’t push; to achieve both flexion and extension of the joints, they are deployed in opposing or antagonist groups. However, an analysis of musculo-skeletal geometry will lead to the counter-intuitive observation that for certain force-production tasks, anatomically antagonist muscles may actually cooperate as agonists or synergists.

A further subtlety of musculo-skeletal biomechanics is that force production challenges skeletal stability. Examining the kinematic details of musculo-skeletal attachments will show that because muscles are deployed to surround the bones (a basic fact of mammalian anatomy) the static stability of skeletal posture is reduced in proportion as muscle tension increases.

Of course, because it is manifestly evident that muscle contraction does not, in fact, cause the skeleton to collapse, we are presented with a paradox. One solution to this puzzle lies in the properties of muscle mechanical impedance. A stabilizing muscle stiffness will be shown to be an essential requirement for controlling force with a muscle-activated endoskeleton.

All of these considerations may be derived from a straightforward mechanical analysis. To begin, the standard robotic analysis of mechanism kinematics is reviewed.

### 1.1 Torque Space

If the human skeleton is regarded as a mechanism\(^1\) then a starting point for its description is a set of variables that uniquely define its configuration. These generalized coordinates, usually identified as angular degrees of freedom relating adjacent rigid limb segments, define a configuration space which is fundamental to the analysis of skeletal mechanics. Knowing the configuration variables and the geometry of the limb segments, the location of all points on the skeleton may be determined. Though not unique, these generalized coordinates are fundamental; for example, the inertial and gravitational dynamic equations of the skeleton are properly defined in configuration space.

To analyze force production, a starting point is to identify the corresponding generalized forces. By definition these are such that the scalar product of generalized forces with incremental displacements in configuration space defines mechanical work done on the mechanism. Just as joint angles are usually

\(^1\) The term “mechanism” is used loosely herein to refer to a collection of kinematically-constrained rigid bodies.
an appropriate choice for generalized coordinates, joint torques are usually an appropriate choice for generalized forces. They define a torque space which is fundamental to a description of how forces are exerted on and transmitted through the skeleton.

1.2 Mapping Torque Space to Contact Space

The position and orientation of any point of contact between the skeleton and the world (i.e., a hand, a foot, etc.) defines a contact space which may always be expressed as a function of the generalized coordinates or configuration variables

\[ X = L(\theta) \] (1)

where \( X \) is an array containing the positions and orientations of the contact point in some appropriate external reference frame (e.g. Cartesian coordinates), \( \theta \) is an array containing the generalized coordinates and \( L \) is an array of algebraic functions.

Conversely, any force or torque exerted at that point of contact may be mapped into torque space, for example by considering the incremental mechanical work it does. Denoting the exerted forces and torques by \( F \), the incremental work is

\[ dW = F^t dX \] (2)

The incremental displacement of the point of contact is determined by

\[ dX = J(\theta) d\theta \] (3)

where \( J \) is the Jacobian of the function relating the two sets of coordinates. By definition, the incremental mechanical work done on the skeleton is

\[ dW = \tau^t d\theta \] (4)

where \( \tau \) is an array containing the generalized forces (joint torques). Substituting and rearranging

\[ \tau = J^t(\theta) F \] (5)

The Jacobian matrix characterizes the mechanical transmission of force and torque between the world and the skeleton. Its columns define the moment arms relating contact forces to joint torques or the “gear ratios” relating contact torques to joint torques. It is always well-defined, even when the dimension of the configuration space exceeds that of the point of contact (i.e., the skeleton is redundant with respect to this contact point).

2 Workless Forces

When we exert ourselves to push on the world, the details of the mechanical transmission affect our action. Efficiency would seem to imply that forces
should be exerted only to do useful work. However, one counter-intuitive aspect of force production with a muscle-activated skeleton is that it may be advantageous and energetically efficient to exert forces that generate no mechanical work [1].

Consider the class of constrained-motion tasks represented by turning a crank. Common examples include opening a door or pedaling a bicycle. The crank defines a holonomic constraint on the motion of the limb, allowing displacement only in certain directions (e.g., tangent to the circle described by the door handle or the pedals). Displacement normal to the constraint is nominally zero; elongation or compression of the pedals is negligible as is the change of the radius of the door handle about its hinges. Any force exerted in the normal direction does negligible mechanical work and no useful work. Only forces tangent to the constraint (e.g., in line with the path of the pedals or the door handle) perform useful work. One basic fact about mammalian muscle is that generating force consumes metabolic energy even when the muscle does no work. One might therefore expect that the most energetically efficient way to turn a crank with the least muscular effort would be to exert exclusively tangential forces. Surprisingly, that turns out not to be true.

