SCIENCE ROBOTICS | REVIEW

ANIMAL LOCOMOTION

Why animals can outrun robots

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Animals are much better at running than robots. The difference in performance arises in the important dimensions of agility, range, and robustness. To understand the underlying causes for this performance gap, we compare natural and artificial technologies in the five subsystems critical for running: power, frame, actuation, sensing, and control. With few exceptions, engineering technologies meet or exceed the performance of their biological counterparts. We conclude that biology's advantage over engineering arises from better integration of subsystems, and we identify four fundamental obstacles that roboticists must overcome. Toward this goal, we highlight promising research directions that have outsized potential to help future running robots achieve animal-level performance.

Animals outperform robots at locomotion. The performance gap is evident across scales, and it is particularly galling given that animal designs respect constraints that need not limit robots; for instance, animals must grow from a single cell, repair their own bodies, and contain all the machinery needed to reproduce. We seek to understand the underlying causes for this performance gap by systematically comparing animals with robots.

Although the preceding observations apply to multiple locomotion modalities, including flight and swimming, for tractability, we focus on legged locomotion, where decades of research have produced a rich robot ecosystem with biocomparable designs. For succinctness and to emphasize high-performance behavior, we will use the catchall phrase "runner" to refer to animals and robots that use intermittent contact between limbs and terrain to move and "running" to refer to the corresponding behavior, regardless of whether it would be more common or accurate to describe a behavior as walking or jumping. Toward these ends, we seek to answer the question, "Why can animals outrun robots?"

Our goal is motivated, in part, by bioinspiration and biomimetic approaches to design (*1*–*3*), that is, the potential to advance robotics by translating natural to artificial technology, as well as robot-inspired approaches to biology (*4*) and physics (*5*), wherein robots are used to advance basic science. Quantifying the performance of "proof-of-concept" designs embodied by extant animals sets aspirational benchmarks for the robotics community, highlights performance limiters, and potentially reveals design principles. We expect that this study will help catalyze advancements in bioinspired and biohybrid robotics and extremes of performance achievable by autonomous robots (*6*).

Engineered and biological runners are built differently. Robots are assembled from discrete components at the macroscale, whereas animals are formed from heterogeneous structures grown at the nanoscale. Additionally, the two technologies use different physical phenomena and materials for power, sensing, actuation, and control. However, both animals and robots are built to run (among other tasks). Given that this shared objective is achieved using vastly different design paradigms, it is not obvious how to compare animal and robot runners. Thus, we consider multiple levels of analysis (*7*, *8*), first by quantifying the performance gap between the systems as a whole, as in Fig. 1, and subsequently by comparing performance across the five subsystems critical for the task of running illustrated in Fig. 2. Last, we conclude by synthesizing our findings to propose fruitful future directions for running robot research.

In the following subsections, we compare performance measurements from the literature on animal physiology and robot design. The metrics that we choose are largely scale invariant, at least above a minimum size where engineered systems struggle, and are measured in diverse taxa, including vertebrates, invertebrates, and robots. We exclude technologies not integrated into existing autonomous runners, for instance: Spider silk is very strong, but it is not used as a structural material in animal locomotion; nuclear reactors can power submarines but have not been integrated into running robots.

A true meta-analysis remains out of reach because we found no principled weighting by which the performance of such diverse organisms and machines could be distilled into an average value. Instead, we selected data from representative systems to informally assess whether and how biological components exceed the performance of their engineered counterparts; these data are summarized in Fig. 3. Because a comprehensive metric table with citations would consume this manuscript, we present the details in a supplementary document. We encourage the reader not to skip the supplement but instead read it for a deeper look at the component metrics, data, and rationale underpinning our assessments.

SYSTEM PERFORMANCE

Although the claim that animals outperform robots at running may sound uncontroversial in 2024, it is, nevertheless, worthwhile to consider how to quantify the performance gap. We think that a runner should have range to operate independently over the distances required, agility to reach and traverse surfaces in its environment, and robustness to maintain range and agility despite changes to the runner and its environment. Although running performance could be measured along other axes, these three nonredundant metrics are commonly studied and of paramount importance for animal fitness and robot autonomy (*9*).

Range can be directly quantified as the distance traveled during autonomous running in a specific environment. This distance is determined by the onboard energy supply as well as the efficiency of energy conversion. The latter factor is conventionally measured by

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the cost of transport, defined as the amount of energy required to move a unit weight of a runner over a unit distance (*10*). The farthest walk by a legged robot on a single battery charge was Ranger's 65-km trek over the course of 31 hours (*11*). Ranger's cost of transport is impressively half that of human walking, but there are important caveats. First, the robot's batteries have about 50-fold less useful energy per unit mass as compared with animal fat; the average human has energy reserves to continue walking long after the robot's batteries are depleted. When allowed to refuel along the way, humans can exhibit extraordinary endurance: Exceptional athletes can run hundreds of kilometers over multiple days in a single outing. They can also do so over rough terrain, whereas Ranger exploits the smoothness of the track that it was designed to walk on—a small rock could cause it to stumble and fall. Outside of controlled environments, robot range is a distant second to that of animals.

