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Supplementary material for this article is available [online](#)

Abstract

Ultrafast movements propelled by springs and released by latches are thought limited to energetic adjustments prior to movement, and seemingly cannot adjust once movement begins. Even so, across the tree of life, ultrafast organisms navigate dynamic environments and generate a range of movements, suggesting unrecognized capabilities for control. We develop a framework of control pathways leveraging the non-linear dynamics of spring-propelled, latch-released systems. We analytically model spring dynamics and develop reduced-parameter models of latch dynamics to quantify how they can be tuned internally or through changing external environments. Using Lagrangian mechanics, we test feedforward and feedback control implementation via spring and latch dynamics. We establish through empirically-informed modeling that ultrafast movement can be controllably varied during latch release and spring propulsion. A deeper understanding of the interconnection between multiple control pathways, and the tunability of each control pathway, in ultrafast biomechanical systems presented here has the potential to expand the capabilities of synthetic ultra-fast systems and provides a new framework to understand the behaviors of fast organisms subject to perturbations and environmental non-idealities.

1. Introduction

Organismal movements propelled by springs and released by latches are renowned for accelerations exceeding 10^6 m s^{-2} and power densities exceeding 10^5 W kg^{-1} (mechanical power output of the movement relative to the mass of the energy source) [3, 6–18]. Organisms successfully operate these mechanisms in diverse environments with

minimal self-destruction such that they are usable for the life of the organism. The shared mechanical basis for these movements is latch-mediated spring actuation (LaMSA). LaMSA comprises a class of mechanical systems propelled by pre-loaded elastic mechanisms and released by latch-like mechanisms that mediate the rate of energy transformation from elastic potential energy to kinetic energy [8, 13]. Engineered LaMSA mechanisms, inspired by

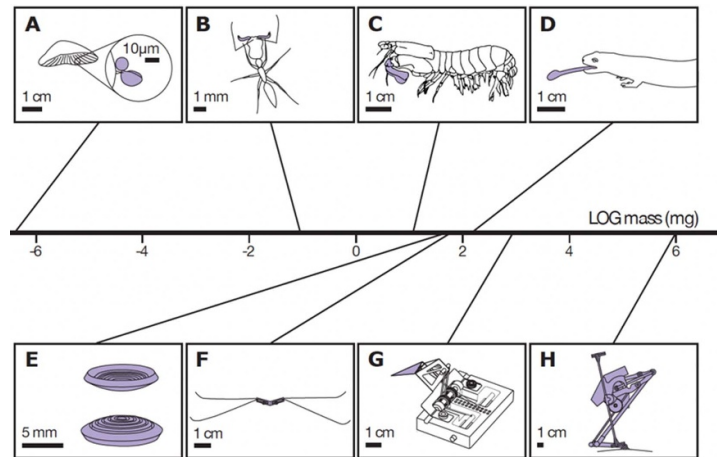


Figure 1. Diverse biological and engineered systems use latch-mediated spring actuation (LaMSA) to propel movement with pre-stored energy in elastic structures and to mediate the transformation from potential to kinetic energy using latch mechanisms. (A)–(D) Biological LaMSA systems span the tree of life, including (A) the ejection of fungal ballistospores [1, 2], (B) the rapid closure of trap-jaw ant mandibles to capture prey and jump [3], (C) the acceleration of mantis shrimp raptorial appendages to break open snail shells [4], and (D) the protrusion of salamander tongues to capture prey [5]. (E–H) Engineered LaMSA systems include (E), (H) devices that jump on land [38, 39], (F) jump on water [40] and (G) perform powerful strikes [41]. (G), (H) Systems use geometric linkage changes to release the elastic energy rather than removing a contact-based latch. Objects colored purple indicate the mass that is accelerated by spring propulsion. The accelerated mass is indicated on the log-transformed mass scale line. (A) Adapted from [1] by permission of the publisher (Taylor & Francis Ltd, www.tandfonline.com). (B) Adapted from [42] with permission from Alex Wild/alexanderwild.com. (C) Adapted from [4] with permission from IOP Publishing Ltd. (D) Adapted from [5] with permission from John Wiley & Sons © 2019 Wiley Periodicals, Inc. (E) Adapted from [38] with permission from Springer Nature. (F) Adapted from [40] with permission from AAAS. (G) Adapted with permission from [41] © 2021 PNAS. (H) Adapted with permission from [43]; photo by Stephan McNally at UC Berkeley.

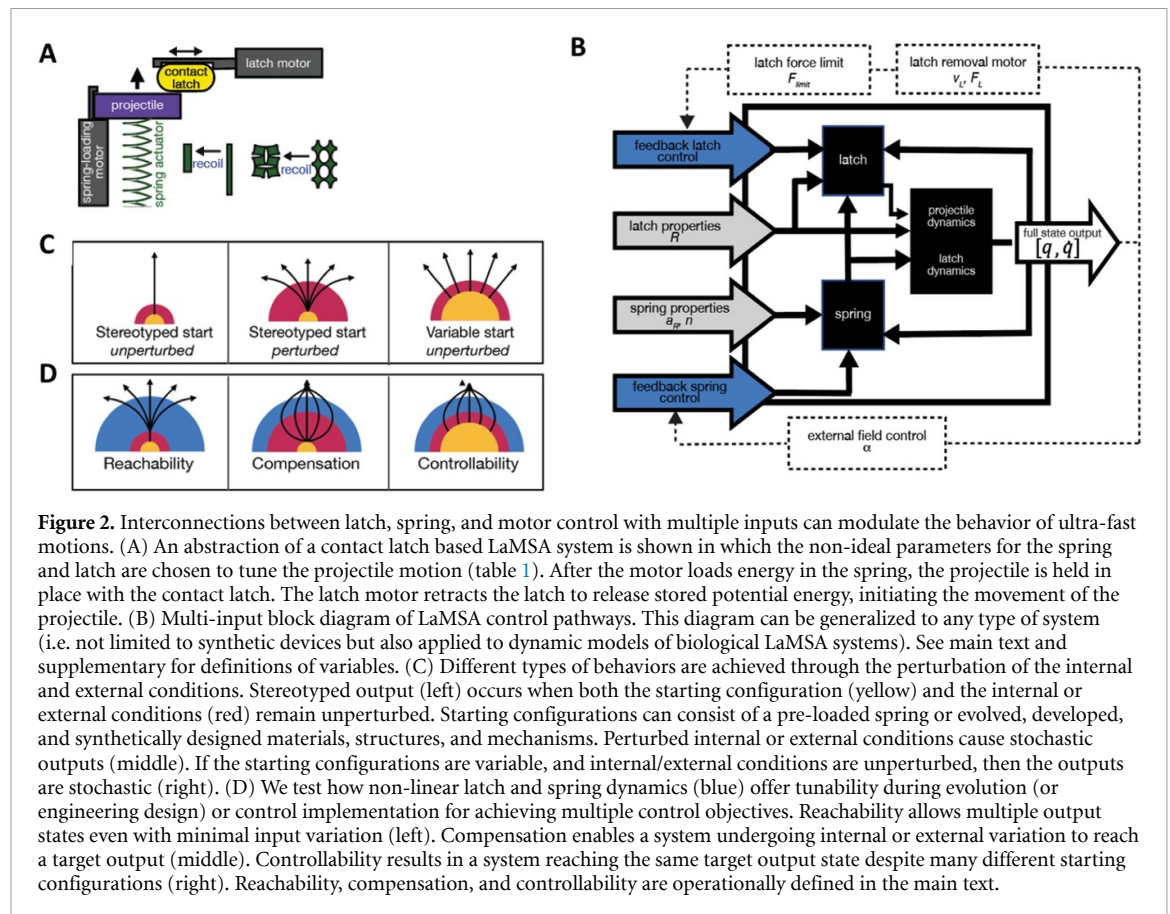
biomechanics, aim for similarly high accelerations and repeated use (figure 1) [19–24, 38, 40, 41].

