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2 **Locomotion**

3 Casey Gähns and Andrés Vidal-Gadea
 4 School of Biological Sciences
 5 Illinois State University, Normal, IL, USA

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6 **Synonyms**

7 [Animal mobility](#); [Animal movement](#); [Animal](#)
 8 [progression](#)

9 **Definition**

10 Locomotion refers to an organism's ability to
 11 translate itself from one place to another. This
 12 can be accomplished by active and passive
 13 means. It spans from the use of simple molecular
 14 machines to complex multi-organ systems acting
 15 in concert.

16 **Introduction**

17 All organisms share a common ancestry along
 18 with a set of enduring biological directives
 19 reflecting their relatedness. Chief among these is
 20 the drive to persist by temporarily overcoming
 21 overwhelming physical and energetic obstacles.
 22 Organisms large and small, simple and complex,
 23 labor to survive long enough to produce viable
 24 offspring. To accomplish this, they evolved

abilities to exploit beneficial resources and envi- 25
 ronments. Some eventually became able to seek 26
 new resources when local supplies became 27
 exhausted, transporting themselves to new 28
 environments. 29

Locomotion refers to an organism's ability to 30
 transport itself from one place to another. This is a 31
 task fraught with uncertainty and danger. Trading 32
 a known environment for an opportunity to find a 33
 better one is risky at best. Many animals are par- 34
 ticularly vulnerable during locomotion. Their 35
 available resources and attention become 36
 repurposed to the completion of this goal, making 37
 them particularly vulnerable to energy depletion 38
 and predation. Therefore, locomotion is a danger- 39
 ous behavior not undertaken lightly. As such, it is 40
 often goal-oriented and used to increase fitness 41
 (e.g., securing nourishment, avoiding death/pre- 42
 dation, reproduction). Because of the associated 43
 risks, many animals locomote in short bouts when 44
 approaching potentially dangerous environments. 45
 This allows them to sample their environment for 46
 dangers. The same animals, however, increase 47
 their bout durations when traveling back toward 48
 safety. 49

The evolutionary race for survival resulted in 50
 the production of highly diverse and complex 51
 sensory systems to probe environments and loco- 52
 motor systems to convey animals to their destina- 53
 tions quickly and safely. How animals accomplish 54
 locomotion, and translate themselves from one 55
 place to another, depends on factors such as their 56

57 evolutionary history, the physics of their environ-
58 ment, and the biological drive being satisfied.

59 Many animals living near the interface of distinct
60 physical environments (e.g., land and water)
61 evolved the ability to exploit multiple environ-
62 ments (e.g., one for sustenance and another for
63 locomotion). For example, many insects and birds
64 walk when foraging but switch to flight when
65 traveling between feeding sites as a more energet-
66 ically efficient form of locomotion. Crayfish and
67 young lobsters walk on the bottom of springs and
68 oceans but will swim away from predators using
69 their powerful tails. Each distinct type of locomotion
70 is made possible by dramatic feats of special-
71 ization in the animals' nervous system, skeleton,
72 and musculature. While there are many examples
73 of transition between environments over evolu-
74 tionary time, most animals are specialized for
75 locomotion through one physical niche through-
76 out their lives. Those capable of locomotion
77 through multiple environments must reconfigure
78 their motor outputs to match the properties of each
79 environment.

80 When studying simple processes, it is often
81 possible to divide them into their components
82 and to dissect and understand the role of each
83 part independent of the whole. Often, single
84 chains of cause-and-effect hierarchies make easy
85 work of understanding the process by sequentially
86 dealing with each aspect of the whole. Animal
87 locomotion defies this type of approach. Locomotion
88 is not the final output of a chain of events;
89 rather, it emerges from the tightly concerted inter-
90 action of numerous organismal systems
91 (Alexander 2003). Thus, our compartmentalized
92 approach to its study is more a reflection of our
93 own limitations than a characteristic of the process
94 we will now discuss.

95 Thus, while the following sections attempt to
96 simplify our task by dealing with intuitive
97 (dissectible) aspects of animal locomotion, the
98 reader should remain aware that these separations
99 are artificial and for our benefit. Furthermore,
100 animal locomotion is not the product of a machine
101 optimized for the performance of a task, but rather
102 the survivable output of the cumulative history of
103 a species. As such, it can only be fully understood
104 in the context of an animal's life history

105 challenges and of its inheritance passed down
106 through evolution. We will next look at some of
107 the challenges this behavior evolved to surmount
108 before looking within organisms at its mechanics.

Goals of Animal Locomotion 109

110 Why do animals move? As mentioned above, one
111 of the primary drives common to all life forms is
112 the directive to survive to reproduce. Thus, loco-
113 motion can be understood as an animal's attempt
114 to improve the odds of this outcome. Some over-
115 arching goals driving locomotion include (i)
116 avoiding death (self-preservation), (ii) finding
117 mates (for sexually reproductive animals), and
118 (iii) ensuring the survival of offspring. These are
119 certainly not all the reasons why animals move.
120 Additionally, some of these goals (e.g., self-
121 preservation) include unique locomotor goals
122 within them. For example, self-preservation
123 includes escaping predators but also energy pro-
124 curement. We will discuss some of these goals, as
125 the (often competing) demands they place on ani-
126 mals have driven the evolution of the distinct
127 types of locomotion we appreciate in the natural
128 world.

Self-Preservation 129

130 Many distinct locomotor activities have the goal
131 of maintaining an organism's viability. The exact
132 locomotor behaviors depend on the animal, but
133 minimally they involve (a) procuring and
134 ingesting other organisms, (b) avoiding ingestion
135 by other organisms, and (c) avoiding environmen-
136 tal risks (e.g., temperature extremes). Each of
137 these tasks presents unique challenges that are
138 often in conflict with one another. For example,
139 searching for food often places animals at
140 increased risk of predation.

141 Animals are unable to manufacture their own
142 complex organic compounds for nutritional pur-
143 poses (i.e., they are heterotrophic). Instead, they
144 must obtain their nutrients by ingesting other
145 organisms in their environment. Some animals,
146 such as sponges, corals, and tunicates, are sessile
147 and able to capture sufficient nutrients as they
148 move pass them. Even here, most of these animals

149 have short motile stages where their larvae seek
 150 promising environments before becoming sessile.
 151 Large, complex animals are unable to reliably
 152 capture sufficient resources without investing
 153 energy to seek them out regularly.

154 Each vital locomotor activity often requires
 155 distinct neural specializations. Finding food
 156 (or mates) requires extreme feats of sensory detec-
 157 tion involving computationally expensive special-
 158 ized search strategies. For example, moths use a
 159 strategy called *casting* when following phero-
 160 mone plumes in search of mates. Similarly, dogs
 161 tracking scents employ active sensing, sampling
 162 their environment at regular intervals. In both
 163 examples, sensory inputs are integrated over
 164 time to deduce the scent's source.

165 Locomotion during the search phase of mate or
 166 food procurement needs to be slow enough to
 167 allow the nervous system enough time to sample
 168 the environment and resolve (often tenuous) gra-
 169 dients. During this type of locomotion, sensory
 170 processing can be the rate limiting factor. Increas-
 171 ing the organism's investment in its sensory sys-
 172 tem can result in higher neural acuity, sampling
 173 speed, and resolution. However, this also carries
 174 heavy energetic costs, which animals must bal-
 175 ance with their needs.

