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An integrative approach to the biomechanical function and neuromuscular control of the fingers

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Abstract

The exquisite mechanical functionality and versatility of the human hand emerges from complex neuro–musculo–skeletal interactions that are not completely understood. I have found it useful to work within a theoretical/experimental paradigm that outlines the fundamental neuro–musculo–skeletal components and their interactions. In this integrative paradigm, the laws of mechanics, the specifications of the manipulation task, and the sensorimotor signals define the interactions among hand anatomy, the nervous system, and manipulation function. Thus, our collaborative research activities emphasize a firm grounding in the mechanics of finger function, insistence on anatomical detail, and meticulous characterization of muscle activity. This overview of our work on precision pinch (i.e., the ability to produce and control fingertip forces) presents some of our findings around three Research Themes: Mechanics-based quantification of manipulation ability; Anatomically realistic musculoskeletal finger models; and Neural control of finger muscles. I conclude that (i) driving the fingers to some limit of sensorimotor performance is instrumental to elucidating motor control strategies; (ii) that the cross-over of tendons from flexors to extensors in the extensor mechanism is needed to produce force in every direction, and (iii) the anatomical routing of multiarticular muscles makes co-contraction unavoidable for many tasks. Moreover, creating realistic and clinically useful finger models still requires developing new computational means to simulate the viscoelastic tendinous networks of the extensor mechanism, and the muscle–bone–ligament interactions in complex articulations. Building upon this neuromuscular biomechanics paradigm is of immense clinical relevance: it will be instrumental to the development of clinical treatments to preserve and restore manual ability in people suffering from neurological and orthopedic conditions. This understanding will also advance the design and control of robotic hands whose performance lags far behind that of their biological counterparts.

Keywords: Hand; Human; Manipulation; Muscle; EMG; Neural; Motor control; Robotics

1. Introduction

Static and dynamic manipulation of objects with the fingertips is essential to the activities of daily living. Manipulation ability is vulnerable to orthopedic/neurological disease and aging because it hinges upon the exquisite interaction between the complex anatomy of the hand and nervous system (Valero-Cuevas, 2000a). The restoration of manipulation ability is the subject of an entire medical field (Tubiana, 1981; MacKenzie and Iberall, 1994; Brand and Hollister, 1999; Green et al., 1999). In spite of these efforts, the legendary complexity of the hand has delayed a comprehensive understanding of biomechanical function and neuromuscular control of the hand.

Given that the neuro–musculo–skeletal complexity of the hand is not well understood, I have found it useful to define a conceptual paradigm to outline the fundamental neuro–musculo–skeletal components of the hand and their interactions (Valero-Cuevas, 2000a) (Fig. 1). Creating a fundamental understanding of manipulation necessitates an integrative paradigm firmly grounded on the mechanics of finger function, but equally devoted to anatomical detail and the meticulous characterization of

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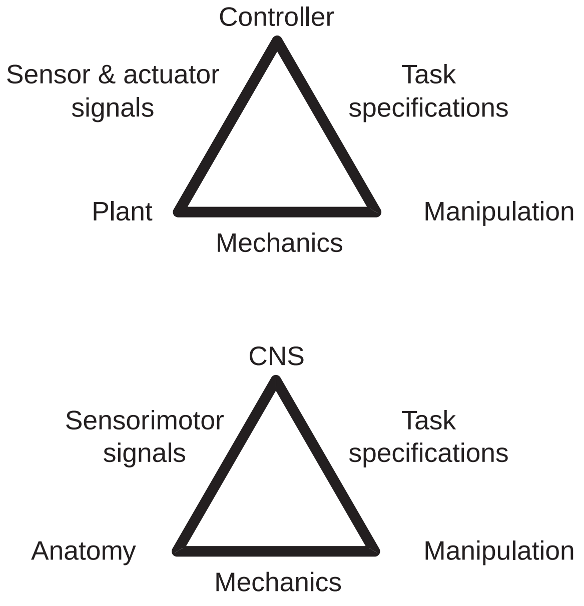


Fig. 1. Conceptual paradigm outlining fundamental neuro–musculo–skeletal components of the human hand and their interactions. For an electromechanical manipulator (Top), laws of mechanics define what grasping function a given manipulator (i.e., plant) can accomplish. Whether and how this function is realized depends on the ability of the controller to appropriately interpret task specifications and sensor signals, implement the appropriate control law, and send actuators signals to the plant. For a biomechanical system such as a human hand (Bottom), the anatomy (articulations, bones, sensory organs, muscles, etc) and central nervous system (CNS) are analogous to the plant and controller, respectively. Both machine and biological systems are part of the same continuum of solutions to the same mechanical challenge of manipulating objects. To date, our investigations have focused on how these fundamental neuro–musculo–skeletal elements of human fingers interact to produce static and dynamic fingertip forces for manipulation tasks such as precision pinch. We interpret "fingertip" loosely to mean the portion of the distal phalanx in contact with the object. (Adapted from Valero-Cuevas, 2000a.)

muscle activity. This paradigm has motivated me to pursue collaborative studies that combine principles of mechanics, anatomy and neurophysiology.

To understand the impairment and restoration of manipulation, I have begun by first comprehending the biomechanical requirements for static and dynamic precision pinch, and how the neuro–musculo–skeletal system meets those requirements. I refer to "static precision pinch" as the sensorimotor ability to regulate the magnitude and direction of the fingertip force/torque vectors in the absence of fingertip motion. "Dynamic precision pinch" also requires the regulation of finger motion (Murray et al., 1994; Valero-Cuevas et al., 1998; Valero-Cuevas et al., 2003b). For simplicity I use "finger" to mean any finger—including the thumb—unless otherwise specified, and "fingertip" as the portion of the tissue surrounding the distal phalanx in contact with the object manipulated. My focus on static and dynamic precision pinch is necessarily limited in that it does not yet address important issues such as neural and anatomical coupling among digits (Leijnse et al., 1993; Zatsiorsky et al., 1998; Latash et al., 2001; Li et al., 2001a; Keen and Fuglevand, 2003; Keen and Fuglevand, 2004a; Keen and Fuglevand, 2004b; Maas et al., 2004) or free finger motion (Cole and Abbs, 1986; Dennerlein et al., 1998b; Santello et al., 1998; Dennerlein et al., 1999; Sancho-Bru et al., 2001).

