

Supplementary Materials for  
**Why animals can outrun robots**

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**The PDF file includes:**

Supplementary Results  
Tables S1 to S41  
References (49, 72, 107–190)

**Other Supplementary Material for this manuscript includes the following:**

MDAR Reproducibility Checklist

# Supplementary Results

This supplement summarizes the quantitative comparisons we made between animals and robots in the five subsystems critical for running: power, frame, sensing, actuation, and control.

The following table summarizes the results of our quantitative comparisons across subsystems between biological and engineered technologies. Each subsystem has an associated color (orange for power, green for frame, red for actuation, blue for sensing, purple for control) that is used in the table to highlight technologies that perform best with respect to each metric. This color is also used in the sections that follow to highlight the specific data tables that are used to populate the summary table. In some subsystems, all tables will be colored; in others, intermediate calculations and datasets are used to derive the quantities that populate the summary table, so those intermediaries are not colored.

			<i>Biological</i>	<i>Engineered</i>	
<b>Subsystem</b>	<b>Metric</b>	<b>Units</b>	<b>Metabolism</b>	<b>Gas engine</b>	<b>Electric battery</b>
<b>POWER</b>	<i>Mass-specific stored energy</i>	kWh / kg	6.7	2.7	0.2
	<i>Mass-specific delivered power</i>	kW / kg	1.2	0.2	10.9
	<i>Mass-specific refueling power</i>	kW / kg	0.8	28,500.0	0.2
	<b>Metric</b>	<b>Units</b>	<b>Bone, Cuticle</b>	<b>Carbon fiber</b>	<b>Aluminum, steel</b>
<b>FRAME</b>	<i>Density-specific stiffness</i>	MPa m <sup>3</sup> / kg	< 10	71.0	< 30
	<i>Density-specific strength</i>	KPa m <sup>3</sup> / kg	< 90	516.1	< 200
	<i>Mass-specific energy</i>	J / kg	< 1000	3753.7	< 1200
	<b>Metric</b>	<b>Units</b>	<b>Muscle</b>	<b>Electric motor</b>	<b>Bimorph piezo</b>
<b>ACTUATION</b>	<i>Mass-specific peak torque</i>	Nm / kg	6 to 133	14 to 164	11
	<i>Mass-specific power</i>	W / kg	50 to 350	1000 to 10,000	160
	<b>Metric</b>	<b>Units</b>	<b>Photoreceptor</b>	<b>Photoreceptor</b>	
<b>SENSING</b>	<i>Light sensitivity</i>	photons	1	1	
	<i># of sensors</i>	#	1.00E+08	1.00E+08	

		Units	Mechanoreceptor	Mechanoreceptor
	<i>Strain sensitivity</i>	strain	1E-5 to 1E-3	1E-11 to 1E-08
	<i># of sensors</i>	#	1E+2 to 1E+4	1E+01
	Metric	Units	Myelinated nerve	Network cable
	<i>Period-specific latency</i>	(none)	4.15E-03	4.58E-06
<i>Communication</i>	<i>Area-and-period specific bandwidth</i>	bits / m <sup>2</sup>	2.50E+13	9.72E+15
CONTROL		Units	Brain	Integrated circuit
<i>Computation</i>	<i># of neurons</i>	#	1E+06 to 8.6E+10	1E+04 to 1E+06
	<i># of synapses</i>	#	1E+10 to 1E+15	1E+07 to 2.56E+08

**Table S1. Summary of quantitative comparisons.** Values and ranges for metrics defined in main text reported for biological and engineered technologies.

# Power subsystem performance

## Body mass fraction

Our aim in this section is to quantify what fraction of the mass of fully-functional runners – such as a human or an autonomous legged robot – is composed of the power system. We treat the energy storage mass fraction separately and consider the mass fraction required for refueling and energy conversion together. We do so as the mass required for energy storage can change depending upon the range requirements, and indeed does so throughout the lifespan, or throughout an extended migration, in biological runners.

For the purpose of making our calculations understandable, we use the following masses to represent animals that are approximately the size of a cockroach, a cat, and a human.

	Body mass $M$ [kg]
<i>Cockroach</i>	0.005
<i>Cat</i>	5
<i>Human</i>	100

**Table S2. Representative body masses for cockroach, cat, and human.**

## Metabolism

What should we consider as the complete subsystem? One approach would be to look at the minimum mass of the storage (fat), energy conversion (mitochondria), and refueling (digestion) components. Although they are not runners, a complete power subsystem of this nature is present in unicellular organisms. Alternatively, we could look at the smallest legged insects or the smallest terrestrial mammals (shrews). Here are some interesting numbers for these possibilities: A single mitochondrion has a mass on the order of  $4E-17$  kg, a single cell has about 300 mitochondria on average, and the smallest unicellular organisms are on the order of  $1E-15$  kg (107). The smallest beetles and spiders are on the order of  $1E-6$  kg (108). The smallest terrestrial mammals (shrews) are on the order of  $1E-3$  kg (87).

Biological power systems can be made on extremely small scales. Here, rather than consider how small this subsystem can be made, we consider what fraction of the mass it comprises in different sized animals.

For mammals, mitochondria as a fraction of body mass scales with  $0.06 M^{-1/4}$  where the units of  $M$  are kg, which we will write as  $[M] = \text{kg}$  (107).

	Mitochondria body mass fraction [(none)]
<i>Cockroach</i>	0.226
<i>Cat</i>	0.040
<i>Human</i>	0.019

**Table S3. Body mass fraction of mitochondria in cockroach, cat, and human.**

Franz *et al.* have the wet gastro-intestinal (GI) tract mass scaling as  $0.075 M^{0.94}$  for 41 species (mass range not reported) (109). The same reference has lizard GI tract mass scaling as  $0.031 M^{1.159}$  for 29 species with a range of body masses 0.008–1.123kg. Gordon and Illius studied African ruminants and found a greater fraction of the body mass dedicated to digestion, as might be expected due to the nature of what they eat and how they extract energy from it. They found  $0.100259 M^{1.1}$  for 21 species with an approximate mass range of 3.7–807 kg (110). Here we use Franz's mammal scaling relationship as the coefficient falls between the three possibilities, and  $[M]$  = kg for all preceding formulas.

	GI tract body mass fraction [(none)]
<i>Cockroach</i>	0.103
<i>Cat</i>	0.068
<i>Human</i>	0.057

**Table S4. Body mass fraction of gastrointestinal tract in cockroach, cat, and human.**

To determine the fraction of body mass dedicated to energy conversion and refueling, we add the mitochondria mass to the gastro-intestinal tract mass.

	Conversion and refueling body mass fraction [(none)]
<i>Cockroach</i>	0.329
<i>Cat</i>	0.108
<i>Human</i>	0.076

**Table S5. Body mass fraction of conversion and refueling components in cockroach, cat, and human.**

The mass of body fat in eutherian terrestrial mammals versus total body mass scales with  $0.075 M^{1.19}$  ( $[M]$  = kg) (111).

A sample of Madagascar hissing cockroaches, *Gromphadorhina portentosa*, has a body mass of 9.59 grams and a measured fat mass of 0.15 grams (112). This equates to about 2% of body mass as fat, which is consistent with the mammalian values.

