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Architectural gear ratio depends on actuator spacing in a physical model of pennate muscle

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Abstract

Pennate muscles are defined by the architectural arrangement of their muscle fibers, which run at an angle to the primary axis of muscle shortening. Pennation angles can vary dynamically over the course of individual contractions, influencing the speed and distance of muscle shortening. Despite their relevance to muscle performance, the physical mechanisms that drive dynamic changes in pennation angle remain poorly understood. Muscle fibers bulge radially as they shorten, a consequence of maintaining a constant internal fluid volume, and we hypothesized that radial interactions between tightly packed muscle fibers are essential to dynamic pennation angle changes. To explore this, we built physical models of pennate muscles in which the radial distance between fiber-like actuators could be experimentally altered. Models were built from pennate arrays of McKibben actuators, a type of pneumatic actuator that forcefully shortens and bulges radially when inflated with compressed air. Consistent with past studies of biological muscle and engineered pennate actuators, we found that the magnitude of pennation angle change during contraction varied with load. Importantly, however, we found that pennation angle changes were also strongly influenced by the radial distance between neighboring McKibben actuators. Increasing the radial distance between neighboring actuators reduced pennation angle change during contraction and effectively eliminated variable responses to load. Radial interactions between muscle fibers are rarely considered in theoretical and experimental analyses of pennate muscle; however, these findings suggest that radial interactions between fibers drive pennation angle changes and influence pennate muscle performance. Our results provide insight into the fundamental mechanism underlying dynamic pennation angle changes in biological muscle and highlight design considerations that can inform the development of engineered pennate arrays.

Introduction

Many skeletal muscles have pennate architectures, characterized by muscle fibers that run at an angle to the primary axis of active muscle shortening. The angle at which fibers run within a pennate muscle can vary dynamically, often by as much as 10–15 degrees of fiber rotation over the course of individual contractions (Narici et al. 1996). These dynamic changes in pennation angle are functionally relevant. Changes in pennation angle impact overall muscle length, allowing whole pennate muscles to operate over a greater

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range of strains than the individual fibers that compose them (Gans and Bock 1965). Dynamic changes in pennation angle also allow pennate muscles to automatically adapt their architectures to favor either high-force or high-speed contractions in response to the size of their load, a phenomenon described as variable gearing (Azizi et al. 2008).

Despite their functional importance, the physical mechanisms that drive dynamic changes in pennation angle during contraction remain unclear. In many early theoretical analyses of pennate muscle, muscle thickness, defined as the distance between sites of fiber origin and insertion within a muscle, was modeled as a constant that does not change over the course of contraction (Pfuhl 1937; Benninghoff and Rollhauser 1952; Gans and Bock 1965; Alexander 1968; Hatze 1978). This constant-thickness constraint helped to satisfy the physiological requirement that muscle maintain a constant volume as it forcefully deforms (reviewed in Otten 1988). It also provided a geometric need for muscle fibers to change pennation angle as they shortened, ultimately allowing dynamic changes in pennation to be modeled trigonometrically without consideration of the forces involved. A fixed muscle thickness is an elegant simplification that allows pennate muscle behavior to be modeled kinematically; however, models that employ this simplification cannot provide insight into the physical mechanisms underlying dynamic pennation angle change in most pennate muscles. Empirical observations show that in the absence of strict anatomical constraints muscle shape changes *in vivo* are complicated, involving expansion in planes orthogonal to the primary axis of shortening (Azizi et al. 2008; Arellano et al. 2016). In the unipennate lateral gastrocnemius muscle of the turkey *Meleagris galapavo*, for example, dynamic changes in fiber pennation angle have been observed even during contractions in which muscle thickness varies by more than 30% (Azizi et al. 2008).

In pennate muscles where a fixed thickness does not require changes in fiber length to be accompanied by changes in fiber orientation, what are the forces driving dynamic changes in pennation angle? We suspect that the constant volume nature of individual muscle fibers is crucial. Muscle maintains an essentially constant volume over the course of individual contractions (Baskin and Paolini 1967) and, consequently, individual muscle fibers must necessarily expand in radius as they shorten. Simultaneously, however, muscles are composed of hundreds or thousands of muscle fibers packed in close proximity with one another. Because of this tight packing, radially expanding muscle fibers must necessarily bulge into neighboring fibers during contraction. We hypothesize that dynamic changes in pennation angle reduce the energy of deformation by increasing the center-to-center distance between neighboring muscle fibers, ultimately minimizing spatial conflict within the muscle belly during contraction.