LaMSA systems are comprised of multiple components, each with their own dynamics, and which must be tuned together to operate effectively [8, 13]. These components include a motor that loads energy into an elastic mechanism, an elastic mechanism that propels the movement, a latch mechanism that both prevents motion during spring loading and mediates energetic transformation from elastic potential energy to kinetic energy, and an accelerated mass (for definitions, see: [8, 13]). The LaMSA motor for biological systems is typically muscle or turgor pressure while for engineered LaMSA systems, this motor can be a linear actuator. Elastic mechanisms (which we henceforth refer to as ‘springs’ for brevity) include tendons, exoskeletons, and synthetic polymers (for engineering systems). Latch mechanisms include adhesive patches, physical blocks, and geometric mechanisms such as torque reversal commonly used in both biological and engineering systems. Motor activity is typically decoupled spatially and temporally from the output movement, such that the rate of energy release (i.e. mechanical power) is determined by spring and latch properties [13, 22]. Latch and spring properties should be tuned to achieve a target output [13].

Variation from individual to evolutionary time scales has been demonstrated in the components, operation, and performance of biological LaMSA systems. Mantis shrimp (Stomatopoda) vary spring

loading to generate variable strike velocities [25] according to the behavioral context of the strike, such as for feeding vs. fighting [26]. Additionally, their spring and spring-loading muscle properties have evolved in tandem with diversification of their strikes for use in, for example, slower fish-catching and ultra-fast snail-smashing species [12, 27–33]. In a different group of shrimp—the snapping shrimp—some species vary their output while others cannot, depending on their particular latch mechanism [3, 25, 34–36]. In plants, intersecting geometry and pressure of Venus fly traps yields rapid, predictable outputs [37]. In fungi, the dynamics of microfluidic processes confers directionality as stored energy in a droplet is transformed into the ballistic launch of a spore [2].

Given that LaMSA systems rely primarily on propulsion by elastic recoil of materials and structures, spring dynamics are central to energy flow and control. LaMSA spring dynamics, as is the case for many small biological and synthetic materials, are more complex than Hookean materials (i.e. linear force-displacement relationship) which store and release energy with maximum efficiency [31, 44, 45]. Indeed, material composition, shapes, and structures of realistic biological springs often result in heterogeneously distributed strain (both spatially and temporally) during loading and recoil [32, 44, 46, 47]. This complexity, although often at the cost of maximum efficiency, may confer other benefits. For instance, the J-shaped stress strain curve of many biological materials results in lower energy storage



than in an idealized Hookean material, but confers other benefits, such as resisting fracture [48, 49]. The multi-structured spring in mantis shrimp (Stomatopoda) with distinct regions of varying stiffness may facilitate the transformation of compressive forces into bending forces [32]. Likewise, the sensitivity of spring stiffness to the biaxial loading of fibrous structures in running wild turkeys allows them to alter effective spring stiffness along the axis of muscle force production in real time [50]. The principles and energetic consequences of hierarchical, structural design—termed “metamaterials”—are centrally important to LaMSA systems using these structures for propulsion and are also of great interest in other synthetic and biological systems [32, 37, 44, 51–56].

For many biological or engineered systems, successfully navigating changing internal and external environments is crucial (figure 2). Performance of biological LaMSA systems suggests a range of responsiveness to environmental changes. The latching mechanism in jumping treefrogs passively adapts to compliant substrates, thereby decreasing energy losses [57]. The spring loading muscles of toad, salamander, and chameleon tongues intrinsically compensate for variation in ambient temperature during spring loading to achieve consistent strikes [58–60]. In terms of internal environments, pH can modulate the stability of dynamic crosslinks,

such as hydrogen bonds within protein assembled biological structures or synthetic hydrogels, leading to changes in structure or direct changes in mechanical properties in real-time [38, 51, 52, 61–64]. Likewise, multilevel structural impacts of changes in environmental conditions on force, velocity, and efficiency are evident in synthetic composite materials [54, 64, 65]. By contrast, when jaw-jumping trap-jaw ants are presented with surfaces at varying angles, their jump trajectories are explained by the angle of the substrate, suggesting that they do not adjust their jaw-jumping strikes according to environmental or behavioral context [66, 67]. Therefore, some, but not all LaMSA mechanisms respond to environmental variation.

Even with substantial research pointing toward LaMSA systems with tuned and tunable inputs and outputs, studies examining pathways for control have been limited—primarily focused on feedback control, specifically through sensorimotor control of a muscle loading a spring [25, 68]. Much of this perspective arises from the assumptions of ideal springs (100% energy efficiency with linear force-displacement behavior) and switch-like latches (either on or off), which, as discussed above, have now been shown to inadequately capture the full capabilities in these systems. In addition, from a neural perspective, sensorimotor control of propulsion has been considered limited in LaMSA

systems, given that the duration of spring propulsion can be shorter than the transit time of an action potential [25, 68–75].

Therefore, taking our cue from the latest research on the diverse capabilities of LaMSA systems, we test how the non-ideal properties of spring and latch components can yield tuned outputs, and test how control systems can be implemented via latch and spring dynamics. In an effort to establish an interdisciplinary framework suitable for biomechanists, biomimeticists, and engineers alike, we adopt the terminology of control systems researchers to capture the range of capabilities conferred by tuning and control implementation. We incorporate and quantify control objectives including compensation, controllability, and reachability (see figure 2 for definitions) [76]. In the first section of the Results, we introduce a block diagram illustrating the interconnection between the latch, spring, and motor with a simple but insightful example of a typical LaMSA system. This system-level approach allows us to explore the effect of multiple inputs, incorporating tunable parameters of the latch, spring, and motor as control pathways for LaMSA behaviors. In the first two sections of the Results, we report how the synthetic mechanical design or biological evolution of structural properties of non-idealized springs and latches can serve as pathways for achieving control objectives, specifically through varying mechanical design, energetic loading, and environmental conditions (which we refer to as ‘externally applied fields’). In the final section, we use Lagrangian-mechanics modeling of feedforward control and feedback control via spring-latch dynamics to assess how the interaction of non-linear springs and latches can yield a range of outputs given the same starting conditions and/or result in consistent output in response to unwanted variation in internal or external conditions. Detailed analyses and a list of variables are included in the supplementary materials.

2. Materials and methods

Please see supplementary materials for detailed methods.

2.1. Spring actuation

We analytically model homogenous and metamaterial springs composed of the same elastomeric material and apply variable global strains (ε) (displacement normalized by spring length) to these springs (figure 3). The metamaterial springs use the same material as the homogenous springs but have circular or elongated pores distributed throughout, allowing both uniaxial displacement and rotation under strain; homogenous springs experience only uniaxial displacement under strain. We simulate applied internal or external fields with a potential energy function

that scales linearly with the strength of the external field (α), providing a mechanism by which spring properties are sensitive to changing environmental conditions. Our model relies on previously published analytical relationships validated by experimental tests of real materials constructed with laser-cut pores in elastomeric materials [64, 65].

For the control pathways offered by the spring, our goal is to move beyond materials or geometries with simple constitutive responses and to demonstrate how materials properties, internal structure (or geometry), and external fields can all play a role in spring mechanics, including recoil. Therefore, a quantitative calculation of spring performance across the hierarchical multivariable space of metamaterial in [64, 65] is used in this study. In addition, hierarchical structures are the norm in biology, such that metamaterials are a good representation of the layered and dynamic materials of biological mechanisms. Whether in the integrated collagens and elastic proteins (Cnidoids) of the stinging structures in jellyfish or the integrated stiff exoskeleton and elastic proteins (resilin) in jumping insects [77–79], these interleaved and highly dynamic materials and composite structures are present throughout biological LaMSA systems.

For both homogeneous and metamaterial springs, we simulate the resulting spring loading force (F_{loading}) and amount of stored elastic energy (W_s) from applied uniaxial stretching displacement (p) to determine the force-length (FL) relationship. For homogeneous, linear elastic springs, the stored elastic energy is a function of their stiffness ($F = kp$, where k is spring stiffness). For metamaterial springs, the relationship between F and p is in general nonlinear due to combined internal bending and stretching deformations in the unit cell ligaments [65]. We simulate spring recoil dynamics based on the elastic wave speed of the elastomeric material (c_0), the mass distribution, and FL relationship [64]. We measure system outputs in terms of the velocity-length relationship of elastic recoil, the corresponding amount of kinetic energy delivered during spring recoil (W_k), and the energy conversion efficiency ($\eta = W_k/W_s$). For the applied field simulations, we analyze these same parameters with the springs additionally experiencing an external field expressed as the ratio, α , of applied potential energy to the stored elastic energy in the spring ($\alpha = 0$; no applied field).