It is informative to represent the task in torque space. For simplicity, consider a two-segment model of the skeleton (e.g., describing planar motion of the arm and forearm). The elbow angle (forearm relative to arm) and shoulder angle (arm relative to thorax) may serve as configuration variables. The corresponding generalized forces are the elbow and shoulder torques and the torque space is depicted in Fig. 1.

![Torque-space diagram](image-url)

Fig. 1. Torque-space diagram illustrating how forces exerted normal to a constraint may reduce muscular effort. The sub-spaces (directions in this example) that generate normal and tangential forces at a particular limb configuration are shown by the light lines; in general they are not orthogonal. Any torque vector with its tip on the dashed line generates the specified tangential force. The torque vector (shown bold) that generates no normal force is not the shortest torque vector that meets the task requirements.
To exert a tangential force requires a particular torque vector (see Fig. 1) determined by equation (5). Consequently, at any given configuration, tangential forces exerted on the crank define a sub-space of torque space, in this two-dimensional example a line or direction in torque space. Normal forces (that stretch or compress the crank) correspond to torque vectors in a different sub-space (a different direction in this example) but, due to the limb geometry, it is rarely orthogonal to the torque vector for tangential force. If workless normal forces are allowed, the specified tangential force can be achieved by any torque vector with its tip on the (dashed) line in Fig. 1.

To assess exertion or efficiency we need some measure of effort, and one convenient candidate is the length of a vector in torque space. By that measure, effort is minimized by the shortest torque vector that meets task requirements. Referring to the figure, it becomes evident that the least muscular effort (by this measure) is generally not achieved by generating a purely tangential force. Except in the (unusual) case that the torque-space directions corresponding to normal and tangential forces are at right angles, minimum effort (the shortest torque vector) will be achieved by exerting a combination of normal and tangential forces.

Many alternative measures of effort (including total metabolic energy consumption, total root-mean-squared stress on the joints, etc.) have been suggested and explored. However, insofar as these measures are equivalent to defining a norm on the torque space, the above argument applies. For example, if metabolic energy consumption is described by a monotonic function of torque, with minimal consumption at zero torque, that function may be used to re-scale the axes of torque space and the argument proceeds as before. Except in the unusual case that the torque sub-spaces corresponding to normal and tangential forces are orthogonal with respect to the particular norm, the minimizing torque vector will generate both normal and tangential forces. In short, attempting to stretch or compress the crank can (almost) always be used to economize the effort need to push tangential to it.

As the dimensions of the torque space and the contact space are the same in this example, it may be analyzed equivalently in terms of the forces exerted at the contact point. However, in general the number of relevant joints exceeds the number of relevant task dimensions, often by a large margin (there are estimated to be about 200 distinct limb segments in the human skeleton). In that case it is not generally possible to identify the contact forces that result from individual joint torques. To do so would require inverting equation (5) but the Jacobian is not square and not invertible. Nevertheless, though it cannot be inverted, the Jacobian is well-defined; it is always possible to project contact forces into torque space. Torque space is fundamental for analysis of how forces are exerted on and transmitted through the skeleton.
3 Coordinating Muscle Forces

A more detailed analysis of force production should consider how muscle forces are coordinated to generate joint torques. Upon doing so, another counterintuitive subtlety of musculo-skeletal biomechanics emerges: anatomical antagonists may be functional synergists. The best way to produce a specified force may require simultaneous contraction of opposing muscles [1].