This overview of our work on the biomechanical function and neuromuscular control of the fingers is presented around three Research Themes: (I) Mechanics-based quantification of fingertip forces; (II) Anatomically realistic musculoskeletal finger models; and (III) Neural control of finger muscles.

2. Research Theme I: Mechanics-based quantification of fingertip forces

Using the scientific method requires that hypotheses be tested against experimental data. Therefore, a rigorous mechanics-based definition of finger function, and appropriate means to measure it, are prerequisites to progress in our clinical and scientific understanding of the biomechanical function and neuromuscular control of the fingers in manipulation. Roboticists, for example, have long been inspired and challenged by the functionality and versatility of the human hand—especially because its musculotendons are relatively sluggish actuators, nerve conduction velocities are much slower than electrical signals, and the musculature appears unnecessarily abundant. In their efforts to create comparably versatile robotic hands, they developed a mathematical framework to study the mechanical effectiveness of multifingered hands based on the function of their fundamental unit: the individual finger (Cutkosky, 1983; Murray et al., 1994). Effective precision pinch depends fundamentally on our ability to move and place the fingertips on an object, and to produce appropriate fingertip force and torque vectors (Cutkosky, 1983; Murray et al., 1994). In this Research Theme, we use a mechanical framework to find ways to define and measure the mechanical output of human fingertips as a necessary step to understanding multi-finger manipulation by the human hand.

From this mechanics perspective, human fingers are modeled as open serial kinematic chains of three rigid links with rotational degrees-of-freedom (DOFs) that allow control over the position and orientation DOFs of the distal phalanx (Fig. 2). The "Jacobian" matrix of this mechanism specifies the vector mapping from net torques at each DOF and fingertip forces/torques, and vice versa (Cutkosky, 1983; Murray et al., 1994). We have used these well-known relationships away from singularities to design experiments that unambiguously define the mechanical task specifications

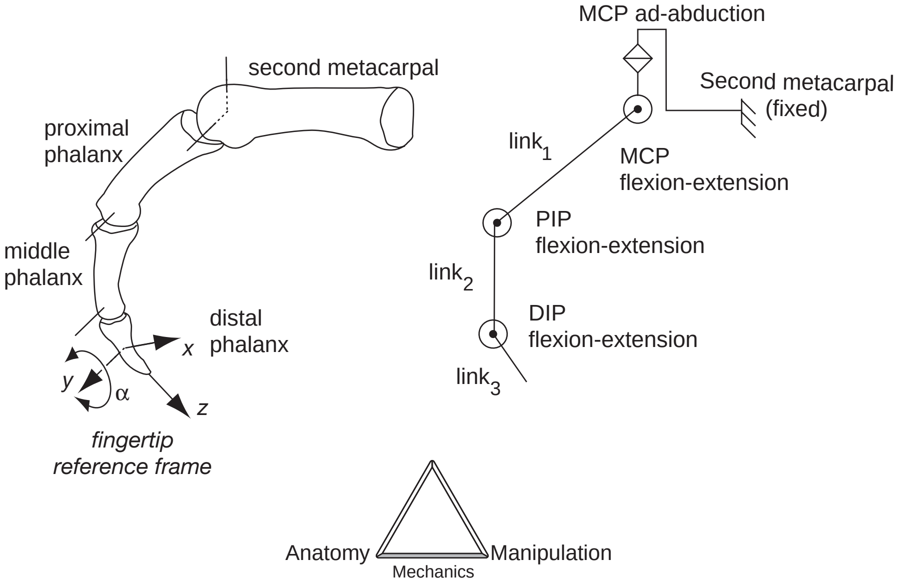


Fig. 2. Mechanics-based description and analysis of human fingers. Human fingers (Right) are assumed to be open serial kinematic chains of three rigid links with at least four rotational DOFs (Left—MCP: metacarpo-phalangeal, PIP: proximal inter-phalangeal; DIP: distal inter-phalangeal joints). Some "finger joints," like the MCP have more than one DOF, such as flexion-extension and ad-abduction (Research Theme II.1). Given that the three flexion-extension DOFs lie roughly in the same plane, the DOFs of the distal phalanx include its orientation (α) in that flexion-extension plane, plus its 3D location (x, y and z). This angular DOF at the distal phalanx grants it the ability to produce torque output in addition to the 3D fingertip force vector (Valero-Cuevas, 1997; Valero-Cuevas et al., 1998). For these idealized mechanisms, well-defined matrix functions like the "Jacobian" map joint angular velocity vectors into the vector of linear and angular velocities at the distal phalanx; as well as relate net torques at each DOF (the "net joint torque vector" in Fig. 7) to the vector of fingertip forces and torque. Such "wrenches" of combined linear/angular elements at the distal phalanx are part of screw theory upon which much of robotics analysis is based (Cutkosky, 1985; Murray et al., 1994).

(i.e., experimental question) to be studied. This mechanics-based approach has the important benefit of promoting mechanical equivalence between measured fingertip output and the predictive biomechanical models described in Research Theme II—which together inform our studies on the control of finger muscles described in Research Theme III.

2.1. Static fingertip forces

In the case of static precision pinch, we developed a thimble with metallic beads embedded on its outer surface, Fig. 3. When asked to produce static fingertip forces against the low-friction surface of a six-axis force sensor, participants had to direct fingertip force vectors within 16° of the surface normal or the thimble would slip, and produce no fingertip torque output (Fig. 2) or the thimble would rotate and change finger posture (Cutkosky, 1983; Murray et al., 1994; Valero-Cuevas et al., 1998; Valero-Cuevas et al., 2003a). In contrast, asking subjects to squeeze pinch meters with their bare fingertips (Mathiowetz et al., 1985) is a more ambiguous task. Higher surface friction allows fingertip force vectors to be directed inside a larger friction cone of about 30°, and finger posture can change by rolling on the finger pad (Cutkosky, 1983; Murray et al., 1994; Valero-Cuevas et al., 1998; Valero-Cuevas et al., 2003a).