The agility of legged robots has been quantified using running speed, jumping height, turning rate, and more. Legged robot development has long been guided by a need for speed, resulting in bipeds, quadrupeds, and hexapods with speeds approaching those of similar-sized animals on regular terrain (*12*–*19*). However, animals are still faster at all scales, and the performance gap widens when considering irregular or deformable terrain (*20*, *21*). Some legged robots have leaped at the task of jumping, either specializing entirely (*22*) or by adapting an existing runner (*23*). New heights have been reached by legged robots using bioinspired elastic energy storage, but even these are still surpassed by animals of similar mass. Rapid robot turning has been occasionally synthesized (*24*, *25*), but animals can redirect momentum "on a dime" (*26*–*31*). Last, although feedback control can enable robots to recover from substantial perturbations (*32*), the ability of animals in this regard is unmatched (*33*). Overall, animals out-run and out-maneuver running robots.

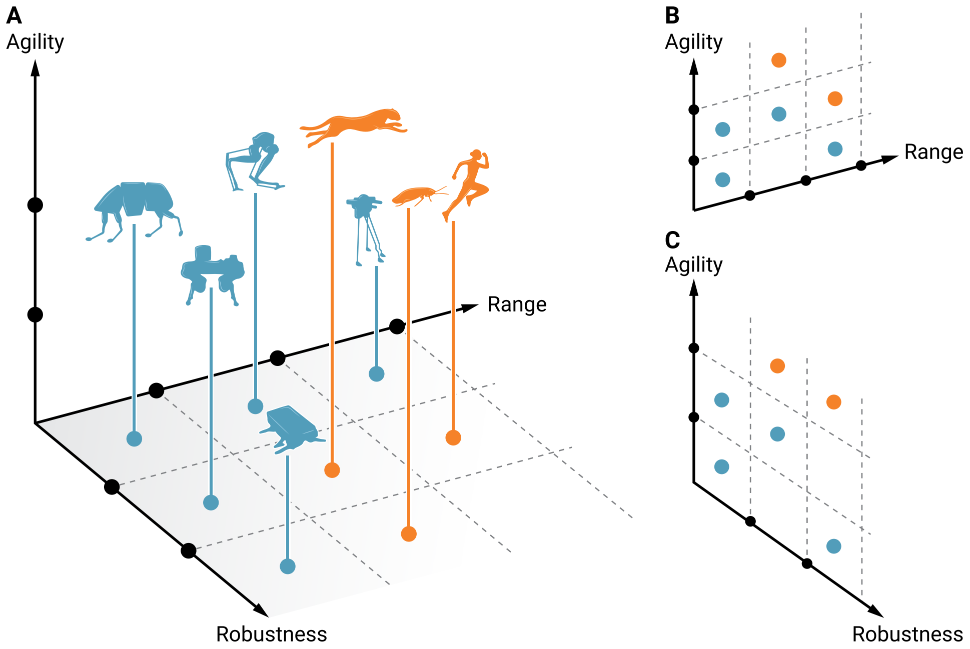

Fig. 1. System-level performance of animal and robot runners. (**A**) Representative performance of robots (blue) and animals (orange) in the three-dimensional space defined by range, agility, and robustness axes. (**B**) Projection of (A) onto agility-range plane. (**C**) Projection of (A) onto agility-robustness plane. Animal running performance now pareto-dominates that of robots at all scales.

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Robustness is deceptively easy to conceptualize yet devilishly difficult to quantify. As a starting point, we consider how agility and range are maintained in the presence of changes to the runner or its environment. Horses can increase body mass 20-fold as they grow from foal to full size, and rhinoceros beetles can carry 30 times their body weight without fatiguing. Animals can survive bone fracture (*34*) or limb loss, with many lizards and insects voluntarily shedding appendages to distract predators (*35*), and the phenomenon is so common in the latter group as to motivate a "spare leg hypothesis" (*36*). In contrast, robot range and agility decrease precipitously when large payloads are added or limbs are damaged. Robots designed to walk or run on flat ground can be made to plod over rough terrain under inclement conditions (*37*), but animals are unimpeded by terrain variations upward of their height (*21*, *38*–*41*) and readily run over, under, and through obstacles like mud, snow, vegetation, rubble, and crevices (*42*, *43*). On granular media, robot running speed can depend sensitively on design, control, and environmental parameters (*44*), with animals handily outpacing robots in their native ecologies (*20*). Overall, animals excel at maintaining performance despite changes that would be catastrophic for existing robots.

