Elephants evolved strategies reducing the biomechanical complexity of their trunk

Highlights

- Elephants evolved strategies reducing the biomechanical complexity of their trunk
- Object transport is achieved by propagating inward curvature from the trunk tip
- The trunk can form rigid segments connected by pseudo-joints for point-to-point motion
- The trunk tip tangential velocity obeys a power law with its path curvature

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In brief

Dagenais et al. uncover the biomechanics of the elephant trunk, showing that complex behaviors emerge from a finite set of basic movements. Curvature, torsion, and strain provide an efficient kinematic representation to decompose trunk trajectories into motion primitives. The trunk forms pseudo-joints and its tip follows a speed-curvature power law.
Elephants evolved strategies reducing the biomechanical complexity of their trunk

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SUMMARY

The elephant proboscis (trunk), which functions as a muscular hydrostat with a virtually infinite number of degrees of freedom, is a spectacular organ for delicate to heavy object manipulation as well as social and sensory functions. Using high-resolution motion capture and functional morphology analyses, we show here that elephants evolved strategies that reduce the biomechanical complexity of their trunk. Indeed, our behavioral experiments with objects of various shapes, sizes, and weights indicate that (1) complex behaviors emerge from the combination of a finite set of basic movements; (2) curvature, torsion, and strain provide an appropriate kinematic representation, allowing us to extract motion primitives from the trunk trajectories; (3) transport of objects involves the proximal propagation of an inward curvature front initiated at the tip; (4) the trunk can also form pseudo-joints for point-to-point motion; and (5) the trunk tip velocity obeys a power law with its path curvature, similar to human hand drawing movements. We also reveal with unprecedented precision the functional anatomy of the African and Asian elephant trunks using medical imaging and macro-scale serial sectioning, thus drawing strong connections between motion primitives and muscular synergies. Our study is the first combined quantitative analysis of the mechanical performance, kinematic strategies, and functional morphology of the largest animal muscular hydrostat on Earth. It provides data for developing innovative “soft-robotic” manipulators devoid of articulations, replicating the high compliance, flexibility, and strength of the elephant trunk.

INTRODUCTION

The elephant proboscis (trunk) functions as a muscular hydrostat:1 the coordinated contractions of antagonist muscles are translated into torsion, bending, elongation, shortening, and stiffening, not via the support of an articulated skeleton, but through shape changes that rely almost entirely on the near-incompressibility (constant volume) of the self-supporting trunk tissues. Remarkably, the elephant trunk can perform very delicate tasks such as manipulating a single blade of grass, but it is also capable of carrying heavy loads up to 270 kg.2,3 The proboscis serves elephants in multiple additional functions: breathing, olfaction, mechanosensation, vocalization, posture-based communication, siphoning/spraying water, sprinkling dust, and tool handling.2–12 In principle, a muscular hydrostat could exhibit a virtually infinite number of degrees of freedom. Hence, simplified control for task-specific trajectories is needed to escape the so-called curse of dimensionality.13 The composition of trajectories from building blocks (motion primitives) provides a solution to reduce the behavioral landscape complexity in muscular hydrostats.14–19

Here, we combine behavioral, kinematic, and functional morphology analyses of the elephant trunk and demonstrate the existence of simplification mechanisms in its integrated form and function. First, we provide evidence of compositionality at the behavioral level by showing that the elephant, when facing the task of grabbing and transporting with its trunk objects of various shapes, sizes, and weights (Figure 1A), resorts to a finite repertoire of basic strategies. Our results indicate that the shortest ballistic trajectories (extension, bending, and twisting) are concatenated into 17 primary behaviors and that changing the size or mass of target objects induces robust transitions in grasping behaviors (Figures 1B–1E). Second, we use high-resolution motion capture to track the trajectories of the continuously flexible trunk and we construct an effective kinematic representation of prototypical sequences via spatiotemporal maps of curvature, torsion, and longitudinal strain. Reproducible kinematic features extracted from these trajectory maps are interpreted as motor primitives, which can be linked directly to the underlying synergistic muscle groups responsible for bending, twisting, and elongating the trunk. We find that these kinematic primitives are specific to tasks and/or phases of motion. For example, when reaching for an object in front, longitudinal strain is the primary motor ingredient as the trunk elongates and retracts in a modular fashion, whereas during the transport phase, the
The dominant feature is the propagation of an inward curvature front. Conversely, when reaching for a target to the side, the trunk can form rigid segments connected by pseudo-joints, analogous to an elbow and wrist in an articulated skeleton.

A fundamental problem in analyzing neural control (and in robotics) is to identify how a specific movement is chosen, among all possibilities, to achieve a given point-to-point displacement. A common answer is that motion primitives might be selected as a compromise between cost functions, such as speed versus accuracy, precision versus efficiency, or velocity versus path curvature. In this perspective, we make a remarkable observation: in all analyzed trajectories, regardless of the specificities of the task, the 3D tangential velocity of the trunk tip obeys a power law with its path curvature, similar to human hand drawing movements in 2D, but with a different scaling exponent. Hence, we propose that the geometry of the path governs the kinematics in elephant trunk trajectories.

Moreover, we suggest that the passive activity of cross-helical connective fibers embedded in different planes, described here for the first time in the trunk, might reduce the trunk energetic expenditure when working through antagonist muscle groups. Finally, a non-trivial relation between longitudinal and cross-sectional strains suggests the contribution of nostril dilation and contraction during trunk elongation and shortening.

In brief, the elephant trunk illustrates how simplified strategies can be adopted by muscular hydrostats to negotiate with their intrinsic complexity. A striking parallel can be drawn with the octopus arm, which has independently evolved the formation of virtual joints during point-to-point motion and the propagation of a bend when reaching for a target. As these two lineages (elephants and octopi) are separated by nearly a billion years of evolution and rely on completely different nervous systems (a centralized cerebral motor cortex in the elephant versus a neural control largely de-localized in the arms in the octopus), it is tempting to conjecture that these strategies (making pseudo-joints and propagating a curvature front) are exceptionally efficient at the level of biomechanics and/or neuronal control.

We discuss our results in the context of so-called soft robotics, an emerging new paradigm with the ambition of developing robotic manipulators replicating the high compliance, flexibility, and strength of natural hydrostats. Web applications are publicly available at https://www.lanevol.org/projects/proboscis.
identify 17 basic behaviors manifested by the trunks of African elephants during the prehension phase of motion (Figure 1; Video S1; Data S1A). Using this ethogram across all 550 successful prehension sequences recorded for both animals, we estimated the probability of executing a specific basic behavior when presented with a specific shape (Figures 1B–1E).