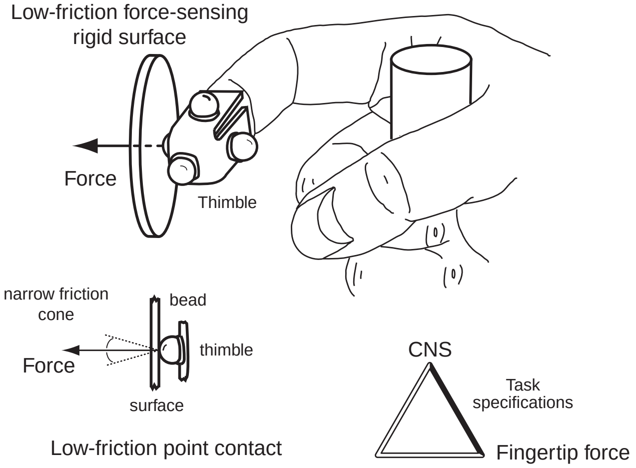


Fig. 3. Fingertip producing force against a rigid surface though a low-friction point contact. (Adapted from Valero-Cuevas, 1997; Valero-Cuevas et al., 1998.) To successfully maximize static force in each of five directions, subjects had to direct fingertip force vectors within 16° of the surface normal or the thimble would slip, and produce no fingertip torque output or the thimble would rotate and change finger posture.

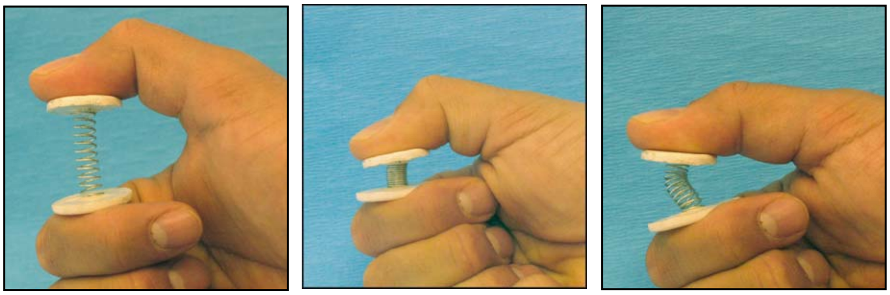
2.2. Dynamic fingertip forces

The effectiveness of dynamic precision pinch (where finger motion is allowed) is determined by our sensorimotor ability to regulate the motion of the fingertips simultaneously with the magnitude and direction of the fingertip force/torque vectors (Valero-Cuevas, 2003; Valero-Cuevas et al., 2003b). This mechanics-based definition led me to develop the Strength–Dexterity (S–D) Test to quantify the simultaneous dynamic regulation of fingertip force vector magnitude (strength) and directional accuracy (dexterity) (Valero-Cuevas, 2003; Valero-Cuevas et al., 2003b). The S–D Test is based on the principle of buckling of compression springs (Fig. 4). The strength requirement is defined as the ability to produce sufficient fingertip force magnitudes to compress the spring. The dexterity requirement (quantified by the Dexterity Index; Valero-Cuevas et al., 2003b) is defined as the ability to prevent buckling by dynamically regulating fingertip movement and the magnitude and direction of fingertip force vectors. Because the S–D Test specifically quantifies one's ability to dynamically regulate finger motion and fingertip force vectors in 3D at submaximal force levels, it has the clinical potential to be informative of people's everyday manipulation ability. Testing maximal finger strength, in contrast, may not be as informative because submaximal forces suffice to accomplish activities of daily living in all but the weakest hands. To shorten the S–D Test for clinical use, we are developing a quick protocol (i.e., <5 min) to analyze the nonlinear dynamical behavior of how subjects delay or prevent spring buckling in physical or haptic virtual-reality systems, which provides valuable information about the sensorimotor capabilities of the fingers during dynamic precision pinch (Venkadesan et al., 2003a, b).

3. Research theme II: anatomically realistic musculoskeletal finger models

The legendary neuro–musculo–skeletal complexity of the human hand makes it challenging for even the most experienced clinicians to understand and predict how specific orthopedic and neurological pathologies and treatments affect finger function and multifinger manipulation. Our scientific community routinely predicts the complex neuro–musculo–skeletal interactions within and among fingers using biomechanical models based on principles of anatomy, biomechanics and neurophysiology (e.g., Chao et al., 1976; Cooney and Chao, 1977; Chao and An, 1978a; An et al., 1979, 1985; Spoor, 1983; Giurintano et al., 1995; Leijnse, 1997a; Santello and Soechting, 1997; Dennerlein et al., 1998a; Valero-Cuevas et al., 1998; Li et al., 2001b; Sancho-Bru et al., 2001; Kamper et al., 2002; Valero-Cuevas et al., 2003a). In spite of these efforts and advances in computer graphics, computational methods and CAD-like packages for biomechanical systems, we still lack validated predictive models of the neuro–musculo–skeletal interactions that produce finger force and/or motion. Our modeling efforts are directed toward overcoming what I consider today's two main computational challenges to creating clinically useful finger models: kinematically complex representations of finger joints with multiple DOFs and viscoelastic tendinous networks.

