PROCEEDINGS B

royalsocietypublishing.org

Research

Article submitted to journal

# The neuroecology of the water-to-land transition and the evolution of the vertebrate brain

Malcolm A. MacIver[1], Barbara L. Finlay[2]

[1]Center for Robotics and Biosystems, Northwestern University, Evanston, IL 60208, USA
[2]Behavioral and Evolutionary Neuroscience Group, Department of Psychology, Cornell University, Ithaca, NY 14850, USA

**Subject Areas:**
evolution, neuroscience, behavior, neuroecology, cognitive evo devo, decision-making, computation, reinforcement learning

**Keywords:**
brain, computation, fish-tetrapod transition, terrestriality

**Author for correspondence:**
Insert corresponding author name
e-mail: xxx@xxxx.xx.xx

The water-to-land transition in vertebrate evolution offers an unusual opportunity to consider computational affordances of a new ecology for the brain. All sensory modalities are changed, particularly a greatly enlarged visual sensorium due to air versus water as a medium, and expanded by mobile eyes and neck. The multiplication of limbs, as evolved to exploit aspects of life on land, is a comparable computational challenge. As the total mass of living organisms on land is a hundredfold larger than the mass underwater, computational improvements promise great rewards. In water, the midbrain tectum coordinates approach/avoid decisions, contextualized by water flow and by the animal's body state and learning. On land, the relative motions of sensory surfaces and effectors must be resolved, adding on computational architectures from the dorsal pallium, such as the parietal cortex. For the large-brained and long-living denizens of land, making the right decision when the wrong one means death may be the basis of planning, which allows animals to learn from hypothetical experience before enactment. Integration of value-weighted, memorized panoramas in basal ganglia/frontal cortex circuitry, with allocentric cognitive maps of the hippocampus and its associated cortices becomes a cognitive habit-to-plan transition as substantial as the change in ecology.

THE ROYAL SOCIETY
PUBLISHING

## 1. Introduction

The water to land transition in vertebrate life nearly 400 million years ago was accompanied by conspicuous changes in two quite different realms: ecological, with 100-fold increases in total living organism mass [1] and visual range [2] over that of aquatic ecosystems; and neuroanatomical, with two of the largest radiations of land animals—mammals and birds—featuring 10-fold larger brains relative to body size than fish [3]. Considering that evolution is definitionally the natural selection of advantageous adaptations *to an environment*, the rarity of systematic analyses of what different kinds of ecosystems prohibit or promote in sensory, motor and cognitive adaptations is a striking gap in our understanding of brain evolution (but see [2,4–7]). The multiple dimensions along which terrestrial environments differ from aquatic environments is an unparalleled opportunity to examine brain functions at a meso-level of analysis. Computational requirements and opportunities that are more general than those that emerge from the neuroethological approach to niche specialists can be identified. While phylogenetic analyses of whole brain volume, or brain/body relationships are necessarily limited to very general descriptions like "increased cognitive capacity" or "cognitive buffer", here we can be more targeted.

In this review, we will first consider key ecological changes relevant to land vertebrate brain evolution, and then examine current evidence for how the brain responded. We suggest several factors at work in the great brain expansion co-occurring with the endothermic land vertebrate radiations—mammals and birds. One is that a 100-fold increase in the mass of living organisms on land creates a demand for more neural resources towards valuation of the ramifying rewards and harms. A million-fold increase in the volume of visually inspected space, from the higher transparency of air to light, enables enough time for this valuation to occur in a less stereotyped manner. This information enrichment includes more mobile sensory surfaces, such as a neck to swivel the greatly expanded visual sensorium, and new ways to integrate their information. Finally, the mechanics of life on land, where aquatic animals feel the full force of gravity from a prior state of near neutral buoyancy, creates a need for stiffening against its onslaught and complex ways of manipulating the highly variable ground through multi-degree of freedom limbs to achieve movement [8]. The multiplication of mobile end-effectors from what is essentially one in the fish (the mouth) results in a need for an easily modified way of coordinating between the reference frames of these freshly endowed musculoskeletal degrees of freedom in the forebrain using a style of computation based on preserving neighborhood relations over topographic maps. A different style of computation centered on events and temporal sequences is found in the olfactory-limbic complex.