We discovered that varying the size or the mass of the objects induces transitions in behaviors, and that such transitions are robust across different geometrical shapes. Figure 1B shows a size-induced behavioral transition: for the smallest objects (d1), the animal tends to either pinch them between the two tip fingers or grasp them with a full tip-grip from the side. The finger pinch is shape-specific and most probable for the thin cylinder. Less probable for d1 objects is a tip-grip from the top, which becomes the single most preferred strategy for slightly larger objects (d2), and one of two preferred prehension strategies (with suction, equally probable) for yet bigger (d3) objects. A distal flip is very frequently used to secure the transport phase after a d1 to d3 object has been picked from the ground. The animal transitions to a distal wrap of the trunk around d4 objects to pick them up from the ground. Bowing the head down in the direction of the object, pressing it against the ground, or sweeping it closer were sometimes used for largest objects. More rarely, the animal used one foot to push the big cylinder against its trunk or wedge it against the tusks before releasing it to the ground in a putative playful behavior.

Second, when varying the mass of the manipulated object, we also observed a transition in prehension strategies (Figure 1C), although not as sharp as when changing the size, suggesting that the tested range of weights was less of a constraint than the tested range of sizes. The combination of tip-grip from the top and distal flip is the preferred strategy for the spheres and cylinders of all tested masses, except for the heaviest cylinder, that the tested range of weights was less of a constraint than changing the size, suggesting that the apparent complexity of grasping behaviors can thus be reduced to a smaller set of basic modules, accounting for the ability to quickly learn new strategies by recombining a pre-defined set of primitive movements. It is likely that such successive choices involve compromises among gain/cost functions, e.g., the probability of a successful prehension and transport, energetic input, number of independent muscle fascicles to activate, or duration of the sequence.

Motion primitives and kinematic invariant
We decompose trajectories into five phases of motion: (1) reaching, (2) prehension, (3) transport, (4) release, and (5) reaching back. We use ellipses-and-backbone reconstructions to quantify the trunk conformations in 3D (Figures 2A and 2B) and extract the dominant motion primitives in each trajectory phase. All sequences analyzed here and virtual animations of the African elephant trunk with projected heatmaps of kinematic variables are available in the online supplemental material (Video S2; online application 1). We first examine a prototypical sequence, in which the trunk uses suction to lift and transport a wooden disk (Video S2).

Multi-axis deformations
Cross-sectional and longitudinal strains compensate (Figure 2C) as expected for a muscular hydrostat. Longitudinal strain moves the trunk end effector front and back without moving the head, and some distal shortening is associated with lifting the trunk up. The profile of longitudinal strain is symmetrically reproduced between the right-to-left and left-to-right sequences (Figure 2D): the whole trunk elongates during the reaching phase up to a maximal strain (>30%) close to the tip (at the trunk index i = 0.85, i.e., 85% of the total distance between the first and last rows of markers). The elongation between i = 0.25 and i = 0.55 is maintained for most of the sequence. On the other hand, the 40% most distal part of the trunk (0.6 ≤ i ≤ 1) retracts during the transport phase but elongates again during the release phase. While reaching back, most of the trunk progressively shortens. Compared to the analogous octopus arm, which uses a distally propagating bend when reaching for a target, the elephant adopts a simpler strategy: modular elongation in the direction of the object.
Curvature and torsion

External variables describing the trunk position, orientation, and velocity are shown in Figure S1. This extracorporeal representation is useful to disentangle the different phases of motion and to distinguish between planned and correctional actions (Data S1D). However, it is tedious to read, and we show below that curvature and torsion constitute a more appropriate parameter space (Figure S2) as they greatly facilitate interpretation of the trunk movements (Figure 3; Data S1E).

In the majority of point-to-point transport tasks, the trunk displacement mainly occurs in the sagittal plane; hence, the dominant ingredients of motion are found in the up-down curvature $\kappa_{12}$, as shown in Figure 3 for prehension tasks with five objects (cylinders with increasing diameter, $d_2$, $d_3$, and $d_4$; with increasing mass, $m_1$ and $m_2$; and a sphere with diameter $d_s$; Video S2). The rate of the sagittal curvature front displacement offers a simple framework to distinguish among categories of movements. Figures 3A–3C illustrate how the trunk adapts to cylinders of increasing size (diameter $d_2$, $d_3$, and $d_4$). The bend typically occurs in two steps. First, the most distal part of the trunk is bent inward during the prehension phase followed by proximal propagation of this curvature front with similar rates ($\approx 0.3 \text{ s}^{-1}$) for all sizes. However, when grasping the largest cylinder ($d_4$), an intermediate step of much slower curvature propagation ($\approx 0.06 \text{ s}^{-1}$) is observed. Note that the inward bend propagates more proximally for larger objects (30%, 40%, and 60% for $d_2$, $d_3$, and $d_4$, respectively). For $d_4$, the inward curvature is delimited by a sharp inflection point on the trunk, i.e., positive curvature (upward bend) is observed in the remaining proximal part, resulting in a S-shaped trunk. Moreover, the maximally curved posture is maintained for longer during the transport phase. Finally, relaxation from the curved state is quite symmetric for $d_2$ and $d_3$, whereas it happens in two steps for $d_4$, the first one with moderate rate ($\approx 0.11 \text{ s}^{-1}$), followed by an abrupt release. The weight of the object also influences the curvature front propagation: in comparison to the light cylinder (Figure 3A), manipulation of a heavier cylinder (Figure 3D) causes a faster and more proximal inward bend propagation, and the trunk stays in its maximally curved state for a longer time.

Figure 3E represents an impressive behavior executed while maneuvering the small wooden cylinder ($d_2$, $m_1$): after having picked up the object with a tip grip, the animal transferred it to the ventral part of its trunk and performed a full-trunk inward bend (bringing the tip fingers up to the mouth), while the cylinder rolled in the middle portion of the curled trunk, nonchalantly intermingling two complex activities (point-to-point trunk tip displacement and point-to-point object transport).

The kinematic profiles of Figures 3C and 3F illustrate the difference of strategy for grabbing a cylinder and a sphere (both with the same large diameter $d_s$) using a vertical and oblique wrap, respectively. The more challenging sphere involved a much longer prehension phase with the curvature propagating at a particularly low rate, immediately followed by a two-step relaxation.