The unifying theme behind these challenges is the need to explicitly distinguish between model topology (i.e., the assumed biomechanical structure) and parameters values (i.e., the particulars of that structure). Today's biomechanical models consist of manually assembled topologies whose parameter values are adjusted to explain and/or reproduce some experimental data. Importantly, the inevitable discrepancies between predicted and measured data can be attributed to unsatisfactory parameter values, inadequate model topology or both. The challenge is to determine if additional or alternative explorations of the parameter space would improve results sufficiently, or if using an alternative model topology would be more fruitful. Improving current models necessitates that we explicitly investigate how the assumed model topology fundamentally determines and limits model behavior (Valero-Cuevas et al., 2003a). Therefore, we should begin to speak of a model space defined by the type, connectivity, properties and interactions of available "building blocks" such as links, tendons, muscles, etc. From this perspective, a specific model topology is, by construction, an instantiation in model space subject to the advantages and limitations of that model space (Lipson and Pollack, 2000). Our engineering training naturally encourages us to create tractable model topologies by using building blocks that are mathematically convenient, such as rigid links for phalanges, hinges for joints, inextensible strings for tendons, etc. There is certainly wisdom in Occam's Razor "Pluralitas non est ponenda sine neccesitate" (plurality should not be posited without necessity): One should not increase, beyond what is necessary, the complexity of model topology required to explain data. I shall nevertheless argue for extending the model space because available finger models do not explain basic motion and/or forces sufficiently well (Valero-Cuevas et al., 2003a). That is, additional or alternative searches of the parameter space may not suffice in cases when the model topology is inadequate. Specifically, I believe we need to add building blocks for (i) kinematically complex representations of finger joints with multiple DOFs (Valero-Cuevas et al., 2003a), and (ii) viscoelastic tendinous networks (Valero-Cuevas et al., 1998). In addition, the simultaneous exploration of model and parameter spaces is likely to be more a powerful means to create truly parsimonious realistic models, the goal of Occam's Razor.



(A) Before use (B) Successful use (C) Buckled system

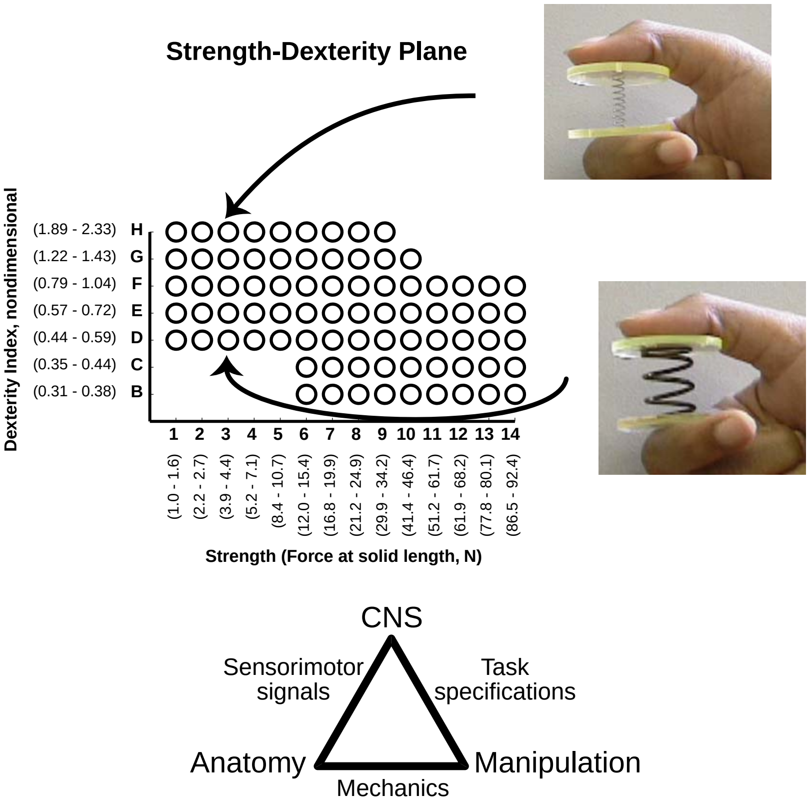


Fig. 4. The Strength–Dexterity Test (Valero-Cuevas, 2003; Valero-Cuevas et al., 2003b). Top: Using the fingertips to compress a helical spring prone to buckling. Fully compressing a helical spring with fingertip forces requires (i) that the magnitude of opposing forces overcome the spring resistance, and (ii) that fingertip movement and the directional accuracy of the forces be dynamically controlled to prevent buckling. (A) Initial configuration; (B) successful compression; (C) buckling of spring due to inappropriate control of fingertip forces, or directional accuracy. Middle: Every combination of strength and dexterity requirements can be represented as a point in the strength–dexterity plane. We have developed a discretized version of the strength–dexterity plane using 87 springs to form a grid, to be administered in random order. The subject is shown using dynamic key pinch with two springs with the same strength requirement (they are in the same strength column), but the top spring requires higher dexterity because it is more prone to buckling (see Valero-Cuevas et al., 2003b) for a detailed description).

3.1. Kinematically complex representations of finger joints with multiple DOFs

My work to date has focused on creating anatomically plausible, 3D biomechanical models to realistically reproduce a basic finger function: static fingertip force production in 3D. We have had encouraging success in creating a 4-DOF, 7-muscle index finger model capable of realistic predictions of static fingertip forces in multiple directions in the plane of finger flexion and the muscle coordination that achieve them (Valero-Cuevas, 1997; Valero-Cuevas et al., 1998). An exception to this finding was the inability of our model to predict the co-contraction of the interossei muscles seen during production of fingertip forces to the sides of the flexed index finger (Valero-Cuevas et al., 1998); which we interpret as a neural strategy to protect the collateral ligaments of the metacarpo-phalangeal (MCP) joint from longitudinal torsional damage, and which our model is inherently unable to predict because the model topology assumed the MCP to be a universal joint impervious to longitudinal torsion (Valero-Cuevas et al., 1998) (see Research Theme III.1).