176 While searching for food might be slow and
 177 involve large sections of the central nervous sys-
 178 tem acting in concert, avoiding predation is often
 179 more straightforward. During predator avoidance,
 180 an animal's reliance on its sensory system comes
 181 down to a single vital piece of information: locat-
 182 ing the threat. This information is used to trigger
 183 often stereotypical escape behaviors that remove
 184 the animal from danger. Because escape speed is
 185 often the variable that separates life and death,
 186 nervous systems show adaptations that optimize
 187 the speed of these behaviors. These include:

- 188 (a) Using as few cells as possible to sense and
 189 trigger the escape response (minimizing delay
 190 associated with synaptic communication).
- 191 (b) Using electrical synapses whenever possible.
 192 Chemical synapses, while malleable and
 193 effective, are also the slowest (each adds at
 194 least 1–5 ms to signal conduction time).

Therefore, many escape behaviors rely on a 195
 few, fast (<0.3 ms), electrical synapses. 196
 (c) Using large diameter nerve fibers and 197
 myelination to maximize the impulse velocity. 198

There are many examples of escape behaviors 199
 making use of these neural optimizations. The 200
 Mauthner cell in fish and amphibians is a large 201
 neuron that makes extensive use of electrical syn- 202
 apses to produce fast escape responses. Similarly, 203
 large diameter neurons and/or electrical synapses 204
 also mediate the tail-flip escape response in cray- 205
 fish, escape jet propulsion of squids, escape jumps 206
 in fruit flies, and more. Similarly, myelination of 207
 escape neurons in some copepod species allows 208
 these animals to perform faster, energetically effi- 209
 cient, escapes than they could perform otherwise. 210

Animals that succeed in consuming (and avoid 211
 being consumed by) other organisms are still 212
 faced with the task of surviving changing envi- 213
 ronmental parameters. The magnitude of this task 214
 varies significantly across species. For animals 215
 unable to regulate their temperature (i.e., ecto- 216
 therms), or those living in harsh environments 217
 (e.g., deserts), the task might pose greater risk 218
 than predation or starvation. Because many envi- 219
 ronmental parameters change between day and 220
 night, or across different seasons, animals often 221
 relocate to avoid environmental extremes. Loco- 222
 motion in response to cyclical environmental fluc- 223
 tuations are responsible for many of the great 224
 animal migrations occurring across the world, 225
 from the daily vertical migrations of jellyfish in 226
 the ocean to the yearly migrations of the monarch 227
 butterfly in North America. 228

However, some environmental parameters 229
 change too fast for animals to successfully relo- 230
 cate once change is underway. Faced with this 231
 challenge, some animals initiate their locomotion 232
 before environmental variables begin to change. 233
 Nervous systems thus evolved internal 234
 (biological) clocks allowing them to predict and 235
 behave in anticipation of impending environmen- 236
 tal changes. Accurately anticipating environmen- 237
 tal variations is of paramount importance in 238
 survival. In addition to these predictive computa- 239
 tions, animals often use environmental cues (e.g., 240

241 photoperiod) to decide when to initiate their
242 migrations.

243 **Finding and Securing Mates**

244 Solitary organisms that rely exclusively on sexual
245 reproduction must travel to find potential mates.

AUJ3 246 Finding a mate can involve returning to a natal site
247 or group (philopatry) or dispersing to new areas
248 and populations (Greenwood 1980). Animals that
249 disperse must seek out and find mates in isolation.
250 For example, moths will orient to chemical signals
251 (pheromones) to find a mate. However,
252 philopatric animals often engage in group migra-
253 tions which increase their odds of finding suitable
254 mates. Examples include crabs, polychaete
255 worms, salmon, and migratory birds. Regardless
256 of their strategy, searching for mates often
257 increases the chances of predation.

258 **Ensuring Offspring Survival**

259 Following reproduction, animals must sometimes
260 protect and feed their young until they are inde-
261 pendent. Some animals travel to find a suitable
262 place to rear their offspring and then to a place to
263 forage for them. Emperor penguins, for example,
264 can travel up to 500 km to forage for food to bring
265 to their offspring.

266 **Molecular Motors**

267 We discussed above some of the reasons why
268 animals elect to translate themselves from one
269 place to another. We now turn to how animals
270 accomplish these feats. In this section we discuss
271 the molecular motors powering all forms of ani-
272 mal locomotion (Schliwa and Woehlke 2003).

273 Cells maintain their shape by means of struc-
274 tural proteins polymerized into rods and tubes that
275 form their cellular skeleton (cytoskeleton). To
276 shuttle proteins and other payloads around, some
277 proteins evolved the ability to use chemical
278 energy (in the form of ATP) to walk their cargos
279 along these cytoskeletal fibers. A key develop-
280 ment in the evolution of animals came when
281 these molecular motors (e.g., dynein and myosin)
282 became harnessed not just to pull a cargo along a
283 polymerized fiber but also to move these fibers

against each other. This endowed these molecules 284
with the ability to generate locomotion by stirring 285
fibrous projections in the surrounding environ- 286
ment (e.g., flagella) or to reversibly reshape cells 287
to produce locomotion (e.g., muscle 288
contractions). 289

290 **Cilia and Flagella**

291 Cilia and flagella are strictly the same cellular 291
organ (henceforth flagella), although they are 292
discerned by their length and number. Eukaryotic 293
cells may have only a few (<10) large flagella but 294
may have thousands of cilia. While both prokary- 295
otic and eukaryotic cells evolved flagella, and use 296
them in locomotion, these organs are structurally 297
distinct. Eukaryotic flagella are powered by 298
dynein ATPase motors and have a cylinder (i.e., 299
axoneme) containing two single microtubules 300
surrounded by nine microtubule doublets 301
(Woolley 2000). The entire assembly lies perpen- 302
dicular to the cell surface and is surrounded by 303
flexible extensions of the cell membrane. Many 304
additional proteins, both in the flagella and at their 305
base (called centrioles), are responsible for the 306
generation and control of its motion. Movement 307
at the base of these structures produces a wave that 308
travels distally and can be either two or three 309
dimensional. Unlike its eukaryotic counterpart, 310
prokaryotic flagella are composed of a hollow 311
cylinder made of flagellin. At the base of these 312
flagella, a small protein assembly creates an elec- 313
tric motor driven by atomic currents derived from 314
(Na⁺ or H⁺) ions entering the cell. 315

316 Cells typically have only a few long flagella 316
but may have thousands of short cilia. Whereas 317
flagella generate propulsion by beating in a con- 318
tinuous corkscrew fashion, cilia generate meta- 319
chronal waves during which their action is 320
divided into the power-generating stroke phase 321
and the recovery phase when there is no propul- 322
sion generated. These differences may reflect their 323
favored use. Flagella are well suited for generat- 324
ing large, propulsive forces (e.g., spermatozoid's 325
flagellum), but cilia can be differentially con- 326
trolled within a single cell, resulting in highly 327
precise movements. 328

329 For billions of years, bacteria, archaea, and 329
later eukaryotes used flagella to seek out viable 330

331 environments. These molecular propellers and
 332 oars continue to translate these microorganisms
 333 to hospitable environments. In animals, flagella
 334 and cilia fulfill a myriad of roles: from propelling
 335 sperm and moving oocytes along to removing
 336 debris in the respiratory system or detecting
 337 light, sound, and gravity. The rise of multicellular
 338 organisms, and their consequent increase in size,
 339 weight, and drag, reduced the effectiveness of
 340 these motors due to their ever-heavier payloads.
 341 Thus, as animals grew in size and complexity,
 342 they evolved alternative means for propulsion
 343 better suited to their larger scales. However,
 344 some small gastropod snails (and even some not-
 345 so-small sea slugs) remain able to achieve propul-
 346 sion purely by the action of their cilia. They
 347 accomplish this by sliding over their mucus secre-
 348 tion. However, unlike their unicellular counter-
 349 parts, the beating of cilia in these animals is
 350 under neural control.

