

# Elephant trunks: Strength and dexterity from mini-fascicles

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Muscular hydrostats, such as the elephant trunk, can perform precise motor actions. A new study has revealed that the elephant trunk contains a dense network of tiny muscle fascicles, suggesting that muscle miniaturization may be a key toward understanding how soft organs achieve both strength and dexterity.

There is a magical scene in Pierre Étaix's classic cinematographic comedy 'YoYo', where the eponymous young circus clown sits in the coiled trunk of an elephant and is gradually elevated above the crowd. What kind of musculature and neuromuscular control can perform such a feat? The elephant's trunk is an organ that offers amazing strength and flexibility. Controlling non-articulated organs like trunks appears to be complex, yet animals can move tongues and trunks with impressive speed and precision. New clues into how animals achieve such feats have been reported in a recent issue of *Current Biology* by Longren, Eigen *et al.*<sup>1</sup>, who utilized state-of-the-art X-ray tomography to generate a high-resolution, three-dimensional segmentation of the musculature along the trunk of an Asian baby elephant.

Flexible, non-articulated body structures are commonly composed almost entirely of muscle. These are referred to as muscular hydrostats: they can elongate, shorten, bend, and twist using local muscle contraction to deform the organ, subject to the hydrostatics of an incompressible fluid<sup>2</sup>. The complexity of these dynamics seems to pose a significant challenge for the motor control system because the possible deformations appear to occupy a very high-dimensional space compared to an articulated system. Yet elephants can both move heavy logs and, as the same research group recently showed, peel a banana with their trunks<sup>3</sup>. This reveals an impressive control of articulation over an extensive range of forces.

Contemporary researchers identify two key issues in the control of motor systems

with many degrees of freedom. First, control can be organized in a hierarchy of commands<sup>4,5</sup>. Ethological work on octopuses and elephant trunks has shown that these animals build behaviors out of a set number of 'motor primitives' as a strategy to simplify their motor control problems<sup>6,7</sup>. Second, the space of possible movement can be restricted through anatomical constraints. In their macro- and micro-anatomy, muscular hydrostats feature specializations that constrain movement in multiple ways. For example, the orientation of non-contractile elements in the octopus arm adds directional stiffness that supports arm bending, a common motor primitive<sup>7</sup>. In this context, detailed descriptions of muscular hydrostat anatomy, like the work of Longren, Eigen *et al.*<sup>1</sup>, are important for resolving questions about potential means for the underlying motor control.