3.1 Mapping Muscle Space to Torque Space

This arises because of the geometry of the skeleton and the way muscles are attached. For simplicity, assume that the lengths of muscles and their associated tendons are uniquely defined by the configuration of the skeleton\(^2\). In that case, the complete set of muscle lengths (which may be taken as the coordinates of a muscle space) may be expressed as a function of skeletal configuration variables (generalized coordinates)

\[
\mathbf{q} = \mathbf{q}(\theta)
\]  

(6)

where \(\mathbf{q}\) is an array containing muscle lengths and \(\mathbf{g}\) is an array of algebraic functions. With this information, muscle forces may be mapped to torque space. As above, one way to do this is to consider the incremental mechanical work done. Denoting the complete array of muscle forces by \(\mathbf{f}\), the incremental work is

\[
dW = \mathbf{f}^t d\mathbf{q}
\]  

(7)

The relation between incremental displacements in muscle length space and configuration space are determined by

\[
d\mathbf{q} = \mathbf{j}(\theta) d\theta
\]  

(8)

where \(\mathbf{j}\) is the Jacobian of the function relating the two sets of coordinates. The incremental mechanical work done on the skeleton is again given by equation (4), hence (substituting and rearranging)

\[
\mathbf{\tau} = \mathbf{j}^t(\theta) \mathbf{f}
\]  

(9)

The Jacobian matrix \(\mathbf{j}\) characterizes the mechanical transmission of force from the muscles to the skeleton. Its columns define the moment arms of the muscles

\(^2\) In fact, the relation between musculo-tendon length and skeletal configuration may depend on the force exerted by a muscle and perhaps by its neighbors. If its tendon passes through an aponeurosis or wraps around a joint, increasing tension may increase or decrease the moment arm of a muscle about the joint even when that joint does not move. Similarly, the line of action of a muscle’s force may change due to the contraction (and hence shape change) of its neighbors, again without any change in skeletal configuration. However, these complications do not change the main result, that anatomical antagonists may be functional synergists.
about the joints. It is always well-defined, even though the dimension of muscle space exceeds that of configuration space, i.e., the number of muscles exceeds the number of skeletal degrees of freedom.

For any given skeletal configuration, each individual muscle force defines a sub-space of torque space, the combination of joint torques generated by that muscle. Assuming that muscles can’t push\(^3\), this sub-space is a “half-space”, the set of vectors pointing in a direction in torque space, but not vectors of the opposite sign. Muscles that actuate a single degree of freedom define a sub-space co-aligned with one of the torque space axes. Consider a two-segment model of planar motion of the arm and forearm as described above. Elbow and shoulder torques define the axes of torque space as depicted in Fig. 2.

\[
\begin{align*}
\tau_{\text{shoulder flexor}} & \quad \tau_{\text{shoulder extensor}} \\
\tau_{\text{elbow flexor}} & \quad \tau_{\text{elbow extensor}} \\
\tau_{\text{two-joint extensor}} & \quad \tau_{\text{two-joint flexor}}
\end{align*}
\]

**Fig. 2.** Torque-space diagram illustrating the joint torque contributions due to single-joint elbow flexor (\(\tau_{\text{elbow flexor}}\)) and extensor (\(\tau_{\text{elbow extensor}}\)) muscles; single-joint shoulder flexor (\(\tau_{\text{shoulder flexor}}\)) and extensor (\(\tau_{\text{shoulder extensor}}\)) muscles; and two-joint flexor (\(\tau_{\text{two-joint flexor}}\)) and extensor (\(\tau_{\text{two-joint extensor}}\)) muscles. Torque vectors of single-joint antagonist muscles are anti-aligned but those of two-joint antagonist muscles need not be.

The action of individual muscles may be represented as vectors in this space. A muscle such as brachialis spans only the elbow joint and generates torque to flex it. In Fig. 2, single-joint elbow flexors such as brachialis define a sub-space which is the positive horizontal axis; i.e., they generate torque vectors oriented positively (but not negatively) along the horizontal axis.

Single-joint muscles have unambiguous antagonists. A muscle such as the deep head of triceps spans only the elbow joint and generates torque to extend it. In Fig. 2, single-joint elbow extensors define a sub-space which is the negative horizontal axis; i.e., they generate torque vectors oriented negatively (but not positively) along the horizontal axis.

\(^3\)This is generally true of skeletal muscles but not necessarily for muscular hydrostats such as the tongue.
Similarly, single-joint shoulder flexor muscles generate torque vectors oriented along the positive vertical axis in Fig. 2 and single-joint shoulder extensor muscles generate torque vectors oriented along the negative vertical axis. The unambiguous mechanical antagonism of these muscle groups is reflected in the architecture of the nervous system that drives them. In general flexors and extensors are endowed with a different density and combination of sensors and may be activated by different neural pathways.