To explore the idea that dynamic pennation angle changes are tied to spatial conflict between radially expanding fibers, we built physical models of pennate muscle in which the radial distance between neighboring fibers could be experimentally altered (Fig. 1, 2). Models were built from McKibben actuators, a type of pneumatic actuator that forcefully shortens when filled with compressed air (Chou and Hannaford 1996). Although they are not isovolumetric, McKibben actuators serve as appropriate muscle fiber analogs for the current study because, like muscle fibers, they necessarily increase in radius as a function of longitudinal shortening. Actuator arrays comprised a total of seven McKibben actuators

anchored on acrylic plates representing abstracted aponeuroses. Arrays of McKibben actuators organized into a pennate arrangement have been used previously to replicate the phenomenon of variable gearing in pennate muscles (Azizi and Roberts 2013; Wang et al. 2022b). Such arrays facilitate a mechanistic understanding of pennate systems by allowing simultaneous monitoring of both global behaviors of the whole array and local behaviors of individual actuators. We measured actuator displacements, pennation angle changes, and architectural gear ratios produced during model contractions, and compared these properties across three distinct fiber spacing conditions that permitted varying degrees of radial interaction between bulging McKibben actuators. We predicted that the magnitude of dynamic pennation angle change produced by models would decrease as the amount of radial interaction between actuators was reduced.

Methods

Muscle models were built from an array of seven pneumatic McKibben actuators operating in parallel. Actuators were anchored at both ends to a pair of acrylic plates that served as abstracted aponeuroses. Three actuator spacing configurations were examined involving 20, 40, or 60 mm of radial distance between neighboring actuators (Fig. 2). In all configurations, actuators were spaced equidistant from their neighbors in the pattern of a regular hexagon, with one central actuator ringed by six peripheral actuators distributed at intervals of 60 degrees. Hexagonal packing provides the highest possible packing density of circles in a two-dimensional plane, minimizing empty space between neighboring actuators. Arrays were oriented to maximize vertical stacking of actuators, with three actuators aligned vertically along the midline of the array and two pairs of actuators flanking the midline laterally.

Each McKibben actuator comprised a 14 cm length of latex tubing (1/4" inner diameter, 1/32" thick walls) sealed with hose fittings and ensheathed in an expandable sleeve of braided plastic fibers (1/2" minimum diameter FlexoPET; Techflex Inc., Sparta, NJ; Fig. 1a). Inflation with compressed air resulted in forceful contraction of actuator length accompanied by radial expansion, as is typical of McKibben artificial muscles (see Chou and Hannaford 1996 for a detailed description of the mechanism underlying this behavior). Actuators were connected to the acrylic plates via custom anchors 3D-printed from polylactic acid (PLA) plastic. Anchors were bolted in place via through-holes drilled in the acrylic plates. Anchors were designed to allow free swiveling of actuators in the vertical direction at their connections with the acrylic plates, facilitating changes in actuator pennation angle during contraction.

All seven actuators composing an array were pneumatically continuous and connected to a common air source. Contractions were simulated by inflating arrays to an internal air pressure of 60 PSI using a hand pump. Air was then slowly bled from the pressurized arrays, allowing them to return to atmospheric pressure (defined as 0 PSI) over the course of approximately 30 seconds. Deflation of the arrays from 60 to 0 PSI was filmed in lateral view using a tripod-mounted digital camera (iPhone SE, Apple Inc., Cupertino, CA). Internal air pressure was recorded via a mechanical pressure gauge (1005 Commercial

Pressure Gauge, Ashcroft Inc., Stratford CT) connected in series with the array and mounted within the frame of the video.

Measurements of actuator length and actuator pennation angle were made from still video frames using ImageJ (Schindelin et al. 2012). Measurements were made at 10 PSI intervals over the 60 to 0 PSI deflation range. Actuator length was measured from the lower of the two flanking actuators nearest the camera. Pennation angle was measured as the orientation of this same actuator relative to gravitational vertical, as indicated by a plumb line suspended near the actuator array. The vertical height of the pennate array was calculated trigonometrically by multiplying the cosine of pennation angle with actuator length (Fig. 1b). The gear ratio at which an array operated over the course of a contraction was calculated by dividing the change in the vertical height of the array by the change in actuator length.

Array contractions were performed over a range of nine lifted loads: 0.5 kg and 2–16 kg in 2 kg increments. Loads were connected to the arrays at the base of the lower acrylic mounting plate, approximately 2 cm below the attachment of the lowest McKibben actuator. Three contractions were recorded and analyzed at each lifted load for each of the three spacing conditions employed, for a total of 81 contractions examined. To reduce the number of statistical tests employed, statistical analyses were performed at three representative loads: 0.5, 8, and 16 kg. One-way ANOVAs combined with post-hoc Tukey tests were used to compare actuator length changes, pennation angle changes, and gear ratios across spacing conditions at each of these representative loads. Statistical analyses were performed in R (<https://www.r-project.org/>).

Results

The largest changes in pennation angle observed in the current study occurred during contractions at the relatively crowded actuator spacing of 20 mm and the relatively light load of 0.5 kg (Fig. 3a). Arrays with less crowded actuator spacings of 40 mm or 60 mm demonstrated noticeably smaller changes in pennation angle when contracting against this same light load (Fig. 3b,c). At 16 kg, the largest load employed, pennation angle changes were relatively small and largely unaffected by spacing condition (Fig. 3a–c). In all contractions, pennation angle changes coincided temporally with decreases in actuator length, indicating that the two processes are mechanically related. In all contractions, the shapes of actuator length vs. inflation pressure curves were similar across the range of loads and array spacings examined (Fig. 3d–f), indicating that actuator spacing influenced the overall performance of pennate arrays without affecting the contractile behaviors of the individual actuators making up the arrays.