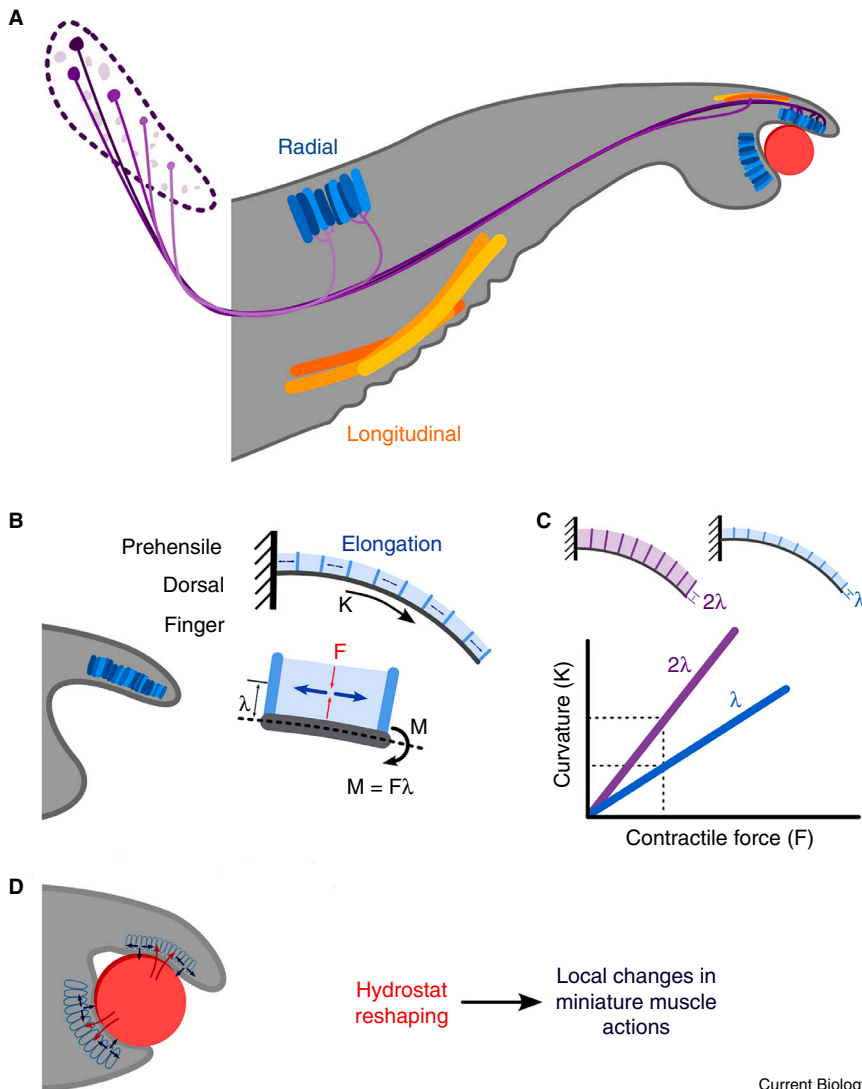
Longren, Eigen *et al.*<sup>1</sup> applied microfocus computed tomography ( $\mu$ CT) to a full Asian baby elephant hemi-trunk and completed the dense segmentation of the musculature of the proximal shaft, the middle shaft, and the tip. Muscles are organized into fascicles, which are bundles of tens to hundreds<sup>8</sup> of muscle fibers ensheathed by connective tissue, forming a functional unit. For the selected regions of the trunk, the authors segmented each individual fascicle, here defined as a muscle volume holding its own unique attachment points. Such a high-resolution reconstruction of trunk musculature was not feasible from earlier data sets<sup>9–13</sup> given limitations of prior technology. The use of  $\mu$ CT permitted Longren, Eigen *et al.*<sup>1</sup> to make a more accurate assessment of the total muscle

fascicle number, which the authors estimate to be an astounding 90,000 for the full trunk. This musculature gives the trunk its strength, while enabling its remarkable dexterity<sup>3,6,14</sup>.

Like articulated body parts, muscular hydrostats have distinct groups of muscle fascicles with antagonistic actions against each other. Longitudinal muscle fascicles, which run with the hydrostat long axis, cause shortening, while radial and transverse fascicles, which lay in the transverse plane, constrict and elongate (Figure 1A). Bending can be achieved by co-contraction of longitudinal fascicles on the inward side and radials on the outer side, which provides counterposed stiffness against which the longitudinal fascicles can pull. Longren, Eigen *et al.*<sup>1</sup> find that longitudinal fascicles are, in the aggregate, larger and longer than radial fascicles. However, longitudinal fascicles are vastly outnumbered by the smaller radials, which make up ~85 % of the total fascicle number. In the middle trunk shaft, an increase in longitudinal fascicle volume on the ventral side, and radial fascicle volume on the dorsal side, could facilitate both dorsal-side extension and inward bending.

The tip of Asian elephant trunks has a ventral lip and a dorsal finger that work in opposition to grasp an object. The tip, and the distal finger especially, is a highly dexterous prehensile structure capable of fine object manipulation<sup>3,6</sup>. Longren, Eigen *et al.*<sup>1</sup> document a large proximal-to-distal size gradient along the trunk, such that the trunk tip is composed of tiny fascicles, with a surprisingly small mean fascicle volume of  $10 \mu\text{m}^3$  in the dorsal finger. Radial fascicles occupy ~80% of the muscle





**Figure 1. Elephant trunk muscle architecture supports dexterous motor control.**

(A) Elephant trunks feature large longitudinal and small radial muscle fascicles oriented perpendicularly to each other. Fascicle composition and size vary along the trunk, and the distal tip is predominantly composed of tiny radial fascicles. (B) The prehensile dorsal finger is composed of miniature radial fascicles exclusively. We can idealize the dorsal finger as an array of elongating elements bending a stiff arm. Within each element, a moment of bending ( $M$ ) is induced by a muscle contraction force ( $F$ ) acting on the arm, applied offset from a neutral axis of bending (dotted line) by a distance  $\lambda$ . Uniform activation of the array causes curvature  $\kappa$  in the arm. (C) For elements with linear material properties, the slope of the force–curvature relationship depends on the distance  $\lambda$ . Miniature muscles, with their short muscle lengths, cause more graded changes in curvature for a given activation force, supporting fine motor control. (D) Deformation changes individual muscle actions in hydrostats by passive mechanisms. Muscle miniaturization may help fine scale tuning of muscle activity.

volume of the entire trunk tip, the remainder being a group of longitudinal fascicles in the dorsal proximal tip, while the finger is exclusively composed of radial fascicles (Figure 1A). Thus, fine motor control of the distal tip and finger is achieved by a dense mesh of thousands of miniature radial fascicles, each of which has distinct attachment points.