	Body fat mass fraction [(none)]
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<i>Cockroach</i>	0.016
<i>Cat</i>	0.102
<i>Human</i>	0.180

**Table S6. Body mass fraction of fat in cockroach, cat, and human.**

## Gasoline

We use *BigDog* as a representative gas-powered runner, which has a mass of 109 kg (49).

The refueling hardware on the robot is quite light as it mainly consists of the pipe/hose that leads to the gas tank. We don't have good values for this mass, but we also didn't think it is important as the refueling rate is many orders of magnitude higher than the biological system so any plausible mass will not change the comparison. Here we neglect it.

From a presentation report, we know the component mass including engine, drive, pump, heat exchanger, and oil tank is 21.4 kg. In addition, we know the mass of a full tank of fuel is 5.68 kg, consisting of 4.73 kg of fuel and 0.955 kg of fuel tank.

	Body mass M [kg]	Engine and fuel mass [kg]	Body mass fraction [(none)]
<i>BigDog</i> (49)	109.000	27.109	2.49E-01

**Table S7. Body mass fraction of engine and fuel for BigDog robot.**

## Batteries

Batteries differ from biological power and gasoline power in that the mass dedicated to refueling, conversion, and storage is integrated into one component, making it difficult to separate the individual component masses. The batteries typically used for robots have a fairly consistent amount of energy per unit mass. Consequently, what determines their contribution to total body mass is the capacity of the battery selected by the robot designers, and the mass of the body components that are not dedicated to power. Here we will use a representative sample of autonomous battery-powered robots to estimate the typical fraction of body mass that the battery-powered system comprises.

Similar to the refueling hardware in gas engines, the mass of the power electronics used to charge and discharge batteries is small relative to the battery mass, so we neglect it here.

	Body mass [kg]	Battery mass [kg]	Body mass fraction [(none)]
<i>MIT Cheetah 2015</i> (113)	33.00	3.00E+00	9.09E-02
<i>MIT Cheetah 2018</i> (114)	45.00	3.00E+00	6.67E-02
<i>ETH StarlETH 2014</i> (115)	25.00	2.58E+00	1.03E-01
<i>ETH ANYmal 2016</i> (116)	30.00	3.00E+00	1.00E-01
<b>Average</b>	3.33E+01	2.90E+00	9.02E-02

**Table S8. Body mass fraction of batteries for quadrupedal robots.**

The values are fairly consistent, so we will use the average in what follows.

As a final note, the *Cornell Ranger 2012* robot (11), which was designed to set range records, had a body mass of 9.9 kg and an estimated battery mass of 2.3 kg, equating to 23% of body mass dedicated to battery – more than double the other robots that were not designed to maximize range alone.

## Specific stored energy

### Metabolism

Stored fat has 39.5 MJ / kg (117). Fat is stored in fat cells (adipocytes) which are 87% fuel (lipids) and 13% other material (48). Mitochondria converts stored fat into ATP with an efficiency that can vary, with 70% being a good approximation (46).

	Mass-specific stored energy [kWh / kg]
<i>Metabolism</i>	6.682

**Table S9. Mass-specific stored energy for metabolism.**

### Gasoline

The mass-specific chemical energy of gasoline is 13 kWh/kg (54). Combining this quantity with the fuel mass of *BigDog* yields a stored energy of 61.5 kWh.

To determine specific stored energy, we consider the energy delivered, rather than that of the raw fuel, because there are efficiency losses in the conversion of energy stored in the fuel's chemical bonds to the potential and kinetic energy of a robot's limbs. Dunn-Rankin *et al.* present a range of efficiencies for automotive engines (~25–30%) with efficiency going down with size (47). Since the engine in *BigDog* is on the small side, here we will use 25% efficiency. Note that this figure captures the conversion of stored chemical energy to the mechanical energy output of the engine as this is what we aim to quantify with our metric. The tank to wheel efficiency is lower, ~13% (54). See also Figure 18 in (47).

The mass-specific stored energy for *BigDog* is thus the fuel energy (in kWh) divided by the sum of the fuel and tank mass (in kg) multiplied by the efficiency of converting that gasoline chemical energy into engine mechanical energy.

	Mass-specific stored energy [kWh / kg]
<i>BigDog</i>	2.704

**Table S10. Mass-specific stored energy for BigDog robot.**

## Batteries

Here we focus on lithium-polymer (LiPo) batteries as they are commonly used in running robots. The reported specific energies tend to range between 0.1–0.3 kWh/kg. Other practical battery technologies can have higher specific power (118).

	Mass-specific stored energy [kWh / kg]
<i>MIT Cheetah 2015 (113)</i>	1.55E-01
<i>MIT Cheetah 2018 (114)</i>	2.17E-01
<i>ETH StarlETH 2014 (115)</i>	1.72E-01
<i>ETH ANYmal 2016 (116)</i>	2.17E-01
<b>Average</b>	1.90E-01

**Table S11. Mass-specific stored energy for quadrupedal robots.**

Again there is modest variation in the values. We report the value for the *MIT Cheetah 2018* robot battery as it was designed more recently than the others and the associated publication reports a complete set of specifications for the battery performance.

## Specific delivered power

### Metabolism

Weibel and colleagues, as summarized by Suarez *et al.*, have found that the maximum rate of oxygen consumption by mammalian mitochondria is 5 ml/min per cubic centimeter of mitochondria (119), essentially independent of animal size. The energy consumed per ml of O<sub>2</sub> is 21 J (120). To obtain the delivered power, we need to account for the efficiency of transforming consumed energy into ATP. As we noted earlier, this efficiency is ~70% (46). If we assume that 1 ml of mitochondria weighs 1 gram, we can solve for specific delivered power.

	Mass-specific delivered power [kW / kg]
<i>Metabolism</i>	1.225

**Table S12. Mass-specific delivered power for metabolism.**

### Gasoline

The delivered engine power in the *BigDog 2018* robot is quoted as 15 hp. The power delivered by the hydraulic actuators is reduced by conversion inefficiencies. But comparing the delivered engine power to the power delivered by ATP or electricity by batteries seems most reasonable.



	Mass-specific delivered power [kW / kg]
Gasoline	0.175

**Table S13. Mass-specific delivered power for gasoline.**

## Batteries

The LiPo robot batteries described in the previous section have discharge rates (C-rates) of 40, 45 and 100. C-rate measures the rate at which a battery is discharged relative to its maximum capacity. Here we will report the specifications for the *MIT Cheetah 2018* robot battery as above, which has a C-rate of 50. A 50C rate means that the discharge current will discharge the entire battery in 1/50 hour. We don't correct for conversion inefficiencies as this is already included in the C-rate calculation.

	Mass-specific delivered power [kW / kg]
Battery	10.850

**Table S14. Mass-specific delivered power for batteries.**

## Specific refueling power

### Metabolism

Resting metabolic rate famously depends on body size according to Kleiber's law. For mammals, we will use  $0.0182 M^{0.737}$  ( $[M] = \text{g}$ ) (121). We are assuming that the resting metabolic rate is well approximated by the basal metabolic rate (basal rate is lower than resting rate). Across a wide range of vertebrates, Diamond and Hammond determined that animals can sustain a metabolic rate that is between 1.3-7.0 times their resting metabolic rate (122). This sustained rate is the maximum metabolic power they can sustain without losing weight. Here we approximate the ratio of the sustained to resting metabolic rate as 5. Finally, we normalize by the masses of the digestive system which is our approximation of the hardware that is responsible for fueling in biological runners.