Dynamic changes in pennation angle, actuator length, and architectural gear ratio were examined as functions of load for each array spacing condition (Fig. 4). Dynamic changes in pennation angle tended to become less pronounced with increased load in arrays with 20 mm and 40 mm actuator spacings, while pennation angle changes remained relatively constant across loads in arrays with 60 mm spacing (Fig. 4a). The magnitudes of pennation angle changes differed significantly across spacing conditions. These statistical differences

are summarized visually in figure 4. At a relatively light load of 0.5 kg, one-way ANOVA indicated that pennation angle changes were not equal across the three spacing conditions examined ($p=1.84*10^{-7}$), and a post-hoc Tukey test confirmed that each of the spacing conditions were significantly different from one another at this load. The same was true at a moderate load of 8 kg; angle changes were not equal across spacing conditions (one-way ANOVA, $p=1.03*10^{-5}$) and a post-hoc Tukey test confirmed significant differences between all conditions. The magnitudes of pennation angle changes produced by models with different array spacings began to converge at higher loads. At 16 kg, one-way ANOVA indicated that pennation angle changes were not identical across spacing conditions ($p=5.36*10^{-4}$); however, a post-hoc Tukey test revealed that there is no significant difference between pennation angle changes produced in the 20 mm and 60 mm array spacing conditions ($p=0.32$). These results illustrate that actuator spacing has large and significant impacts on dynamic pennation angle changes during low-load contractions, but that the impact of spacing is reduced at higher loads where dynamic changes in pennation angle are negligible regardless of spacing condition.

Actuator length changes were consistent across all contractions examined (Fig. 4b), averaging 41.67 ± 0.93 mm (mean \pm SD) of shortening across all actuator spacing conditions and loads. One-way ANOVAs performed at 0.5, 8, and 16 kg confirmed that the magnitudes of actuator length changes were not significantly different ($p=0.82, 0.06, \text{ and } 0.10$, respectively), and post-hoc Tukey tests performed at each of these three highlighted loads confirmed that no significant differences existed between spacing conditions at any load. These findings confirm that spacing condition has a negligible impact on the length changes produced by individual actuators during contraction.

Architectural gear ratios were calculated mathematically from changes in pennation angle and changes in actuator length. Since actuator length changes remained essentially constant across all spacing conditions and loads examined (Fig. 4b), architectural gear ratios followed a qualitatively similar pattern to pennation angle changes in response to increased load (Fig. 4c). At a low load of 0.5 kg, one-way ANOVA indicated that gear ratios were not equal across the three spacing conditions examined ($p=2.43*10^{-8}$), and a post-hoc Tukey test confirmed that each of the spacing conditions were significantly different from one another at this load. At 8 kg, one-way ANOVA again indicated that gear ratios were not equal across spacing conditions ($p=5.31*10^{-6}$), and a post-hoc Tukey test revealed the 20 mm spaced array to be an outlier from the 40 and 60 mm spacing conditions. This pattern held true at 16kg. Gear ratios were not equivalent across spacing conditions at a load of 16 kg (One-way ANOVA, $p=4.01*10^{-5}$), and a post-hoc Tukey test again revealed the 20 mm condition to be an outlier. Gear ratios for the three spacing conditions were never found to be statistically equivalent at the loads examined in the current study. However, the trend of decreasing differences in gear ratios as load increases suggests that architectural gear ratios for the three spacing conditions are converging at a ratio of 1.0 at high loads.

Discussion

Consistent with the behavior of biological muscle, the pennation angles of our pneumatic actuator arrays changed dynamically over the course of individual contractions. The

magnitude of these pennation angle changes ranged from approximately 1 to 15 degrees and varied as a function of load, consistent with previous examinations of automatic variable gearing in pennate actuator arrays (Azizi and Roberts 2013; Wang et al. 2022b). The salient finding of the current study is that in addition to varying with load, dynamic pennation angle changes produced during contraction were also significantly influenced by actuator spacing, the radial distance between neighboring actuators within an array. Increasing actuator spacing reduced the magnitude of dynamic pennation angle changes exhibited by the pennate arrays and brought the architectural gear ratios at which they operated closer to 1.0. Increasing spacing to the point where neighboring actuators did not bulge into one another during contraction effectively eliminated both dynamic pennation angle changes and automatic variable gearing. These results indicate that radial interactions between actuators are essential to the mechanisms of dynamic pennation angle change and automatic variable gearing in pennate arrays. They inform our fundamental understanding of the mechanism of dynamic pennation angle change in both biological and engineered pennate actuator systems.