2.2. Latch mediation

We use reduced-parameter models of latches mediating spring recoil; we model an ideal spring (linear) so that our findings represent latch-specific dynamics and not the non-linear interactions of spring-latch dynamics. The contact-based latch model (derived from: [13, 22]) abstracts the system to a physical structure with a constant dimensionless latch

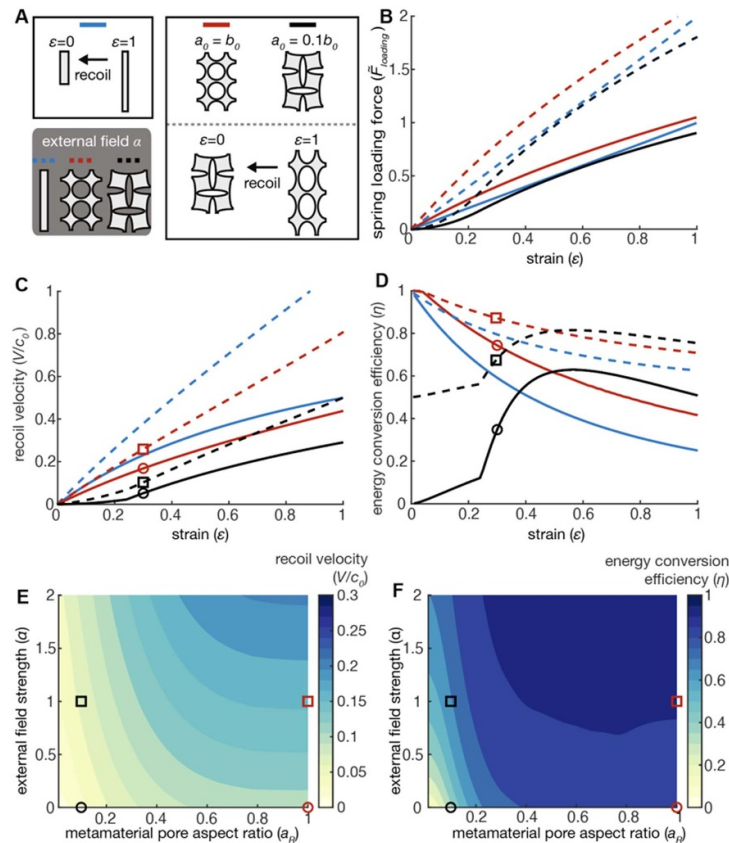


Figure 3. Reachability is expanded in metamaterial springs compared to homogeneous springs and further expanded in metamaterials with externally applied fields. (A) We analyzed three recoiling strips made of the same elastomeric material: one is a homogeneous strip (no pores, blue lines) and two are metamaterials which effectively operate as square plates connected by slender ligaments (circular pores, red lines; elongate pores: pore width, a_0 , is 0.1 times the pore length, b_0). The materials are additionally subjected to an external field, α , which is the ratio of applied potential energy to the stored elastic energy in the spring (dashed lines; in (B)–(D), $\alpha = 1$). (B) Spring loading force is enhanced through the application of an external field with the greatest range achieved in the circular pore metamaterial (red). Spring loading force is normalized by the elastic modulus of the elastomeric sheet and the cross-sectional area of the spring unit cell. (C) Recoil velocity (V) is enhanced via applied external fields with greatest range in the homogeneous strip (blue) and most substantial non-linear behavior in the elongate pore metamaterial (black). Recoil velocity curves represent maximum recoil velocity of the spring for a given value of global strain on the x-axis, rather than representing the temporal velocity as the spring relaxes. A spring will not follow the same velocity trajectory with time if strained to a different value. Slender ligament geometry permits stretching and bending, and associated internal rotation of the plates, as the pore aspect ratio decreases from 1 to 0.1. The combination of internal bending and stretching deformation in the metamaterials modulates the stiffness (slope of force versus global strain) and recoil velocity as the global strain is applied. Recoil velocity is normalized by intrinsic elastic wave speed (c_0) for the elastomeric sheet. (D) Energy conversion efficiencies (η , ratio of kinetic energy to stored elastic energy) are highest for metamaterial springs with the most elongate pore metamaterials. (E) By varying metamaterial structure (pore aspect ratio) simultaneously with external field strength beyond the ranges of the individual plots in (B)–(D), a six-fold range of recoil velocities can be reached for a given global strain ($\epsilon = 0.3$). (F) When the same simulation in (E) is run for energy conversion efficiency, the more circular pore metamaterials exhibit less tunable variation compared to the wide range in elongate pore metamaterials. Symbols in (E) and (F) correspond to points on the curves in (C) and (D), respectively.

radius that blocks the release of the projectile. Similar contact latch mechanisms are present in many arthropods [15, 16, 22, 71, 72, 80–84]. The antagonist muscle-pair latch model is comprised of two opposing muscles: the extensor which loads a spring, and the flexor which provides a holding force and then releases that force like a relaxing flexor muscle. The forces imparted by these muscles are balanced through a geometric mechanism that can be varied through the extensor offset angle (figure 4). This model is primarily based on grasshopper legs [85–87] which have similar geometric and antagonistic muscle latch configurations to many other animal systems [3, 9, 25, 27, 32, 41, 69, 71, 81, 88, 89]. For

each latch model, we explore how variation in geometric/structural properties (contact latch model: latch radius, R ; antagonistic muscle model: extensor offset angle, ϕ_{ext}) and temporal properties (contact latch: latch removal velocity, v_L ; antagonistic muscle model: unlatching duration, δ_L) alter the reachability of the system. Here we calculate reachability as the range of energy delivered to the projectile (E_{out}) (figure 4).

2.3. Control implementation

We developed a Lagrangian mechanics-based approach for analysis of integrated LaMSA systems which is generalizable to any latch profile,