These curvature maps exemplify how intrinsic kinematic variables can encode the unfolding of trunk conformations in serial phases of motion. The propagation of a curvature front initiated at the tip suggests the existence of a propagating front of muscle activation, analogous to what has been discovered in the octopus arm during the reaching phase.31–34

Joint-like twist

A “joint-like twist” movement was often recorded while the trunk reached behind to grab a treat (Figure 4A; Video S2): a sharp bend about halfway through the trunk length (with the ventral side of the trunk facing up distally to the joint), followed by a second bend before the tip of the trunk (with fingers wide open), creating the illusion of an arm with an elbow and a wrist. Three independent kinematic ingredients are necessary to
properly encode this posture (Figure 4A, right panel): the abrupt development of a sideway curvature front \(k_{na}\) is combined with a gradual accumulation of torsion \(t_{ba}\), whereas the inward curvature \(k_{nb} < 0\) exhibits two maxima (one just before the first virtual joint and a second one at the very tip, contributing to the second virtual joint). The longitudinal strain completes the picture: the trunk is contracted by 10%–15% everywhere except at the very tip, where it is close to zero. Elephants were previously described to form a joint at the distal part of the trunk forming a stiff pillar to apply vertical force and pick up granular food.41 Once more, a parallel can be drawn with the octopus arm, whose solution for point-to-point movements (food to mouth) is a combination of virtual joints and stiffened segments.28,30

**Sharp self-wipe twist**

Another behavior involving a spectacular twist was observed when the elephant attempted in early experiments to remove markers by using the trunk to wipe itself (Figure 4B; Video S2). Note that the capacity of a flexible arm to clean itself is of prime interest from a robotics point of view. In the first half of the trajectory, the trunk shortens homogeneously across its length (by 10%). Halfway through, the distal part elongates by \(\sim 20\%\) and the proximal part (until \(i \approx 0.6\)) relaxes back to the reference length. Concomitantly, (1) a front of sagittal curvature \(k_{nb} < 0\) is initiated at the tip and propagates very fast up to half the trunk length, (2) torsion \(t_{ba}\) is generated clockwise in a large interval \(0.5 < i < 0.9\) and anti-clockwise more locally near the tip, and (3) a slight curvature toward the left \(k_{na} < 0\) adds the final touch to the posture (Figure 4B, right panel).

**Velocity and path curvature relationship**

One key result of our analyses is that trunk tip trajectories exhibit a power law between 3D tangential velocity and the path curvature \(v_{\text{tip}} \sim \kappa_{\text{tip}}^{p}\) with \(p \approx 0.8\) (Figure 5). Other values of the scaling exponent have been measured in various biological systems such as human hand drawing movements \(p \approx -1/3\),24 human locomotion paths \(p \approx -0.26\) and -0.13\),22 human tongue movements \(p \approx -0.55\) and -0.33\),22 and Drosophila larval locomotion \(p \approx -0.24\) and -0.22\).26 Different arguments have been proposed to link these kinematic invariants with control aspects of motion such as minimization of trajectory variance, of jerk, or of mechanical power.22,24,27

**Escaping the high-dimensionality problem**

In brief, complex trunk trajectories are decomposed into reproducible piece-wise primitives expressed in the profiles of curvature, torsion, and longitudinal strain. These motion primitives are highly relevant from a motor control point of view as they can be mapped directly to the activity of specific muscle groups responsible for bending, twisting, and elongating the trunk. Certain
mechanical and kinematic parameters uncovered here (Table S2; Data S1F) can be directly used in a soft robotics biomimetic approach.

Muscular synergies
Using state-of-the-art computer tomographic (CT) scan, magnetic resonance imaging (MRI), an in-house developed macro-scale serial-sectioning method (STAR Methods), and histology, we characterized the anatomy of the African and Asian elephant trunks in unprecedented detail. A combination of longitudinal, radial, transversal, and oblique muscle groups, traversed and clothed by nervous and connective tissues and wrapped in a hyperkeratinized skin, have been previously identified in the elephant trunk. Here, we produced high-resolution images (30 microns/pixel) of transversal (Figure 6), sagittal, and coronal sections of the trunks as well as MRI virtual sections. MRI series are also presented in Videos S3 and S4. In addition, we generated high-resolution polygon meshes of (1) the skin surface (Figure S3A) and (2) the six muscle groups (Figure S3B). In the online supplemental applications 2–9, the complete series of anatomical sections can be examined at full resolution and meshes can be manipulated in 3D. Anatomists from the previous century have reported up to 150,000 muscles in the Asian elephant trunk, but our images indicate that they were in fact counting muscle fascicles. Below, we explore the anatomy of the trunk in relation to each specific mechanical function of muscular hydrostats, which present a one-to-one correspondence with the intrinsic kinematic variables described above (strain, curvature, and torsion).

Elongation and shortening
The basic function of the radial dorsal, radial ventral, and transversal (rectus nasi) muscle groups (in red, dark blue, and green, respectively, in Figures 6 and S3B) is to reduce the diameter of the trunk, inducing its passive elongation. Muscle groups work in antagonist pairs: contraction of the dorsal longitudinal group (maxillo-labialis, orange in Figures 6 and S3B) or the superficial and deep oblique groups on the ventral side (pars rimana and pars supralabialis, in pink and pale blue, respectively, in Figures 6 and S3B) causes shortening of the trunk, inducing a passive increase in diameter. We measured an exceptional elongation capacity of the trunk of 135% (length ratio between the longest and shortest trunk states).

The muscles’ relative volumes are very well conserved between the two species, with 28% and 24% of the total trunk volume occupied by muscles in the African and Asian elephant trunks, respectively.
volume occupied by the longitudinal muscle group for the African and Asian elephants, respectively; 10% and 15% by the superficial oblique; 14% and 15% by the deep oblique; 28% and 21% by the radial dorsal; 13% and 15% by the radial ventral; and 7% and 10% by the transversal muscle group. Note that the proximal end of the longitudinal muscle group attaches anteriorly on the cranium43 (Video S3), similarly to the protruding tongues of certain animals (lizard, armadillo, opossum, and pangolin) that originate outside the oral cavity.1,46

The relation between longitudinal and cross-sectional strain is captured by four components of the strain-dependent Poisson’s ratio (\(n\)), which were estimated from the graphs of \(D_{aL} = a_0\) versus \(D_{L} = L_0\) and \(D_{b} = b_0\) versus \(D_{L} = L_0\) (where \(a\) and \(b\) are, respectively, the radii of the large and small axes of the ellipse cross-section): \(n_{aL} = 0.33\), \(n_{bL} = 0.28\), \(n_{La} = 0.38\), and \(n_{Lb} = 0.35\) (Figures S4D–S4F; Data S1G). These values reflect approximate isotropy between the cross-sectional and longitudinal directions, as well as between the two antagonist processes of elongation and shortening. It is also consistent with the maximal change in volume of \(DV/V_0 \sim \pm 5\%\) for \(\pm L/L_0 \pm 15\%\), which we recorded (Data S1G). The apparent compressibility of the trunk \((v_{La} + v_{Lb} \neq 1)\) might be due to the presence of the nostrils, two air-filled cavities with variable cross-sectional areas.47 For example, dilating the nostrils while contracting the outer diameter would contribute to the elongation of the trunk without being accounted for in the overall diameter change \((\Delta D/D_0)\), thus causing Poisson’s ratios to be underestimated.