351 Myosin II

352 To achieve propulsion, cilia and flagella must be
 353 exposed to the environment. A second type of
 354 molecular motor evolved from the novel
 355 rearrangement of core proteins. It allowed
 356 single-celled organisms, and eventually multi-
 357 cellular animals, to move through their environ-
 358 ment by causing entire cells to act as motors.
 359 Myosin heavy chain II is a molecule capable of
 360 transforming chemical energy (ATP) into
 361 mechanical energy (Raymet et al. 1993). Myosin
 362 is comprised of two light chains and two heavy
 363 chains that combine to give rise to the molecule's
 364 characteristic two heads, neck, and tail domains.
 365 The N-terminal halves of the heavy chain give rise
 366 to the globular heads, while the tail of myosin is
 367 assembled from the C-terminal halves. The tails of
 368 the molecule can polymerize together to form a
 369 filamentous backbone lined with the globular
 370 heads along its surface. Each head of myosin II
 371 consists of a motor domain that binds to the thin
 372 filament actin when allowed to hydrolyze ATP.
 373 Myosin successively binds, deforms, and releases
 374 an ordered lattice of actin proteins. These addi-
 375 tively transfer the combined mechanical deforma-
 376 tion of all myosin molecules to effectors such as

membranes, tendons, and skeletons, thereby gen- 377
 erating propulsion. 378

Myosin II predates animals and is found in 379
 amoeba and fungi, as well as in primitive animals 380
 lacking muscles such as sponges and cnidarians. 381
 Amoebas are large unicellular organisms that 382
 locomote through the protrusion and retraction 383
 of cellular pseudopodia and rely on the activity 384
 of the actin-myosin II complex. Besides locomotion, 385
 myosin also functions in cell division, migra- 386
 tion, and shape. 387

Cellular Motors 388

Muscles 389

Cilia and flagella are feats of evolution, allowing 390
 (mostly) small unicellular organisms to move 391
 effectively in their native aqueous environments. 392
 To be propulsive, these structures must act at the 393
 interface of the animal and its environment. For 394
 mostly sessile animals (e.g., sponges), flagella 395
 function by propelling food particles into diges- 396
 tive cavities. However, as many organisms grow 397
 in size and cell numbers, their surface area to 398
 volume ratio rapidly drops. Under these condi- 399
 tions, fluid flow changes from laminar to turbu- 400
 lent (see Reynolds numbers below), reducing the pro- 401
 pulsive effectiveness of flagella. 402

Unlike flagella, myosin II acts within cells. 403
 Their numbers and effective forces can therefore 404
 scale with the volume of cells, rather than just 405
 with their surface area (i.e., flagella). This allows 406
 these molecules to generate forces strong enough 407
 for large cells to deform (and even divide), allo- 408
 wing them to interact physically with other cells 409
 and their environment to generate propulsion. 410

One limitation to the use of myosin in propul- 411
 sion is the necessity to effectively transfer these 412
 large forces to the environment without structur- 413
 ally compromising the cells themselves in the 414
 process. This challenge becomes significant in 415
 multicellular animals, where myosin and actin 416
 allow many cells, even those buried deep within 417
 an animal, to become motors and generate com- 418
 bined forces far greater than those previously pos- 419
 sible. When the structural elements responsible 420
 for transferring these forces are absent (e.g., loss 421

of dystrophin in Duchenne muscular dystrophy), the powerful forces generated by the actomyosin complex are strong enough to rip muscle cells apart (Nowak and Davies 2004). Arguably, when properly harnessed, the versatility and scalability of the actomyosin complex can give rise to the enormous diversity of animal forms, sizes, and locomotion we observe in the animal kingdom.

Skeletal Muscle Structure

In vertebrates, three types of muscles are recognizable by their structure, their function, and the forces they generate. Skeletal muscles are responsible for locomotion and are discussed below (Lieber 2002); cardiac muscles are structurally similar to skeletal muscle but are capable of myogenic contractions (i.e., able to initiate contractions autonomously); and smooth muscles are also capable of myogenic contractions but possess unique myosin organization (see below). We will restrict our discussion to skeletal muscles as they are responsible for producing locomotion.

In vertebrate skeletal muscles, each myosin filament is surrounded by six actin filaments. Actin filaments are fixed to a z-disk (comprised of a vast array of interlinked proteins and fibers) at one end. The ends of the actin filaments not bound to the z-disk bind to one of the distal ends of the centrally located myosin fibers. The sarcomere is the smallest contractile unit of a muscle, and the z-disks themselves are ultimately responsible for transferring the force generated by actin and myosin within the sarcomere. Sarcomeres are aligned in series (end-to-end) within elongated threads called myofibrils. In humans, myofibrils can be up to 1 cm in length. Myofibrils are like threads in a rope; they are bundled together to form thicker and longer fascicles.

The head of the myosin molecule has two binding sites (one for ATP and one for actin). When ATP binds to a myosin head, it causes it to release an actin filament. Following the release of the previously bound actin filament, myosin hydrolyzes the bound ATP to ADP + P_i and uses the energy released to change conformation and weakly bind to an actin filament. On the actin filament, two free Ca²⁺ ions bind to troponin, causing the protein tropomyosin to slide and

allowing actin filaments to fully bind to the myosin head. Finally, myosin releases the inorganic phosphate and initiates the power stroke in which it changes conformation and slides the actin filament toward the center of the sarcomere, shortening the sarcomere as a consequence. Myosin then releases the bound ADP and remains in this (rigor) state until a new ATP binds to its free site, restarting the contractile cycle.

Animals can alter their muscle architecture in a variety of ways to generate different types of forces. At the ultrastructural level, long series of sarcomeres activated simultaneously generate quick muscle shortening and allow animals to generate fast motion. Conversely, arrangements of sarcomeres in parallel allow the generation of large powerful forces. In vertebrates, myosin can be found polymerized into thick filaments with their long axes aligned with the fiber and their globular heads pointing away from a bare center zone (e.g., striated muscle). Alternatively, myosin can be at an angle to the filaments' long axis with their globular heads, covering the whole length of the filament. This arrangement is found in smooth muscle.

Invertebrate muscles display even more diversity. Many species alter their myosin diameter, length, and myosin-to-actin ratio even within a single muscle cell. A type of invertebrate muscles termed "asynchronous muscles," found in flying insects, are capable of contraction rates an order of magnitude faster than is possible through other muscles. Used to power flight, these muscles are driven by mechanical stretch rather than neural stimulation.

Additional Function of Muscles during Locomotion

The most intuitive role for muscles during locomotion is that of generating propulsive force. Besides acting as motors, muscles can perform other functions during locomotion (Dickinson et al. 2000). For example, muscles can stiffen to become force transmitters rather than generators. This "strut" function allows the optimal transmission of force from multiple muscles into a single effector organ. For example, in fish that use their caudal fin for propulsion, posterior muscles

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516 become stiff and act as struts to convey anteriorly
517 generated forces to the tail. Once these forces
518 pass, the muscles resume their propulsive role to
519 generate force by contracting, then conveyed to
520 the (still stiff) posterior muscles of the tail.