In addition, we still lack such a model for the thumb. We are investigating whether the limitations of previous thumb models (Cooney and Chao, 1977; Chao and An, 1978a; Giurintano et al., 1995) arise from an incomplete search of the parameter space (i.e., uncertainty about parameter values and their variability) or inadequate model topology. We began by constructing a 3D, 5-DOF, 8-muscle thumb model with carpo-metacarpal (CMC) and MCP joints defined by two orthogonal and intersecting hinges (i.e., a universal joint; Valero-Cuevas et al., 2003a). We used Monte Carlo simulations to find the type and range of possible behavior for this model topology (Fishman, 1996; Hughes and An, 1997; Chang et al., 2000), where each of the 50 musculoskeletal parameters is described by a statistical distribution instead of a specific value. We explored the parameter space for this model topology by running to convergence iterative simulations with different random combinations of parameter values sampled from those distributions. We found this kinematic model topology could not map net joint torques into realistic thumbtip forces, regardless of parameter adjustments. Moreover, our recent cadaveric work suggests load-dependent motion of the trapezium (Pearlman et al., 2004) such that the thumb may act as a "floating digit" whose kinematics are affected by tendon loading, as suggested previously for the trapezium (Brand and Hollister, 1999) and carpus in general (Valero-Cuevas and Small, 1997). These results not only justify but also demand that we enlarge the model space to include alternative model topologies for thumb joints with multiple DOFs. We are currently exploring the model and parameter spaces with more kinematically complex representations of thumb CMC and MCP joints that (i) consider non-orthogonal and non-intersecting axes of rotations (the virtual 5-link thumb model; Giurintano and Hollister, 1992; Giurintano et al., 1995); or (ii) abandon mathematically convenient hinges in favor of model topologies where joint kinematics emerge from the interactions among joint forces, contact surfaces and ligamentous structures (Piazza and Delp, 2001).

3.2. Viscoelastic tendinous networks

The network of viscoelastic tendinous interconnections among intrinsic and the extrinsic extensor muscles is called the "extensor mechanism" or "dorsal aponeurosis" of the fingers (Bunnell, 1944; Zancolli, 1979; Tubiana, 1981; Garcia-Elias et al., 1991a, b; Zancolli and Cozzi, 1992; Netter, 1997). Sadly, Bunnell's words remain as true today as in 1944, especially with regards to biomechanical modeling of the extensor mechanism: "In the literature regarding the function of the intrinsic muscles controlling the fingers, one finds such a wide divergence of opinion that it is evident that the subject is still in the controversial stage. Textbooks of anatomy largely agree but are incomplete as they fail to consider synergic action between the muscles, stabilization and coordination, and the conception that lumbricales and interossei have a different action when the proximal finger joints are in their first half (45°) of flexion, than when in their second half, and a different function, depending on whether or not the extensor tendon stabilizes the proximal finger joints in extension.... The thin sliding dorsal aponeurosis of a finger [the extensor mechanism] is a complicated mechanism which makes for ingenious coordination in the action of the long extensors and flexors, and the lumbricales and interossei." (Bunnell, 1944, pp. 350, 351) (see also Bunnell, 1944; Tubiana, 1981; Ikebuchi et al., 1988; Garcia-Elias et al., 1991a, b; Netter, 1997; Brand and Hollister, 1999). There is clinical urgency to understanding the function of the extensor mechanism in the presence of anatomical variability (Ikebuchi et al., 1988) because muscle damage and imbalance often produce finger impairment and deformities such as clawing (Littler, 1973; Srinivasan, 1976; Mentari, 1978; Malaviya, 1991; Leijnse et al., 1992, 1993; Malaviya and Husain, 1993; Leijnse, 1997b; Brand and Hollister, 1999).

Biomechanical modelers understandably use simplified representations of the extensor mechanism for the sake of computational feasibility. Our work has shown that only when we represent the extensor mechanism as a 3D "floating net" (as a truss network in equilibrium) can models reproduce measured maximal isometric forces and the coordination patterns that produce them (Valero-Cuevas, 1997; Valero-Cuevas et al., 1998). Subsequent studies have successfully used this floating net approach to study finger movement (Sancho-Bru et al., 2001). However, there is still lack of an anatomically realistic comprehensive model of the extensor mechanism that can account for finger force, motion, and their pathologies. Achieving these research goals requires that we broaden the model space to include building blocks that allow representing the extensor mechanisms as topologies with 3D wrapping, non-symmetric deformable networks of viscoelastic bands. To this end we have created a modeling environment that can simulate load transmission in complex viscoelastic tendinous networks such as the extensor mechanism (Fig. 5) (Valero-Cuevas and Lipson, 2004; Lipson, in review; Valero-Cuevas and Lipson, in review).

3.3. Model validation

To validate our finger models we need to use experimental measurements beyond those presented in Research Theme I. One of our approaches is to use

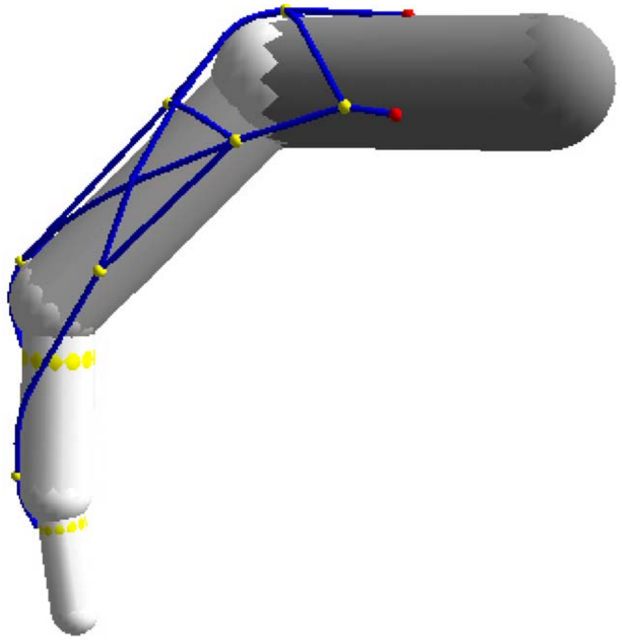


Fig. 5. Extensor mechanism of the fingers. Graphical user interface of a modeling environment capable of simulating viscoelastic tendinous networks to represent the extensor mechanism (Lipson, in review; Valero-Cuevas and Lipson, in review). This modeling environment is a computational implementation of a 3D model space to assemble arbitrary finger topologies from building blocks that include rigid bones, joint contact mechanics, and wrapping deformable networks of viscoelastic tendons to simulate the extensor mechanism. We are using this modeling environment to create realistic finger models by simultaneously exploring both the model and parameter spaces.

direct actuation of the tendons of cadaveric fingers with simultaneous measurement of fingertip force/torque output (Valero-Cuevas et al., 2000; Valero-Cuevas and Hentz, 2002; Pearlman et al., 2004). These methods have helped validate modeling predictions in the tetraplegic hand, such as that bowstringing of the flexor profundus tendon at the PIP joint can greatly increase index finger strength (Valero-Cuevas and Hentz, 2002), and compare the force production capabilities of alternative tendon transfers for the thumb (Pearlman et al., 2004). The computer-controlled tendon actuation of cadaveric fingers (Pearlman et al., 2004) now allows us to combine parameter estimation techniques with on-demand data collection to quickly explore model and parameter spaces. At convergence, these finger models would reproduce experimental finger motion and force data in a maximal likelihood sense.