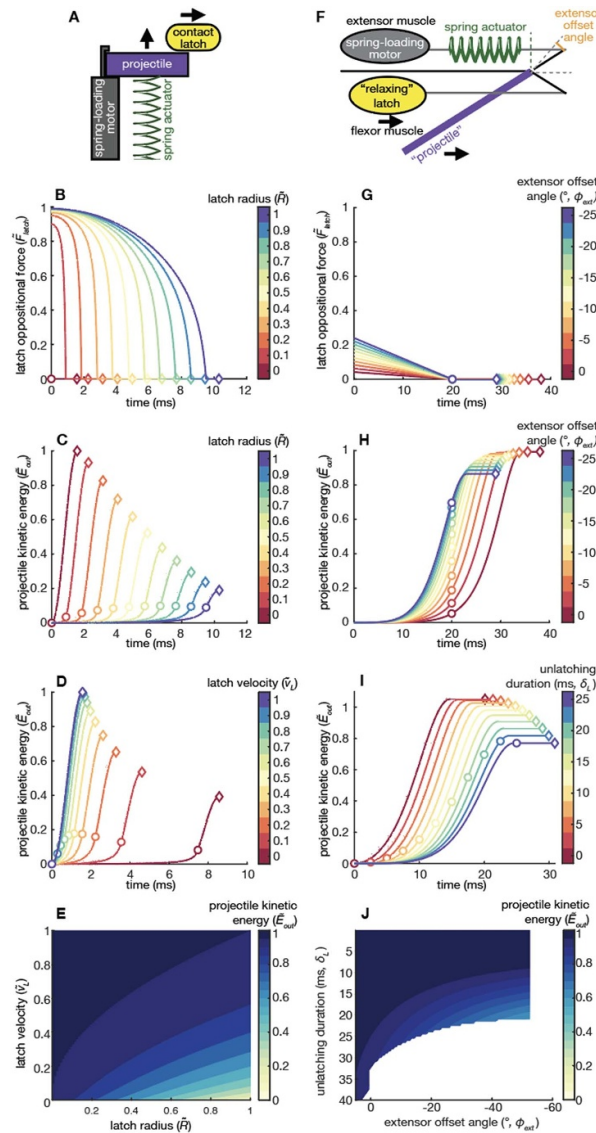


Figure 4. Models of two latch types — contact latch (A)–(E) and antagonistic muscle-pair latch (F)–(J) — reveal how latch dynamics yield reachability through temporal variables or structural components (shape or geometry). (A)–(E) The contact latch model consists of a latch structure moving perpendicularly to the direction of spring recoil to mediate the transformation of stored elastic energy to the kinetic energy of the projectile. We measure the effect of latch radius (R ; with increasing radius, the contacting edge with projectile is more curved and less sharp) and latch removal velocity (v_L) on the force applied by the latch to the mass-spring pair (F_{latch}), projectile kinetic energy (E_{out}), and the timing of unlatching (circles; latch force decays to zero) and takeoff (diamonds; projectile is no longer powered by spring recoil). Latch force and projectile kinetic energy are normalized to the maximum spring force and maximum possible kinetic energy, respectively ($\bar{F}_{\text{latch}} = F_{\text{latch}}/k\delta$, $\bar{E}_{\text{out}} = E_{\text{out}}/KE_{\text{max}}$). Latch radius and velocity are normalized to the spring length (L) and threshold velocity (v_L^{thresh}) respectively ($\bar{R} = R/L$, $\bar{v}_L = v_L/v_L^{\text{thresh}}$). (B) Reachability is expanded by varying latch radius while keeping latch removal velocity constant. Given consistent starting conditions at unlatching time (circle), varying latch radius results in a wide array of decay rates for the oppositional force, and takeoff times (diamonds). (C) Using the same simulation as in (B), reachability emerges through the effect of latch radius on projectile energy ($\bar{E}_{\text{out}} = \frac{E_{\text{out}}}{KE_{\text{max}}}$). Through the resulting constrained spring recoil arising from varying latch radius, variable projectile energy, unlatching time and takeoff time are controlled. (D) Varying latch removal velocity is a pathway for real-time adjustments to achieve reachability. While keeping latch radius constant ($\bar{R} = 0.6$), adjusting latch removal velocity allows for control of projectile energy, unlatching time, and takeoff time. (E) The interaction of latch velocity and latch radius creates a substantial range of projectile outputs that can be manifested through synthesis/evolution of different latch structures alongside temporal adjustments to latch removal velocity. (F) The antagonistic muscle-pair latch model consists of a pair of muscles that generate opposing torques to elastically load and subsequently release stored elastic energy. Latch dynamics are varied through the extensor offset angle (ϕ_{ext}) and the duration of flexor muscle relaxation (δ_L), both of which can be varied after synthesis and during use of the system. (G) Reachability occurs through varying extensor offset angle: given an array of starting conditions, the extensor offset angle can be varied such that identical unlatching time and minimally varying takeoff times are achieved. (H) The same simulation as in (G) reveals reachability in the context of projectile dynamics; for a constant latch relaxation duration ($\delta_L = 20\text{ms}$), increasing extensor offset angles offer pathways to varying takeoff timing and projectile kinetic energy. (I) For a constant extensor offset angle ($\phi_{\text{ext}} = -25^\circ$), varying unlatching duration enables fine-tuned control of projectile kinetic energy as well as the time between unlatching and takeoff: a shorter unlatching duration yields greater projectile kinetic energy and a longer time window between unlatching and takeoff. (J) Combining these parameters together reveals the reachability of projectile kinetic energy through adjustments to timing (unlatching duration) and orientation (offset angle) of the antagonistic muscle latch system.

Table 1. Categorization of multi-input control in a modeled LaMSA system.

Component	Properties	Real-time changes to system	Control type
Latch	Radius, R	Removal velocity, V_L	Feedforward (figures 5 and 6)
Spring	Metamaterial pore aspect ratio, a_R Power law spring exponent, n	Removal force, F_L External field, α	Feedback (figure 7) Feedforward (figures 5 and 6)
		External field, α (state dependent)	Feedback (figure 7)

spring potential energy, and other latch types (e.g. antagonistic muscle latches) (table 1). Building on two prior models [13, 22], we parameterize our model as a contact latch LaMSA system in which generalized coordinates represent the position of the spring (p) and latch (l). The spring is loaded with an initial displacement, p_0 . As the rounded latch (radius R) is removed perpendicularly to the spring force, spring energy is transformed into projectile movement. This continues until the projectile reaches the take-off position after which it is no longer actively powered. The projectile and spring are constrained to one degree of freedom movement. The latch and projectile maintain contact via sliding along a frictionless interface during the latched and unlatching phases. We set length, mass, and time scales to represent systems with high natural frequencies (on the order of 1 kHz; calculated based on spring stiffness and projectile mass) [22], which are similar to a mathematical synthetic LaMSA model analyzed to understand the various mediated energy releases during the multiple strikes of the Dracula ants (*Myrmica camillae*) mandibles [15]. We simulate metamaterial springs and generalized homogeneous springs with both linear and non-linear force-distance relationships (represented by a power law spring recoil force $F_s \sim p^n$ with a variable exponent). Spring properties representing potential control inputs in our model include the exponent, n , of the homogeneous, power law spring, in addition to pore geometry, a_r , and external field, α , for the metamaterial spring (figure 3). Latch properties representing control inputs include latch radius and latch removal velocity, both of which affect the decay of the latch force (figure 4). Integrating our control objectives metrics—transmission efficiency ratio (TER) and variability compensation (VC)—with our Lagrangian modeling approach, we

apply and test feedforward and feedback control in LaMSA systems.

The two metrics, TER and VC are used to quantify the change in the impulsive behaviors of the systems. First, we operationalize reachability in terms of TER, which assesses the range of possible outputs when controlling the system through changes to a particular input. A TER of 1 indicates the greatest control authority through the variable of interest, while a TER of 0 indicates no control over system output (TER should not be confused with energy conversion efficiency which quantifies the ratio of stored potential energy converted to projectile kinetic energy). Next, we assess compensation and controllability control objectives in terms of VC which quantifies the ability to compensate for internal or external perturbations through control over a particular variable. VC is calculated as the change in the control input required to compensate for undesired variation, such that large changes are needed to compensate for relatively small perturbations. Therefore, our two focal metrics—TER and VC—encompass reachability, compensation, and controllability of integrated LaMSA systems (figure 2).

In general, the feedforward control provides a predefined behavior of the systems with a known disturbance without using any sensory information. On the other hand, the feedback control allows for constant behavior correction based on real-time state measurement. In this paper, the feedforward control is implemented via changes in desired latch removal velocity. We use a simplified model assuming that latch inertia is substantially larger than projectile inertia. This assumption allows latch dynamics to be ignored and allows a constant latch removal velocity regardless of the force required to remove the latch (F_{remove}) or other inputs to the latch dynamics such as perturbations. This configuration reflects the reasonable assumption that for many biological LaMSA systems, the combined forces of the spring and projectile on the latch do not move the latch (either due to the relative magnitude of latch removal force, large inertia, or the direction of the spring and projectile forces). Each simulation is normalized to the same initial spring potential energy so that the control objective metrics reflect variation in spring and latch designs (figures 5 and 6).