A mechanistic basis for dynamic pennation angle changes

We suspect that neighboring fibers bulging into one another is the crucial physical interaction that drives dynamic changes in pennation angle. Because of their constant volume nature, contracting muscle fibers that forcibly decrease in length must necessarily forcefully increase in radius. With hundreds or thousands of muscle fibers bundled in close proximity within a muscle, this need to change radius as a function of length presents a potential packing problem. If they are to actively decrease in length, closely packed muscle fibers must necessarily bulge into one another, pushing on their neighboring fibers and contributing to the development of intramuscular pressure. Shifting from a low pennation angle, in which actuators run relatively parallel to the primary axis of shortening, to a high pennation angle, in which actuators run relatively perpendicular to the shortening axis, increases the center-to-center distance between neighboring actuators within a pennate array. This phenomenon is easily demonstrated by manually changing the pennation angle of an actuator array and observing the difference in free space available between neighboring actuators (Fig. 5). It also underlies the established concept that pennate muscle architectures allow for a greater cross-sectional area of muscle fibers to be packed into a given volume of muscle than parallel architectures (Gans 1982). We suggest that dynamic changes in pennation angle in biological muscle arise purely as a means of reducing the energy of muscle deformation by decreasing spatial conflict within the muscle belly. Under this framework, dynamic pennation angle changes can be viewed as a natural consequence of a pennate system deforming along the path of lowest mechanical work.

Implications for muscle biology

A conceptual model of muscle mechanics in which radial interactions between fibers influence dynamic shape changes and pennate gearing carries several biologically relevant implications. Under such a model, any perturbation that alters the radial interaction of fibers within a muscle should be expected to influence pennation. Muscle hypertrophy, for example, which is characterized by increased muscle fiber diameter typically resulting from strength training, would be expected to result in an increase in pennation angle

that allows fibers of increased diameter to occupy a fixed area of origin and insertion. Consistent with this idea, hypertrophied muscles have been shown to display higher resting pennation angles relative to muscles from a control population (Kawakami et al. 1993), and muscles of individuals undergoing strength training have been shown to adopt higher resting pennation angles (Aagaard et al. 2001). Though they operate on vastly different timescales, we suspect that active bulging of muscle fibers during shortening contractions and growth-driven bulging of fibers during hypertrophy have analogous effects on muscle architecture. Both induce an increase in pennation angle that alleviates spatial conflict within the muscle belly.

Deformation of the attachment sites onto which muscle fibers originate or insert would also be expected to influence muscle performance. The acrylic mounting plates employed in the current study serve as infinitely stiff aponeuroses, resisting any appreciable deformation over the range of loads and contractile forces examined. In contrast, biological aponeuroses display in-plane straining during muscle contraction (Scott and Loeb 1995; Azizi and Roberts 2009; Arellano et al. 2016). This deformation has the potential to alleviate spatial conflict by facilitating radial displacement of neighboring fibers. Under this framework, the material stiffness of muscle aponeurosis becomes an important variable influencing dynamic muscle shape changes and gearing behaviors. Like an acrylic plate with relatively crowded actuator spacing, a stiff aponeurosis will keep muscle fibers in close radial contact throughout contraction, resulting in relatively large dynamic pennation angle changes to accommodate increases in muscle fiber diameter. In contrast, a compliant aponeurosis will allow bulging muscle fibers to be displaced radially into a conformation more akin to an acrylic plate with increased fiber spacing, providing an alternative means of reducing spatial conflict between fibers and reducing the need to alleviate spatial conflict through dynamic changes in pennation angle. Consistent with this idea, aged pennate muscles with increased aponeurosis stiffness have been found to display a consistently high gear ratio regardless of load (Holt et al. 2016), and experimentally weakening the aponeuroses of isolated pennate muscles through the introduction of longitudinal incisions has been shown to decrease gear ratio during high force contractions (Eng and Roberts 2018). Continued study of the influence of aponeurosis material properties on muscle performance is needed, especially when considering that biaxial strains have been shown to dynamically modulate aponeurosis stiffness (Azizi and Roberts 2009), suggesting that the force required to stretch the aponeurosis and displace muscle fibers radially will vary over the course of individual contractions and as a function of muscle shape.

Our physical model of pennate muscle focuses exclusively on the effects of actuator spacing; however, chronic or transitory changes in the bulk modulus of muscle are likely to have analogous effects on gearing behaviors. Contractions of our pennate physical model involve simultaneous inflation of all seven actuators composing the array. This is mechanically analogous to a muscle contracting under maximal stimulation such that all fibers across the entire cross section of the organ are active simultaneously. Most muscle contractions occurring *in vivo* do not involve maximal activation, and instead involve submaximal activation in which only a portion of the muscle cross-sectional area is active at any given time. Thus, the ability of a muscle fiber or group of muscle fibers to expand radially during shortening contraction may depend partly on the contractile state of neighboring

fibers. To date few studies have explored muscle dynamics under submaximal conditions, though recent findings suggest little change in architectural gear ratio under submaximal conditions (Tijs et al. 2021). Additional studies exploring the effect of submaximal muscle activation on gearing behaviors are needed. Other phenomena that have the potential to alter the bulk modulus of muscle include increased connective tissue deposition, as occurs in the pathological condition of muscle fibrosis (Lieber and Ward 2013) or increased fat deposition between fibers, as in the phenomenon of white striping (Kuttappan et al. 2013). Such changes have the potential to alter the magnitude of intramuscular pressures present within contracting muscle and influence the degree of dynamic shape change.