	Mass-specific refueling power [kW / kg]
<i>Cockroach</i>	2.89E-04
<i>Cat</i>	7.11E-02
<i>Human</i>	7.74E-01

**Table S15. Mass-specific refueling power for cat, cockroach, and human.**

## Gasoline

The rate of refilling a gas tank in a consumer car is a controlled standard, and the energy liberated from gasoline is also well known. Previously we assumed the mass of the refueling hardware was negligible – for the purpose of this calculation, we assume it is 1 kg. The resulting quantity is consistent with the figure in (47).

	Mass-specific refueling power [kW / kg]
<i>Gasoline</i>	28,500

**Table S16. Mass-specific refueling power for gasoline.**

## Batteries

The LiPo robot batteries described in the *Specific Stored Energy* section have charge rates of between 1 and 5C. This measures the rate at which a battery is charged relative to its maximum capacity. Here we will report the specifications for the battery in the *MIT Cheetah 2018* robot (114) as we have a complete battery data set and the specifications are similar to the other comparison robots and hobbyist batteries. We don't know its exact charge rate, but let's assume it is 1. A 1C rate means that the charge current will charge the entire battery in 1 hour.

	Mass-specific refueling power [kW / kg]
<i>Battery</i>	0.217

**Table S17. Mass-specific refueling power for battery.**

# Frame subsystem performance

A robot or animal's frame is the primary means of mechanical interaction with its environment, propelling the body forward while overcoming gravity. During these interactions, the frame is subject to substantial dynamic forces that often exceed the body weight depending on the locomotion modality (123). For example, peak forces during constant average speed human running are typically twice the body weight (124). But, during dynamic movements like jumping, they can exceed over 100 times for small animals (125). These interactions can result in the structural or functional failure of a frame. Our motivation is to define a set of possible metrics to capture the performance limits that frames might impose on the agile movement.

## Material and shape

We consider frames as structures, combining material properties (for instance, strength, stiffness, density) and shape (for instance, length, section modulus, moment of area) to support loads and restrict or control motion. Viewed at the level of a component, such as a leg segment, shape and material are independent but interacting factors that together determine structural performance. This coupling must be taken into account when analyzing this subsystem.

To illustrate this challenge, we first consider a foundational function of a runner's limb: support the body's weight. As a first approximation to understand a limb's mechanical properties, consider a thin-walled tube (such as a bone or strut). When subject to axial forces, such a column can fail either by axial compression or buckling as determined by the following governing expressions. For a detailed discussion on this topic, we refer the readers to the comprehensive textbook by Ashby (126), specifically Appendix A5 on page 482.

During *axial compression*, the governing equation is

$$\sigma_{ax} = \frac{F}{A} < Y$$

where:

- $\sigma_{ax}$  is the compressive stress;
- $F$  is the axial force;
- $A$  is the cross section area; and
- $Y$  is the compressive strength (Yield or Ultimate).

During *buckling*, the governing equation is

$$\frac{F_{cric}}{A} = \frac{\pi\lambda^2 E}{2(L/R)^2}$$

where:

- $F_{cric}$  is the critical force after which buckling occurs;
- $A$  is the cross section area;
- $\lambda$  is the half wavelength signifying the buckling mode;
- $L$  is the column length; and
- $R$  is the gyration radius.

The above expression for compressive stress can be rewritten as,

$$\sigma_{bk} = K \frac{E}{s^2} < Y$$

where:

- $\sigma_{bk}$  is the compressive stress;
- $K$  is a proportionality constant determined by the bending mode;
- $E$  is the elastic (Young's) modulus (*a material factor*);
- $s$  is the slenderness ratio (*a shape factor*); and
- $Y$  is the compressive strength (Yield, Ultimate, or Modulus of Rupture as appropriate for elastic, plastic, or brittle materials).

These constraints highlight the strong interdependence of material and shape in determining the performance of a frame element.

Failure of a column will occur in purely axial compression if the stress ( $\sigma_{ax}$ ) in the column reaches the yield stress ( $Y$ ) of the material (*strength-dominated*). On the other hand, if the critical buckling stress ( $\sigma_{bk}$ , determined by the modulus  $E$ ) is less than the yield stress ( $Y$ ), then the column will fail by buckling before yield stress is reached (*stiffness-dominated*).

Our subsequent analyses will focus specifically on thin-walled tubes. We believe this simplification is reasonable because thin-walled tubes are remarkably common in the diversity of bones across vertebrates or tibia across insects (127). Choosing one specific shape enables us to focus on the *material* properties of biological and engineered frames without having to simultaneously consider the *shape*. Methods to incorporate the effect of shape are discussed in detail as 'shape indices' in Chapters 5 and 11 of (126).

We will focus on material indices that determine a limb's functional performance primarily dependent on stiffness ( $E$ ) and strength ( $Y$ ) as discussed above. Furthermore, we assume that we want the lightest possible limbs for reducing actuation and power subsystem constraints and therefore we normalize these material properties by their density ( $D$ ). Thus, we will consider *density-specific stiffness* ( $M1 = E/D$ ) and *density-specific strength* ( $M2 = Y/D$ ), which both contribute to the above failure modes. We compute these for common biological (bone and cuticle) and robotic (aluminum and carbon fiber) materials. We also include Stainless Steel, a popular engineering material for various non-robotic applications, for contrast. Below is the range of material properties derived from (55, 59, 126, 128).

	Stiffness $E$ [GPa]	Strength $Y$ [MPa]	Density $D$ [ $10^3$ kg/m <sup>3</sup> ]
<i>Cuticle</i>	0.001-120	10-1200	1-1.3
<i>Cortical bone</i>	7-30	100-230	1.8-2.1
<i>Tendon</i>	1-2	50-150	1.1-1.2
<i>Natural rubber</i>	0.0015-0.0025	22-32	0.92-0.93
<i>Kevlar</i>	76	1240	1.38

<i>CFRP (carbon fiber reinforced plastic)</i>	69-150	550-1050	1.5-1.6
<i>Aluminum</i>	68-82	58-550	2.5-2.9
<i>Stainless Steel</i>	180-210	480-2240	7.6-8.1

*\*approximate due to small data points and/or large variance.*

**Table S18. Stiffness, strength, and density ranges for biological and engineered materials.**

Note that Kevlar and natural rubber are examples of specialized materials as described in Metric 3 (below) and not used for Metrics 1 & 2.

We choose typical numbers within the above range to evaluate our metrics.

	<b>Stiffness <math>E</math> [GPa]</b>	<b>Strength <math>Y</math> [MPa]</b>	<b>Density <math>D</math> [<math>10^3</math> kg / m<sup>3</sup>]</b>
<i>Cuticle</i>	9	100	1.15
<i>Cortical bone</i>	19	165	1.95
<i>Tendon</i>	1.5	100	1.15
<i>Natural rubber</i>	0.002	26	0.92
<i>Kevlar</i>	76	1240	1.38
<i>CFRP</i>	110	800	1.55
<i>Aluminum</i>	75	302	2.7
<i>Stainless Steel</i>	195	1350	7.85

*\*approximate due to small data points and/or large variance*

**Table S19. Representative stiffness, strength, and density values for biological and engineered materials.**

## Specific stiffness

It is straightforward to compute this metric from the preceding data tables. Carbon fiber outperforms all other materials by a wide margin.