We conclude that animals outperform robots at running along the three key axes of range, agility, and robustness, as illustrated in Fig. 1 and corroborated in other recent work (*45*). In what follows, we seek to understand the cause of this performance gap. Given that animals and robots are generally designed and built using different technologies, it is possible that differences in the parts give rise to differences in the whole. To test this hypothesis, we coarsely divided runners into the five subsystems illustrated in Fig. 2: a power system to store and deliver energy; a frame for support and leverage; actuators to modulate mechanical energy; sensors to perceive self and environment; and a control system to transmit and transform sensor and actuator signals. Of course, our "subsystems" are abstractions, and runners cannot always be cleanly divided, particularly in the case of animals. We will take care in what follows to note when separating subsystems is messy work.

POWER SUBSYSTEM PERFORMANCE

The ideal power supply for running stores a large amount of useful energy and delivers it efficiently to the other subsystems with minimal added mass. The three main types of power plants used in autonomous runners are gas engines, electric batteries, and metabolism. All three convert stored chemical energy to power running: Engines convert gas to movement, batteries convert chemical bonds to electricity, and metabolism converts fat to adenosine triphosphate (ATP).

Because a runner's endurance is ultimately limited by its stored energy, we compare mass-specific stored energy, defined as the energy delivered by the power plant normalized by fuel mass. Biology outperforms engineering by this metric, with values more than double those of combustion engines and 50-fold more than batteries. There are two main reasons for biology's edge: Oxidative metabolism within mitochondria converts fat to ATP with a remarkable efficiency of about 70% (*46*) compared with 25% in engines (*47*); and, whereas adipose tissue is almost 90% fuel (*48*), gas tanks can be 20% of the mass of the fuel they carry (*49*).

Because locomotion is among the most power-intensive behaviors that runners perform, we compare mass-specific delivered power, defined as the sustainable power delivered normalized by total power plant mass. Metabolism meets or exceeds engine performance by this metric (*47*, *50*), but batteries outperform both using the natively high power output of lithium-ion cells and relatively light electronics and packaging. Although animals may transiently achieve higher peak power outputs by depleting the supply of ATP in muscles, the energy in stored ATP is quite limited and, if used on its own, could only sustain performance for a few seconds (*51*, *52*).

Because fuel can potentially be harvested from the environment to extend running distances, we compare mass-specific refueling power, defined as the energy rate of refueling divided by the mass of the refueling frame. By this metric, gas tanks can be refueled an order of magnitude faster than a battery can charge or digestion can process biological matter. To put this in perspective, a human would only need to refuel at the gas rate for a fraction of a second to gain the energy it needs for each day. The actual human refueling rate limits 100-day running to a range of about 40 km per day (*53*).

In summary, the performance of engineered power plants can exceed that of their biological counterparts in the rates at which they refuel and deliver energy, although biology now has the edge in energy storage. The development of portable power plants capable of delivering both high specific energy and high specific power is considered one of the grand challenges for mobile robots (*6*). Fortunately, there is no known fundamental barrier to creating engineered power plants that have a superior combination of storage and energy-delivering capabilities (*54*).

FRAME SUBSYSTEM PERFORMANCE

The ideal frame for running combines material and geometry to support and propel the body overground while being light and failure resistant. Running robot frames are generally built from rigid connections between steel, aluminum, or carbon fiber struts using linear or rotary joints. Animal frames have two primary forms: Vertebrates have an endoskeleton made from bone connected by soft tissue, and insects have an exoskeleton made from hard cuticle connected by soft flexures (*55*). A runner's frame is loaded by multiaxial forces that vary over time (*56*), making it susceptible to multiple modes of failure, including buckling and yielding. Failure modes are affected by the frame's geometric and material properties, and bracing against one failure mode may weaken the frame against another (*57*). A simple yet instructive analysis is to consider a macroshape shared between robot and animal frames (*55*), a cylindrical tube, and evaluate material resistance to failure modes dominated by stiffness and strength.

Because the body's weight must be supported throughout running without buckling, we compare density-specific stiffness, defined as a material's modulus of elasticity normalized by its density. Carbon fiber outperforms the other materials by this metric by a factor of 3 to 5, with cuticle, bone, aluminum, and steel being roughly comparable. Because limbs must generate large forces to propel the body overground without breaking, we compare density-specific strength, defined as a material's stress before fracture normalized by its density. Carbon fiber again outperforms the other materials by this metric by an order of magnitude; the substantial density of steel makes it the lowest performer in the group. In practical terms, this means that a carbon fiber limb could support a heavier body and enable more agile maneuvers that would otherwise break a bone, fracture an exoskeleton, or snap a strut made of aluminum or steel with similar mass.