Finally, the findings of the current study imply that changes in pennation angle may influence the mechanical work required for active muscle deformation. In the absence of pennation angle changes, bulging muscle fibers can only forcefully shorten if they also forcefully displace or deform their neighboring muscle fibers. This radial pushing would require either the deformation of neighboring fibers or deformation of the aponeuroses onto which fibers attach, representing additional mechanical work that must be done by contracting fibers. Multiple empirical observations indicate that radial loads that inhibit muscle bulging influence muscle performance. Whole muscles loaded laterally with a weighted plunger exhibit reduced isometric contractile force that scales with the size of the lateral load (Siebert et al. 2014a; Siebert et al. 2014b), isolated muscles squeezed by a pneumatic pressure cuff exhibit reduced isometric force in some conditions (Sleboda and Roberts 2020), and isolated muscles fully encased in a rigid glass tube that confines their diameter exhibit decreased ability to perform mechanical work in the shortening direction (Azizi et al. 2017). Dynamic pennation angle changes provide a means of decreasing spatial conflict between bulging fibers, ultimately facilitating radial expansion of fibers. Any perturbation that alters the ability to change pennation angle, such as excess connective tissue deposition between the fibers of fibrotic muscles, may thus be associated with an altered energetic burden of contraction.

Implications for pennate actuator design

Multiple actuators that draw inspiration from pennate muscle architectures have been developed in recent years (Jenkins and Bryant 2020; Wang et al. 2022a; 2022b; Xie et al. 2023). In addition to informing our theoretical understanding of dynamic shape changes in biological muscle, our results highlight fundamental design considerations that can inform the construction of engineered pennate arrays. The key finding of the current study is that radial interactions between neighboring actuators are essential to the production of dynamic pennation angle changes during contraction. These interactions cause actuators to deform into a new conformation that we suspect minimizes strain energy within the array. It follows then that if a pennate array is to demonstrate variable gearing it must be composed of actuators that physically encroach upon one another during contraction. Specifically, the actuators must increase in size radially during contraction and they must be spaced closely enough together that this expansion causes spatial conflict. An array composed of actuators that decrease in length without increasing in diameter (via a telescoping mechanism or conformational change, for example) would not be expected to demonstrate variable pennate gearing no matter the arrangement of actuators. Similarly, an array with actuators spaced so

far apart that they never come into spatial conflict during contraction would not be expected to demonstrate variable gearing regardless of the mechanism of actuation.

Additionally, although physical encroachment is essential to the phenomenon of dynamic pennation angle change, actuator arrays must maintain the ability to deform internally throughout contraction. Actuators must be free to swivel or bend at their attachment sites and must also maintain some ability to move independently of their neighboring actuators. Reducing friction forces between neighboring actuators using lubrication or low-friction materials may be essential to increasing performance in situations where energetic efficiency is valued, as shear forces developed within an array will tend to inhibit dynamic changes in pennation angle. Pennate actuators must balance the need for forceful spatial conflict between neighboring actuators with the need to accommodate internal deformation at low force. These competing design constraints lie at the heart of the mechanism of dynamic pennation angle change. Continued study of the functional morphology and biomechanics of pennate skeletal muscle has great potential to inform the design of pennate actuator arrays and, reciprocally, continued study of the mechanics of pennate actuators will inform new approaches to understanding the physiology of skeletal muscle.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Data Availability

Any data that support the findings of this study are included within the article.

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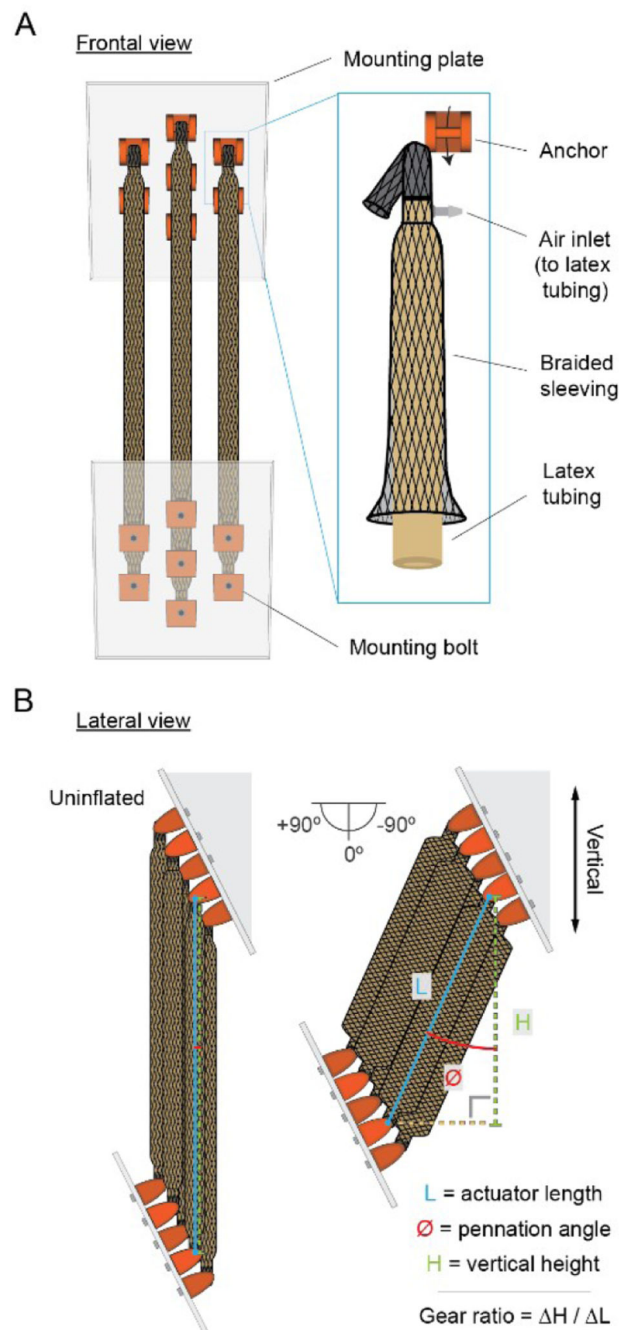