Other muscles span multiple degrees of freedom or multiple joints and generate torques about each of them. The torque sub-space defined by a polyarticular muscle corresponds to positive displacement in a direction that does not co-align with the torque space axes. For example, biceps brachii generates torque to flex the elbow and also to flex the shoulder. The moment arms that map the single muscle force onto torques about the two different joints may vary with limb configuration and, in general, are not equal. In Fig. 2, two-joint flexor muscles generate a combination of shoulder and elbow flexion torques represented by a vector oriented between the positive (but not negative) horizontal and vertical axes.

Like single-joint muscles, multi-joint muscles typically have anatomical antagonists. For example, the long head of triceps brachii generates torques to extend the elbow and also to extend the shoulder. Again, the moment arms that map the single muscle force onto torques about the different joints may vary with limb configuration and, in general, are not equal. In Fig. 2, two-joint extensor muscles generate a combination of shoulder and elbow flexion torques represented by a vector oriented between the negative (but not positive) horizontal and vertical axes.

For the most part, multi-joint flexor and extensor muscle groups act antagonistically; i.e., the long head of triceps generally opposes biceps brachii. However, the muscle moment arms about the two joints are not generally in the same ratio. At any given limb configuration, force in biceps brachii may generate flexion torques about elbow and shoulder in a different ratio than triceps long head generates extension torques about the same joints. Whereas the torque vectors generated by single-joint flexor and extensor muscles are always exactly opposed, the torque vectors generated by two-joint flexor and extensor muscles are not always exactly in opposition.

3.2 Antagonists or Synergists?

One important consequence is that anatomically antagonist muscles may contribute synergistically to force production. Because the two-joint flexor and extensor torque vectors are not anti-aligned (i.e., they do not exactly oppose one another), there exists a region of torque space (a sector in Fig. 2) onto which both flexor and extensor poly-articular muscles have positive projections. Any force to be generated where the limb contacts the world, (e.g., the hand, the foot, etc.) requires a combination of joint torques that may always be represented by a vector in torque space (as described above). If the required
joint torque lies in the region in which flexor and extensor poly-articular muscles have positive projections, then both can make a positive contribution to producing the required force. In that case, these anatomical antagonists become functional synergists.

To what extent are these theoretical considerations biologically meaningful? After all, if these antagonist muscles project weakly onto the required torque, then their contribution to force production will come at a heavy cost, e.g., in the consumption of metabolic energy. To the author’s knowledge, this question has not been fully explored. However, if a situation requires maximal force production, then every contribution matters, however costly. Reasoning along similar lines, if a force is to be produced with minimal effort, where the measure of effort is equivalent to defining a norm on the torque space, then for certain forces the minimum-effort solution will include contributions, albeit small, from both of these anatomical antagonists.

Given that muscles spanning multiple degrees of freedom are more the rule than the exception in the mammalian musculo-skeletal system, the identification of antagonists requires care. Though the distinction between flexors and extensors may have a sound neural basis (possibly a legacy of phylogeny) their functional definition as antagonists is ambiguous and depends sensitively on the task. The same pair of muscles may act as antagonists in one case and synergists in another—even if the configuration of the limb remains fixed and the only change is the direction of the force to be produced.

4 Kinematic Instability

In the analysis above, the configuration of the skeleton serves to parameterize the mappings between contact forces, joint torques and muscle forces. In effect, the analysis is equivalent to assuming an instantaneous static equilibrium, with the skeleton remaining at a fixed configuration as force is produced. However, a further subtlety of musculo-skeletal mechanics is that co-contraction of antagonist muscles may cause the skeletal configuration to become statically unstable.

Naturally, an equilibrium posture cannot be maintained if a joint torque is generated without any opposing equilibrating load. However, even when net joint torque is zero (a necessary condition for static equilibrium) muscle contraction may still destabilize the limbs. To understand how, consider the relation between muscle forces and joint torques described by equation (9). The columns of the Jacobian, $\mathbf{j}$, define the moment arms of the muscles about the joints. However, those moment arms depend on limb configuration so that incremental changes of the joint angles may increase or decrease the moment arms. Any non-zero muscle force will result in a joint torque that depends on joint angle. That produces a behavior analogous to that of a spring, but with a stiffness that may be positive or negative, depending on the details of musculo-skeletal attachment.
The details may be quantified simply by differentiating equation (9), the relation between muscle force and joint torque (which has been transposed for clarity).