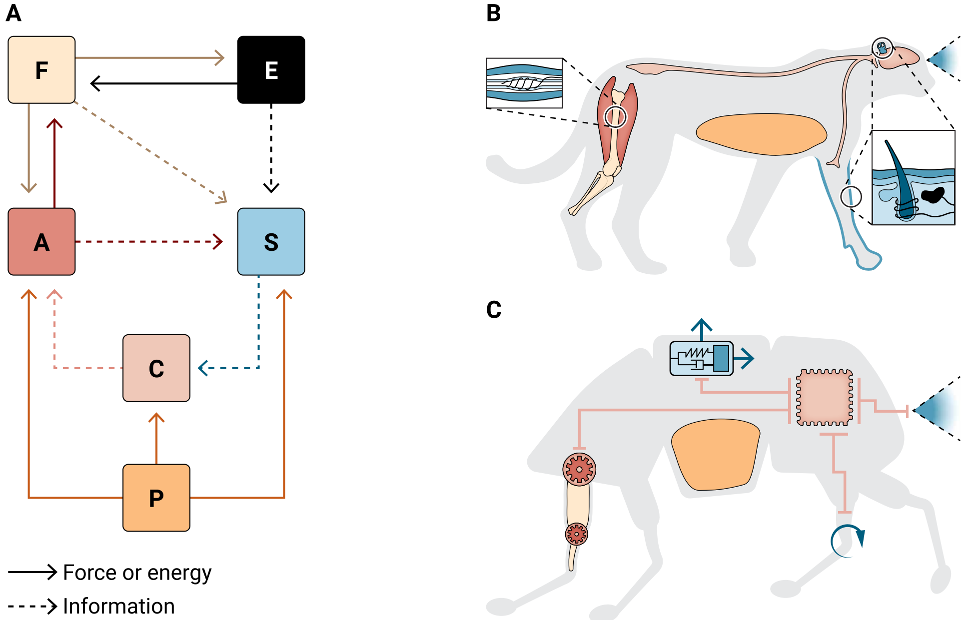

Fig. 2. Five subsystems critical for running. (**A**) Block diagram showing interconnections among the power, frame, actuation, sensing, and control subsystems as they interact with the environment (orange, yellow, red, blue, light red, and black, respectively). Solid arrows indicate transduction of force or energy, and dashed arrows indicate transmission of information. (**B**) Illustration of the five subsystems overlaid on the fastest running animal (cheetah): fat and metabolism; bone skeleton; muscles; visual, vestibular, and proprioceptive sensors; nervous system. (**C**) Illustration of the five subsystems overlaid on the fastest autonomous running robot (WildCat): gas engine or electric battery; metal or carbon fiber struts; hydraulic or (piezo)electric motors; vision, IMU, and joint sensors; computer network.

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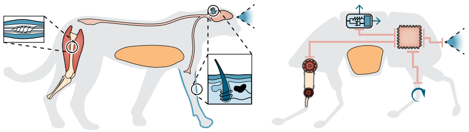
Because frames and joints often store and return energy, we compare mass-specific energy, defined as a material's strength squared normalized by its stiffness and density. In this metric, carbon fiber outperforms the other materials above by a factor of 3 to 10. However, there are other materials, both engineered and biological, that have exceptional specific energy that can be used for the sole purpose of storing and returning energy. For example, resilin is used in insect jumpers (*58*) and tendon in vertebrates (*59*). Both have higher specific energy than carbon fiber, but not higher than what is achievable by engineered rubber and Kevlar (*60*).

In summary, engineered frames built from carbon fiber can be much stiffer and stronger than biological skeletons built from bone, cuticle, aluminum, or steel; metals may outperform biology with respect to stiffness but underperform in strength. Animal frames now exhibit a greater diversity of microshapes (for instance, trabecular bones have remarkable crack propagation resistance) that offer advantages beyond our metrics (*61*). However, a growing catalog of materials and fabrication techniques available to robots may provide similar advantages (*6*, *62*).