Figure 1: Schematic diagram of a pneumatic artificial muscle array. Primary components and variables of interest are depicted. [A] Frontal view of an actuator array, consisting of seven McKibben actuators. Inset image shows an individual McKibben actuator with key components exposed. [B] Lateral view of an array shown in both uninflated and inflated states. Actuator length (L, blue line) is measured as the distance between proximal and distal anchor points. Pennation angle (\emptyset , red arc) describes actuator orientation relative to gravitational vertical (denoted 0°). Clockwise rotation from zero is indicated with positive angles and

counterclockwise rotation with negative. Vertical height (H , green dashed line) is calculated trigonometrically from actuator length and pennation angle. Gear ratio quantifies the amount of vertical displacement produced per unit of actuator shortening and is calculated as the ratio of vertical height change and actuator length change produced over the course of a single contraction.

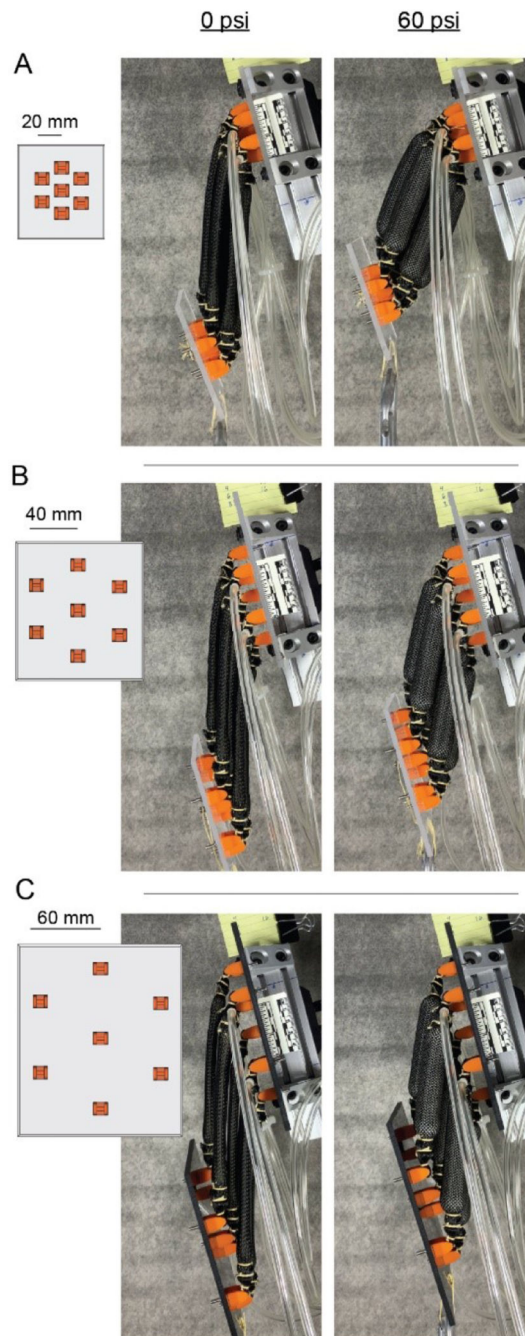


Figure 2:

Visual summary of actuator spacing patterns and their influence on array deformation. Arrays are fixed to an aluminum frame with their distal ends suspending a hanging load. All arrays are shown suspending a relatively light load of 0.5 kg. Left-column photographs show arrays in an uninflated state (0 psi), and right-column photographs in an inflated state (60 psi). Inset illustrations depict spacings of anchor points scaled to their accompanying images. [A] An array with anchors spaced 20 mm apart, allowing neighboring actuators to bulge into one another during inflation. [B] Anchors spaced 40 mm apart, decreasing the

amount of radial interaction between neighboring actuators. [C] Anchors spaced 60 mm apart, preventing neighboring actuators from contacting one another during inflation.