521 Many invertebrate muscles possess a myosin
522 binding protein (i.e., paramyosin), which allows
523 them to display a property called “catch” in which
524 they can maintain force in the absence of actomy-
525 osin activity. The best-known examples of catch
526 muscle fibers are those of bivalve mollusks, which
527 they use to hold their shells tightly closed for long
528 periods of time.

529 Another role muscles can perform during loco-
530 motion is that of brakes. During running, extensor
531 muscles in the legs of cockroaches do not act to
532 generate power, but rather to slow the velocity of
533 the swing phase of the motion. This type of activ-
534 ity provides a metabolically inexpensive way to
535 slow down locomotion.

536 **Muscle Contraction**

537 Contractions are initiated when calcium ions are
538 released from intracellular storage compartments
539 and bind troponin. In order for the many sarco-
540 meres in a muscle to act in synchrony, the release
541 and removal of calcium ions must be under pre-
542 cise control. As mentioned above, muscles that
543 achieve this endogenously are known as
544 myogenic. Cardiac, arterial, and intestinal mus-
545 cles are examples of myogenic tissues. It is likely
546 that the ancestral muscle was similarly myogenic
547 and able to independently respond to environmen-
548 tal stimuli. Myogenic contractions work well for
549 (relatively) independent organs such as arteries or
550 guts (Horowitz et al. 1996). While hormonally
551 regulated, these organs function in partial auton-
552 omy. However, myogenic contractions are not
553 well suited for most forms of animal locomotion,
554 where different muscles acting remotely from one
555 another must achieve precise timing to produce
556 accurate locomotor patterns. For these complex
557 muscular ensembles, endogenous or reflexive
558 activation could not produce the fast, reliable,
559 and diverse array of activities associated with
560 locomotion. Therefore, around the same time
561 muscles evolved, a second type of specialized
562 excitable tissue evolved which could coordinate

muscle activity. These cells could detect meaning- 563
ful environmental information, compute appropri- 564
ate responses, and mount an appropriate 565
organismal activity by synchronizing patterns of 566
muscular activation. They gave rise to the nervous 567
system. 568

569 **Neural Control of Locomotion**

The movements of charged atoms (i.e., ionic cur- 570
rents) are important drivers of prokaryotic flagella 571
and eukaryotic muscular contractions. In muscles, 572
the magnitude and speed of intracellular calcium 573
release allow quick and synchronous activation of 574
millions of myosin molecules throughout these 575
large cells. Around the same time as muscle cells 576
were getting their evolutionary start, a second type 577
of specialized cell evolved to also harness ionic 578
currents to communicate distant parts of large 579
multicellular organisms. Neurons are specialized 580
cells that can detect and integrate environmental 581
changes as well as select and elicit adaptive pat- 582
terns of muscular activity. 583

Neurons can communicate with one another 584
(and with muscles) using chemical molecules 585
released across intercellular approximations 586
called (chemical) synapses (Jessell and Kandel 587
1993). Chemical synapses are by far the most 588
common way by which neurons communicate. 589
Because of the large number of proteins involved 590
in this type of communication, they lend them- 591
selves to the modification and modulation char- 592
acteristic of learning. Most forms of proactive 593
locomotion, that is, locomotion initiated in 594
response to internal drives, rely primarily on 595
chemical synapses coordinating the activation of 596
different muscle groups. 597

A second form of neuronal communication is 598
the electrical synapse or gap junction (Bennett 599
1997). Gap junctions rely on proteins creating 600
physical channels between adjacent neurons. 601
These allow ions and small molecules to travel 602
freely between cells. By connecting the cytoplasm 603
of two cells electrically, gap junctions are respon- 604
sible for the fastest form of cell-to-cell communi- 605
cation. This speed, however, comes at the cost of 606
plasticity. Electrical synapses lack the degree of 607

608 modulation that chemical synapses champion.
 609 However, the velocity of these synapses makes
 610 them ideal for synchronizing different cells and
 611 for driving reactive locomotion or locomotion that
 612 is initiated in response to external perturbations.
 613 For example, electrical synapses are responsible
 614 for coordinating many escape behaviors in the
 615 animal kingdom such as the C-star escape in fish
 616 or the tailflip of crayfish.

617 A third way in which neurons control locomotion
 618 is by the action of molecules released into
 619 systemic circulation (Harris-Warrick and Marder
 620 1991). The release of chemical modulators by
 621 neurons is a way of altering the function of multiple
 622 and remote locomotor systems in an organism.
 623 Whereas diffusion of chemicals across an organism
 624 makes this the slowest form of neural control,
 625 its global effects (simultaneously reaching
 626 multiple tissues), coupled with its combinatorial
 627 potential (using multiple signaling molecules),
 628 make this one of the most diverse and robust
 629 ways of generating behavioral diversity. For
 630 example, the simple stomatogastric ganglion
 631 driving mastication in crustaceans is comprised
 632 of about 30 neurons interconnected by electrical
 633 and chemical synapses. Although the number of
 634 neurons may seem small, the patterns of muscular
 635 activation this network can produce are vastly
 636 increased by an even larger number of modulatory
 637 substances, which can act singly or in combination
 638 to produce many behavioral patterns.

639 Central Pattern Generators

640 Whether it is the crawling of a worm, or the
 641 swimming of a whale, successful locomotion
 642 relies on the appropriate pattern of muscular
 643 activation, which must be initiated and maintained
 644 throughout the duration of the behavior. This
 645 necessitates synchronization of distant muscles,
 646 which must be contracted and relaxed in precisely
 647 the correct order and with the appropriate duration
 648 and intensity. In addition, sensory information
 649 about changing environmental and internal
 650 conditions must be allowed to modify the initial
 651 motor output. For example, a strong gust of
 652 wind, a change in terrain inclination, or a misstep
 653 could prevent the completion of a locomotor goal
 654 unless the animal used sensory feedback to correct

655 motor outputs to match new available information.
 656 In the next section, we discuss sensory modulation
 657 of locomotion, but first we will consider the
 658 generation of motor outputs.

659 Most forms of animal locomotion rely on the
 660 rhythmic activation of groups of muscles. These
 661 cyclical patterns of activity are often the product
 662 of specialized neural tissues dedicated to the
 663 production of these rhythms. They are known as
 664 central pattern generators (CPGs), and they are
 665 capable of producing rhythmic outputs in the
 666 absence of rhythmic inputs (Marder and Bucher
 667 2001). Extensive work on cats demonstrated that
 668 the mammalian spinal cord houses CPGs for the
 669 production of walking and running. Similar
 670 central rhythmic centers have been identified
 671 across taxa, including nematodes and jellyfish.

672 Motor patterns are usually produced by one or
 673 several cells, which act as pacemakers for the
 674 rhythm. Pacemakers can consist of a single
 675 rhythmically active neuron, a pair of mutually
 676 inhibiting neurons, or a group of three or more
 677 cells. Although CPGs do not require inputs to
 678 generate an output, sensory feedback is crucial
 679 for modifying outputs and obtaining rhythms
 680 that reflect the changing needs of an animal. For
 681 this reason, rhythms recorded from isolated
 682 nervous systems (termed “fictive”) generally
 683 match rhythms observed in intact animals only
 684 partially. In the absence of sensory feedback,
 685 rhythms tend to be faster and less variable than
 686 those recorded in intact preparations. The
 687 importance of sensory feedback to modulate
 688 motor output is exemplified in box jellies. These
 689 animals, among the simplest to possess nervous
 690 systems, use CPGs to produce locomotion.
 691 Nevertheless, the activity of their CPGs is
 692 modulated by input from rudimentary sensory
 693 organs (eyes), which help the animal steer
 694 their locomotion.