ACTUATION SUBSYSTEM PERFORMANCE

The ideal actuators for running enable rapid changes in runner momentum with minimal added mass. Animal runners exclusively actuate their limbs with muscle, and most autonomous running robots use electromagnetic motors at vertebrate scales or piezoelectrics at insect scales. The physical principles governing motors, piezos, and muscle are different: Motors produce force from the flow of current in a magnetic field, piezos use crystal properties to convert electric fields to mechanical pressure, and muscles produce force through chemical reactions that generate length changes in nanoscale proteins. We exclude other actuators that have been deployed in running robots, including hydraulics and artificial muscles (*63*), because motors and piezos are sufficient to justify our quantitative conclusions below.



Power	**Metabolism**	**Engine, battery**
Specific stored energy [kWh/kg]	**~10**	~1, 0.2
Specific delivered power [kW/kg]	~1	**~0.2, 10**
Specific refueling power [kW/kg]	~1	**$\sim 10^4$, 0.2**
Frame	**Bone or cuticle**	**Carbon fiber**
Specific stiffness [MPa m^3/kg]	<10	**~100**
Specific strength [kPa m^3/kg]	<90	**~500**
Specific energy [J/kg]	<1000	**>3000**
Actuation	**Muscle**	**Motor**
Specific torque [Nm/kg]	6 to 133	**14 to 164**
Specific power [W/kg]	50 to 350	**10^3 to 10^4**
Sensing	**Photoreceptor**	**Photoreceptor**
Light sensitivity [photons]	**1**	**1**
Number of sensors	**$\sim 10^8$**	**$\sim 10^8$**
	Mechanoreceptor	**Mechanoreceptor**
Strain sensitivity [strains]	10^{-5} to 10^{-3}	**10^{-11} to 10^{-8}**
Number of sensors	**100 to 10^4**	<100
Control	**Myelinated nerve**	**Network cable**
Specific latency	$\sim 10^{-3}$	**$\sim 10^{-6}$**
Specific bandwidth [bits/m^2]	$\sim 10^{13}$	**$\sim 10^{16}$**
	Brain	**Integrated circuit**
Number of neurons	**10^6 to 10^{11}**	10^4 to 10^6
Number of synapses	**10^{10} to 10^{15}**	10^7 to 10^8

Fig. 3. Subsystem-level performance of animal and robot runners above 1 kg. Performance in each subsystem is compared using multiple performance metrics and one or more engineering technologies. The highest-performing quantities in each row are bold (see the Supplementary Materials for comparisons at smaller scales).

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Because running requires high forces to support the body and move the limbs, we compare mass-specific peak torque, defined as the maximum torque normalized by the mass of the actuator and its transmission. Muscles can outperform direct-drive motors and bimorph piezos (*64*) by a factor of 2 to 5 in this metric. Although transmissions can theoretically multiply torques by arbitrarily high gear ratios, the mass added and efficiency lost yield diminishing returns in this metric. Nevertheless, the performance gap between motors and muscles can be eliminated at the vertebrate scale by pairing motors with higher-ratio transmissions, like harmonic drives (*65*) or ball screws (*66*), and series compliance to provide backdrivability (*67*).

Because running agility is limited by the rate at which actuator output can be converted to a change in momentum of the runner, we compare mass-specific power, defined as the mean mechanical power over a gait cycle normalized by the mass of the actuator and its transmission. By this metric, peak performance of EM motors exceeds that of muscle by one or more orders of magnitude, and piezos are comparable to muscle when used for running. Sustained performance in motors, piezos, and muscles alike is constrained by thermal management and energy supply. Although animals use spring-assisted power amplification to overcome actuator limitations (*68*), robots can also use these mechanisms (*22*).

In summary, the performance of motors with high-ratio transmissions and series compliance can meet or exceed that of muscles in torque and power density, whereas piezos only match muscle in the latter and are at a disadvantage in the former. Motors and piezos have an advantage over muscles in their efficiency of energy transduction, which can exceed 90%, whereas muscle fiber efficiency in most animals is closer to 30% [under 63% in the most extreme case measured; (*69*)]. Hydraulic actuators may exceed the torque and power density of motors and muscles, but their efficiencies are often much lower than either, and they require a complex and heavy fluid system in parallel with the electrical systems used for sensing and control. Natural muscles' variable shapes and inherent scalability provide packaging advantages not available in motors, easily adding degrees of freedom where needed, distributing actuation mass elegantly across the body, and providing failure tolerance through redundancy. The diverse linear actuator technologies known as "artificial muscles" may offer similar advantages but now have an equally diverse set of limitations compared to motors.

SENSING SUBSYSTEM PERFORMANCE

The ideal sensor suite for running delivers the actionable information (*70*) needed to move quickly overground. There are two fundamental sensing modalities relevant to running: electromagnetic and mechanical. Eyes, cameras, and LIDAR (light detection and ranging) are examples of the former; vestibular systems, inertial measurement units, and force transducers are examples of the latter. The mechanistic details differ in biology and engineering: Animals sense light via chemical excitation from photon absorption and strain via ion channels that open in response to the physical deformation of membranes or molecules; robots sense light via electrical excitation from photon absorption and mechanical deformations via strain, magnetic fields, and optics. However, both vision and mechanosensation technologies generally transduce sensory cues into analog electrical signals that are subsequently encoded into digital signals.