These two styles of computation, the first based on spatial/nearest neighbor co-occurrence characteristic of the neocortex, just described, versus a second based on events and temporal co-occurrence characteristic of olfactory cortices and hippocampus are progressively separated and expanded in land animals compared to aquatic vertebrates. Finally, the more challenging environments occurring on land may generate a selective benefit for learning with few or no trials. This occurs via planning, a process that can be thought of as learning from hypothetical experience, and abstraction. Learning from hypothetical experience is particularly advantaged in action selection where irreversible outcomes are present, such as when evading predation. The ability to learn a high-acuity, value-tagged egocentric visual panorama characteristic of the cortex and its homologues and integration with the temporal-sequence computations of the hippocampus together seem critical to planning.

## 2. The neuroecology of the water to land transition

Air is more electromagnetically permissive than water and thereby results in a massive 100x jump in visual range, if unblocked by irregular topography or exuberant plant life [2]. Adding eye and head rotation, the total volume of space containing visual information to guide action grows with

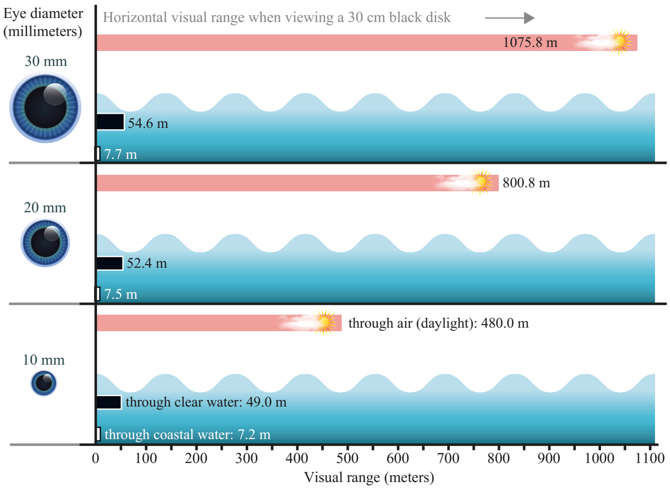

**Figure 1.** Computationally estimated change in visual range for a 30 cm black disk through two types of water and through air for the tripling of eye size that occurred as vertebrates transitioned from water on to land over 300 million years ago. Visual range was calculated for bright daylight (noon, no clouds), clear water, and coastal water [2,5]. For reference, typical human eye diameter is 24 mm. Note how underwater visual range hardly varies across the tripling of eye size from 10 to 30 mm, in contrast to the doubling in range that occurs for overwater visual range. The water clarity used for the clear water range estimate (in full sun, at a depth of 10 m) is based on a very clear sample taken in the Bahamas. The water clarity used for the coastal water estimate (also full sun) is based on water typical of freshwater bodies and along the coastlines of oceans (Baseline Model [2]). These values are an upper bound on possible visual range for a black disk (as detailed previously [2]). For less than full sun, or for more naturalistic contrast ratios than a black disk provides, range decreases rapidly [2]. This results in aquatic visual ranges on the order of one body length [2,10] for coastal and freshwater domains where much of aquatic life is concentrated. Figure modified from [5].

the cube of range, or a million-fold. Easy passage of light benefits plants as well, increasing food availability on land 100-fold—95% due to plants [1]. Ironically, this plant bounty can render the visual signs of predators or other perils absent or cryptic as photosynthesis requires absorbing and blocking the same light that would disclose them. To access this resource, vertebrates had to master a vastly different mechanical milieu, one that favors jointed limbs in order to structure the ground reaction forces on flowable substrates such as soil, sand, and mud, since movement easily fails without such conformation [9]. Movement through the resource-dense but partially occluded space of land increases the selective benefit of planning if the necessary computational resources can be afforded [5], a point we will return to after considering what happened to the brain.

### (a) Light in water, light in air, and visual perception

Sensory ecologists have charted the many sensory signal differences between water and air environments. A few sensory modes could not survive the transition, such as electrosense, which depend on electrical charge flow in water that is not possible in air. Similarly, the mechanosensory lateral line—critical for detecting the velocity and accelerations of adjacent water flows around aquatic animals relating to locomotion and the movement of other animals nearby—has no analog in terrestrial vertebrates, although the key sensory receptor, the hair cell, continues within auditory organs. Visual, sound, chemical, geomagnetic and mechanical signals are the remaining external signals. Here, we focus on visual signals, as the change in how light works on land is so large, reasonably easy to quantify, and accompanied by clear changes in the brains of terrestrial animals.