\[ d\tau^t = f^t (\partial j (\theta) / \partial \theta) d\theta = f^t h (\theta) d\theta \]  

(10)

where the partial derivative of the Jacobian matrix \( j \) with respect to the array \( \theta \) denotes the Hessian \( h \) of the function relating configuration variables to muscle lengths. It is a three-index array of partial derivatives of the elements of the Jacobian matrix with respect to each of the configuration variables. The product of the Hessian and the muscle force vector yields a two-index matrix that defines what may be termed a configuration-dependent “kinematic stiffness”, \( \Gamma \).

\[ \Gamma^t (\theta) = f^t h (\theta) \]  

(11)

Though it is a second-order effect of the relation between joint angles and muscle lengths, kinematic stiffness is important nonetheless. Most mammalian muscles span joints in such a manner that their torque acts to move the limbs in a direction that increases the muscle’s moment arm. For example, brachialis is connected between the arm and forearm such that its origin, insertion, and the axis of the elbow form an approximate triangle. Brachialis acts to flex the elbow and as it does, the perpendicular distance between its line of action (joining its origin and insertion and forming the base of the triangle) and the elbow axis (the apex of the triangle) increases. Consequently, if brachialis exerts a constant force, the corresponding elbow torque increases as the elbow flexes and decreases as it extends. This resembles a negative spring and has a destabilizing effect on the joint. For example, if brachialis were opposed by a constant torque so that static equilibrium was achieved at a particular elbow angle, small displacements towards flexion would increase the net torque acting to flex the elbow; similarly, small displacements towards extension would increase the net torque acting to extend the elbow.

Though the details vary, this example is typical of the muscles of the mammalian skeleton: because muscles are deployed outside the bones, their moment arms tend to increase as they move the limbs. Consequently, muscles with this destabilizing kinematic connection are typically opposed by muscles which also exhibit the same behavior, and that compounds the destabilizing effect. In essence, the skeleton may be regarded as a set of columns of rigid links connected by joints of negligible torsional stiffness. The links are surrounded by tensile elements, the muscles, which act to load the columns in compression. As the column has negligible torsional stiffness, it is vulnerable to buckling. Force production in a muscle-activated endoskeleton\(^4\) may destabilize its posture and cause it to collapse.

\[^4\text{It may be otherwise for an exoskeleton.}\]
4.1 Muscle Mechanical Impedance

Despite this observation, a moment of personal experimentation will confirm that simultaneous contraction of opposing muscles (that’s what we do when we tense our muscles or clench a fist) does not destabilize the limbs. How can this be? An answer lies in the special properties of muscle.

Muscle powers movement but is remarkably different from engineering power sources. For example, electrical voltage sources are painstakingly designed so that (as nearly as resources and engineering expertise can achieve) their output voltage is independent of current delivered. Electrical current sources (e.g., commonly used with permanent-magnet electric motors) deliver current largely independent of the required voltage. These properties are quantified by electrical impedance, where zero is the ideal impedance for voltage sources and infinity (equivalent to zero admittance) is the ideal for current sources. Mechanical power sources are similar; for many applications the ideal is an actuator that produces force (or torque) independent of translational (or angular) speed and displacement. This property is quantified by mechanical impedance (the ratio of force/torque change to motion change) with zero being the ideal for a torque or force source. Conversely, an ideal motion source has infinite mechanical impedance (zero mechanical admittance).

In striking contrast, mammalian muscle is neither an ideal force source nor an ideal motion source. Quite aside from variations due to fatigue or pathological conditions, for a constant activation of the alpha-motoneuron that drives it, the force developed by a skeletal muscle is a strong function of muscle length and its rate of change. Its mechanical impedance is certainly not infinite (the speed at which a muscle shortens depends strongly on the load it moves) but neither is it zero; force developed may change by several hundreds of percent as muscle length and shortening velocity vary within their physiological range. With mechanical impedance far from either ideal extreme, muscle appears to be a poor power source (by engineering standards).