Because the information provided by a sensor is fundamentally limited by its ability to perceive change in the world, we compare threshold sensitivity, defined as the smallest unit of input that results in a resolved response from the sensor. Both biological and engineered sensors can nearly achieve theoretical limits: single photons and microstrains. For example, biological photoreceptors can resolve individual "quantum bumps" of electrical activity from absorption of single photons (*71*), similar to single-photon avalanche diodes in semiconductors (*72*). The ubiquitous invertebrate campaniform sensilla can detect strains as small as proteins (*73*), whereas hair cells in the mammalian vestibular and auditory system go further still (*74*). However, engineered strain gauges can be many orders of magnitude more sensitive (*75*).

Robots generally use a handful of sensors, whereas animals have large numbers distributed throughout their bodies. Because redundant distributed sensors can yield richer data more robustly, we compare the number of sensors in each modality. The number of rod and cone cells in a human eye (*74*) is comparable to the number of pixels in the latest smartphones. Invertebrate compound eyes have far fewer individual receptors, with cockroaches having comparable numbers to LIDAR arrays (*76*). However, animals have many orders of magnitude more strain sensors than robots. Humans, for instance, have roughly 200,000 tactile receptors in addition to 50,000 stretch receptors (*77*, *78*). Insects can have thousands of individual campaniform sensilla to detect exoskeleton strains, thousands of mechanosensitive neurons in chordotonal organs that detect internal strains, and hundreds to thousands of other less well-characterized mechanosensory hairs and sensilla (*79*).

In summary, biological and engineered photoreceptors are comparable in their overall counts and ability to detect visual stimuli. Although engineered mechanoreceptors can detect much smaller stimuli than biological ones (*74*, *75*), biology's ability to integrate staggering numbers of mechanosensors distributed throughout bodies, including the electrical system needed to innervate the sensors, is remarkable. There are robustness advantages to the redundant mechanosensing streams in animals, given that failure of any particular sensor need not halt a runner in its tracks. Further, the ability to sense throughout the body may also confer advantages for agility, because actionable information may arise in any nook or cranny.

Another potentially interesting comparison is the cost associated with sensing. In animals, neural activity in sensory regions can be substantial (for instance, 8% of resting metabolic rate for the blowfly retina), placing evolutionary pressure on the size and processing of nervous systems (*80*, *81*). However, during movement, metabolic rate increases up to 50-fold (*82*). Together, these observations imply that the contribution of sensing to the overall energy budget during running is low and therefore is not predictive of overall performance differences, even if they might still be important in the overall fitness of the animal.

CONTROL SUBSYSTEM PERFORMANCE

The ideal controller for running transmits and transforms sensor and actuator signals to produce versatile behavior. Although animals can walk in the absence of large parts of their nervous systems (*83*) and robots can walk without computers (*84*), electrical control systems are used to run. The physical components and mechanisms differ in biological and engineered control systems: Neurons transmit action potentials through axons and synapses using the diffusion of charged molecules; electrical circuits and networks transmit binary or analog signals on wires using electromagnetic waves. Because implementing a control policy requires communication and computation, we consider both in what follows. For the former, we compare axons to network cables; for the latter, we compare natural and artificial spiking neural networks. Larger runners have more time to react to sensor signals before they hit the ground, so we normalize time by the natural period of a runner's limb.

Bandwidth and latency fundamentally limit controller performance (*85*), so we compare both. Many axons can be bundled into a single nerve to increase bandwidth without affecting latency, so we normalize bandwidth by the cross-sectional area of the communication channel. The bandwidth of a standard Ethernet cable at 10 megabit/s is at least 10,000 times greater than the fastest single axon, but a bundle of 1 million human axons has comparable area- and period-specific bandwidth (*86*), whereas gigabit Ethernet and other computer network protocols are orders of magnitude faster still. In addition, period-specific latency is at least 1000 times longer in nerves than an Ethernet cable, and it is impractical for biology to close this gap (*87*). At the smallest scales, buses connecting integrated circuits can have orders of magnitude higher bandwidth and lower latency than Ethernet and, thus, even greater advantages over axons.