694 Locomotor Gaits

695 Simple pattern generators such as the jellyfish’s
 696 may be restricted to the generation of one or,
 697 at most, a few patterns of activity. This places
 698 limits on the behavioral repertoire they are able
 699 to produce. As animals increased their number
 700 of neurons, the number of possible synaptic
 701 connections between them grew exponentially. Increased

702 interconnectivity permitted finer modulation of
703 motor outputs and led to the evolution of alterna-
704 tive motor circuits animals could now select
705 between. The neural networks responsible for
706 these distinct programs could be independent or
707 partially overlapping. Many of these circuits are
708 highly conserved between species, and only
709 minor modifications are needed to produce pro-
710 found changes in outputs. In the case of distinct
711 locomotor outputs, these are referred to as gaits
712 (Alexander 1989).

713 The term gait is historically associated with the
714 patterns of leg movements in pedestrian locomotion
715 on land. Work pioneered by Eadweard
716 Muybridge and his stop motion photography in
717 1878 allowed the study of the patterns of limb
718 movements in freely moving animals. The study
719 of animal locomotion has since expanded from
720 animals walking on land to all animals (limbed
721 or limbless) moving in every kind of environment
722 by means of rhythmic movements. Locomotion
723 researchers modified the usage of “gait” to include
724 other types of locomotion. In general, two patterns
725 of animal locomotion are considered to be distinct
726 gaits if their production represents the output of
727 nonidentical neural circuits. Animals thus may
728 produce flying, swimming, crawling, walking,
729 burrowing gaits, etc.

730 The production and selection of different gaits
731 is associated with the distinct energetic costs of
732 locomotion in different environments or speed
733 ranges. For example, a person on an accelerating
734 treadmill can increase their pace as the treadmill
735 speeds up. However, beyond roughly 2 m/s, most
736 people become unable to keep pace and are forced
737 to switch from walking to running. This transition
738 occurs at the point where walking faster would
739 consume more energy than running slow. Walking
740 and running gaits are optimized to minimize
741 energy expenditure for a particular range of veloc-
742 ities. We discuss the energetics of locomotion in a
743 later section.

744 While the transition between walking and run-
745 ning might be subtle and occurs within the same
746 environment (on land), some gait transitions are
747 more dramatic and involve different environ-
748 ments. For example, crawling and swimming
749 involve the activity of the same muscles, but

using distinct patterns of activity. These patterns 750
of muscle activity involve different pattern gener- 751
ators and often rely on distinct sensory feedback. 752
The ability to appropriately select and transition 753
between distinct motor patterns is of paramount 754
importance to survival. For many animals, getting 755
this transition wrong once spells demise. Because 756
of this, the mechanisms employed to effect these 757
transitions tend to be highly conserved across 758
evolution. For example, leeches and nematodes 759
are evolutionary distant animals that use the sig- 760
naling amines dopamine and serotonin to trigger 761
transitions from swimming to crawling 762
(dopamine) and vice versa (serotonin). Dopamine 763
is an ancient molecule universally used to modu- 764
late locomotion. Loss of dopamine in Parkinson’s 765
disease, or through other insults, results in the 766
inability to initiate locomotor patterns in worms 767
just as much as it does in humans. Natural selec- 768
tion does not act on all processes equally. While 769
the genes involved in the synthesis and use of 770
signaling molecules are highly conserved across 771
taxa, genes coding the receptors for these mole- 772
cules have been free to diverge and increase in 773
number. They are key contributors to the diversity 774
of locomotor programs we see in the natural 775
world. 776

777 **Sensory Feedback**

778 The production of meaningful locomotion
779 depends on an animal’s ability to monitor (a)
780 changes on its environment, (b) the position of
781 its limbs during the performance of the behavior,
782 and (c) its changing orientation and position with
783 respect to its intended trajectory (Ausborn et al.
784 2009). Higher-order sensory systems, such as the
785 olfactory, visual, and auditory systems, modulate
786 the direction and speed of locomotion. These are
787 instrumental in achieving the locomotor goal of
788 translating an animal to its destination. At a more
789 basic level, internal organs such as the inner ear
790 (or statocysts in invertebrates) allow animals to
791 maintain appropriate body orientation during the
792 performance of locomotion. Lastly, proprioceptor
793 organs distributed throughout the organism pro-
794 vide ongoing feedback to central motor centers
795 that allow the continuous adjustment of motor
796 outputs. It is through the continuous and

797 combined inputs of these sensory streams that
798 locomotion becomes relevant and meaningful to
799 the survival of the organism.

800 **Physical Variables Influencing** 801 **Locomotion**

802 Animals adapted to move in every niche afforded
803 by our planet. These include environments with
804 physical properties that place unique demands or
805 constraints on the strategies available. For exam-
806 ple, demands faced in aquatic and aerial locomo-
807 tion are distinct from those encountered during
808 terrestrial or subterranean locomotion.

809 **Environment**

810 Our planet is lush with diverse environments ani-
811 mals can exploit in their quest to survive and
812 reproduce. The seas were the first biotic environ-
813 ment and remain home to millions of animal spe-
814 cies. Locomotion through a fluid (liquid or
815 gaseous) is dominated by the friction and inertia
816 experienced by an animal as it collides with the
817 molecules in the fluid around it (Sfakiotakis et al.
818 1999). To minimize resistive (drag) forces experi-
819 enced while swimming (or flying), animals often
820 evolved hydrodynamic (or aerodynamic) shapes
821 that reduce the number and intensity of collisions
822 with the particles making up their environment. In
823 physical terms, the primary distinction between
824 aquatic and aerial locomotion resides in the rela-
825 tive density of animals to their environment. Ani-
826 mals that are denser than their environment sink
827 and must continually spend energy to remain air-
828 or waterborne. Both aerial and aquatic animals
829 often possess adaptations that allow them to mit-
830 igate the effects of this differential density. For
831 example, birds have hollow bones that consider-
832 ably reduce their weight, while most bony fish
833 have swim bladders that allow them to control
834 buoyancy without having to swim continuously.
835 These adaptations reduce the energy required to
836 maintain the animal within its locomotor
837 substrate.

838 The familiar shape and locomotor strategies of
839 swimming animals evidence their commitment to
840 a single physical environment (Gleiss et al. 2011).

The similarities between aquatic and aerial envi- 841
vironments allowed many birds to become apt 842
swimmers without compromising their flight 843
abilities. 844

Subterranean locomotion places unique physi- 845
cal demands on animals. We define subterranean 846
locomotion as locomotion through solids such as 847
soils, sands, or even other organisms. These envi- 848
ronments are characterized as being overwhelm- 849
ingly dominated by resistive forces and the 850
absence of inertia. Although mostly understudied, 851
burrowing is one of the most commonly used 852
forms of animal locomotion (Gans 1973). 853

Like swimming and flying, the physical 854
demands that burrowing places on animals have 855
resulted in the evolution of an optimal burrowing 856
shape adopted by most animals that burrow regu- 857
larly: the vermiform or wormlike shape. Like fish 858
and birds, most worms are bilaterally symmetri- 859
cal. However, because their density is often lower 860
than that of their environment, worms often adopt 861
a cylindrical shape that allows them to exert forces 862
equally well in every direction. For example, peri- 863
staltic waves allow worms to maximize propul- 864
sion by generating thrust in every direction. For 865
burrowing animals, the relative density of the 866
media determines the optimal burrowing strategy. 867