This might reflect nothing more than a biological imperfection or an incomplete evolutionary adaptation. Skeletal muscles generate force by deforming myosin molecules after they have been attached to binding sites on actin filaments [2]. Dependence of contractile force on muscle length might be an epi-phenomenon arising in part from incomplete overlap of myosin heads and actin binding sites; or from mechanically parallel passive tissue that encapsulates a sarcomere; or from some other mechanisms. However, available evidence favors the view that finite muscle mechanical impedance is not an imperfection but is highly adaptive, solving some of the problems inherent in a muscle-activated endoskeleton and supporting the remarkable motor abilities of biological systems.

4.2 Mammalian Actuators

From neurophysiology we learn that mammalian muscle is richly endowed with muscle spindles [2]. These sensory organs are the origin of afferent nerve fibers
carrying signals related to (at least) muscle length and its rate of change. They make monosynaptic excitatory connections in the spinal cord to at least the homologous alpha-motoneurons innervating the muscle containing the spindle. Both these afferent fibers and the efferent alpha fibers are myelinated, with nerve conduction velocities among the highest in the nervous system. The result is one of the body’s fastest feedback connections, giving rise to the well-known stretch reflex: abrupt stretch of a muscle evokes a brisk, involuntary contraction a short time later. Other prominent muscle sensors include Golgi tendon organs, which respond almost exclusively to muscle-generated force in the tendon. Their afferents are also myelinated (hence fast-conducting) and act to inhibit the alpha-motoneurons of homonymous muscles. One plausible role of these nested feedback loops is to enhance (and perhaps regulate) the apparent mechanical impedance of the actuator that drives the skeleton [3, 4]. That is, the apparent stiffness of the actuator is increased; more precisely, because of reflex loop dynamics, apparent impedance\(^5\) is changed.

4.3 Neural Feedback Complements Intrinsic Mechanical Impedance

Although muscle responds rapidly to activity of its embedded sensors, the delay in neural transmission is nevertheless substantial: about 30 milliseconds or more for muscles of the human upper limbs, 50 milliseconds or more for muscles of the human lower limbs. To avoid instability due to this delay, feedback gain must be limited, which in turn limits impedance bandwidth: an effective opposing force is generated in response to stretch only at lower frequencies. Feedback-generated impedance declines at higher frequencies.

It is a remarkable fact that intrinsic muscle impedance due to actin-myosin interactions exhibits a complementary variation with frequency. Broadly speaking, as muscle is stretched, deformation of each myosin molecule bound to an actin filament contributes to apparent muscle stiffness. At the same time, the rate at which myosin molecules detach from their actin binding sites increases with deformation but is limited by the dynamics of the ATP-driven reactions that provide the energy to separate myosin heads from actin filaments. The result is that the steady force generated in response to rapid stretch is much smaller than the transient force. Intrinsic muscle impedance is high at higher frequencies and declines at lower frequencies.

It therefore appears that feedback-generated impedance properties of the peripheral neuromuscular system may complement those due to intrinsic muscle contractile mechanics [5]. Rather than think of the skeleton being driven by muscles, it is probably more useful to consider the skeletal actuator to be a neuro-muscular system comprised of the muscle, its sensors and the associated reflex loops, acting in concert to manage mechanical impedance over a wide frequency range.

\(^5\) Mechanical impedance may be considered a dynamic generalization of stiffness.
4.4 The Stabilizing Effect of Muscle Impedance

The analysis presented above demonstrated that the static equilibrium of the skeleton may be compromised by force production; muscle tension may cause the skeleton to collapse upon itself. Muscle stiffness (the static component of muscle mechanical impedance) counteracts this effect. A sufficient condition to ensure static stability is readily obtained by extending the differentiation of equation (9) and assuming that muscle forces $f$ depend on muscle lengths $q$ (as well as other variables such as neural drive)

$$f = f(q, u)$$

where $u$ is an array containing at least the neuro-muscular control inputs$^6$. Using equations (8) and (11) yields

$$\frac{\partial \tau}{\partial \theta} = \Gamma(\theta) + j^t(\theta) \left( \frac{\partial f}{\partial q} \right) j(\theta)$$

In words, the net joint stiffness is the sum of a kinematic stiffness and a neuro-muscular stiffness. Positive-definite net joint stiffness is sufficient to ensure static stability. This may be achieved if neuro-muscular stiffness is positive-definite (i.e., stabilizing) and larger than kinematic stiffness. Furthermore, note from equation (11) that the destabilizing kinematic stiffness is proportional to muscle force. To stabilize skeletal posture, neuro-muscular stiffness must increase with muscle force at least as rapidly.