In the feedback control model, we remove the large inertia assumption on the latch, previously imposed to maintain a constant latch removal velocity for the feedforward analyses. Because the spring pushes against the latch during recoil in this simple model, a latch resistance force, F_{res} , is necessary to oppose spring recoil and more realistically control latch removal velocity. Therefore, this model assumes that the physical latch is held in place by a latch motor with an upper force limit, F_{limit} , that sets the upper bound of the latch motor force (F_L) which

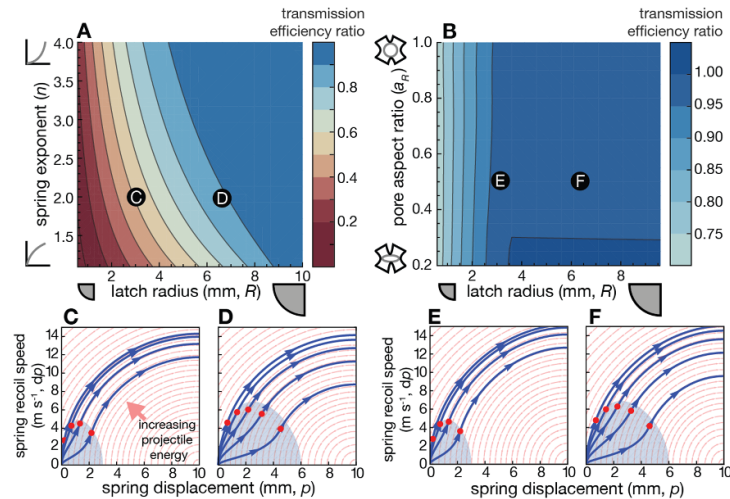


Figure 5. Feedforward control implementation via latch removal velocity enhances the range of projectile outputs as quantified by the reachability metric, transmission efficiency ratio (TER). (A) Higher spring exponents in polynomial springs combined with greater latch radius yield greater reachability (higher TER). (B) Metamaterial springs across a range of pore aspect ratios yield high TER given a sufficiently large latch radius. (C)–(F) Each phase plot corresponds to the white letters on the heat maps in (A) and (B). The projectile state trajectory depicts selected combinations of spring and latch properties. Red contour lines represent projectile energy in systems with instantaneous latch removal at a spring displacement of 0; highest projectile energy is in the upper left-hand corner of each plot. Blue lines indicate the projectile's energy trajectory with a contact latch operated at different latch removal velocities. The shaded blue region represents the approximate space over which the latch is removed; the red dots indicate the precise location of latch removal. The latch can vary projectile energy while its state is within the blue region. Once out of the blue region, the latch is fully removed and the projectile is accelerated by the spring, such that the projectile's energy state changes according to the spring's viscoelastic properties. To traverse the red contour lines (for controlling output energy), adjustments must happen during unlatching (blue region). The trajectories of the blue contours demonstrate that TER is primarily determined by latch radius (larger latch radius yields greater output range).

can be applied in opposite directions depending on how the motor is operating (latch resistance force, F_{res} , pushing the latch to oppose recoil; latch removal force, F_{remove} , pulling the latch to allow spring recoil) (figure 7). This is similar to the muscle antagonist pair latch, where the flexor muscle opposes the spring's recoil force (figure 4). While any accessory component is expected to be tuned to normal operation of the system during engineering design or evolutionary time, we can also consider the upper force limit of this latch motor to represent a perturbation to the system from either internal or external factors, such as a reduction in force capacity of a muscular motor with decreasing temperature. Therefore, we explore the ability of this LaMSA system to respond to perturbation of the upper force limit of the latch motor (F_{limit}) through real-time feedback control of the latch and spring inputs, assuming that the full state ($\mathbf{x} = [p \dot{p} l \dot{l}]^T$) can be sensed (position of the spring, p , and latch, l).

3. Results

3.1. Tunability of LaMSA mechanisms through the interplay between spring, latch, and motor control pathways

The fundamental components of LaMSA systems include a latch, a spring, and one or more motors (e.g. muscles). The interplay between these components diversifies the behaviors of ultra-fast motions,

ranging from stereotypical binary triggering of latch removal to strategic modulation of spring energy release dynamics (figure 2(B)). Thus, the ability to tune the properties of each component in LaMSA mechanisms has the potential to open new control pathways and explore non-stereotyped behaviors in biological and synthetic LaMSA systems subject to perturbations, muscle/motor limits, and non-ideal operating conditions and environments.

We study how tuning the three essential components of LaMSA systems expand the range of output motions by analyzing a simple example of LaMSA containing all three components (figure 2(A)). The full dynamics, based on Lagrangian mechanics, illustrates the interconnection between these three components in a parameterized way (see the list tunable parameters in table 1). The aim of this paper is to provide a quantitative framework for modeling and understanding how multiple pathways can be used to provide diverse and robust behavior of ultra-fast motions via an empirically informed, simulation-based approach. The expansion of the proposed multiple-input control framework for LaMSA systems is not limited to synthetic systems and may also be applied to simplified models of biological organisms with latches. In the following two sections, we first define the tunability of individual LaMSA components, specifically the spring and latch, in order to later incorporate robust parameters that can be

used as control inputs to the whole system (table 1; figure 2(B)).

3.2. Spring actuation: reachability through hierarchical structure and externally applied fields

We find that adding hierarchical structure and external fields to springs enhances their range of outputs, thereby providing a pathway for achieving reachability (figures 2 and 3; variable output in stable conditions) in LaMSA systems [76]. We operationalize reachability here as the range of energy delivered to the projectile when varying system morphology or dynamics. As detailed in the Methods and supplementary, we compare unstructured (homogeneous) springs to structured (metamaterial) springs. We test their responses with and without an applied external field (externally applied forces representing changing environmental conditions). We incorporate the following measurements and calculations: spring input parameters (spring composition, metamaterial structure, applied external field), spring recoil output parameters (force, displacement, velocity), and the energetic efficiency of the conversion from elastic potential to kinetic energy.

In comparison to homogeneous springs, we find that metamaterials enhance reachability through nonlinear associations among force, recoil velocity, conversion efficiency, and global strain (figure 3). A tradeoff between bending and stretching modes within the metamaterial enables tunability of local strain and, therefore, tunability of the efficiency of energy conversion between stored and released strain energy. Non-linear responses of the metamaterial springs are caused by their hierarchical structure: some regions strain and recoil at different rates than other regions. Non-monotonic dependency of energy conversion efficiency with global strain also enhances reachability. Metamaterials with narrow pores achieve maximum energy conversion efficiency at a finite global strain. Increased reachability occurs because a spring can be stretched to a global strain to achieve peak recoil performance or can be slightly under-stretched to decrease energy conversion efficiency and thereby dampen and reduce system damage through adjustments to the energetic losses of the system.

For metamaterials, this complex response of energy conversion efficiency with global strain arises from the non-linear relation between the local and global strain and the sequential activation of local displacements of ligament and plate mass during impulsive recoil [64]. These responses enable refined structural design and compositional variation to achieve reachability. However, the pores in our metamaterials create structures prone to internal rotation, causing decreased energy density compared to homogeneous springs. This diminished energy density is most evident in decreased maximum recoil velocity relative to the intrinsic elastic wave speed

(figure 3). A homogenous spring recoils more than two times faster than a metamaterial with narrow elliptical pores when stretched to the same force. While this tradeoff may initially seem unacceptable, it is commonly encountered: helical springs are often made of stiff metals (e.g. steel)—their effective energy density is considerably less than the metal's intrinsic energy density, but their structure allows enhanced displacement by transforming stretching displacements into local bending deformations, like our metamaterials. In nature, helices are often used as a bundle or integrated assembly; similarly integrated assemblies of metamaterial springs may increase energy density while enabling control objectives.

Reachability is further expanded through application of an external field: spring loading force, recoil velocity, and energy conversion efficiency are enhanced as a function of global strain when compared to no external field (figure 3). In LaMSA systems, a spring can be stretched to a fixed force in the absence of a field, then the field is activated prior to latch release, allowing the spring to recoil at higher velocity. Field effects can be realized in homogeneous and metamaterial springs, but metamaterials offer additional control opportunities. For metamaterials with narrow aspect ratio pores, modest changes in applied field alter energy conversion efficiency from nearly perfectly resilient (high energy conversion efficiency) to nearly perfectly dissipative (low energy conversion efficiency) (figure 3). This change, which is beneficial for reducing system damage, only causes modest changes to peak recoil velocity. Nonetheless, sensitivity to external environmental conditions exacerbates vulnerability to unexpected environmental shifts, thus exemplifying the tradeoffs among these different control objectives and pathways.

3.3. Latch mediation: reachability in contact latches and antagonistic muscle pair latches through changes in structural and temporal parameters

The key finding of this section is that latch dynamics offer pathways to reachability through both their structure and real-time operation. We operationally define a latch as a force enabling spring loading, opposing spring recoil, and mediating the transformation of elastic potential energy to kinetic energy (*sensu*, [8, 13]). Latches include physical obstructions opposing spring recoil (e.g. [15, 16, 22, 80, 81]) as well as contact (adhesion, friction), fluidic (e.g. cohesion, coalescence, pressure) and geometric (e.g. buckling, linkage-based torque-reversal, changes in mechanical advantage) (e.g. [2, 3, 8, 11, 13, 35, 40, 41, 88, 89]) mechanisms. As explained in the Methods and supplementary, maximum elastic potential energy can be determined by the latch force constraint opposing spring recoil, as well as the FL relationship of the motor and the FL relationship of the spring loaded by the motor. Additionally, latches control

the proportion of stored spring energy converted to kinetic energy through decreasing oppositional latching force through time [22].