We now turn to the issue of neuronal control of the trunk. In the prototypical example of an articulated prehensile structure, the primate hand, fine motor control is achieved via a large expansion of the upstream neural circuitry for this body region<sup>15</sup>. Yet such representation expansion does not hold for the trunk. Rather, the number of trunk-innervating

motoneurons is slightly less than the estimated number of fascicles<sup>1,16</sup>, consistent with the notion of one motoneuron innervating many fascicles. How does the tip achieve dexterous manipulation of objects? While the mechanisms are not known, the answer may lie in the unique properties of hydrostats.

We idealize the dexterous distal tip finger as an array of elongating elements attached to one side of a stiff arm<sup>17</sup> so that the finger radial muscles can act against inherent or induced stiffness in the tissue (Figure 1B). Uniform contraction of radial muscles along these elements would cause unilateral elongation and bending of the arm. In this toy model, a limited number of control elements — motor neurons — activate an array of muscle fascicles to cause bending. This aligns the output actions of many individually controlled motor elements in parallel, both restricting the space of possible movement and permitting fine gradients of control. Based on the predicted contraction force–curvature relationship, initial activation of short versus long muscles would cause more graded changes in curvature (Figure 1C). Thus, the miniaturization of the muscle fascicles would provide a means for fine motor control.

The miniaturization of the muscle fascicles may help achieve dexterity in soft bodies by other mechanisms. As soft bodies deform in response to internal muscle contractions and interaction with external objects, tissue pressure is redistributed inside the hydrostat, and muscle architecture is reshaped. Hydrostat reshaping is known to change regional output forces<sup>18</sup>. In this regime, it is possible that miniaturization of the fascicles enhances passive mechanisms that match local muscle actions to the overall shape contours on a finer scale (Figure 1D).

Lastly, Longren, Eigen *et al.*<sup>1</sup> and prior work<sup>19,20</sup> demonstrate that elephant trunks possess extensive sensory innervation, especially at the trunk tip. The trunk tip not only contains different types of sensory nerve endings but also contains short and regular vibrissae, both densely innervated by sensory nerves. The tip can easily adapt its shape to an object being touched to pick it up<sup>6</sup>. This raises an interesting question about how

this dense sensory innervation interfaces with the motor control system to achieve haptic perception, that is, stereognosis and flexible object manipulation. Given the rich sensorimotor capabilities of trunks and organs like the mammalian tongue<sup>2</sup>, these interactions are likely to be a critical component of fine motor control in these complex, flexible organs.

#### DECLARATION OF INTERESTS

The authors declare no competing interests.

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## Epithelial homeostasis: Cell size shapes cell fate

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A new study shows that cell size, in conjunction with specific signaling pathways, controls apoptosis within developing tissues. Cells with smaller sizes and relatively smaller sizes compared to their neighbors exhibit an increased likelihood of undergoing apoptosis. These processes are regulated by the Hippo/YAP and Notch pathways, respectively.

In 1849, the French physiologist Claude Bernard introduced a concept<sup>1</sup> that would later be coined as ‘homeostasis’ by the American physiologist Walter Cannon in 1926<sup>2</sup>. Homeostasis is a crucial process that comes into play as living organisms mature, enabling the body to maintain a delicate balance in changing conditions.

When it comes to tissues, preserving their sizes and the number of cells within them is a fundamental aspect of this equilibrium. While it is intuitive to imagine that homeostasis of a number of cells is accomplished by a precise balance between cell division and death, we tend to use the word ‘precise’ in a naïve way.

Even in something as simple as a single layer of epithelial tissue, containing several tens of thousands of cells per square centimeter, the process of when and which cells divide and die remains far from predictable.

Apoptosis, or programmed cell death, serves as a crucial mechanism for