Embedded crossed-fiber connective tissues play a major role in shape control (limiting deformations) and elastic recoil during antagonist movements.46,48,49 Here, we show that intramuscular connective fibers in the transversal plane (Figures 6 and S5B; Data S1H) might store potential energy when the cross-sectional area of the trunk is passively increased, allowing the trunk to elongate again with less active force. Note that histological sections of the large nerve bundles running longitudinally into the trunk (Figures 6, 7, S5C, S6D, and S6E) reveal an undulated arrangement (Figure S6E) that allows the nerves to sustain large trunk elongation without undergoing strain-induced damage (Data S1H).

**Torsion**

The fiber angle of the oblique muscle groups (measured from the longitudinal axis) is determinant for the mechanical behavior: below or above the critical angle \(\theta_c = 54^\circ 44'\), their contraction induces, in addition to torsion of the trunk, its overall shortening or elongation, respectively.1 The superficial and deep oblique muscles show angles \(\theta = 20^\circ 30'\) (Figure 7A). Hence, these are also trunk shorteners. The concomitant \(-10\%\)–\(-15\%) negative strain that we observed during the joint-like twist and the sharp self-wipe twist (where torsion plays an important role) is compatible with this suggestion.

Oblique muscles run with opposite angles on the left and right sides of the trunk, forming a V-shape with the open side facing the tip of the trunk for the superficial oblique group and with the pointy side facing the tip for the deep oblique group. Given

![Figure 5. Power law between tangential velocity and path curvature at the trunk tip](current_biology≦ð'5 injecting 54727.png)
that these fibers follow the curvature of the trunk surface, the right and left superficial oblique muscles form a left-handed and right-handed helix fiber arrangement, respectively, and inversely for the deep oblique muscles. Therefore, torsion of the trunk can be amplified by the activation of the fibers with the same helix-handedness, i.e., in different muscle groups on opposite sides of the trunk. Note that, because of its more external location from the central axis, the superficial oblique group generates larger torque ($r \times F$) than the deep oblique muscles, for an equal force.

The superficial and deep oblique groups are tightly entangled at their junction, displaying a braided design of alternating muscle strands (Figure 7A). The confinement of the muscle groups responsible for torsion to the ventral side might be a morphological adaptation granting greater dexterity to that side of the trunk, specialized in wrapping, squeezing, holding, transporting, and pressing items against surfaces. The stress generated by the ventral oblique muscles can be transmitted to the dorsal side by the connective tissue wrapped around the muscular core, with a cross-helical arrangement visible in the most lateral parasagittal sections of the trunk (Figure 7B), at the junction of the obliques and longitudinal muscles (with helix angle $\psi = 42^\circ$). Moreover, the ventral side presents a concave surface (akin to the palm of a hand), covered with large transversal wrinkles (Figure S3A), which aid in gripping and holding objects.

**Bending**

There are two possible mechanisms of bending: either via longitudinal contraction on one side (the dorsal longitudinal or the ventral obliques for an upward or inward bend, respectively, or an appropriate lateral combination of those three groups for sideways curvature) while actively keeping a constant diameter by contraction of cross-sectional muscle groups (transversal and/or radial), or via a reduction of the diameter while actively keeping a constant length on one side, resulting in a passive elongation on the convex side of the bend. Accordingly, we have shown that upward curvature ($\kappa_{\text{ob}}>0$) is accompanied by a dorsal longitudinal shortening ($\Delta L/L_0<0$), and vice versa. For trajectories involving the propagation of an inward bend from the tip, we typically observe a negative peak in the longitudinal strain of about $-15\%$ at the location of the inflexion point (where $\kappa_{\text{ob}}$ changes sign or goes to zero), indicating that the dorsal longitudinal muscle group is locally shortened at the curvature wave front.

Activating both sides (left and right) of the same oblique group (deep or superficial) or both oblique groups (superficial and deep) on the same side (left or right) with equal strength would suppress any undesired torsional effect due to their opposite handedness. The external location of the longitudinal/oblique groups allows them to generate greater moment arm for bending. Note that intramuscular connective tissue fibers oriented in the transverse plane (Figures 6 and S5B) might help the trunk to bend with more energetic efficiency, by resisting the passive increase in diameter imposed by the unilateral longitudinal contraction, and thus reducing the amount of active force needed from the cross-sectional muscle groups. The muscle arrangements in the dorsal and ventral tip fingers (Figure S7) reflect a greater ability for bending (Data S1I), compared to a reduced capacity for torsion.

**Stiffening**

One additional muscular synergy consists in multi-axial contractions allowing the elephant to produce localized stiffening of the trunk. During our prehension experiments, we observed that the ventral side of the trunk sometimes applied downward forces on objects, prior to a distal wrap. In this case, stiffening allows resisting diametrical compression. It is likely that the animal is finely adjusting the local stiffness of its trunk to control the surface contact with the manipulated object.

**DISCUSSION**

In the present study, we combined kinematic analyses with anatomical measurements to uncover the fundamental...
biomechanics of the elephant trunk. First, we quantified the prevalence of 17 basic prehension strategies of African elephant trunks in point-to-point transport tasks, reflecting the compositionality of motion as a crucial simplification mechanism for controlling this muscular hydrostat. Our results highlight robust behavioral transitions as a function of the size or mass of the target objects. The catalog of actions reported here only encompasses a small subset of all possible trunk behaviors and many other movements would be worth investigating, especially focusing on the trunk tip region. Second, we reconstructed the dynamics of 3D conformations of the African elephant trunk from high-resolution motion capture data, and we showed that specific actions are translated as signature patterns in the spatiotemporal maps of strain, torsion, and curvature. Out of a virtually infinite conformational space, we identified simple kinematic solutions accounting for distinct trajectory phases. This suggests a potential mechanistic solution for a nervous system to control the complexity of muscular hydrostats. In particular, the elephant adopts basic strategies such as successively elongating and retracting specific portions of the trunk when reaching for a target in front, or propagating an inward curvature front (initiated at the tip) during the transport of objects. We also revealed that the elephant trunk can form functional joints when achieving point-to-point displacements, reminiscent of a strategy of the octopus arm and reinforcing the idea that joint formation in soft manipulators is an efficient solution (both in terms of mechanics and control) for point-to-point motion.\(^{26,30}\) Additionally, we extracted invariance principles from the kinematic analyses, demonstrating that a power law exists between the tangential velocity and path curvature at the trunk tip \((\nu \sim \kappa^{-2/3})\), which differs from the relation found in human hand movements \((\nu \sim \kappa^{-1/3})\).\(^{24}\)

Finally, we investigated the internal morphology of the elephant proboscis with unparalleled precision, revealing the orientation of muscles and connective fibers and their microscopic structure. By analyzing the anatomical data in the light of our kinematic results, we draw a strong connection between the muscular system of the trunk and its biomechanical functions. Electromyographic investigations of the proboscis and recording of the elephant brain activity would clearly deepen our understanding of the underlying neuromotor control, although such experiments would be particularly difficult to implement in elephants compared to smaller species.