4. Research theme III: neural control of finger muscles

The fingers and their musculature are the interface between the central nervous system (CNS) and the objects being manipulated. Understanding the neuromuscular control of the fingers is, therefore, helpful to improving our understanding of how the nervous system interacts with the physical world. The problem of how the nervous system selects and regulates the coordination of "redundant" (or "abundant") musculature is central to the field of motor control. The production of submaximal static and dynamic fingertip forces is an under-constrained problem because multiple coordination patterns can achieve a mechanical task equivalently (Close and Kidd, 1969; Chao and An, 1978a, b; Darling and Cole, 1990; Valero-Cuevas et al., 1998; Valero-Cuevas, 2000b) (even though each coordination pattern has particular consequences in other functional dimensions such as musculoskeletal loading, metabolic cost, signal-dependent noise, etc.). Our insistence on mechanically well-defined experimental protocols (Research Theme I) stems from our attempt to leave as few aspects of the task as possible open to interpretation to mitigate the confounding effects of anatomical, neuromuscular and cognitive variability inherent to psychophysical studies of voluntary function. This approach also enhances the mechanical equivalence between the task specifications presented to human subjects and biomechanical models. The unifying theme of our studies described in Research Theme III is to drive the system to some limit of performance (i.e., constraining the task sufficiently; Raasch et al., 1995; Loeb, 2000) as an effective means to elucidate principles of biomechanical function and neuromuscular control.

4.1. *Muscle coordination patterns necessary to reach limits of biomechanical performance*

Our experimental approach has been to ask motivated subjects to maximize fingertip force magnitude to estimate the limit of biomechanically feasible fingertip forces, where muscle redundancy is predicted to disappear (Valero-Cuevas et al., 1998; Valero-Cuevas, 2000b). Not surprisingly, investigators have reported subject-dependent coordination patterns for submaximal finger forces (Close and Kidd, 1969; Maier and Hepp-Reymond, 1995). By designing experimental paradigms with well-defined mechanical task specifications, and refining fine-wire electromyogram (EMG) techniques (Burgar et al., 1997), we have shown that different people use similar muscle coordination patterns to produce maximal voluntary fingertip forces in the index finger (Valero-Cuevas et al., 1998) and thumb (Johanson et al., 2001; Valero-Cuevas et al., 2003a). Moreover, such coordination patterns depend on the accuracy with which fingertip force vectors need to be directed and regulated (Johanson et al., 2001). These results are important because they motivate and justify seeking out task-specific and general principles for motor control of the hand.

One such line of research is to test the hypothesis that the neural control of finger musculature can be

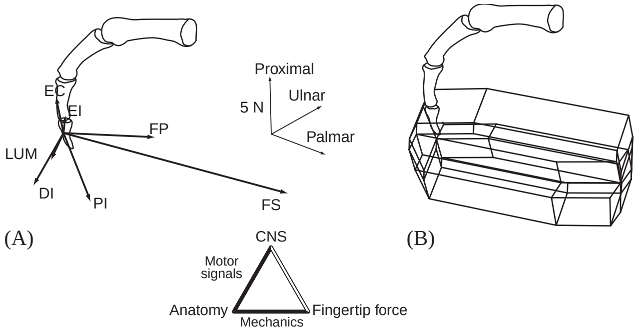


Fig. 6. The feasible force set of the index finger. The maximal biomechanically feasible fingertip forces, and the unique coordination patterns that achieve them, can be found by calculating the finger's "feasible force set": the 3D vector space representing maximal force production in all directions in "force space" (Lee and Rim, 1990). Each muscle produces a force vector at the fingertip (Valero-Cuevas et al., 2000; Pearlman et al., 2004) (Fig. 6A). The "convex hull" of all positive linear combinations of these vectors is the finger's FFS (Fig. 6B) (Valero-Cuevas et al., 1998; Valero-Cuevas, 2000b; Valero-Cuevas and Hentz, 2002; Yokogawa and Hara, 2002). Nonlinearities in the transformation from tendon tension to fingertip force may distort the feasible force set (Pearlman et al., 2004), but it serves, at the very least, as a linearized approximation of the force production capabilities of a fingertip.

preferentially driven by the mechanical specifications of the task, as opposed to, for example, driven by possible sensorimotor interactions among motor unit pools within and across fingers (Schieber and Hibbard, 1993; Keen and Fuglevand, 2004b). In support of this hypothesis, we found the subject-independent coordination patterns measured during maximal voluntary static fingertip forces to compare favorably with the unique coordination patterns predicted to achieve those forces (Valero-Cuevas et al., 1998; Valero-Cuevas, 2000b). See Fig. 6 for a description of these predictions. This evidence encourages and justifies developing mechanics-based models to investigate the clinical impairment and restoration of hand function (Valero-Cuevas et al., 2000; Valero-Cuevas and Hentz, 2002), but only for those tasks where such mechanics-based control has been established. Importantly, distinguishing between what is or is not "task-driven" control depends on what we consider the task to be. For example, the co-contraction of the interosseous muscles seen for lateral forces with the flexed finger (Research Theme II.1) can be interpreted as a ligament-protecting neural strategy, or alternatively as an artifact of our incomplete definition of the task specifications of the nervous system that we are trying to meet. The next section discusses other aspects of co-contraction.