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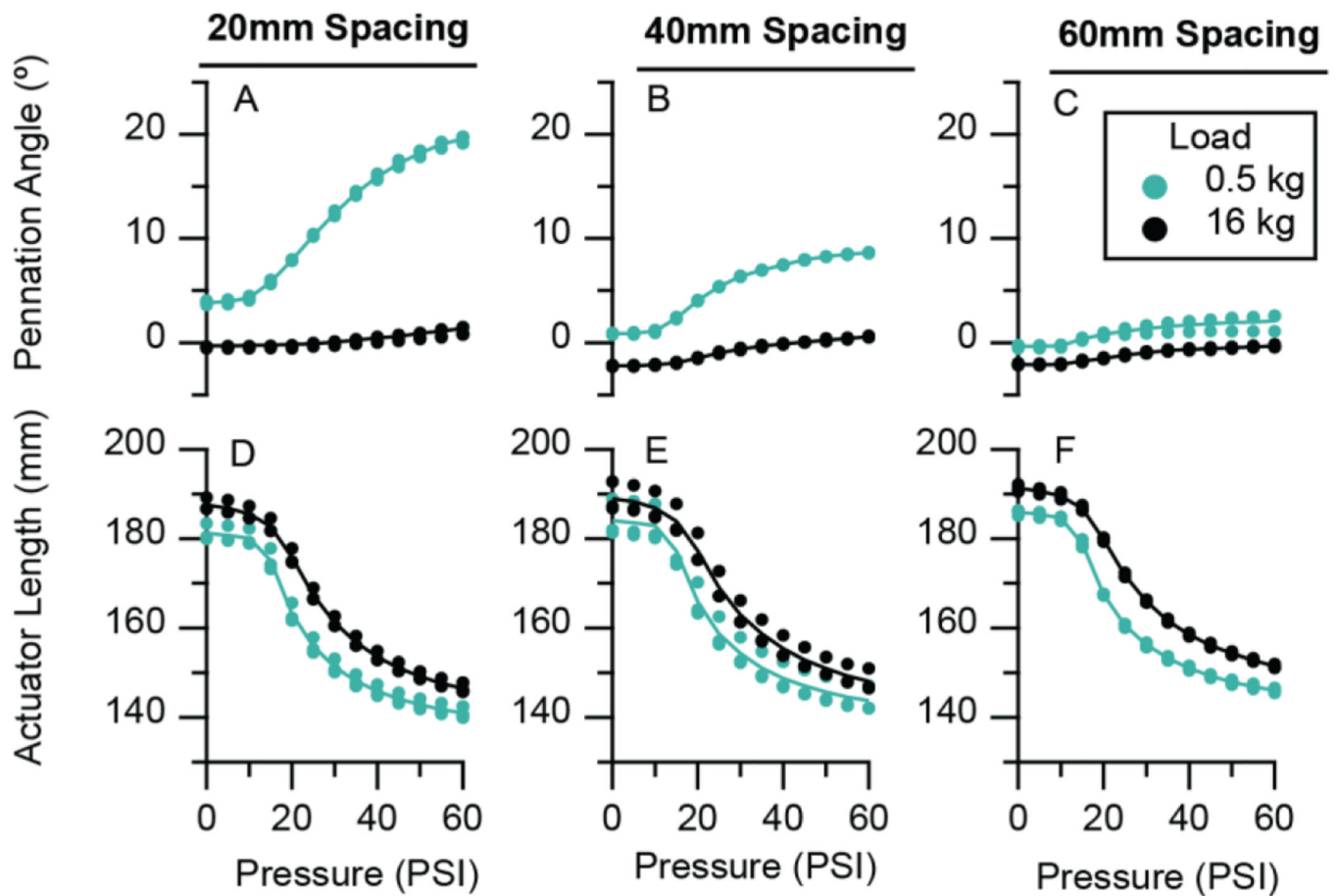


Figure 3:

Summary of the effect of array spacing on pneumatic deformation at two representative loads. Graphs depict pennation angles and actuator lengths measured from actuator arrays at a series of incremental inflation pressures. Teal markers denote values measured from arrays lifting a relatively light load of 0.5 kg. Black markers denote values measured from arrays lifting a relatively heavy load of 16 kg. $n=3$ inflation trials at each load. Solid lines connect average values calculated at each incremental pressure.