Swimming and burrowing are modes of loco- 868
motion in which animals inhabit and locomote 869
through a single physical environment. However, 870
many animals evolved the ability to exploit the 871
interphase between distinct physical environ- 872
ments as a way to reduce the energetic cost of 873
locomotion. Terrestrial and benthic animals take 874
advantage of the differences between different 875
physical environments to effectively locomote at 876
their interface. For example, walking animals 877
exploit the resistive differences between soil and 878
air, using the high resistance in the ground to 879
generate propulsion and the lower resistance of 880
the air to move large, heavy payloads. Walking 881
evolved multiple times in aquatic and terrestrial 882
animals. Tetrapod walking first evolved in 883
sarcopterygian fishes. Arthropods, including crus- 884
taceans and insects, produced some of the most 885
sophisticated walkers nature has to offer. Even apt 886
swimmers like cephalopods can produce bipedal 887
walking under certain conditions. 888

889 Birds and insects are the most proficient and
 890 prolific users of multiple physical environments.
 891 Many species spend considerable time locomot-
 892 ing in two or more distinct media. Locomotion in
 893 multiple physical environments poses distinct
 894 challenges depending on the environments in
 895 question. For example, as discussed above,
 896 aquatic and aerial locomotion share some similar
 897 challenges that allow many flying animals to
 898 swim effectively using the same machinery they
 899 use for flight. However, there are limits to this
 900 overlap. Other forms of locomotion are consider-
 901 ably less synergistic. For example, the demands
 902 placed by walking and flying are so different that
 903 animals must maintain distinct neuromuscular and
 904 skeletal machineries dedicated to each type of
 905 locomotion. The high energetic costs of
 906 maintaining two independent locomotor systems
 907 result in animals dedicating more resources to one
 908 form of locomotion over another. As such, many
 909 birds are better flyers than they are walkers or
 910 swimmers. Alternatively, there are examples of
 911 birds where walking or swimming is preferred
 912 over flying; however this usually leads to the
 913 loss of flight (e.g., ostriches and penguins). An
 914 alternative to this type of compromise or commit-
 915 ment is found in arthropods. Insects often have
 916 complex life histories that allow them to sequen-
 917 tially specialize for distinct forms of locomotion
 918 during different life stages. For example, dragon-
 919 fly larvae are voracious aquatic predators capable
 920 of walking, swimming, and even jet propulsion,
 921 while their adult form is one of the most effective
 922 flying hunters in nature. Therefore, dragonflies
 923 and other insects can exploit distinct environ-
 924 ments by using them during different life stages.
 925 Of course, before some swimming larvae can
 926 become an aerial adult, they must invest a consid-
 927 erable amount of energy and time undergoing the
 928 process of metamorphosis with all the dangers and
 929 costs associated with it.

930 The physical properties on an environment
 931 clearly place unique challenges and opportunities
 932 for animal locomotion. We now discuss the chal-
 933 lenges and opportunities associated with the ani-
 934 mals themselves and with their locomotor
 935 strategies.

Stability and Maneuverability

936 Stability refers to the ability of a system to with- 937
 stand perturbations that would bring it away from 938
 equilibrium (Full et al. 2002). For standing ani- 939
 mals, *static stability* is dictated by the interaction 940
 between an animal's center of mass and its base of 941
 support. We will use the analogy of a painter's 942
 folding ladder to visualize how this interaction 943
 works. In the opened position (with the legs 944
 placed well apart), the ladder is in its most stable 945
 configuration. Considerable force can be applied 946
 to it before this stability is compromised. This is 947
 because the ladder's center of mass lies well 948
 within a base of support. As long as destabilizing 949
 forces do not move the center of mass outside of 950
 their base of support, the ladder will remain stable. 951
 If the legs of the ladder are brought closer 952
 together, the base of support decreases in size, 953
 and the ladder becomes less (stable) able to with- 954
 stand perturbations. Most ladders have rectangu- 955
 lar bases of support (wider than long). Therefore, 956
 ladders can withstand greater perturbations in one 957
 direction (it is easier to tip a ladder sideways than 958
 forward or backward). Animals follow the same 959
 rules of stability as the ladder in the analogy 960
 above. For example, standing quadrupeds with 961
 narrow bases of support (e.g., a horse) are less 962
 stable than animals with wider base of support. 963

964 One of the most consequential properties of 964
 stability is that it is independent of the source of 965
 the perturbations. A system that is highly stable 966
 will resist environmental perturbations (e.g., 967
 wind) as much as they will resist perturbations 968
 they themselves cause (e.g., locomotion). 969
 Because of this, animals must carefully balance 970
 an equation where on one hand they have their 971
 ability to withstand unwanted perturbations and 972
 on the other is their ability to disrupt their stability 973
 to achieve locomotion. One way by which many 974
 animals solve this problem is by altering their 975
 posture depending on their changing needs. For 976
 example, many animals adopt a sprawled stance 977
 when engaged in withstanding environmental per- 978
 turbations and a more upright stance during 979
 locomotion. 980

981 Once locomotion is initiated, stability is not 981
 discarded. Instead, the challenge increases in 982
 complexity as it must be achieved for a body in 983

984 motion. This is termed *dynamic stability*, and it
 985 pertains to the ability of a moving body to with-
 986 stand perturbations. Like the static stability
 987 discussed above, an animal's dynamic stability is
 988 realized as a compromise between competing
 989 needs, namely, the animal's need to resist
 990 unwanted perturbation versus its need to produce
 991 quick, intentional disruptions such as turning,
 992 dodging, abrupt breaks, etc. (e.g.,
 993 maneuverability).

994 It is easy to underestimate the challenge that
 995 animals face to achieve both high stability and
 996 maneuverability. On first approach, animal loco-
 997 motion can seem simple: an animal exerts force on
 998 its environment and produces acceleration
 999 (locomotion) in the opposite direction. However,
 1000 this bears little resemblance to reality. Locomo-
 1001 tion in most animals is accomplished by the oscil-
 1002 lation of bodies or appendages that exert nonlinear
 1003 forces on their environment. Indeed, if animal
 1004 locomotion consisted of straight, steady-state
 1005 motion, one would not expect to see animals
 1006 invest in the large number of muscles, neurons,
 1007 or appendages they often have for the purpose of
 1008 propulsion. The heavy investment in the genera-
 1009 tion and control of locomotion can only be under-
 1010 stood in light of both the important role of
 1011 locomotion in survival and in the unpredictable
 1012 nature of the external and internal perturbations
 1013 that challenge its completion.

1014 Energetics of Locomotion

1015 Locomotion in animals requires the expenditure
 1016 of large amounts of energy (Schmidt-Nielsen
 1017 1972). Due to its energetic cost and incurred
 1018 risks, animals do not generally engage in locomo-
 1019 tion unless there is a physiological need being
 1020 served that justifies the expenditure. When ani-
 1021 mals do move, only part of the energy spent is
 1022 transformed into propulsion. A significant frac-
 1023 tion of the energy spent in locomotion is
 1024 converted into unproductive motion or lost
 1025 entirely to the environment.