In conclusion, our study offers unprecedented insights into the anatomy and biomechanics of the largest muscular hydrostat on Earth: we characterized the elephant trunk motion as a partition of building blocks, both at the biomechanical level (expressed as muscular synergies) and at the kinematic level (translating into trajectories encoded via intrinsic trunk variables). The description of motion based on a finite set of primitives and the identification of kinematic invariants can greatly reduce the complexity of control in animal motion and robotics. Solutions derived from natural systems can inspire engineers to select proper approaches, and our study has the potential to guide the design of an innovative biomimetic soft manipulator (https://www.proboscis.eu).

Figure 7. Muscular anatomy in the proximal part of an Asian elephant trunk
(A) Coronal sections (MRI virtual sections in left halves and physical sections in right halves) in ventral, central (below the nostrils), and dorsal (above the nostrils) portions. The white dashed lines highlight the braided arrangement of the two oblique muscle groups.
(B) Sagittal sections (MRI in proximal halves and physical sections in distal halves) in lateral, mid-lateral, and central (intersecting the nostril) portions. Black lines highlight the cross-helical connective fibers at the junction of the oblique and longitudinal muscles. Muscle groups are indicated as in Figure 6. Star symbol, proboscideal nerve bundles; arrow, blood vessel.
See also Figure S7, Videos S3 and S4, and online applications 6 and 7.
STAR METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.08.029.
A video abstract is available at https://doi.org/10.1016/j.cub.2021.08.029#mmc8.

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AUTHOR CONTRIBUTIONS

M.C.M. supervised all aspects of the study. P.D., M.C.M., and S.H. designed and conducted the behavioral study with assistance of V.H. P.D., V.H., and M.C.M. performed the anatomical study. Histology was performed by V.H. P.D. and M.C.M. analyzed all data and wrote the manuscript. All authors read and approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare that they have no competing interests.