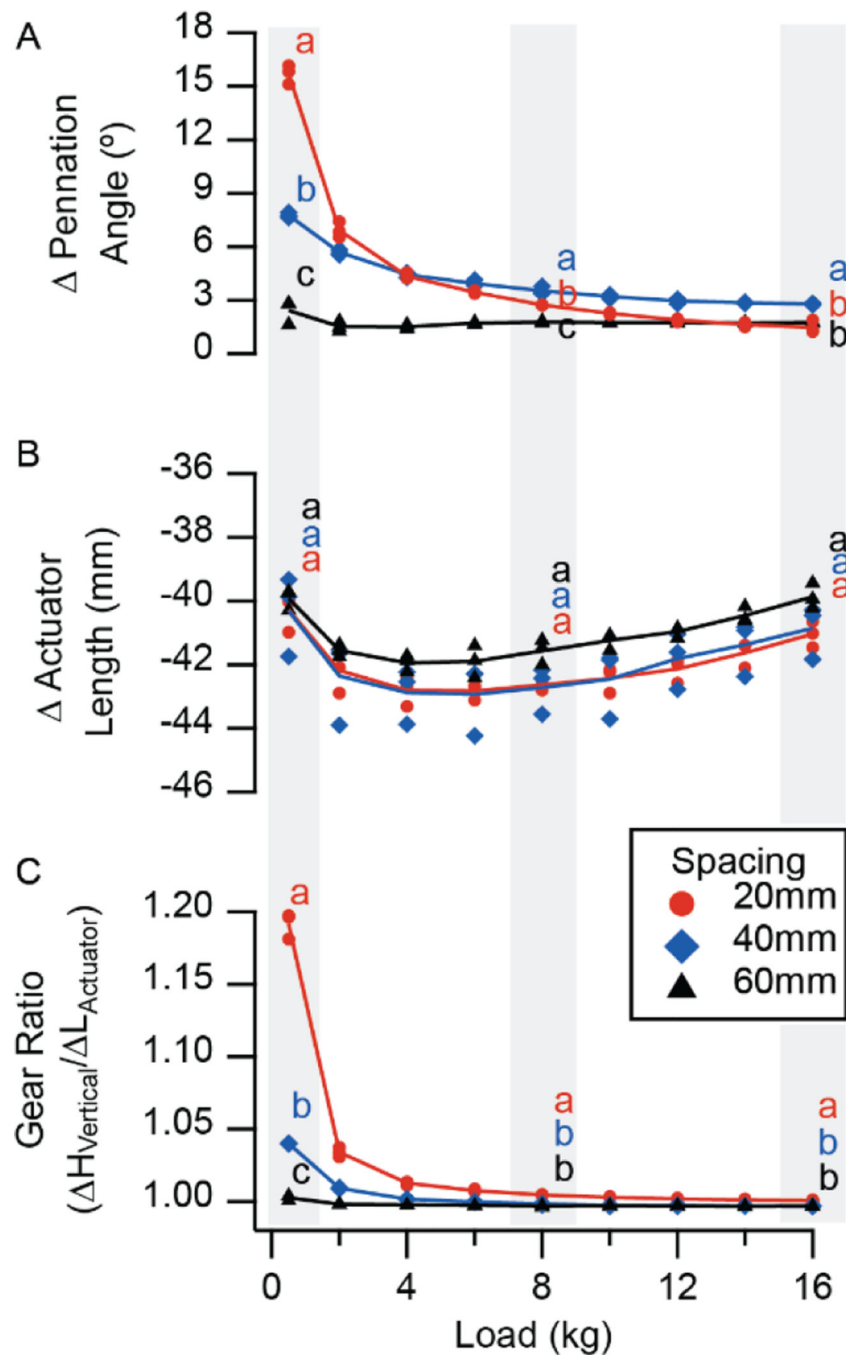


Figure 4: Summary of [A] changes in pennation angle, [B] changes in actuator length, and [C] gear ratio as a function of suspended load. All delta (Δ) values are calculated as differences between inflated (60 psi) and uninflated (0 psi) states over the course of a single contraction. Markers represent data collected from arrays with anchors spaced 20 mm (red circles), 40mm (blue rhombuses), and 60 mm (black triangles) apart. Solid lines connect average values calculated at each incremental load. Gray bars highlight loads at which statistical

analyses were carried out. Lowercase letters associated with gray bars denote statistical differences across spacing conditions and are color coded to their associated condition.

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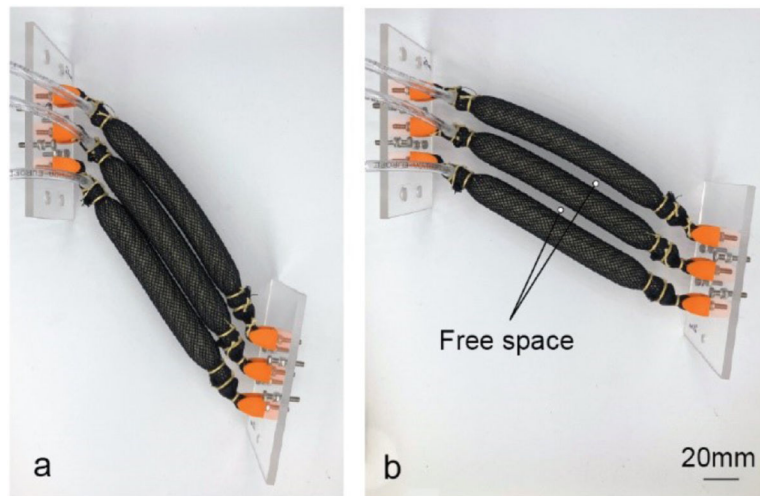


Figure 5: Demonstration of the effect of pennation angle on free space between actuators. A simplified pennate array consisting of three McKibben actuators resting on a horizontal tabletop is shown from above, in lateral view. No load is present. The array has been manually positioned to illustrate the space available between actuators at low (a) and high (b) pennation angles. Actuators have the same internal pressure in both conditions.