	Density-specific stiffness $M1 = E / D$ [MPa m <sup>3</sup> / kg]
<i>Cuticle</i>	7.8
<i>Cortical bone</i>	9.7
<i>Tendon</i>	1.3
<i>CFRP</i>	<b>71.0</b>
<i>Aluminum</i>	27.8
<i>Stainless Steel</i>	24.8

**Table S20. Density-specific stiffness for biological and engineered materials.**

## Specific strength

Similar to the previous metric, it is straightforward to compute this metric from the data tables. Carbon fiber outperforms all other materials by a wide margin.

	Density-specific strength $M2 = Y / D$ [KPa m <sup>3</sup> / kg]
<i>Cuticle</i>	87.0
<i>Cortical bone</i>	84.6
<i>Tendon</i>	87.0
<i>CFRP</i>	<b>516.1</b>
<i>Aluminum</i>	111.9
<i>Stainless Steel</i>	172.0

**Table S21. Density-specific strength for biological and engineered materials.**

## Specific energy

The preceding metrics focused on the frame's ability to support the body's weight. We now combine these metrics to evaluate the performance of frames as they propel the body overground. In this capacity, an important function of the frame is to store and return energy for increasing the range of locomotion – the frame should function as a spring. We assess a spring's ability to store and release mechanical energy using the material's capacity to store energy defined as the area under the stress-strain curve of the material and normalized by density. This material metric is defined by the following equation, which also relates it to the previous two metrics.

$$M3 = \frac{Y^2}{ED} = \frac{M2^2}{M1}$$

	<b>Mass-specific energy <math>M3 = Y^2 / E * D = M2^2 / M1</math> [J / kg]</b>
<i>Cuticle</i>	966.2
<i>Cortical bone</i>	734.8
<i>Tendon</i>	<b>5797.1</b>
<i>Rubber</i>	367391.3
<i>Kevlar</i>	14660.6
<i>CFRP</i>	3753.7
<i>Aluminum</i>	450.4
<i>Stainless Steel</i>	1190.6

**Table S22. Mass-specific energy for biological and engineered materials.**

Carbon fiber again outperforms bone, cuticle, aluminum, and steel in this metric. However, tendon outperforms carbon fiber. This is not surprising given that tendon's remarkable role in energy storage and release during energy-intensive locomotion is well-documented (129, 130).

However, there are other engineering materials with more exceptional performance if we consider this metric alone. For example, Kevlar has more than twice the mass-specific energy of tendon, and natural rubber is nearly an order of magnitude better than Kevlar by this metric. However, tendon, Kevlar, and rubber have low specific stiffness and are therefore much less effective for load-bearing than the other materials considered. These springy materials are best employed within the frame to add specific functionality like passive energy storage and return.

# Actuation subsystem performance

A dazzling array of technologies have been deployed in the quest for an actuator that could equal or exceed muscle in the pursuit of robotic running. It is a daunting prospect to collect comparative metrics for all of them. Luckily, to substantiate our hypothesis we need not do so. Here we compare the only natural technology for actuating running (muscle) to the most ubiquitous engineered actuator, electric motors, and find that except at small scales, electric motors can perform similarly or substantially better than muscle. At smaller scales, we compare muscle to the most commonly used solution for autonomous microrobots, the piezo bimorph. We find piezos slightly lacking in comparison to muscles at the same scale, but within a similar order of magnitude.

## Overview of technologies

Some general principles constrain the types of actuators available for running. By definition runners have legs, and although simple machines might use prismatic (131) or flexible structures (132), most animals and robots use jointed structures with multiple segments. Thus we consider an actuator for running to be a device that generates rotary motion around a joint. Linear actuators like muscle accomplish this with a moment arm, which affords some torque-speed adjustment at design time.

*Muscles* are hierarchical molecular machines in a matrix of elastic material. They produce a tension force by inducing a conformational change (via a chemical reaction with ATP) in a myosin protein, which then ratchets along another protein. Despite the universality of muscle as Nature's actuator, maximum stress and power values range widely, even within the same organism. As in engineered actuators, muscles exhibit specialization for tasks (for instance, some may be slow but strong, others the opposite). In all muscles, force falls nearly logarithmically with shortening speed, producing a maximum power near 1/3rd the maximum speed. They have a density near water and have intrinsic stiffness much lower than the metals that comprise EM motors.

*Electric motors* vary in their construction and mechanism of operation but generally harness the Lorentz force that arises when a current-carrying wire is placed in a magnetic field. They typically spin much faster than joints need to during legged locomotion, so EM motors benefit from speed-reducing transmissions. Unlike muscle, EM motor torque need not fall with increasing speed, if voltage is high enough.

*Piezo bimorphs* are cantilever actuators consisting of two active piezo crystal layers sandwiching a passive flexible layer. When an electric field is applied, the cantilever bends; mechanical output is taken at the tip of the cantilever (133). Piezos typically require relatively high voltages, so power electronics can be a challenge at small scales.

Since running necessitates repeated collisions with the ground, the effective inertia at the foot is extremely important. The bandwidth of high-speed impacts is typically much faster than that of the actuator, so impact forces are not directly controllable and energy loss is inevitable (134). Thus actuators must be fairly backdrivable and must isolate as much inertia as possible from the end effector. This precludes many transmission approaches like worm gears, lead



screws, and harmonic drives unless some compliance is added between the joint and the transmission.

## Specific peak torque

In the context of running, actuators most frequently create motion by applying torque at joints. Since stronger actuators tend to weigh more, we first compare *mass-specific peak torque*.

### Muscle

Values for muscle can be found from direct experiments, or more commonly by making assumptions about the maximum stress available in combination with measurements of area and moment arm. Maximum muscle force can be calculated by the product of stress and area; in the biological literature area is often estimated by physiological cross-sectional area, defined as the ratio of muscle volume and fiber length. Therefore, *mass-specific torque* can be estimated by the product of the maximum stress and moment arm over the product of fiber length and density.

This calculation assumes parallel fibers; a correction for pennation can be added by dividing the specific torque by the cosine of the pennation angle (135). Muscles with large moment arms and short fiber length will maximize specific torque. The ratio (moment\_arm/fiber\_length) varies from 0.1 to 0.3 in the cockroach hind limb (136), from 0.3 to 1.0 in the human lower limb (137), and generally from 0.1 to 1.0 in the greyhound (135), though more extreme values are found for postural muscles especially. Combined with a representative value of maximum stress of 20 N / cm<sup>2</sup>, this rough calculation suggests a possible range of ~20 to 200 Nm / kg in running animals. Values found in the literature for invertebrates, dogs, and humans lie within that interval.