Using two latch types common in biological systems—contact latch and antagonistic muscle-pair latch—we find that latch release dynamics and the influence of geometry can influence kinematics (figure 4). With a contact latch, energy delivered to the projectile is affected by the timing and magnitude of the latch oppositional force. The latch oppositional force is, in turn, determined by the geometric and temporal properties of the latch [22]. A contact-based latch with a sharp edge ($\dot{R} = 0$) causes the latch oppositional force to disappear instantly. For a larger latch radius, holding all else constant, latch oppositional force decays more slowly.

Latch shapes determine initial conditions of spring recoil, such that a projectile could reach a fraction of maximum kinetic energy or experience delayed energy release. When latch geometry is constant, though, slower latch removal results in longer unlatching duration and lower output energy. Therefore, for a given latch geometry, output energy is proportional to latch removal velocity. When examining variation in shape and speed, slower latch removal rates yield systems more sensitive to latch geometry. At sufficiently high latch removal speeds, even a curved latch can instantaneously disappear, with the latch oppositional force decaying at a time constant smaller than spring recoil, thus mimicking a sharp latch.

We find that output energy from the antagonistic muscle pair latch is also affected by latch geometric and temporal properties (figure 4). Similar to our findings for the contact latch, both latch geometry and unlatching duration influence the magnitude and timing of the latch oppositional force. A shorter unlatching duration can increase energy delivered to the projectile, while an extensor offset angle closer to zero maximizes energy conversion efficiency, resulting in greater kinetic energy. When the extensor offset angle is set to an angle close to 0° , as found in biological systems [90], the energy conversion is less efficient, but the geometric advantage of the latch requires only a small latch oppositional force to oppose spring recoil. In sum, reachability with an antagonistic muscle pair latch is also increased by altering latch properties.

3.4. Control implementation and control objective metrics for LaMSA systems

Leveraging spring and latch reachability established in our above analyses, we test how interacting LaMSA components enable control systems implementation and control objectives (table 1). In the following sections, we apply TER (defined in section 2.3) in

the context of latch and spring properties across different models of control implementation. We apply VC and TER (defined in section 2.3) by measuring the change in spring and latch properties required to achieve target projectile takeoff energy given variation in preloaded spring energy. Adjustments to spring and latch properties that do not necessarily occur during real-time motion are analogous to developmental, behavioral, or evolutionary adjustments in biology or to changes in design or environmental sensitivity in engineered systems.

3.5. Feedforward control

We find that feedforward control yields reachability given an unperturbed system with stereotyped starting conditions (figure 5). Latch dynamics influence TER similarly to previous findings in which a large latch removal velocity results in instantaneous unlatching and higher projectile energy, while infinitesimally small latch removal velocity results in maximally attenuated projectile energy [22]. Therefore, increased TER occurs with increased range of latch removal velocities and latch radius. Nonlinear recoil forces and spring structure expand the influence of latch radius on TER. Stiffening springs (convex FL curve) access a greater range of outputs than softening springs (concave FL curve); for a given amount of spring displacement (during unlatching), there is greater sensitivity to changes in latch removal velocity in the case of a stiffening spring, even with the same initial energy before the onset of unlatching (figure 5(A)). Metamaterial springs with an applied external field manifest an even larger output range than homogeneous springs (figures 5(A) vs. (B)), largely due to the affordance provided by the external field, α , for any fixed geometry. Finally, metamaterial springs generate larger unlatching regions compared to homogeneous springs.

We also find that feedforward control enables compensation for variation in initial conditions to achieve controllability. We considered spring loading as the initial condition, but for other LaMSA systems, spring loading can serve as part of the run-time of the mechanism subject to feedback control. Latch design has a greater influence than spring design (figures 6(A) and (B)) and metamaterial springs exhibit superior performance compared with homogeneous springs (figure 6). Changing the spring exponent, n , does not significantly change VC in contrast to the findings with TER; VC is relatively invariant to the spring exponent. These findings suggest optimization of spring-latch-control properties which are mutually tuned for a particular use (e.g. maximum kinetic energy and/or controllability). For feedforward systems, spring design coupled with latch design is consequential for achieving compensation. Furthermore, if recoil time constants

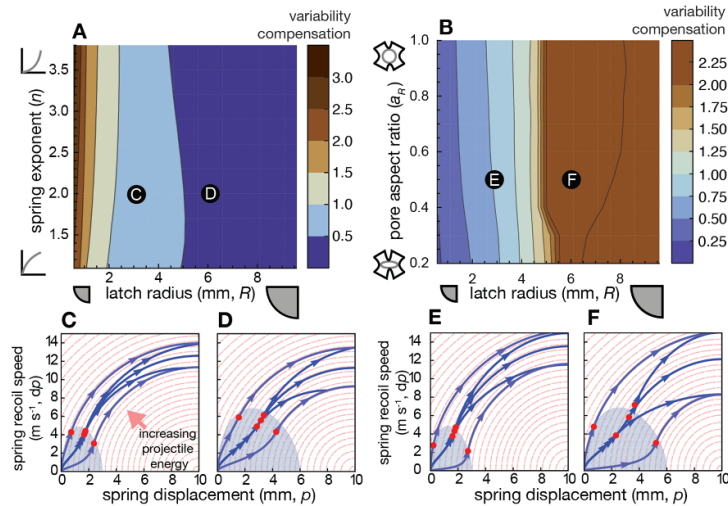


Figure 6. Feedforward control implementation via latch removal velocity minimizes the changes needed to compensate for perturbations due to variation in elastic potential energy thereby achieving controllability and compensation. (A) In polynomial springs, variability compensation (VC) is reduced primarily by increasing latch radius. (B) Metamaterial springs across a range of pore aspect ratios primarily reduce VC by decreasing latch radius, with the shifts in VC more directly tied to latch radius changes than in (A). (C)–(F) Each phase plot corresponds to the white letters on the heat maps in (A) and (B). Projectile state trajectory is shown for several combinations of spring and latch properties. Red contour lines represent projectile energy in systems with instantaneous latch removal at a spring displacement of 0; highest projectile energy is in the upper left-hand corner of each plot. Unlike in figure 5, which varied latch removal velocity while holding elastic potential energy constant, this figure depicts variation in latch removal velocity across simulations with varying elastic potential energy. The shaded blue region represents the approximate space over which the latch is removed; the red dots indicate the precise location of latch removal. Once out of the blue region, the latch is fully removed and the projectile is accelerated by the spring, such that the projectile's energy state changes according to the spring's viscoelastic properties. Variation in elastic potential energy varies behavior during the spring-driven movement (outside of the blue region). Latch retraction velocity compensates for variation in elastic potential energy during unlatching by dissipating energy to a greater or lesser extent. Since larger radius latches enlarge this unlatching region (E, F), those systems also enhance VC and controllability. Increased size of the blue region in (F) compared to (E) shows that larger latch radius enhances the ability of the latch retraction to compensate for preload variability. Note that in (B), the effect of normalization of the spring geometric parameters as the preload is varied counteracts the effect of the enlargement of the controllable region by increasing latch radius (as visible in E, F). Note that orientation of the contours in (A, B) indicates that latch radius has a greater influence on VC than the spring type. The metamaterial spring exhibits superior controllability compared to the polynomial spring, but counterintuitively, smaller latch radii are favored in VC by the metamaterial spring while the opposite is true for the polynomial spring.

are too fast for feedback (i.e. reactive) control in biomechanical systems, then these pathways for feedforward control are particularly important in the evolution of these systems.