1026 The locomotor strategy employed by animals
 1027 depends on the most energy-efficient options
 1028 available in a given environment. Walking ani-
 1029 mals use the high friction conditions of the ground
 1030 to generate propulsion but must minimize ground

1031 contact to not lose energy to this very friction. For
 1032 example, at low speeds, walking animals use an
 1033 inverted pendulum strategy where the body mass
 1034 moves up over each leg in a motion reminiscent of
 1035 an inverted pendulum. Part of the energy spent in
 1036 propulsion is transformed into forward displace-
 1037 ment, while part of it is saved as potential energy
 1038 as the body moves up. The potential energy is then
 1039 harvested during the second part of the stance
 1040 phase when the body falls forward toward the
 1041 next step. The maximal velocity walking animals
 1042 can achieve is constrained by the earth's gravity,
 1043 as this force field powers the second half of each
 1044 step. For animals that are able to temporarily
 1045 generate accelerations greater than that of the
 1046 earth's gravity, a second type of motor gait
 1047 becomes available. At faster speeds, these animals
 1048 transition to a form of locomotion called running
 1049 (or hopping, trotting). Here, motion by the center
 1050 of mass resembles a pogo stick. All muscles are
 1051 used to generate forward and upward propulsion
 1052 (which might lead to an aerial phase). During the
 1053 second part of the stride, as the animal accelerates
 1054 downward, the tendons, muscles, and ligaments
 1055 absorb the vertical forces (decelerating the body
 1056 vertically in the process) and store these as elastic
 1057 energy ready to propel the first part of the next
 1058 stride. The use of elastic body components to store
 1059 energy is also in use in the horizontal plane. Many
 1060 animals such as lizards and crabs have sprawled
 1061 postures that generate significant lateral motion
 1062 while walking. The energy spent in lateral dis-
 1063 placement is stored and partially recovered during
 1064 successive steps. For slower walkers, this strategy
 1065 is useful in more than one way. It also enhances
 1066 stability by allowing the animal to absorb and use
 1067 disruptive forces such as those experienced when
 1068 pushed. Because these strategies are based on
 1069 physical constraints posed by the environment,
 1070 they are observed in most walking animals (Full
 1071 and Koditschek 1999).

1072 The energy-saving or recovering strategies
 1073 described above are not only used by walkers
 1074 but also by swimmers and fliers. As they push
 1075 against a fluid (air or water), these animals impart
 1076 forces on their environment, causing it to move in
 1077 vortices. Many animals ranging from insects to
 1078 salps, fish, and birds control the shape and

[AU6]

[AU7]

1079 distribution of these vortices to recover part of the
 1080 energy lost in their generation. For example, gen-
 1081 eration of tightly packed vortex rings allows
 1082 swimmers higher velocities and efficiencies. Sim-
 1083 ilarly, flying insects generate lift with their wings
 1084 in large part due to the vortices created above at
 1085 the leading edges of their wings.

1086 **Size and Reynolds Numbers**

1087 Organisms locomoting through fluids constantly
 1088 crash with the particles in their surrounding
 1089 media. They therefore must spend energy to
 1090 move the fluid out of their way, and they must
 1091 overcome the internal friction of the fluid (i.e., its
 1092 viscosity). Osborne Reynolds determined that
 1093 flow patterns in fluids could be predicted by the
 1094 ratio of the inertial forces over the viscous forces
 1095 present in a system (Reynolds 1883). This rela-
 1096 tionship turned out to predict a great deal of nat-
 1097 ural phenomena from flow through pipes to the
 1098 locomotor strategies available to animals. The
 1099 ratio of these forces (Reynolds number) is a
 1100 widely used, dimensionless number. For animals
 1101 (solids) moving through a fluid, the Reynolds
 1102 number (Re) can be calculated as the product of
 1103 the density of the media (ρ), the velocity of the
 1104 animal (V), its length factor (L), and the inverse of
 1105 the viscosity (μ) of the medium: $Re = (\rho VL)/\mu$.
 1106 For biological systems, this number ranges from
 1107 $\sim 10^{-6}$ (bacteria) to $\sim 10^{14}$ (whales).

1108 At high Reynolds numbers, inertial forces
 1109 dominate animal locomotion. However, as the
 1110 fluid viscosity increases ($Re = 1$), viscous forces
 1111 dominate, and animals produce purely laminar
 1112 patterns of flow over their bodies. Above
 1113 $Re = 40$, turbulence develops in the wake of the
 1114 animal (see above). Beyond $Re = 10^6$, the cost of
 1115 overcoming turbulence to increase speed becomes
 1116 challenging. Animals can push the velocity at
 1117 which turbulence becomes insurmountable by
 1118 streamlining their shape. This is a widely used
 1119 strategy by larger swimming and flying animals
 1120 (e.g., fish, birds), but that would present no advan-
 1121 tage for small swimmers operating in the absence
 1122 of turbulence (e.g., bacteria). Many animals exist
 1123 within Reynolds numbers characterized by both
 1124 viscous and inertial components (e.g., the nema-
 1125 tode, *C. elegans*). Others can span Reynolds

numbers posing distinct physical demands as 1126
 they grow in size or transition between different 1127
 environments. 1128

1129 **Survey of Locomotor Forms**

1130 Animals adapted distinct forms of locomotion to 1130
 best suit their physical environment and to accom- 1131
 plish the goals of self-preservation, finding and 1132
 securing mates, and ensuring the survival of off- 1133
 spring. We discuss a few examples of the numer- 1134
 ous types of locomotion that animals use to 1135
 achieve these goals relative to their physical envi- 1136
 ronments: aquatic, terrestrial, and aerial 1137
 (Alexander 2003). 1138

1139 **Aquatic Locomotion**

1140 Aquatic environments lend themselves to several 1140
 types of locomotion, from walking and swimming 1141
 to sailing and jet propulsion. 1142

1143 **Walking** is accomplished by the cyclical 1143
 motion of body appendages against a solid sub- 1144
 strate. Many aquatic species evolved the machin- 1145
 ery required for this type of locomotion. Because 1146
 walking entails generating force against a solid 1147
 substrate, most walking is performed using rigid 1148
 limbs (e.g., arthropods and some fish). Some ani- 1149
 mals, however, evolved the ability to walk using 1150
 different means. Echinoderms such as starfish 1151
 walk by means of tube feet, which rely on a 1152
 water vascular system to inflate and deflate them 1153
 during locomotion. Nudibranch sea slugs and 1154
 other mollusks walk by means of their foot cilia, 1155
 and some octopus use their arms to walk on the 1156
 ocean floor. 1157

1158 **Burrowing** is a form of locomotion that takes 1158
 place through solid media. Many aquatic species 1159
 tunnel through the benthos using peristaltic waves 1160
 of body contractions. Most of these animals 1161
 developed vermiform (wormlike) shapes. Exam- 1162
 ples of this type of animal are nematodes and 1163
 annelids. Their locomotion usually relies on the 1164
 presence of a hydrostatic skeleton capable of pre- 1165
 cise rhythmic deformations. There are, however, 1166
 many burrowing species that rely on other means 1167
 for burrowing. For example, bivalves use their 1168

1169 muscular foot to dig themselves into the
1170 substratum.

1171 **Swimming by undulation** is one of the most
1172 commonly used forms of aquatic locomotion.
1173 Animals across taxa, from platyhelminths to mol-
1174 lusks and annelids, nematodes, arthropods, and
1175 chordates, evolved the ability to move through
1176 water by undulations generated along the longitu-
1177 dinal axis of their bodies. These undulations can
1178 be lateral, as in the case of most fish and reptiles,
1179 or dorsoventral, as in the case of marine mammals
1180 like dolphin, whales, or seals (Sfakiotakis
1181 et al. 1999).