	Mass-specific peak torque [Nm / kg]
<i>Cockroach hind limb extensors (136, 138)</i>	10-60
<i>Hunting spider flexor (139)</i>	30

**Table S23. Mass-specific peak torque for insect muscle.**

An extensive set of morphological data in the greyhound provides insight into a range of hindlimb muscles in one of the fastest known runners (135). Direct force measurements were not available, and a constant specific force (stress) of 30 N / cm<sup>2</sup> was used to estimate muscle forces. The larger muscles have remarkably low torque density, suggestive of specializations for high shortening velocity and high power production in fast running. Some smaller muscles with much larger fiber length to moment arm ratios like gracilis and gastrocnemius reach values of 33–47 Nm / kg. Data from the three largest muscles are below.

	Mass-specific peak torque [Nm / kg]
<i>Greyhound biceps femoris</i>	6
<i>Greyhound sartorius</i>	10
<i>Greyhound rectus femoris</i>	7.5

**Table S24. Mass-specific peak torque for dog muscle.**

In humans, values arise from measurements of (typically) volitional maximum isometric torque collected on an isokinetic dynamometer, combined with morphometrics collected from MRI or ultrasonography, often combining muscle groups across a joint because humans can't selectively activate single muscles reliably (140, 141).

	Mass-specific peak torque [Nm / kg]
<i>Human elbow flexors (140)</i>	133
<i>Human elbow extensors (140)</i>	100
<i>Human ankle extensors (141)</i>	120

**Table S25. Mass-specific peak torque for human muscle.**

## Electric motor

Direct drive machines have a distinct disadvantage in torque density. Flux saturation limited direct drive motors can reach values of ~25 Nm / kg with large gap radius designs (23). Adding low-ratio gearboxes (typically single-stage planetary) can improve torque density further.

Higher ratio gearboxes can increase torque density but have diminishing returns due to the added weight of the drive. One popular approach, especially in robot arms, is to use Harmonic drives, also known as strainwave gears, which use a novel flexible spline ring gear to produce very high ratios in a compact single-stage drive. Ratios beyond 100:1 are common. Multi-stage planetary drives and cycloids are alternatives. To meet the backdrivability requirement, all high-ratio drives must use series elastic elements. Walking robots with stiff, high-ratio drives typically exhibit stiff gaits and high cost of transport (ASIMO for instance, which uses harmonic drives with no series compliance).

Converting an electric motor's torque to linear motion (for instance, via ball-screw mechanism) and back to rotary joint torque via moment arm is another popular approach that results in very high torque density.

	System type or configuration	Total Motor + Transmission Mass [kg]	Torque [Nm]	Mass-specific peak torque [Nm / kg]
<i>T-Motor U8 (23)</i>	Direct drive	0.25	3.5	14
<i>MIT Cheetah 2017 (142)</i>	Gearbox (5.8:1), no SEA	3.65	313.2	86
<i>DLR FSJ Variable Stiffness Joint (143)</i>	Harmonic drive (100:1), SEA	1.41	67	48
<i>Harmonic drive + Robodrive LM (Not likely capable of running, included for comparison) (144)</i>	Harmonic drive (100:1), no SEA	1.8	182	101

<i>Univ. Texas UT-SEA, with a moment arm of half the stroke (6cm) (66)</i>	Ball-screw with series coil spring	1.17	84	72
<i>MIT TF8 Ankle; omitting ankle structure (145)</i>	Ball-screw with series leaf spring	1.064	175	164

**Table S26. Mass-specific peak torque for electric motor.**

## Piezo bimorph

At very small scales, electric motors see dramatically reduced power and torque density. Some of the most well known high-performance microrobots use piezo bimorphs for actuating wings or legs. The robot HAMR-jr (146) (smaller successor to HAMR (147)) uses 24 mg bimorphs to achieve torque density below muscles found in cockroaches but above those found in greyhounds. The bimorph motion is amplified with a linkage that is integrated into the limb; therefore we omit the linkage mass.

	<b>System type or configuration</b>	<b>Motor mass [kg]</b>	<b>Torque [Nm]</b>	<b>Mass-specific peak torque [Nm / kg]</b>
<i>Piezo bimorph with flexures (146)</i>	Flexure linkage with mechanical advantage	2.40E-05	2.70E-04	11

**Table S27. Mass-specific peak torque for piezo bimorph.**

## Specific power

Since running is dynamic, torques must be generated over a wide range of speeds. A common way to compare this ability is through mechanical power (the product of speed and torque). Again, more powerful motors are heavier, so we compare *mass-specific power*.

## Muscle

Since power amplification mechanisms abound (for instance, latch-mediated springs (68)), the gold standard for measurements is the workloop (148) – an in vitro technique that cycles isolated muscle or its subcomponents while applying electrical stimulation, analogous to a motor dynamometer. The technique allows the full performance space to be explored, including muscle activation and phase that are not part of the typically observed motor pattern. Here we consider power averaged over a whole cycle, since instantaneous power may reflect elastic energy storage and return. Specific power values found via this technique still vary over ~2 orders of magnitude, especially between vertebrates and invertebrates (149). The highest known value comes from quail flight muscle. Values for limbs are generally lower, but this number gives an "existence proof" of extreme power adaptation to compare against.

When these invasive techniques are not available (for instance, in humans), estimates exist for muscle groups across a joint. Joint power can be measured with an isokinetic dynamometer or other instrument, or during behaviors that generate mechanical work (for instance, acceleration or climbing)

Note that muscle is single-acting and antagonistic in most animals; over one cycle of motion, a kilogram of muscle can only contribute power while shortening (for instance, during extension only), whereas a kilogram of electric motor produces power in both directions (i.e., flexion and extension). In many cases, muscles even actively absorb power while their antagonist works, especially when cycling quickly. Although muscles may instantaneously produce higher power levels (for instance, over 1000W/kg for quail flight muscle (150)), instantaneous values make for a misleading comparison. Therefore, we use cycle-averaged power in the following comparison.

	Measurement method	Mass-specific power [W / kg]
<i>Quail flight muscle (150)</i>	Workloop	350
<i>Lizard (148)</i>	Workloop	150
<i>Mouse (151)</i>	Workloop	107
<i>Frog hindlimb extensor (152)</i>	Workloop	94
<i>Locust hindlimb extensor (150)</i>	Workloop	75
<i>Cockroach hindlimb extensor (138)</i>	Workloop	50
<i>Turkey hindlimb (153)</i>	Acceleration; whole hindlimb mass used	150
<i>Human knee extensors (154)</i>	Cycle dynamometer; test duration 5-10 minutes	117

**Table S28. Mass-specific power for muscle.**

## Electric motor

Electric motors produce torque proportional to the supplied current, up to a maximum typically determined by magnetic saturation (or more practically, due to heat build up). Unlike muscles, motors do not experience intrinsic reduction in force with increased velocity, unless supply voltage is limited. Like muscle, motors can be specialized, trading torque, maximum speed, and other parameters, so performance values vary. Because high currents can heat a motor quickly, the maximum torque and power can be very sensitive to the time horizon. Still, many papers cite “maximum” numbers, and we will use those here. At the highest speeds, mechanical limits arise due to centripetal forces.

Compared to muscle, electric motors can generate extremely high power densities, typically at high rotary speed. Even over longer time horizons, motors can sustain high power density. Values near 1 kW / kg can be found for continuous power in commercial off-the-shelf motors. When integrated into structures with high ratios, power density can be substantially degraded (especially when power supplies are limited), but values still typically meet or exceed that of muscle.