3.6. Feedback control

We find that feedback control can reject perturbations during run-time (i.e. real-time) use of LaMSA systems. While spring recoil duration appears to preclude neural feedback control, other systems suggest that passive reactive behavior could enable real-time adjustment [37, 50, 91–95]. We find that real-time adjustments of latch forces and external fields can reject perturbations. Above, we demonstrated that increasing latch exponent, n and metamaterial springs (aspect ratio, a_R) (figure 7) radius increases TER for softening, linear, and stiffening springs; however, adding latch dynamics and an upper limit to the force required to remove the latch (F_{remove}) changes this conclusion. TER is more sensitive to variation in the exponent of the homogeneous spring than the aspect ratio of the metamaterial spring when a feedback linearization controller is applied to simulations with varying homogeneous (figure 7). As the latch motor's force limit is decreased, the

difference between the maximum and minimum TER is reduced, because latch removal force no longer maintains a constant latch removal velocity and retracts more quickly than desired, resulting in a lower TER (figure 7). The TER at lower latch velocities is more likely to be affected by the upper force limit of the latch motor, which indicates that more force is required for latch feedback control to slowly release spring potential energy than during faster latch retraction. Therefore, we apply a maximum of two feedback controls: a latch retraction force, $F_{\text{remove}}(\mathbf{x})$, from a latch motor with a maximum force F_{limit} , and a spring force, $F_S(\mathbf{x})$, when using a metamaterial spring sensitive to an external field (figure 7). When a spring without an external field control input is used, the system has one control input, $F_{\text{remove}}(\mathbf{x})$, to control spring position, p . When an external field-controlled metamaterial spring is used, the system becomes over-actuated (more control inputs than the number of controllable degrees of freedom). The over-actuation provides an additional pathway to design the feedback controller and can also help overcome actuation limits. Our derived feedback control is essentially a feedback linearization

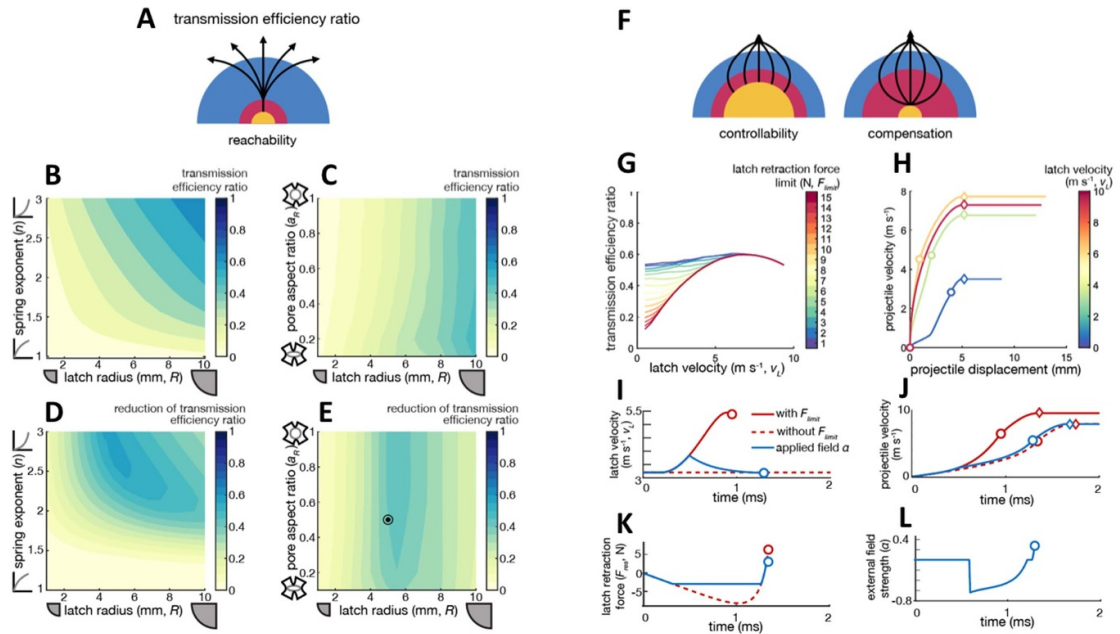


Figure 7. Transmission efficiency is enhanced through spring and latch properties, such that controllability and compensation of projectile velocity is achieved through cooperative negative feedback control of latch force limits and applied field in metamaterial springs. (A) Transmission efficiency ratio (TER) represents reachability and change in reachability in polynomial and metamaterial springs. (B) TER is greatest with larger radius latches with higher exponents, when latch retraction force is constrained to less than or equal to 3 N in the simulation ($|F_L| \leq 3\text{ N}$). (C) TER increases with increasing radius latches regardless of pore aspect ratio in metamaterial springs, when simulated latch retraction force is constrained to $\leq 3\text{ N}$. (D) Reduction of TER occurs when latch retraction force limit is removed. The heat map shows the difference between (B) with the latch force limit and the same simulation without a force limit. The darker blue region at the middle of the latch radius range indicates the intermediate radius latches most affected by the latch force limit. (E) The difference between the metamaterial spring simulation with and without a latch force limit reveals that reduction in TER occurs at intermediate radius latches, but with less reduction than in the polynomial spring in (D). Regions with greatest change (i.e. reachability) indicate particularly effective pathways for implementing feedback control to achieve controllability and compensation; we perform subsequent feedback control simulations in the high-change region as indicated by the black dot. (F) With a reachability configuration identified, we implement feedback control and assess how systems overcome or compensate for perturbations as expressed by these conceptual diagrams from figure 2. (G) Using the configuration indicated by the black dot in (E) ($R = 5\text{ mm}$, $a_r = 0.5$) TER increases as latch retraction force decreases at low latch removal velocities. Highest TER occurs at 6.4 m s^{-1} latch velocity. At high latch removal velocities, equivalent to an instantaneous latch release (9.4 m s^{-1}), TER decreases and converges regardless of latch retraction force limit. The configuration from (E) demonstrates a relatively large reduction in TER due to the latch retraction force limit (3 N). Latch retraction force limit of 15 N is equivalent to having no force limit, because the feedback controller is not saturated. (H) Using the state space trajectories in (C), mid-range latch velocity (orange, $v_L = 6.4\text{ m s}^{-1}$) yields a higher projectile velocity than faster latch removal velocity (red). Circles indicate when latch force decays to zero and diamonds indicate when the projectile is no longer powered by spring recoil. (I, J) Using the same state space configuration as the black dot in (E), we simulate latch velocity and projectile velocity with the latch retraction force limit (solid red line), without the limit (dashed red line), and with a feedback-controlled applied field that controls spring recoil (blue). Imposing the latch retraction force limit enhances latch and projectile velocity. Application of an applied field to control spring recoil allows control of latch velocity and projectile velocity (blue lines) to match the kinematics without a force limit (red dashed lines). (K) As latch retraction force is saturated due to the force limit (blue line; illustrates the output of the combined latch force limit and applied field), latch velocity cannot be regulated to the desired speed, $v_L = 3.2\text{ m s}^{-1}$. Instead, the latch is pushed away more quickly by the spring, resulting in the higher latch velocity in G (red solid line). Therefore, the projectile also moves faster (I, red solid line). (L) The applied field serves as feedback control of spring recoil and compensates for perturbation of the latch retraction force. This real-time control of the applied field is active 0.3 ms after latch retraction force saturation, thereby incorporating triggering delay. By decreasing the applied field, the spring is softened, and latch velocity is regulated to the desired speed before latch release, as shown in (G). Similarly, as shown in (I), maximum projectile velocity can be regulated using these cooperative feedback controls.

controller commonly used for analyzing nonlinear control systems [96].

Adding a metamaterial spring to this simulation further upends conventional wisdom. The previous study of the same exemplar model for an ideal Hookean spring (i.e. spring exponent $n = 2$) [22] shows that maximum transmission efficiency is achieved by instantaneous latch removal (also shown in figure 4). However, with a metamaterial spring, the fastest latch removal velocity does not yield the highest takeoff energy (figure 7), because of the non-monotonic nature of the metamaterial spring energy

efficiency when recoiling (figure 3). Instantaneous latch removal results in the start of unobstructed spring recoil at a larger global strain where efficiency is lower and more energy is dissipated. A slightly slower latch removal velocity allows the spring to start its recoil at a more optimal global strain—ultimately achieving higher projectile energy.