One robust observation of mammalian muscle is that its neuro-muscular impedance is positive and increases with force exerted. The a-reflexic (intrinsic) contribution to muscle stiffness is positive at zero operating force and increases in proportion to force over the full range of contraction [4]. With reflexes intact, neuro-muscular stiffness is substantially larger. It is also positive at non-zero operating force and increases in approximate proportion to force (though about three times more rapidly) up to about 50% of maximum voluntary contraction [4]. Furthermore, while the torque contributions of antagonist muscles usually oppose each other, the impedance contributions of all muscles always add to net joint impedance [6].

Taken together, these properties of muscle-generated impedance offset the destabilizing effects of configuration-dependent muscle moment arms. In fact, the increase of neuro-muscular impedance with force exerted more than compensates for the static instability due to musculo-skeletal kinematics. It is easily verified that voluntary co-contraction of antagonist muscles increases the externally-observable net joint stiffness [7, 8].

$^6$ For a-reflexic muscle, the neural input is alpha-motoneuron activity. However, if we consider the basic neuro-muscular actuator to comprise the muscle and its associated reflex feedback loops, the neural control input to that actuator has not yet been identified unambiguously.
5 Concluding Remarks

One important conclusion to be drawn from this analysis is that it is inadequate or at best incomplete to consider muscle as just a force generator. While engineering actuators are often painstakingly designed to minimize mechanical impedance, that would be quite unsuitable for a machine with the kinematic structure of the mammalian musculo-skeletal system. The minimum competent description of muscle should include its mechanical output impedance, and almost certainly the fact that muscle stiffness increases with force.

Once the importance of mechanical impedance is recognized, it affords a wealth of alternative approaches to problems in both robotics and biology. For example, the stabilizing properties of neuro-muscular mechanical impedance may simplify motion control. They endow the skeleton with dynamic attractor properties (e.g., a tendency to converge to a certain pose or trajectory) so that trajectory details could then emerge from dynamic interaction between skeleton, muscle and peripheral neural circuits with minimal intervention from higher levels of the central nervous system. That is one key element of the so-called “equilibrium-point” theories of neural control, which remain appealing (though controversial!) after four decades of research [9, 10].

Modulating net joint stiffness may be used to regularize ill-posed problems such as the “inverse kinematics” of a redundant multi-joint system. The challenge is to determine trajectories of the joints that will achieve a specified trajectory of, say, the hand. Approaches equivalent to computing a pseudo-inverse of the Jacobian have been proposed, but the resulting map is not integrable; that is, closed paths of the hand do not yield closed paths of the joints. However, taking advantage of the natural stabilizing properties of joint stiffness yields an inverse map that is fully integrable [11]. In fact, the full theoretical implications of muscle mechanical impedance for motion control of redundant mechanical systems remain to be articulated; see especially the recent work by Arimoto et al. [12].

The ability to modulate externally-observable mechanical impedance also provides a robust way to control physical interaction with the world. Impedance control of robots has been investigated and applied extensively; see [13] for a review. Observations of human subjects interacting with unstable objects have verified that they can skillfully tune the stiffness of the hand to maintain stability [8]. This may be an essential requirement for effective use of tools which destabilize limb posture [14].

The unique challenges of force production in a muscle-activated endoskeleton raise the intriguing possibility that muscle mechanical impedance may be an evolutionary adaptation of the biological actuator. To prevent muscle activation from collapsing the skeleton, muscle stiffness must increase with muscle force at least as rapidly as the destabilizing effects of musculo-skeletal kinematics. If that is achieved, muscle stiffness that increases even more rapidly with muscle force enables antagonist co-contraction strategies to modulate mechanical impedance at the hand, which then enables sophisticated
behavior such as the use of tools. To the author’s knowledge, the biological validity of these speculations remains untested.

Acknowledgements

This work was supported in part by the New York State Spinal Cord Injury Board and by the Eric P. and Evelyn E. Newman Laboratory for Biomechanics and Human Rehabilitation. Figures 1 and 2 and portions of Sections 4.1 to 4.3 are reproduced from [15] with permission from World Scientific Publishing Co. Pte. Ltd., Singapore.

References