4.2. *Using the "feasible set" analysis to understand co-contraction and important anatomical features*

A fingertip needs to be able to produce force in every direction to be versatile (Spoor, 1983; Leijnse, 1996; Valero-Cuevas et al., 1998; Brand and Hollister, 1999; Valero-Cuevas, 2000b; Valero-Cuevas and Hentz, 2002). Said mathematically, the "feasible force set" of the fingertip (the description of the maximal fingertip force vector achievable in every direction of "force space;" Fig. 6B shows a 3D example; Lee and Rim, 1990) must span portions of all Cartesian quadrants. This functional requirement has important consequences to the routing of tendons and muscle co-contraction. Consider the 2-joint, 5-muscle planar finger in Fig. 7A, simplified to have only two DOFs to helps visualize coordination patterns. At a nonsingular finger posture, the Jacobian matrix relates fingertip forces and net joint torques to each other (Research Theme I). Thus for the fingertip to be versatile, the "feasible torque set" of the finger (the description of the maximal net joint torque vector achievable in every direction of "torque space") must also span portions of all Cartesian quadrants. See Fig. 7C for a 2D example for this planar finger. That is, finger musculature must be able to produce any combination of net joint torques. Fig. 7 shows how the multiarticular muscles m1 and m5 are particularly helpful to span quadrants I and III, respectively), which would otherwise require two uni-articular muscles (Leijnse, 1996; Valero-Cuevas et al., 1998; Brand and Hollister, 1999). Note that no finger muscle can produce torque exclusively at the distal joints (the vertical axis in Figs. 7B–D) because all tendons cross the most proximal joint. I now use the "feasible set" analysis to highlight three ideas. First, every muscle or tendon transfer, no matter how weak, contributes uniquely to the size and shape of the feasible force set of the fingertip. Thus, impairment or rehabilitation of any muscle will degrade or enhance the feasible force set, respectively (Valero-Cuevas and Hentz, 2002; Kuxhaus et al., in review). This perspective challenges current notions of "muscle redundancy" by making it difficult to decide which finger muscle we would rather do without; and suggests means to quantify the impairment and rehabilitation of subsets of muscles (Kuxhaus et al., in review). Second, spanning of quadrant IV of torque space benefits greatly from a multiarticular muscle (i.e., m4) that flexes the proximal joint and extends the distal joint (Figs. 7D). Interestingly, this tendon cross-over from flexor to extensor is a defining anatomical feature of the extensor mechanism (Research Theme II.2). Enlarging coverage of quadrant IV can only enlarge the feasible force set of the fingertip in some directions. Fig. 6 shows that the muscles acting on the extensor mechanism of the index finger (lumbrical and palmar interosseous) contribute to fingertip force vectors in directions useful to opposing the thumb during grasp and manipulation. While the opposite cross-over tendon route is also possible, those fingertip force vector directions would be in directions roughly opposite to those needed to oppose the thumb, which I speculate did not have as strong an evolutionary advantage. This view of the extensor mechanism