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REFERENCES

1. Kier, W.M., and Smith, K.K. (1985). Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. Zool. J. Linn. Soc. 83, 307–324.
2. Dehnhardt, G.F.C., and Sachser, N. (1997). Sensitivity of the trunk of Asian elephants for texture differences of actively touched objects. Proceedings of the International Symposium on Physiology and Ecology of Wild and Zoo Animals 2, 37–39.
3. Shoshani, J. (1997). It’s a nose! It’s a hand! It’s an elephant’s trunk! Nat. Hist. 106, 37–43.
4. Chevalier-Skolnikoff, S., and Liska, J. (1993). Tool use by wild and captive elephants. Anim. Behav. 46, 209–219.
5. Rasmussen, L.E., and Munger, B.L. (1996). The sensorineural specializations of the trunk tip (finger) of the Asian elephant, Elephas maximus. Anat. Rec. 246, 127–134.
6. Shoshani, J. (1998). Understanding proboscidean evolution: a formidable task. Trends Ecol. Evol. 13, 480–487.
7. Hart, B.L., Hart, L.A., McCoy, M., and Sarath, C.R. (2001). Cognitive behaviour in Asian elephants: use and modification of branches for fly switching. Anim. Behav. 6262, 839–847.
8. Garstang, M. (2004). Long-distance, low-frequency elephant communication. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. 190, 791–806.
9. Martin, F., and Niemitz, C. (2003). “Right-trunkers” and “left-trunkers”: side preferences of trunk movements in wild Asian elephants (Elephas maximus). J. Comp. Psychol. 117, 371–379.
10. Shoshani, J., Kupsky, W.J., and Marchant, G.H. (2006). Elephant brain. Part I: gross morphology, functions, comparative anatomy, and evolution. Brain Res. Bull. 70, 124–157.
11. Niimura, Y., Matsu, A., and Touhara, K. (2014). Extreme expansion of the olfactory receptor gene repertoire in African elephants and evolutionary dynamics of orthologous gene groups in 13 placental mammals. Genome Res. 24, 1485–1496.
12. Plotnik, J.M., Brubaker, D.L., Dale, R., Tiller, L.N., Mumby, H.S., and Clayton, N.S. (2019). Elephants have a nose for quantity. Proc. Natl. Acad. Sci. USA 116, 12566–12571.
13. Bellman, R.E. (2015). Adaptive Control Processes (Princeton University Press).
14. Mussa-Ivaldi, F.A. (1999). Modular features of motor control and learning. Curr. Opin. Neurobiol. 9, 713–717.
15. Mussa-Ivaldi, F.A., and Bizzi, E. (2000). Motor learning through the combination of primitives. Philos. Trans. R. Soc. Lond. B Biol. Sci. 355, 1755–1769.
16. Wolpert, D.M., and Grillner, S. (2000). Computational principles of movement neuroscience. Nat. Neurosci. 3 (Suppl.), 1212–1217.
17. Flash, T., and Hochner, B. (2005). Motor primitives in vertebrates and invertebrates. Curr. Opin. Neurobiol. 15, 660–666.
18. Anderson, D.J., and Perona, P. (2014). Toward a science of computational ethology. Neuron 84, 18–31.
19. Wiltschko, A.B., Johnson, M.J., Furlani, G., Peterson, R.E., Katon, J.M., Pashkovski, S.L., Abraira, V.E., Adams, R.P., and Datta, S.R. (2015). Mapping sub-second structure in mouse behavior. Neuron 88, 1121–1135.
20. Todorov, E. (2004). Optimality principles in sensorimotor control. Nat. Neurosci., 7, 907–915.
21. Fitts, P.M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. J. Exp. Psychol. 47, 381–391.
22. Harris, C.M., and Wolpert, D.M. (1998). Signal-dependent noise determines motor planning. Nature 394, 780–784.
23. Viviani, P., and Terzuolo, C. (1982). Trajectory determines movement dynamics. Neuroscience 7, 431–437.
24. Lacquaniti, F., Terzuolo, C., and Viviani, P. (1983). The law relating the kinematic and figurative aspects of drawing movements. Acta Psychol. (Amst.) 54, 115–130.
25. Hicheur, H., Vieilledent, S., Richardson, M.J.E., Flash, T., and Berthoz, A. (2005). Velocity and curvature in human locomotion along complex curved paths: a comparison with hand movements. Exp. Brain Res. 162, 145–154.
26. Zago, M., Matic, A., Flash, T., Gomez-Marín, A., and Lacquaniti, F. (2018). The speed-curvature power law of movements: a reappraisal. Exp. Brain Res. 236, 69–82.
27. Matic, A., and Gomez-Marín, A. (2020). Geometric purity, kinematic scaling and dynamic optimality in drawing movements beyond ellipses. J. Math. Psychol. 99, 102453.
28. Sumbre, G., Fiorito, G., Flash, T., and Hochner, B. (2005). Neurobiology: motor control of flexible octopus arms. Nature 433, 595–596.
29. Hooper, S.L. (2006). Motor control: the importance of stiffness. Curr. Biol. 16, R283–R285.
30. Sumbre, G., Fiorito, G., Flash, T., and Hochner, B. (2006). Octopuses use a human-like strategy to control precise point-to-point arm movements. Curr. Biol. 16, 767–772.
31. Gutfreund, Y., Flash, T., Yarom, Y., Fiorito, G., Segev, I., and Hochner, B. (1996). Organization of octopus arm movements: a model system for studying the control of flexible arms. J. Neurosci. 16, 7297–7307.
32. Sumbre, G., Gutfreund, Y., Fiorito, G., Flash, T., and Hochner, B. (2001). Control of octopus arm extension by a peripheral motor program. Science 293, 1845–1848.
33. Zeilmann, I., Titon, M., Yekutieli, Y., Hanassy, S., Hochner, B., and Flash, T. (2013). Kinematic decomposition and classification of octopus arm movements. Front. Comput. Neurosci. 7, 60.
34. Hanassy, S., Botvinik, A., Flash, T., and Hochner, B. (2015). Stereotypical reaching movements of the octopus involve both bend propagation and arm elongation. Bioinspir. Biomim. 10, 035001.
35. Zullo, L., Eichenstein, H., Maiole, F., and Hochner, B. (2019). Motor control pathways in the nervous system of Octopus vulgaris arm. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. 205, 271–279.
36. Tsukagoshi, H., Kitagawa, A., and Segawa, M. (2001). Active hose: an artificial elephant’s nose with maneuverability for rescue operation. In Proceedings 2001 ICRA IEEE International Conference on Robotics and Automation, pp. 2454–2459.
37. McMahan, W., Jones, B.A., and Walker, I.D. (2005). Design and implementation of a multi-section continuum robot: Air-Octor. In 2005 IEEE/RSJ International Conference on Intelligent Robots and Systems, pp. 2578–2585.
38. Walker, I., Dawsona, D., Flash, T., Grasso, F., Hanlond, R., Hochner, B., Kier, W., Paganog, C., Rahn, C., and Zhangi, Q. (2005). Continuum robot arms inspired by cephalopods. Proceedings of SPIE, 5804.
39. Mazzoli, B., Margheri, L., Cianchetti, M., Dario, P., and Laschi, C. (2012). Soft-robotic arm inspired by the octopus: II. From artificial requirements to innovative technological solutions. Bioinspir. Biomim. 7, 025005.
40. Yang, Y., and Zhang, W. (2014). ET arm: highly compliant elephant-trunk continuum manipulator. International Conference on Intelligent Robotics and Applications, 288–299.
41. Wu, J., Zhao, Y., Zhang, Y., Shumate, D., Braccini Slade, S., Franklin, S.V., and Hu, D.L. (2018). Elephant trunks form joints to squeeze together small objects. J. R. Soc. Interface 15, 20180377.
42. Kuberski, S.R., and Gafos, A.I. (2019). The speed-curvature power-law in tongue movements of repetitive speech. PLoS ONE 14, e0213851.
43. Boas, J.E.V., and Pauli, S. (1925). The Elephant’s Head: Studies in the Comparative Anatomy of the Organs of the Head of the Indian Elephant and Other Mammals (Carlsberg-Fund).
44. Wilson, J.F., Mahajan, U., Wainwright, S.A., and Croner, L.J. (1991). A continuum model of elephant trunks. J. Biomech. Eng. 113, 79–84.
45. Martins, A.F., Bennett, N.C., Clavel, S., Groenewald, H., Hensman, S., Hoby, S., Joris, A., Manger, P.R., and Milinkovitch, M.C. (2018). Locally-curved geometry generates bending cracks in the African elephant skin. Nat. Commun. 9, 3865.
46. Kier, W.M. (1992). Hydrostatic skeletons and muscular hydrostats. In Biomechanics (Structures and Systems): A Practical Approach, A.A. Biewener, ed. (IRL Press at Oxford University Press), 1247–1257.
47. Schulz, A.K., Ning Wu, J., Ha, S.Y.S., Kim, G., Braccini Slade, S., Rivera, S., Reidenberg, J.S., and Hu, D.L. (2021). Suction feeding by elephants. J. R. Soc. Interface 18, 20210215.
48. Kier, W.M., and Stella, M.P. (2007). The arrangement and function of octopus arm musculature and connective tissue. J. Morphol. 268, 831–841.
49. Kier, W.M. (2012). The diversity of hydrostatic skeletons. J. Exp. Biol. 215, 1247–1257.
50. Kreyszsig, E. (1991). Differential Geometry (Dover Publications).
51. Miller, J. (2009). Shape Curve Analysis Using Curvature (University of Glasgow).
52. Wagner, P.H., Luo, X., and Stelson, K.A. (1995). Smoothing curvature and torsion with spring splines. Comput. Aided Des. 27, 615–626.
STAR METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---------------------|--------|------------|
| Biological samples  |        |            |
| trunk of a deceased adult elephant *Loxodonta africana* | Réserve Africaine de Sigean, France | CITES certificate 1470 |
| trunk of a deceased adult elephant *Elephas maximus* | Zurich zoo, Switzerland | N/A |
| Experimental models: Organisms/strains |        |            |
| 2 adult male elephants *Loxodonta africana* | https://adventureswithelephants.com/ | N/A |
| Software and algorithms |        |            |
| Qualisys Track Manager | https://www.qualisys.com/software/qualisys-track-manager/?gclid=EAIaIQobChMIyLTbosOl8AIVg6Z3Ch3tAn4EAAYAAlAEgLq5fD _BwE | N/A |
| MATLAB | https://www.mathworks.com/products/matlab.html | N/A |
| Amira | https://www.thermofisher.com/ch/en/home/industrial/electron-microscopy/electron-microscopy-instruments-workflow-solutions/3d-visualization-analysis-software/amira-life-sciences-biomedical.html | N/A |
| Hugin | http://hugin.sourceforge.net/ | N/A |

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Michel C. Milinkovitch (Michel.Milinkovitch@unige.ch).

Materials availability
This study did not generate new materials.