Effective controllers quickly compute complex policies. The time required for computation in spiking neural networks is proportional to the period-specific latency of a neuron, the time constant of which is on the order of milliseconds for natural neurons (*88*) and shorter than microseconds for artificial neurons (*89*). However, the number of neurons and synapses differs vastly in natural and artificial networks, with biology outperforming engineering in this metric by orders of magnitude at scales ranging from insects to people. However, it is worth remembering that animals rely on their nervous systems to implement a rich repertoire of behaviors, including attracting a mate, finding food, and avoiding predators. It is unclear how much brain is needed for locomotion, given that parasitic wasps with fewer than 400 neurons can fly, feed, and find hosts (*90*).

In summary, computer networks vastly exceed the performance of nervous systems in latency and bandwidth of communication and computation, but artificial neural networks are at a substantial disadvantage relative to the size and connectivity of biological networks. Animals cannot practically decrease sensorimotor delay by the orders of magnitude that would be required to compete with robots' communication channels; this fundamental limit surely affects control strategies, for instance, by favoring the use of internal models (*87*). Although neuromorphic circuits will continue to increase in complexity, it remains to be seen whether bigger brains are better (*91*) for running and how to make most effective use of the limited brainpower available to robots in the meantime (*92*).

DISCUSSION

Returning to the hypothesis posed at the outset, we found some limited evidence, summarized in Fig. 3, that performance differences at the level of subsystems favor biology, partly explaining why animals outrun robots. Fat stores a lot of energy per unit mass, giving animals an advantage in range, particularly compared with robots powered by batteries. Muscle has higher torque density than piezos and motors paired with conventional transmissions, likely conferring some advantage in agility. Although biological sensors are no more sensitive than their engineered counterparts, a large number of them can be distributed throughout the body, lending robustness through redundancy and benefitting agility by providing rich sensor streams from each body part. Last, brains can theoretically implement much more complex transformations than current integrated circuits because of their vastly greater quantities of neurons and synapses, potentially leading to advantages in range, agility, and robustness. Biological subsystems fare better with respect to robots at insect scales than at human scales, indicating substantial headroom for component performance improvements in roach-sized runners.

However, a simple thought experiment demonstrates that these differences in runner parts do not explain most of the gap in running performance. Suppose we could build cyborg runners using the highest-performing components and subsystems from biological and engineering technologies: a fat-burning, carbon-fibered, muscle-bound monstrosity with distributed sensors and low-latency engineered communication channels, all controlled by mind-bogglingly complex spiking neural networks. Would roboticists be able to create cyborgs whose running performance competes with those of animals? This experiment could be carried out in the world of computational simulations, where runner designs are not constrained by the innumerable practical obstacles that make our imagined cyborg physically unrealizable. Even in the most favorable of these worlds, where frames never break and nearly unlimited computational resources control ideal torque sources using perfect state information, we suspect that the performance of simulated runners would not approach the agility or robustness of animals in the real world.

If not the performance of subsystems, what is the explanation for why animals can outrun robots? By elimination, the problem must lie with our lack of understanding of how to construct and control a high-performance "whole" using existing high-performance "parts." This is a forgivable shortcoming because at least four fundamental obstacles must be overcome to tackle this integration challenge. First, we lack quantitative metrics for evaluating the many dimensions of running performance, yet these are necessary for improving robot designs using systematic engineering processes. We qualitatively discussed agility and robustness at the outset, but there are only a handful of narrowly defined ways to measure these properties. Even range, which we conflated with distance, is only well-defined once the runner's behavior and environment are specified. The second and third obstacles are trade-offs and emergence. Stringent trade-offs potentially arise when subsystems combine because performance of one component might constrain that of another. The opposite is also possible during integration, because emergence is where the behavior of the whole is different than, and irreducible to, the behavior of the parts. The composition of subsystems, especially when feedback is involved, can transform the dynamics for better or worse. These two obstacles are two sides of the same coin in the sense that, at their core, they are unknown but potentially transformative interaction dynamics and that performing the integration is the only way to expose these dynamics. However, there are a huge number of ways that the parts can be combined, each producing different possibilities for trade-offs and emergent behavior. Unfortunately, the fourth obstacle, the curse of dimensionality (*93*, *94*), admonishes us that these high-dimensional integration spaces cannot be explored by brute force alone. Consequently, it is challenging to find good mechanical designs in the high-dimensional space of candidate designs and good control policies in the high-dimensional space of candidate policies.