	System type or configuration	Motor mass [kg]	Power [W]	Mass-specific power [W / kg]
<i>Typical direct-drive 3-</i>	Direct drive	(see ref)	(see ref)	1000-10,000

<i>phase motors (134)</i>				
<i>Maxon EC frameless DT50</i>	Direct drive	0.225	150	667
<i>DLR FSJ Variable Stiffness Joint (143)</i>	Harmonic drive (100:1), SEA	1.41	600	426
<i>Univ. Texas UT-SEA, with a moment arm of half the stroke (6cm) (66)</i>	Ball-screw with series coil spring	1.17	110	94
<i>MIT TF8 Ankle; omitting ankle structure (145)</i>	Ball-screw with series leaf spring	1.064	350	329

**Table S29. Mass-specific power for electric motor.**

### Piezo bimorph

Piezo bimorphs can generate high power at high frequencies, but may be more limited in limb structures with lower resonant frequency. HAMR's actuators resonate at 1600 Hz, generating over 300 W/kg, but when integrated into a robot resonate at 75 Hz and generate only 38 W/kg. HAMR-Jr's legs resonate at higher frequencies, enabling about 4X more power density of 160 W/kg, substantially more than its biological inspiration.

	<b>System type or configuration</b>	<b>Motor mass [kg]</b>	<b>Power [W]</b>	<b>Mass-specific power [W / kg]</b>
<i>Piezo bimorph with flexures (146)</i>	Flexure linkage with mechanical advantage	2.40E-05	3.84E-03	160

**Table S30. Mass-specific power for piezo bimorph.**

## Sensing subsystem performance

Our motivation is to capture the performance limits that sensors might impose on the generation of controlled, agile movement. Biological sensing is classically partitioned into exteroception and proprioception. But the former strictly is the sensing of external cues, whereas the latter is typically defined as the sensation of self-movement, pose, and internal mechanical state. As a result, these are not a true dichotomy. Internal sensing can be chemically mediated and the detection of external cues through force transmitted through the body such as vibration and load sensing belie this partition. An exoskeletal strain receptor or even a muscle stretch receptor could therefore detect deformations produced by self-motion or respond to externally applied forces, especially during unsteady movement. Nonetheless, it is a useful heuristic for discussing the use case of sensors in behavior. Interestingly such a dichotomy does not seem to exist in the engineering literature, likely because specific sensors are often designed to capture only specific single modalities. In these cases, roboticists often design control of specific task variables to utilize a specific few sensory modalities leading to dichotomies like force versus positional control that do not align with organisms' typically multimodal strategies.

The most common metrics for sensors in engineered systems are sensitivity and resolution. The former is a ratio of the change in the sensor to the sensor output. The resolution is the smallest amount of change in the input that can be resolved as a change in the output. Similar definitions have been used in the biological literature with the output of a sensory neuron often quantified by the firing rate of action potentials or the membrane potential of the neuron. A challenge with comparing sensitivity and resolution across systems is that their values are context-dependent: they can depend both on the design of the sensors themselves, the power supplied, and the situation in which they are deployed.

### Threshold sensitivity

We define *threshold sensitivity* as the minimum amount of input needed to register a detectable change in the sensor's output. The units depend on the type of sensors (for instance, photons, nm, concentrations).

### Photoreceptors

Vision thresholds are defined by the number of photons needed to produce a response. Both invertebrates and vertebrates can achieve single photon thresholds with quantized bumps in their photoreceptor's membrane potential (71). The best engineered semiconductor photodiodes can also achieve this resolution (72).

	Photoreceptor threshold sensitivity [#]
<i>Vertebrates &amp; Invertebrates</i>	1 photon
<i>Single Photon Avalanche Diodes (SPAD)</i>	1 photon

**Table S31. Biological and engineered photoreceptor threshold sensitivity.**

## Mechanosensors

For mechanosensation there are a larger variety of ways to measure displacement or deformation, but both biological and engineered systems often rely on strain ( $\epsilon = \Delta L/L$ ). Campaniform sensilla are typically between  $10^1$  and  $10^2 \mu\text{m}$  and have a detection threshold of 10 nm (73). Mammalian hair cells are used in both audition and vestibular sensation, with some modifications. Auditory hair cells can resolve displacements down to 0.3 nm and at  $10^1$  to  $10^2 \mu\text{m}$  is size, this gives a threshold sensitivity of  $\sim 10^{-5}$  strain (155). However, Brownian motion at these scales is often  $\sim 1\text{--}3$  nm (156) so the actual limit may be thermodynamic at  $\sim 10^{-4}$  strain. Most engineered strain sensors can achieve better threshold strain sensitivities from  $10^{-8}$  to  $10^{-11}$  but are often longer in absolute size by design in order to achieve this (157). So, the absolute threshold in both cases may again be down to biophysical limits of thermal noise.

	Mechanosensor threshold strain sensitivity [(strain)]
<i>Cockroach campaniform sensilla</i>	1E-03
<i>Guinea Pig hair cells</i>	1E-05
<i>Engineered strain sensors</i>	1E-11 to 1E-08

**Table S32. Biological and engineered mechanosensor threshold sensitivity.**

## Number of sensors

Our second metric is the number of sensors. This is a common sensor metric (sometimes reported as a density, for instance, pixels /  $\text{cm}^2$ ) and draws an important distinction between biological and engineered runners.

## Photoreceptors

For vision, the number of sensors is just the number of photoreceptors in the eye. In invertebrate compound eyes, each facet is called an ommatidium (plural: ommatidia) and each has usually between 6–10 photoreceptors (71).

	Number of photoreceptors [#]	Explanation
<u>Biological:</u>		
Cockroach <i>Periplaneta americana</i> (76)	1.4E4	2000 ommatidia, 7 photoreceptors per ommatidium
Fly <i>Drosophila melanogaster</i> (158)	5.6E3	700 ommatidia, 8 photoreceptors per ommatidium
Moth <i>Paysandisia archon</i> (159)	1.8E5	20,000 ommatidia, 9 photoreceptors per ommatidium
Feather-wing beetle <i>Ptiliidae</i> (160)	$\sim 4E2$	$\sim 50$ ommatidia, 8 photoreceptors per ommatidium
Human <i>Homo sapiens</i> (155)	1E8	

Engineered:		
<i>100 MP camera (engineering)</i>	1E8	found in high-end smartphones

**Table S33. Biological and engineered number of photoreceptors.**

## Mechanosensors

Quantifying the total number of mechanosensors for animals is very species specific and in the case of mechanoreceptors it is unclear if the appropriate comparison point is all mechanosensors or only those thought to be used in proprioception. Such distinction is likely to be important for investigations of specific systems, but our broad point is captured by a very general comparison.