The two previous simulations used latch retraction force as the only feedback control input, but our final feedback simulation establishes a novel control approach for integrated LaMSA systems through cooperative feedback control between latch removal

force (F_{remove}) and spring recoil force (F_s) (figure 7). This cooperative feedback approach can overcome the force limit on the latch removal actuator (F_{limit}) that inhibits regulation of latch removal velocity. If latch feedback control is insufficient to maintain a constant latch removal velocity, then the spring can be softened (figure 7) to lower spring recoil force, thereby pushing the latch below the upper force limit of the latch removal actuator. This cooperative feedback control between the latch and spring recoil force is possible only during the latched or unlatching phase when both feedback control terms appear in the latch dynamics. This coincides with our intuition that after latch release, feedback control from both the spring and the latch is unlikely to be implemented simultaneously for aperiodic LaMSA systems.

4. Discussion

Our analyses demonstrate that the output of LaMSA systems can be varied, not only through changes in spring loading, but also through spring and latch geometry and dynamics. These findings indicate distinct mechanical pathways and strategies with which LaMSA systems can perform diverse uses while operating in and compensating for diverse environments. This controllability arises only when relaxing the traditional assumption that springs and latches are idealized components (i.e. the assumption that springs and latches are neither influenced by external conditions nor introduce energy losses in the system). We establish how these pathways of control can be realized. We establish a pathway through the non-linear dynamics of the recoiling materials that actuate these systems, including by actively adjusting the environmental conditions of these springs (i.e. through our applied fields). We establish a pathway by using latches to both control the rate of energy transformation and compensate for perturbations. Our approach and findings are unconventional given the historical focus on negative feedback control of the motor loading the spring, yet, at the same time, our findings are commensurate with the observed diversity of capabilities, uses, and environments of LaMSA systems in the natural world.

We find that feedback and feedforward control implemented through the non-linear dynamics of interacting LaMSA components can yield consistent outputs in variable conditions and variable outputs under constant conditions (figure 2). Feedforward control yields reachable outputs given the same starting conditions and consistent output in response to unwanted variation in starting conditions (figures 5 and 6). Likewise, feedback control, including cooperative control through spring and latch components, enables compensation for perturbations

during the running of the mechanism and consistent output (figure 7). Rather than deriving new control laws, we have applied existing control theory in new ways: we redefine control inputs by analyzing subsystems to identify variable component properties (figures 3 and 4), and we demonstrate the benefits of multiple and cooperative control in an over-actuated system (figures 5–7). Using quantitative metrics for comparing controllability, compensation, and reachability, we have demonstrated pathways for ultrafast, multi-component systems to achieve control objectives. Our mathematical modeling approach integrates the empirical data of spring metamaterial behavior and contact latch variation with a dynamic systems control framework. Thus, while the results presented here are specific to the pathways and dynamics of our models, these metrics and analyses apply to other LaMSA systems, the analyses of biomechanical systems in general, and to the synthesis of bioinspired mechanisms.

Latch dynamics are the most readily adjusted and tuned component during active use of LaMSA [88]. Our results offer insights into well-studied systems, such as how relaxation of the grasshopper's flexor tibiae muscle [85] triggers the jump and how the jump can be influenced during spring recoil by allowing the flexor to act as an 'imperfect latch'—in other words, absorbing undesirable energy from the spring (figure 4). Variation in flexor muscle activity [86, 87] can thus mediate the amount of energy released even with a maximally-loaded spring. This could be advantageous if organisms cannot reduce spring loading, either due to mechanical constraints or because conditions change. Additionally, this finding indicates the benefits of shorter relaxation durations for trigger muscles in order to minimize energetic losses of the latch. Indeed, fast-relaxing muscles are found in the latch muscles of mantis shrimp [97]. The control and tunability evidenced in our analyses have substantial implications for the as-yet unrealized capabilities of biological LaMSA systems and design strategies for broadly useful synthetic systems.

A key next step for this research is to incorporate bandwidth (the range of frequencies the system can produce) and latency (time required to respond to an input) for sensing and responding to stimuli in synthetic and biological LaMSA systems. Even so, biomechanical systems can be remarkably responsive to brief events, suggesting that LaMSA systems also have these abilities. Biological reflexes can be extremely brief: the reflexive roll correction of the fruit fly lasts 5 ms [98] and the squid startle reaction occurs within 50 ms [99]. 'Preflexes'—materials or structures that confer rapid responses to perturbations without needing nervous system activation [92]—include rapid responses to brief perturbations in cockroaches (13 ms), running birds

(<40 ms), flying birds (80 ms), and arboreal ants (<1 ms) [93–95, 100]. These material and structural-based rapid responses embedded in these highlighted biomechanical systems are almost certainly present in LaMSA systems. In addition, exploring the higher bandwidth of the actuators (e.g. piezoelectric and electrostatic) with a different size scale to understand the limits of fast dynamics control would provide the control bounds of the ultra-fast synthetic systems.

Biologists experimentally deducing mechanics, and engineers emulating integration and tunability, are both challenged and informed by organismal biomechanics [19, 68, 101]. These interdisciplinary challenges often converge in the realm of control systems and control objectives [102–108]. Control objectives [76] are not commonly defined as such in biomechanics research, yet biologists routinely experiment with robustness and responsiveness of mechanical systems in varying conditions. Therefore, our incorporation of these terms is intentional, encouraging an interdisciplinary language for the broad and diverse capabilities of biomechanical systems, while allowing our field to address broader capabilities beyond a focus on particular kinematic achievements, such as high acceleration. Furthermore, by recognizing the potential for components and their non-linear dynamic interactions to serve as control inputs, particularly via the spring and latch, we address control and component design simultaneously, ultimately revealing feedforward and feedback pathways for control in LaMSA. These insights and analytical approaches apply to LaMSA systems and to many other extraordinary mechanical systems in biology that have evolved the tuning and tunability among multiple components with complex dynamic interactions—ultimately serving as the foundation for their remarkable performance in complex and changing environments.

Our discoveries reveal multiple avenues for experimental analysis of biological LaMSA, controller design for diverse objectives in synthetic LaMSA systems, and, more broadly, analytical approaches that are applicable for many multi-component dynamic systems. For mechanisms with variable components, a system-level approach considering control contemporaneously with design is necessary to fully explore pathways for reachability, compensation, and controllability. In biology, control systems evolve in tandem with the mechanisms under control; therefore, selection for control objectives can shape the mechanism to have variable properties that are well-suited for different control schemes. Our findings are synergistic with analogous discoveries in other biomechanical and bioinspired systems, such as the non-linear dynamics of variable environments [109], dynamical systems modeling using losses and nonlinearities for control implementation [110], and feedforward control and distributed (decentralized) materials-mediated pathways for control [104, 105]. Finally, our

focus on leveraging the non-ideal properties of spring and latch dynamics—which have substantial losses at the small, ultrafast scales of LaMSA systems—follows in the illustrious, historical footsteps of leveraging losses in electronics to achieve and implement control, such as through the use of resistors and capacitors.

Organisms perform remarkable feats in ever-changing conditions—from maneuverable flyers to multi-terrain runners [111–113]—because the process of evolution yields integrated and tunable mechanical systems [30, 114, 115]. Biomechanical systems routinely achieve exceptional performance through integration of subsystems operating at different timescales [53, 105, 116, 117]—yet these are the very features that present the greatest challenges for testing and building these systems [53, 118, 119]. Examining one element by holding others constant often does not resolve the dynamics of these integrated systems [120]; furthermore, negative feedback control, feedforward control, and control objectives are well-defined in linear systems, but are difficult to define in non-linear, multi-component systems operating in diverse environments, which is the norm for biomechanical systems. Extending beyond linearized, feedback control of actuators mediated through sensorimotor systems, our study yields interdisciplinary principles of control pathways and objectives for feedforward and feedback control implementation via non-linear dynamics of biomechanical systems. The constraints and opportunities posed by tuning of complex components to yield control objectives are key to the rich diversity of biological LaMSA systems, offer principles for the design of synthetic LaMSA systems, and ideally reveal solutions to challenging control systems approaches and control objectives in diverse systems with similar characteristics.

Data availability statement

The data reported in this paper are presented in the manuscript, and the code to analyze the data is accessible at Dryad Depository [10.5061/dryad.tqjq2bw3g](https://doi.org/10.5061/dryad.tqjq2bw3g).

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Conflict of interest

Authors declare that they have no competing interests.

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