How can the daunting challenges of integration be overcome? Given that tackling the entire system-level problem is daunting, decomposing into subproblems is helpful. The conventional subsystems that we evaluate above are one such decomposition. However, performance in these subsystems has been driven by industry's need to efficiently manufacture at scale rather than the roboticist's desire to build the ideal subsystem for running. Instead, we advocate for decomposing into "functional subunits": groupings of parts that reveal the trade-offs and emergent behavior arising from their integration. As an example, consider the series elastic joint actuator (*95*, *96*): Composed of elements of frame, sensing, actuation, and low-level control, its design is subject to the integration challenges and trade-offs that we argue are central to the performance deficit of running robots. At the same time, it features emergent behavior greater than the sum of its parts, because it is torque- and power-dense while maintaining backdrivability and robust force control, simplifying high-level control. The complexity of functional subunits should be more tractable than that of a whole robot, enabling tight integration and performance optimization for their subtasks. They should have reduced and predictable ways of interacting mechanically and electrically with other functional subunits to simplify integration into the broader system. The reduced subset of possibilities ought to make the overall design space more feasible to navigate while still allowing a rich set of runners to explore. As a final note, functional subunit decomposition is compatible with proven tools for building and analyzing runners. For instance, hierarchical models of varying degrees of complexity (*97*, *98*) have revealed how reduced-order emergent behavior is embodied in more complex machines (*99*, *100*)—functional subunits could facilitate this embodiment. Additionally, information-based metrics of control architectures like centralization (*101*) and control effort (*102*, *103*) provide potential design criteria at an integrative level applicable to functional subunits and whole robots alike. Although we believe that this approach of decomposing the problem of runner design into functional subunit design will be fruitful, we also understand that it will require creativity, inspiration, and discovery.

Lest roboticists feel sheepish about their machines' performance, we note that biology has a substantial head start over engineering to explore design and policy spaces. At the lineage level, there have been 1000 to 10,000,000 times as many generations of animals as robots. Considering population size, there have been 1000 times more humans than robots (of all kinds) and perhaps 1 quintillion times as many individual insects. In terms of individual experience, animals are less sedentary and have longer lifespans than robots, with ambulatory adult humans taking roughly 10,000 steps per day over decades. In light of these observations, it strikes us that the rate of advancements has been markedly faster in robots than in animals.

There are several key factors contributing to the disparity between the pace of technological innovation in biology and engineering. Designing and prototyping in engineering is a rapid and systematic process compared with the undirected search of evolution. Animals must survive to pass on their genes, limiting experimentation from generation to generation. Additionally, animals in one phylogenetic branch generally cannot benefit from innovations in any other: An adaptation that improves running in a cockroach provides no benefit to a cheetah. In contrast, advancements demonstrated in one robot are readily transferred to others. Furthermore, robots have access to sources of parallelism unavailable to animals: Experience can be accumulated on multiple physical and simulated robots simultaneously, and these data can be shared directly. Further, these advantages are only limited by the resources invested, for example, by the number of researchers in robotics labs, robots on the ground, or servers in the cloud.

We are optimistic that legged robots will someday outrun animals. To hasten this outcome, we conclude by highlighting emerging approaches that we regard as potentially transformative. The multidirectional exchange of principles and approaches among engineering, biology, and physics (*1*, *2*, *4*–*6*, *92*) has yielded a wonderful constellation of insights and creative designs that have pushed the boundaries of knowledge and possibility. Going forward, systematic comparative studies (rather than single-species inspiration) could reveal generalizable principles for exceptional performance by providing evolutionary context for the factors shaping organisms (*104*). Distributing energy, sensing, actuation, and control throughout robot frames, as animals do, may advance autonomy (*62*, *105*). Bridging the “sim-to-real” gap with better computational models of robot interaction with the environment (*20*, *44*) could markedly accelerate exploration of design and policy spaces by reducing the number of physical prototypes that need to be built. Bodies can be made easier to control by offloading computation into morphology (*84*, *106*); this approach remains underdeveloped, but continued advances in material robotics may prove transformative (*62*). Systematically exploring trade-offs with respect to multiple performance metrics promotes reuse of parts in disparate behaviors (*6*).

The lesson that we take from biology is that, although further improvements to components and subsystems are beneficial, the greatest opportunity to improve running robots is to make better use of existing parts. We advocate for integrative exploration of design and policy spaces.

Supplementary Materials

This PDF file includes:
Supplementary Results
Tables S1 to S41
References (*49*, *71*, *107*–*190*)

Other Supplementary Material for this manuscript includes the following:
MDAR Reproducibility Checklist

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Why animals can outrun robots

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Editor's summary
Strategies for robot locomotion have often taken inspiration from animals. But robots still fall short when compared to the inherent performance of animals. Burden *et al.* review the literature and discuss why animals outrun robots in categories such as agility, range, and robustness. The authors highlight that, with few exceptions, engineering outperforms biology in the components critical for running, so they conclude that there must be as-yet-undiscovered principles of integration and control that give animals their advantage over robots. —Amos Matsiko

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