Data and code availability
All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplemental Information. The online web applications are available at https://www.lanevol.org/projects/proboscis.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Two adult male African bush elephants (*Loxodonta africana*) were involved in the motion capture experiments, one with an intact trunk and the second with severed fingers in the prehensile tip as the result of an accident that occurred several years prior to the experiments. All experiments have been approved by the University of Geneva ethical regulation authority and performed according to South-African law. Two trunks from adult males of African bush and Asian elephants (*Loxodonta africana* and *Elephas maximus*) were collected from deceased zoo animals and used for the anatomical study.

METHOD DETAILS

Motion capture experiments
Motion capture was performed at Adventures with Elephants (https://adventureswithelephants.com/) in Bela Bela, South Africa. The animals were trained to grasp objects (of various shapes and sizes) with the trunk and transport them from one point to another on the ground (or from/to the hands of a person). During the experiments, one animal handler was standing on each side of the elephant to distribute food items as rewards for executing tasks.

Multiple objects were designed for the prehension experiments (Table S1). Four shapes (sphere, cube, cylinder and cone), each in four different sizes (diameter or side length d1 = 3.75 cm, d2 = 7.5 cm, d3 = 15 cm, d4 = 30 cm) were made of wood (plywood and spruce; fabricated by https://www.richard-rohart.com). The cylinders have a length/diameter ratio of 3, the cones have a height/diameter ratio of 3. To limit the change in mass in that series of objects, the larger shapes (d3 and d4) were made hollow with a
wood thickness of 1 cm. Three shapes (sphere and cylinder of diameter d₂, and disk with a 30 cm diameter and 1 cm length) were also fabricated, each with three different mass densities (m₁ = 500 kg/m³, wood; m₂ = 3000 kg/m³, aluminum; m₃ = 8000 kg/m³, steel). The aluminum sphere was not tested. The steel sphere (m₃) was fabricated in two versions: one with a smooth surface and one with a carved (rough) surface. The smooth steel sphere was presented to the animal either with a clean surface, or with its surface covered with lubricant (glycerin and water-based) in order to make it slippery. The metallic objects were fabricated in the mechanical workshop of the physics department at the University of Geneva, Switzerland. Granular material (rice) was used for additional prehension experiments. We also tested the ability of elephants to pick up uncooked spaghetti sticks (Data S1A).

We used a motion capture system (Qualisys, Göteborg, Sweden), combining 10 infrared cameras (Oqus 7+, 100 Hz, 12 megapixels) with sun filters and two video cameras recording in the visible range (Miqus, 30 Hz, 2 megapixels) positioned in a semi-circle around the scene, placed on tripods with alternating heights of 1 m and 2 m. Retroreflective markers (1.6 cm in diameter) were screwed in flexible bands of bio-compatible adhesive kinesiology tape. Eight to 10 rows of markers were placed on the dorsal side of the trunk with 3 (near the tip) to 6 (at the proximal base) markers per row. Distances in between markers were 5 cm near the tip and 10 cm at the base. An example of the markers configuration on the trunk can be seen in Figure 2A. The animals accepted the presence of the kinesiology bands on the dorsal side of their trunk, but not on the ventral side or on the tip fingers. Before placing the kinesiology bands, the trunk was thoroughly brushed to remove excessive dust. Calibration was performed inside the measurement volume by placing an L-shaped frame with 4 markers on the floor (to set the coordinate system) and by sweeping a wand (with one marker at each end of its T-shaped end) across the full volume. We obtained very high spatial resolution (uncertainty ≈ 2 mm) for the tracking of the 3D markers positions.

**Trunk imaging procedures**

Following the approach of the Visible Human Project (https://www.nlm.nih.gov/research/visible/visible_human.html), we explored the internal anatomy of the trunk from adult males of African bush and Asian elephants using a combination of CT scans, MRI and physical sectioning. The time between death and freezing the trunk was longer for the African elephant sample, resulting in a more advanced degradation of the tissues which is reflected in the MRI scans but less so in physical serial sections.

The MRI and CT scanning sequences were optimized to reveal the soft tissues (dermis, epidermis, muscles, connective tissues). CT scan yields a better contrast for dermis and epidermis, and was thus used to extract precise skin morphology. MRI offers better contrast for muscular and connective tissues than for the skin but also takes a much longer time for comparable resolution (4 h for the MRI of a full trunk versus 30 min for a CT scan). The trunks were unfrozen a few days before imaging so that they would be at room temperature during the scans. For the Asian elephant trunk, CT scanning and MRI were performed at the Tierspital (Zurich, Switzerland). For the African elephant trunk, CT scanning was performed at the University Medical Center in Geneva (Switzerland) and MRI was performed at Geneva University Hospital (HUG, Geneva, Switzerland). The resolution of the CT scan (pixel spacing) is 0.75 mm. MRI sequences were acquired with the so-called ‘T2’ protocol, which offers better contrast but can only be acquired as 2D series, and the ‘Proton Density (PD)’ method which yields slightly reduced contrast but produces a 3D image with isotropic resolution. The T2 scans were acquired in 3 orientations (coronal, sagittal and transversal) with a slice thickness (i.e., out-of-plane resolution) of roughly 2 mm and in-plane resolution dependent on the field of view (FOV): from 0.6-0.7 mm (smallest FOV at the tip) to 0.9-1.1 mm (largest FOV at the head base). The isotropic resolution for the PD sequence is equivalent to the in-plane resolution of the T2 sequences. Six successive and overlapping portions of the trunk were scanned using different receptor antenna so as not to displace the antennas nor the trunk during the whole procedure.

The image series (DICOM files) were imported in Amira (Thermo Fisher Scientific, Massachusetts, USA) where the piecewise scans were stitched and used to segment and export surface meshes for the skin and the six main muscle groups. Segmentation was done automatically (using an intensity threshold) for the skin, whereas segmentation of muscle groups was manually performed in about 40 selected planes and then interpolated over the full trunk volume.

After CT and MRI scanning, the trunks were frozen again in a straight position before being sliced on a vertical bandsaw in regular 1 cm-thick sections. The African elephant trunk was entirely sliced in about 160 serial transversal sections. The Asian elephant trunk was sliced in about 130 serial transversal cuts, and the remaining 45 cm most proximal part of the trunk was sagittally divided in two halves: the left half was sliced in serial sagittal cuts (~20 slices) and the right half was sliced in serial coronal cuts (~25 slices). Each trunk slice was washed in tap water, placed over a green background in a plastic container, fully immersed in 2 L of tap water (to avoid reflections) and covered with a glass plate (to prevent the slice from floating). Physical sections were imaged with the following high-resolution photography system. A 45 mega-pixel camera (Nikon D850 with 60 mm objective, f16, shutter speed=1/50 s, iso 200) was fixed facing down over the slice at a distance of 74.5 cm. The plastic container with the slice was positioned on an in-house developed motorized stage for controlled horizontal (in x and y) movements. Nine overlapping pictures were taken to cover the largest slices (about 45 cm x 35 cm) whereas more distal sections of the trunk could be imaged with six, four, and one picture. Images were stitched using the Hugin software (http://hugin.sourceforge.net/). Alignment and cropping of the green background was done in Photoshop. This procedure allowed us to generate the same very high resolution (= 0.03 mm/pixel) for all images. Note that this resolution is much higher than for the corresponding virtual section images obtained with CT and MRI scans. This also proved to be crucial for delineating the muscle groups in the tip of the trunk. All serial sections are available (for both species) in high resolution in the form of a virtual scroller of the internal structures of the trunk (online applications 2 and 5–7).