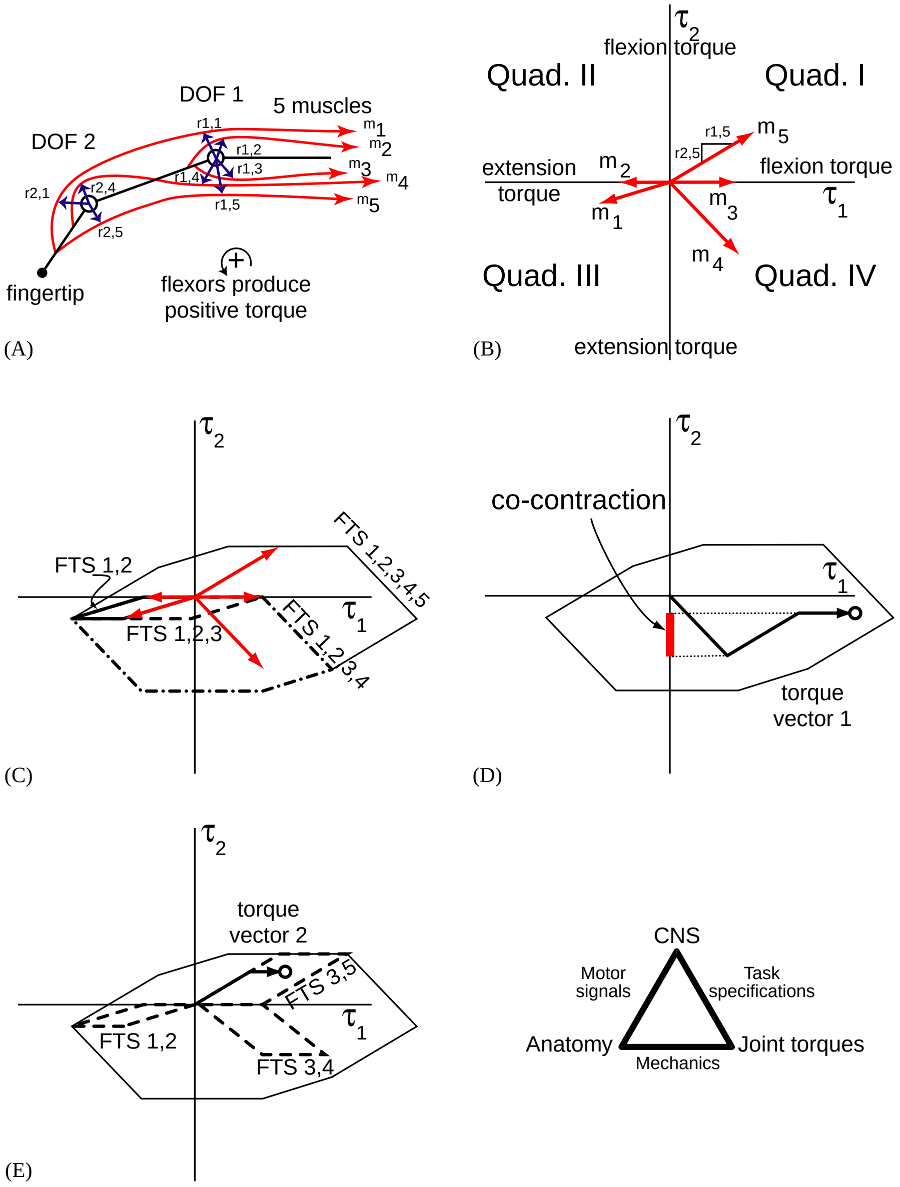


Fig. 7. Graphical interpretation of muscle coordination patterns for static force production in force and torque spaces. (A) Consider the 2-joint, 5-muscle planar finger, simplified to have only two flexion DOFs to helps visualize coordination patterns. To be versatile, the finger should be able to produce fingertip force vectors in all directions of force space (i.e., the plane of the finger in this case, or 3D space in Fig. 6). The anatomical routing of tendons results in a moment arm $r_{i,j}$ at DOF i for muscle j. (B) These moment arms determine the contribution of each muscle force to the net joint torque at each joint, which can be shown graphically as a vector in "torque space" (An et al., 1983; Leijnse, 1996; Valero-Cuevas et al., 1998; Brand and Hollister, 1999). Any net joint torque combination is simply a point described by a vector in torque space. To be versatile, the finger should be able to produce net joint torques in all quadrants of torque space. (C) The feasible torque space (FTS) defines all possible net joint torque vectors a group of muscles can produce. The FTS is calculated by finding all positive linear combinations of muscle actions in torque space (muscles can only actively pull). All possible torque vectors that m1 and m2 can produce are described by FTS1,2, and so on. Thus FTS1,2,3,4,5 specifies all biomechanically possible net joint torque vectors the musculature can produce. Note that (i), every muscle or tendon transfer, no matter how weak, contributes uniquely to the size and shape of the feasible torque set (and thus to the feasible force set). And (ii) spanning of quadrant IV of torque space benefits greatly from a multiarticular muscle (i.e., m4) that flexes the proximal joint and extends the distal joint—which is a defining anatomical feature of the extensor mechanism. (D) The simultaneous activation of agonists and antagonists at a DOF (i.e., co-contraction) is necessary to reach most regions of FTS 1,2,3,4,5 (Valero-Cuevas et al., 1998). Co-contraction is described graphically by a reversal along a torque DOF during production of a net torque vector. For example, producing net joint "torque vector 1" unavoidably requires reversing direction in at least one torque DOFs, as shown by the wide bar on the vertical axis for a solution combining the actions of muscles m3, m4 and m5. E: Only in the subset regions FTS 1,2, FTS 3,4 and FTS 3,5 is it possible to achieve a net joint torque vector without reversing direction, as in the case of "torque vector 2". Note that producing net joint torque vectors inside feasible FTS 1,2,3,4,5 is a redundant task because it can be accomplished by multiple strategies (Valero-Cuevas, 2000b). Thus, while reaching points in regions FTS 1,2, FTS 3,4 and FTS 3,5 can be done without co-contraction at any joint, there exist numerous other coordination strategies where co-contraction can be used (i.e., using a more circuitous vector addition). In contrast, co-contraction along at least one DOF is unavoidable anywhere else in FTS 1,2,3,4,5 (the total FTS for this finger).

provides a framework to investigate the degeneration of force and motion capabilities of the fingers when the tendinous or muscular balance of the extensor mechanism is disrupted (Bunnell, 1944; Srinivasan, 1976; Mentari, 1978; Malaviya, 1991). And third, co-contraction at some DOFs (i.e., simultaneous activation of agonists and antagonists of the same DOF) is in many instances not an option, but an unavoidable consequence of having multiarticular muscles (e.g., m3, m4 and m5 in Fig. 7D) (Valero-Cuevas et al., 1998). See Fig. 7D for examples of how producing vectors in most regions of torque space (and thus force space) necessitates co-contraction. The above three ideas naturally: (i) demand that we consider carefully the implications of the biomechanical structure of fingers before drawing conclusions about the neural selection of coordination patterns, or their optimality with respect to a given cost function. And (ii) suggest that drawing conclusions about the unique roles of "bi-articular" muscles may be premature without first considering the "tri-" and "tetra-" articular muscles of the fingers. See Prilutsky (2000) for a review of the current state of these issues.

4.3. Scaling and regulation of muscle coordination patterns for static precision pinch

Researchers have long proposed task-specific neural strategies to tolerate inaccuracies in the motor command and simplify the control of multiple muscles (Bernstein, 1967). By quantifying the similarity among coordination patterns—estimated via fine-wire EMG—during modulation of static fingertip force magnitude, I found evidence that the nervous system can control multiple muscles by simply scaling their relative activations (Valero-Cuevas, 2000b). This was important experimental evidence that simplifying strategies might exist at the level of the neural command. Prior evidence of simplifying strategies came from kinematic and kinetic data, which can often be produced by different neural commands (Latash et al., 2004). Recently, we (Valero-Cuevas and Todorov, 2003) have begun to investigate whether the control of multiple muscles of the fingers obey a "minimal intervention" principle (Todorov and Jordan, 2002). This ongoing work seeks to establish if the nervous system improves task-relevant performance by actively accumulating the inevitable variability and inaccuracy in the motor command in task-irrelevant output dimensions (the "uncontrolled manifold;" Scholz and Schoner, 1999; Latash et al., 2004). Our preliminary results suggest that variability in EMG (indicative of noise in the motor command) is actively combined in ways that attenuate noise in the desired fingertip force vector magnitude and direction (Valero-Cuevas and Todorov, 2003).

4.4. Limit of sensorimotor integration for dynamic precision pinch

The S–D test is different from maximal force production tasks in that it brings the fingers to a limit of sensorimotor integration at low force magnitudes comparable to those used in everyday tasks (Valero-Cuevas et al., 2003b).We have found the S–D test for key and tip pinch to be repeatable and able to distinguish between unimpaired hands and those with thumb osteoarthritis (Valero-Cuevas et al., 2003b). More recent results suggest that this limit of sensorimotor integration is independent of the person's pinch strength (Venkadesan et al., 2003a, b). In collaboration with neurophysiologists and radiologists, we are combining the S–D test with fMRI to characterize cortical activity correlated with sensorimotor processes necessary for successful manipulation (Talati et al., 2003). Extending this work has the potential to help us understand the association between specific brain disorders and loss of specific features of manipulation function (e.g., strength vs. dexterity).

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