	Number of mechanosensors [#]
<i>Insect campaniform sensilla (79)</i>	1000 to 10,000
<i>Insect chrodontonal organs (79)</i>	Many with 100s of sensors per organ
<i>Insect other mechanosensitive hairs and sensilla (79)</i>	100 to 10,000
<i>Human tactile receptors (77)</i>	20,000
<i>Human muscle spindles (161)</i>	5,000
<i>Angular encoders (engineering)</i>	< 100; typically equals # of degrees-of-freedom

**Table S34. Biological and engineered number of mechanosensors.**

## Perceptual threshold

It is important to draw a distinction between the threshold sensitivity of the sensor and the behavioral or perceptual threshold, which is the smallest unit of input that an organism can perceive consciously (i.e. discriminate when asked) or respond to behaviorally. For vision, perceptual thresholds can still occur at the single photon level (162), but for mechanosensation, they are typically much higher than the threshold sensitivity (163). However, these perceptual limits are a consequence of the integration of sensing, control, and behavior rather than of fundamental limits on the sensors themselves.

	Perceptual threshold about a limb joint [deg]
<i>Human elbow flexion (164)</i>	1
<i>Locust scratching (165)</i>	< 10

**Table S35. Perceptual threshold about a limb joint in human and locust.**



# Control subsystem performance

Since control consists of transmission and transformation of signals, we compare the communication channels and computational elements available to animals and robots.

## Communication

Our goal is to quantify the bandwidth and latency of communication channels found in nervous systems and computer networks of runners. Before quantitatively comparing these metrics, we motivate their definition using fundamental performance constraints in control systems.

### Data-rate Theorems

Latency and bandwidth constrain control system performance via *data-rate Theorems (85)* by placing lower bounds on the steady-state error that can be achieved by any controller.

Consider the discrete-time linear time-invariant system,

$$x^+ = A x + B u.$$

Since stable modes do not need to be stabilized by feedback, we assume without loss of generality that a change-of-coordinates has been applied to extract only the unstable modes for consideration, so all eigenvalues of  $A$  have magnitudes larger than 1.

Define the intrinsic entropy rate  $H$

$$H = \log_2 | \det A |.$$

Note that  $H > 0$  since all eigenvalues of  $A$  have magnitude larger than 1 and the determinant of a matrix equals the product of its eigenvalues.

Theorem 1 and Proposition 1 in (85) tell us that:

- if the bandwidth  $R$ , measured in units of bits per sample, is smaller than the intrinsic entropy rate, so  $R < H$ , then the system cannot be stabilized;
- if  $R > H > 0$  and the communication channel has latency (i.e. delay)  $L > 0$ , measured in units of samples, then the norm of the steady-state error is lower-bounded by a function that increases without bound as  $R$  and  $L$  increase.

These theoretical results comport with the intuition that a controller can perform better when more information (measured by  $R$ ) is available more quickly (measured by  $L$ ). Importantly, these performance constraints apply regardless of how the controller is implemented, so we compare bandwidth and latency of communication channels implemented in nervous systems and computer networks.

### Application of data-rate Theorems

Consider the dynamics of an inverted pendulum,

$$m l^2 \ddot{q} = m g l \sin (q) + u,$$

where:

- $m$  is the pendulum mass;
- $l$  is the pendulum length;
- $g$  is the acceleration due to gravity;
- $q$  is the pendulum angle,  $\dot{q}$  its velocity,  $\ddot{q}$  its acceleration; and

- $u$  is the control torque applied to the pendulum.

Since runners must be capable of maintaining an upright posture, stabilization of an inverted pendulum defined by the runner's mass and leg length is a simple representative control problem solved by a nervous system or computer network in a runner.

By time-discretizing the pendulum dynamics with sampling interval  $d$  and linearizing about the vertical equilibrium point, the intrinsic entropy rate can be shown to be

$$H = \log_2 (1 + d \sqrt{g/l}).$$

Note that this expression decreases as the natural frequency  $\sqrt{g/l}$  of the pendulum increases. This finding comports with intuition, as larger runners have more time to correct for errors before they hit the ground, so less bandwidth is required to attain the same steady-state error (166). We normalize latency and bandwidth by the natural period  $\sqrt{l/g}$  to obtain dimensionless quantities for comparison across scales.

	Leg length [m]	Natural period [sec]
<i>Cockroach</i>	0.02	0.284
<i>Cat</i>	0.25	1.003
<i>Human</i>	1	2.006

**Table S36. Leg length and natural period of cockroach, cat, and human.**

### Specific bandwidth

The maximum bandwidth of a single axon is 1 kilobit per second; this bound has been posited theoretically (167) and measured empirically (168). Although the length of axons that approach this upper bound is generally much shorter than a cat's or human's leg length, this upper bound suffices for comparison with computer networks.

EtherCAT (IEC 61158) (169) is a standardized communication protocol for control systems that runs on CAT 5 Ethernet cables. This standard can update 100 servo axes with 16 bit precision every 100 microseconds for cable lengths up to 100 meters.

InfiniBand (170) is a proprietary communication protocol and medium for computer clusters that uses copper wires with lengths ranging from 0.5 to 1 meter and transmits data at up to 100 gigabits per second.

Many axons can be bundled into a single nerve, yielding a communication channel whose bandwidth theoretically scales linearly with the number of axons. However, the cross-sectional area of the channel also scales linearly with the number of axons, so we normalize bandwidth by cross-sectional area.

Axon diameters range from 0.2 to 20 micrometers in mammals (171, 172), and there are theoretical reasons to believe smaller sizes are not practical (173), leading to a range of cross-sectional areas.

Ethernet wires range from 22 to 28 AWG, corresponding to diameters of roughly 0.5 mm, and the outer cable diameter is roughly 5mm.

Infiniband has 0.25 mm wires and roughly 10mm cable diameters.

To obtain a single representative diameter for subsequent calculations, we average these extremes. Since many orders of magnitude will separate the performance of a computer network from that of an axon, this choice does not influence the outcome of the comparison.

	Diameter [micrometer]		
	<i>lower bound</i>	<i>upper bound</i>	<i>representative</i>
<i>Axon</i>	0.2	20	10.1
<i>EtherCAT</i>	500	5000	2750
<i>InfiniBand</i>	250	10000	5125

**Table S37. Diameter of axon, EtherCAT cable, and InfiniBand cable.**

	Area-and-period-specific bandwidth [bit / m <sup>2</sup> ]
<i>Axon</i>	2.50E+13
<i>EtherCAT</i>	5.40E+12
<i>InfiniBand</i>	9.72E+15

**Table S38. Area-and-period-specific bandwidth of axon, EtherCAT cable, and InfiniBand cable.**

As a sanity-check for our rough calculations, we note that (86) estimates a bandwidth of approximately 10 megabits per second for the human retinal nerve, which has a 5 mm diameter (174), corresponding to an area-specific bandwidth of 5.09E+11.

This figure is lower than our estimate, but that outcome is unsurprising since we gave axons the advantage at every stage of the preceding calculation: we used the maximum theoretical bandwidth and didn't account for the adipose tissue (myelin) that insulates nerves, which can take up a substantial fraction of a nerve's area as summarized in Table B.1 of (175).

We find that a nerve (axon bundle) may theoretically outperform EtherCAT whereas having the same cross-sectional area, but there are faster communication protocols like InfiniBand that outperform the nervous system by two or more orders of magnitude.

### Specific latency

Axonal conduction velocity is theoretically proportional to axon diameter; experimentally, conduction velocities top out at 120 m / sec for the myelinated nerves of terrestrial mammals (176, 177) and 4 m / sec for the unmyelinated nerves of insects (178). Since latency is equal to distance divided by conduction velocity, signals transmitted the length of a runner's leg are delayed by more than a millisecond.