1182 **Swimming with appendages** is the main man-
1183 ner by which organisms inhabiting the low Reyn-
1184 olds number space generate thrust (Purcell 2014).
1185 When viscous forces dominate locomotion, sym-
1186 metrical (reciprocal) forces such as body undula-
1187 tions become ineffectual. Many small animals
1188 rely on nonreciprocal motion generated by fla-
1189 gella or on swimming appendages that evolved
1190 multiple times in most animal groups. Append-
1191 ages generate propulsion through nonsymmetrical
1192 motion that is divided into the power-generating
1193 phase (when interaction with the medium is max-
1194 imized) and the recovery phase (when interaction
1195 with the medium is minimized). Many cartilagi-
1196 nous fish, arthropods, and other animals locomote
1197 through water (and other environments) using
1198 their appendages. Examples of swimming
1199 appendages include fins (e.g., fish), swimmerets
1200 (e.g., krill), wings (e.g., penguins), and legs (e.g.,
1201 cormorants).

1202 **Sailing** is a passive form of locomotion used
1203 by some aquatic animals. Cnidarians are among
1204 the most prolific sailors with several species tak-
1205 ing to this form of locomotion. For example, the
1206 by-the-wind sailors form disks that dwell on the
1207 water surface on top of which a triangular fin sits
1208 able to harness wind force in locomotion. Another
1209 sailing cnidarian is the Portuguese man-of-war,
1210 which, unlike the permanent stiff sail of the by-
1211 the-wind sailor, has an inflatable gas-filled sail it
1212 can use to travel.

1213 Just like cnidarians are able to exploit the
1214 water-air interface for locomotion, many animals
1215 exploit the benthos (the water-ground interface) to
1216 the same end. Like swimming, benthic

locomotion can be achieved by body undulations
1217 or by the motion of specialized appendages. 1218

1219 **Jet propulsion** evolved convergently in many
1220 aquatic animals as a mechanism for evading pred-
1221 ators and approaching prey. The most well-known
1222 example of jet propulsion comes from jellyfish,
1223 which propel themselves by ejecting water from
1224 their oral cavity. Cephalopods (e.g., squid and
1225 octopus) draw water into their mantle cavity
1226 under low pressure; water is quickly expelled
1227 through the siphon under high pressure. The gen-
1228 erated force propels the animal in the opposite
1229 direction, which can be controlled by movements
1230 of the siphon. Additional examples of jet propul-
1231 sion come from scallops and dragonfly larvae,
1232 which are capable of jet propulsion by using
1233 their rectal chamber to hold and expel water. Jet
1234 propulsion is limited by the volume of water used
1235 for reaction mass (which is dependent on the
1236 animal's cavity size). Many coleoids adapted
1237 undulatory fins for fish-like locomotion.

1238 Terrestrial Locomotion

1239 Many animal orders transitioned from aquatic to
1240 terrestrial environments. Whereas some locomo-
1241 tor approaches used in aquatic environments are
1242 ineffective on land (e.g., jet propulsion and swim-
1243 ming), many approaches that first evolved in
1244 aquatic environments remain effective.

1245 **Burrowing** is a widely used locomotor strategy
1246 for many animals including nematodes, annelids,
1247 arthropods, and vertebrates.

1248 **Walking** is one of the most effective forms on
1249 locomotion on land. Terrestrial environments
1250 offered walkers decreased drag and buoyancy
1251 compared to aquatic walking. This increased
1252 their ability to generate greater propulsive forces
1253 (due to their increased effective weight) and to
1254 experience less resistance. The result of these
1255 improved conditions was the evolution of the
1256 fastest forms of pedestrian locomotion for both
1257 vertebrates and arthropods.

1258 **Crawling** is mostly performed by limbless ani-
1259 mals that produce either axial bending to produce
1260 propulsive forces as in the case of snakes and
1261 some fishes or by peristaltic waves as in the case
1262 of many arthropod larvae.

1263 **Jumping** or hopping involves the simulta-
 1264 neous retraction or extension of the hind legs,
 1265 followed by an aerial phase of movement.
 1266 Jumping is the dominant mode of terrestrial loco-
 1267 motion in frogs, and it is also found among mam-
 1268 mals and arthropods. Whereas most animals use
 1269 muscular contractions to power their jumps, some
 1270 arthropods evolved additional mechanisms,
 1271 enabling them to attain greater accelerations and
 1272 improved jumping performances. For example,
 1273 jumping spiders use hemolymph pressure to
 1274 extend their legs, and planthopper insects evolved
 1275 biological gears to power their ballistic jumps.
 1276 Most terrestrial animals locomote on, or
 1277 through, the ground; however, some terrestrial
 1278 animals evolved the ability to locomote through
 1279 the air.

1280 Aerial Locomotion

1281 True flight has evolved independently at least
 1282 seven times among insects, birds, and mammals.
 1283 By sheer number of species, and flight modes,
 1284 insects are the most prolific aerial group.

1285 **Active flight** refers to flight produced by mus-
 1286 cular exertion of an animal's flight machinery.
 1287 Insects, the undisputed champions of this form
 1288 of locomotion, began flying during the Carbonif-
 1289 erous (~350 mya). In insects, flight can be pro-
 1290 duced by the action of direct, or indirect, muscles.
 1291 With *direct flight*, muscles attach directly to the
 1292 wings. Examples of this arrangement are dragon-
 1293 flies and mayflies. Most insects, however, use
 1294 *indirect flight*. Here, flight muscles attach not to
 1295 the wing, but rather to the thoracic skeleton. Com-
 1296 pressions of the thoracic cavity result in the
 1297 (indirect) movement of the attached wings. In
 1298 birds, active flight dates back to the earliest
 1299 avian ancestors (e.g., Archaeopteryx) some
 1300 150 mya and is responsible for the great success
 1301 and diversity of this group. Among mammals,
 1302 bats alone evolved the ability for powered flight.
 1303 Unique among animals, squids are capable of
 1304 flight by means of rocket propulsion. This
 1305 involves the generation of lift by means of force-
 1306 ful ejection of water from their mantle cavity
 1307 during flight.

1308 **Gliding** refers to the use of gravity to power
 1309 forward locomotion. By harnessing and

controlling the drag forces experienced during 1310
 free fall, gliding animals travel with only minimal 1311
 energy expenditure. Birds are the champions of 1312
 this type of locomotion, with albatrosses being 1313
 able to harvest up to 20 times in horizontal dis- 1314
 placement what it invests in falling vertically. 1315
 Gliding also occurs among mammals (e.g., flying 1316
 squirrels), amphibians (e.g., gliding frogs), rep- 1317
 tiles (e.g., geckos), fish (e.g., flying fish), and 1318
 mollusks (e.g., squid). 1319

Ballooning refers to the passive aerial dis- 1320
 persal of animals using silk threads to harness 1321
 the wind. This process is best understood in spi- 1322
 ders that use it to disperse following hatching, but 1323
 it also takes place among mites and some insect 1324
 larvae. 1325

1326 Cross-References

- ▶ [Adaptedness of Behavior](#) 1327
- ▶ [Behavior Systems](#) 1328
- ▶ [Bird Migrations](#) 1329
- ▶ [Catarrhine Locomotion](#) 1330
- ▶ [Cetacean Locomotion](#) 1331
- ▶ [Escape Response](#) 1332
- ▶ [Fitness](#) 1333
- ▶ [Fixed Action Patterns](#) 1334
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- ▶ [Mustelidae Locomotion](#) 1336
- ▶ [Natural Selection](#) 1337
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- ▶ [Pinniped Morphology and Locomotion](#) 1339
- ▶ [Platyrrhine Locomotion](#) 1340
- ▶ [Predation Risk](#) 1341
- ▶ [Predator Defense](#) 1342
- ▶ [Prosimian Locomotion](#) 1343
- ▶ [Terrestrial](#) 1344

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