Finally, small blocks from different regions of the trunk (muscles and skin) were fixed in formalin, and histological slides were prepared with two standard staining procedures: (i) Mallory’s trichrome and (ii) Methyl blue and Acid fuchsin.
QUANTIFICATION AND STATISTICAL ANALYSIS

Catalogue of prehension behaviors
Analyzing the 550 recorded prehension sequences (Table S3) for both animals, we constructed an ethogram with 17 basic trunk behaviors (Video S1). We counted the number of occurrences for each behavior over all the prehension sequences, which can be used to estimate the probability of executing a behavior when presented with a specific shape.

Kinematic calculations
After post-processing of the motion capture data (cleaning the trajectories with Qualisys software QTM), the 3D positions of all markers in each time point were exported for analyses of specific trajectories. We fitted an ellipse to each row of markers. Each ellipse has 8 parameters to be fitted (3 coordinates of its center, 3 angles for its orientation around the 3 cartesian axes and 2 parameters for the lengths of its axes). The initial guess for the optimization process is based on the real anatomy of the trunk, using the eccentricity (ratio of large over small diameter) of the trunk at the position of each ellipse. We imposed that the large axis of the ellipses decreases in length toward the tip. Due to the fact that markers are only present on the dorsal perimeter of the trunk, some deviations are expected between the fitted values for the two principal axes a and b and the real cross-sectional geometry of the trunk. Nevertheless, despite not having imposed incompressibility (constant volume), this feature is captured by the reconstruction, with a maximal total change in volume of ±5%. We then fit a cubic spline through the ellipse centers and extract 50 points from this spline as an approximate virtual backbone of the trunk. The resulting model can be visualized in Figures 2B and S2A.

The velocity and acceleration are calculated using the virtual backbone spline positions and finite centered differences between subsequent time frames. A reference sequence was selected in which the trunk was in a relaxed posture for 3 s. Longitudinal and cross-sectional strains (\(\Delta L/L_0\), \(\Delta a/a_0\) and \(\Delta b/b_0\)) are defined using the arc length between subsequent ellipses and the radii (for the large and small axes) of each ellipse, relative to the reference frame, yielding a local description of the strains.

The curvature and torsion are typically defined in differential geometry using the Frenet-Serret framework. Preliminary analyses revealed some pitfalls of this approach while evaluating those quantities across the trunk. Indeed, torsion is prone to artifacts and difficult to interpret, as very sharp peaks of torsion can appear along the curve without any physical intuitive meaning, as observed by Miller in his work on human face shape analysis. Curvature thus defined is also prone to artifacts, especially when the number of spline segments is small and at the extremities of the curve. Therefore, we used an alternative definition for the torsion and the two curvature components, which is much more relevant from a biomechanical point of view. This definition is based on local orthogonal frames constructed from the ellipses: unit vectors \(\hat{a}\), \(\hat{b}\) and \(\hat{n} = \hat{b} \times \hat{a}\) pointing respectively along the ellipse large axis (toward the right of the animal), the ellipse small axis (toward the dorsal side of the trunk) and the axis of the trunk (the cross product being in the direction of the trunk tip). This allows to define the torsion \(\tau_{ba}\) as the tendency of the trunk to twist in a clockwise direction, \(\kappa_{ab}\) as the upward/downward curvature component and \(\kappa_{na}\) as the left/right curvature component:

\[
\hat{a} = \kappa_{ab} \hat{b} + \kappa_{na} \hat{n}
\]

\[
\hat{b} = -\kappa_{ab} \hat{n} + \tau_{ba} \hat{a}
\]

\[
\hat{n} = -\kappa_{na} \hat{b} - \tau_{ba} \hat{a}
\]

with \(\hat{a}\) denoting the partial derivative with respect to \(i\), the normalized position index on the trunk, starting at 0 at the most proximal ellipse and ending at 1 at the most distal ellipse.

Or, in matrix form:

\[
\begin{bmatrix}
\hat{n} \\
\hat{b} \\
\hat{a}
\end{bmatrix}
= 
\begin{bmatrix}
0 & \kappa_{ab} & \kappa_{na} \\
-\kappa_{ab} & 0 & \tau_{ba} \\
-\kappa_{na} & -\tau_{ba} & 0
\end{bmatrix}
\begin{bmatrix}
\hat{n} \\
\hat{b} \\
\hat{a}
\end{bmatrix}
\]

These quantities are dimensionless; to obtain the usual units (m\(^{-1}\)) for torsion and curvature, we must divide by the (time-dependent) trunk length. In the relaxed posture, the dimensionless torsion has maximal values of \(\tau_{0,\text{max}} = \pm2.5\), or 1.4 m\(^{-1}\) when normalized by the trunk length. To avoid including biased torsion coming from an asymmetrical placement of the markers, \(\tau_{ba}\) is always expressed as a relative difference with the reference pose: \((\tau - \tau_0)/\tau_{0,\text{max}}\). The torsion can be intuitively interpreted as the tendency of the ellipse cross-section to rotate around the trunk central axis, since \((\tau - \tau_0) \approx \hat{a} \theta\), where \(\theta\) is the rotation angle (in radians) of the ellipse around its center. For example, \((\tau - \tau_0) = 2\pi\) would mean that the trunk effectuates a full twist of 2\(\pi\) radians around its central axis over its full length (from \(i = 0\) to \(i = 1\)).
In addition to the instantaneous curvature of the trunk posture ($\kappa_{na}$ and $\kappa_{nb}$), we also calculate the path curvature of the trunk tip (defined in the Frenet-Serret frame), using the time-dependent position $r'(t)$ of the trunk tip (position of the center of the most distal ellipse):

$$\kappa_{tip} = \frac{\| r''(t) \times r'''(t) \|}{\| r''(t) \|^3} = \frac{\| \dot{v}(t) \times \ddot{a}(t) \|}{\| \dot{v}(t) \|^3}$$

where $\dot{v}$ and $\ddot{a}$ are the velocity and acceleration of the trunk tip. Additional information is provided in Data S1.