EtherCAT can update 100 servo axes every 100 microseconds for cable lengths up to 100 meters.

InfiniBand latency is 1.3 microseconds for cables up to 1 or 2 meters.

	Period-specific latency of <i>communication</i> [(none)]	Notes
<u>Biological:</u>		
<i>Cockroach</i>	1.76E-02	
<i>Cat</i>	2.08E-03	
<i>Human</i>	4.15E-03	
<u>Engineered:</u>		
<i>EtherCAT</i>	3.52E-04	<i>scale-invariant; cockroach natural period used to get worst-case value</i>
<i>InfiniBand</i>	4.58E-06	

**Table S39. Period-specific latency of communication for axon, EtherCAT cable, and InfiniBand cable at cockroach, cat, and human length scales.**

We find that EtherCAT may outperform axons by an order of magnitude in time required to transmit a signal the length of a runner's leg, and InfiniBand is hundred times faster still. It is impractical for animals to approach the latencies of computer network protocols, since doing so would require scaling up axon diameters by multiple orders of magnitude (87, 177), which would not fit inside legs.

## Computation

Our goal is to quantify the complexity of computations that can be performed in runners and the time required for the computation.

Intuitively, a controller's computation consists of transforming sensor signals to actuator signals. Mathematically, this transformation is a function. It is not clear what specific function or class of functions are necessary for high-performance running – all we have is the proof-of-concepts in animals, whose transformations are implemented in (biological) neural networks.

Robots have access to artificial and spiking neural networks in neuromorphic integrated circuits (179) as well as the fundamentally different von Neumann architecture (180). It is conceivable that digital computers based on von Neumann architectures could meet or exceed the performance of animals' neural networks in their implementation of effective controllers, but in the absence of robots that are better at running than animals, we focus on the most direct comparison between natural and artificial spiking neural networks.

As a brief aside, it is worth noting that the von Neumann architecture is inefficient at "simulating" a spiking neural network – a supercomputer simulation of a leaky integrate-and-fire network on the scale of the human cerebellum required 82,944 von Neumann CPUs and ran six hundred times slower than realtime (181).

We are thus motivated to compare natural and artificial neural networks: on the one hand because they are the only option for general-purpose computation in the nervous system; and on the other because they are capable of solving complex optimization problems (88) and they are universal approximators (182) – any function can be approximated to any desired degree of accuracy by a network with a sufficiently large number of "neurons" (termed *units*) and "synapses" (the weighted connections between units).

We will not consider neural network architecture here for two reasons. First, feedforward neural networks with only one "hidden" layer have the "universal approximation" property, so there is no theoretical advantage in terms of the complexity of transformations that can be represented by considering deep networks (183). Second, there appear to be no practical constraints on the architecture that can be implemented in neuromorphic circuits, so if a particular network were discovered that solved a control problem particularly well, current design and fabrication technologies ought to be able to reproduce the circuit in silicon, so long as a sufficient number of units and connections were available in the integrated circuit.

Instead, we will focus on the number of units and connections that can be implemented in a runner's neural network, since these counts place limits on the space of transformations available to the runner. But we first repeat our analysis of latency to confirm a similar separation in performance holds between engineered and biological networks.

### Specific latency

In a feedforward neural network, a "computation" is performed when a vector of inputs is transformed to a vector of outputs. This process does not occur instantly and is instead proportional to the latency or characteristic time constant of the network's units (88). This latency is on the order of milliseconds for natural neurons (88) and can be shorter than microseconds for artificial neurons (89).

Period-specific latency of <i>computation</i> [(none)]	
<u>Biological:</u>	
<i>Cockroach scale</i>	3.52E-03
<i>Cat scale</i>	9.97E-04
<i>Human scale</i>	4.98E-04
<u>Engineered:</u>	
<i>Cockroach scale</i>	3.52E-06
<i>Cat scale</i>	9.97E-07
<i>Human scale</i>	4.98E-07

**Table S40. Period-specific latency of computation for axon, EtherCAT cable, and InfiniBand cable.**

We find, perhaps unsurprisingly, that artificial units in specialized integrated circuits can be activated several orders of magnitude faster than biological neurons. Decades of intensive research and development into the design and fabrication of integrated circuits by the

semiconductor industry has yielded engineered units that dramatically outperform their biological counterparts in this regard.

### Number of neurons and synapses in a spiking neural network

Neuromorphic integrated circuits are undergoing something of a renaissance in recent years, motivated in part by the impressive performance of large-scale neural network architectures on machine learning challenges in perception, language, and control.

Industry research labs have created chips with the largest numbers: IBM's TrueNorth (184), which has an area of 430 mm<sup>2</sup>, has 1e6 neurons and 2.56e8 synapses. Intel's Loihi (185), which has an area of 60 mm<sup>2</sup>, has 1.3e5 "leaky integrate-and-fire" (LIF) neurons and 2e6 1-bit synapses.

The numbers have been more modest in academic research labs, with Tianjic (89) having an area of 14.4 mm<sup>2</sup> containing 4e4 neurons and 1e7 synapses. But Tianjic was notably used to control an autonomous robot (electric bicycle), whereas applications of the industrial chips have focused on more general-purpose machine learning tasks (186, 187).

In stark contrast, animal nervous systems have staggering numbers of neurons and synapses: cockroach nervous systems have 1e6 neurons and 1e10 synapses on a characteristic length scale of 0.5 mm (188); cat brains have 7.6e8 neurons and 1e13 synapses, and the largest linear dimension of the brain is 50 mm; human brains have 8.6e10 neurons and 1e15 synapses, and the largest linear dimension of the brain is 150 mm.

	Neurons [#]	Synapses [#]	Length scale [mm]	Neurons [words]	Synapses [words]
<u>Biological:</u>					
<i>Cockroach</i>	1.00E+06	1.00E+10	0.5	1 million	10 billion
<i>Cat</i>	7.60E+08	1.00E+13	50	760 million	10 trillion
<i>Human</i>	8.60E+10	1.00E+15	150	86 billion	1,000 trillion
<u>Engineered:</u>					
<i>Tianjic</i>	4.00E+04	1.00E+07	4	40 thousand	10 million
<i>Loihi</i>	1.30E+05	1.26E+08	8	130 thousand	126 million
<i>TrueNorth</i>	1.00E+06	2.56E+08	21	1 million	256 million
<i>Supercomputer</i>	6.80E+10	5.40E+12	100,000	68 billion	10 trillion

**Table S41. Number of neural units and synaptic connections in biological and engineered spiking neural networks.**

We find support for the colloquial understanding of animal brains being remarkable computing machines relative to integrated circuits, specifically in terms of the complexity of transformations that can theoretically be implemented. But in conclusion, we recall the obvious fact that animal brains are used for a staggering variety of tasks beyond sensorimotor control, so it is unclear how much brain is needed to achieve high performance in any particular task

like running. There are many competing theories for whether and why bigger brains are better (91). One observation is that primate brain size correlates with social network size (189), motivating the "social brain hypothesis" (190) that bigger brains evolved primarily in service of interactions with others, rather than to increase proficiency in tasks like locomotion that much smaller brains perform extremely well.