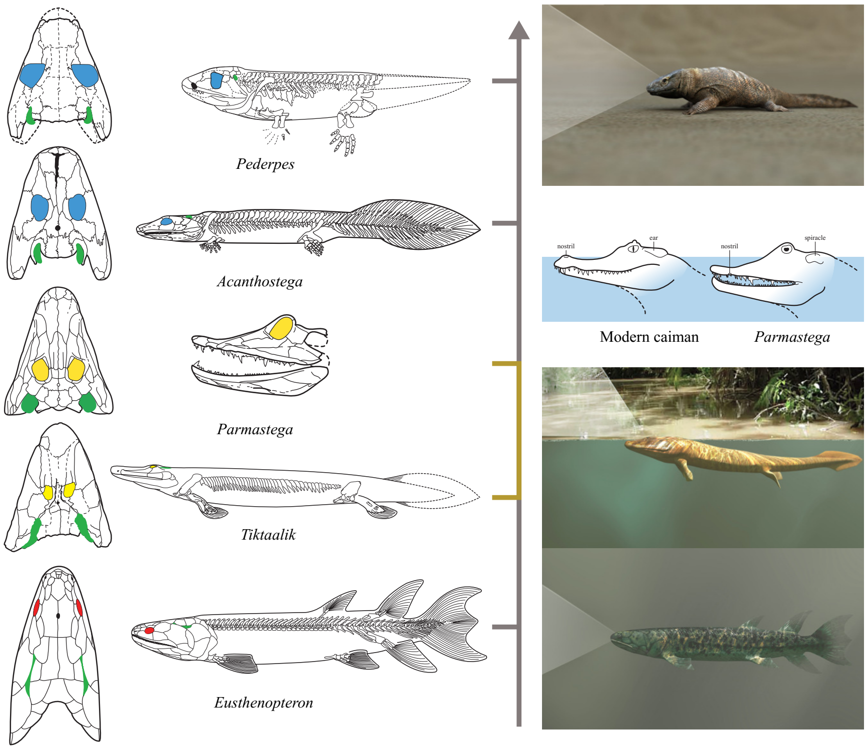

**Figure 2.** Eye orbit size tripled as fish morphed into their terrestrial form, during which time their skulls became flattened with eyes on top, probably for viewing out over the water surface. Bottom to top shows a finned representative (red orbits), two transitional representatives (yellow orbits), and two digited representatives of this period. Holes in the top of the head (spiracles) thought to be used for breathing in these taxa and later giving rise to the Eustachian tube in the auditory organs of more derived tetrapods, are shown in green. In terrestrial taxa that later return to the water, orbit size recedes to the values typical of ancestral fish [2]. For time reference, *Eusthenopteron* is ≈385 Ma, while *Pederpes* is ≈348 Ma. Figure modified from [2], with addition of *Parmastega* from [21]. Caiman comparison modified from Extended Data Fig. 8 of [21].

Light is rapidly scattered and absorbed in water, while it passes unimpeded through long distances in air [2,11,12]. The "beam attenuation length", defined as the distance a parallel beam of light of a given wavelength travels at which 37% of the light remains, demonstrates this. For the most penetrating wavelengths of light (bluish) this distance can be 24 meters in the clearest deep ocean water [13,14], to several meters in coastal waters [10,13] and down to 2 m and less in fresh water [15–17]. In air, the attenuation length for similar wavelengths is easily over 25,000 m [18,19]. For example, the longest line-of-sight photograph from a mountain in Spain to a mountain in France is 443,000 meters [20]. Estimation of visual range from visual system and water parameters coheres with empirical measurements. For fish, these give detection ranges for ecologically relevant objects on the order of a body length [2,10]. The thousand-fold higher transparency of air translates to a hundred-fold increase in visual range (figure 1).

After the minor corneal shape changes required for the change in refractive index, a hundred-fold improvement in visual range for simply surfacing the eyeball has major implications for animal behavior. Adding the onset of targeted eye movements [22], the evolution of necks in transitional tetrapods [23] along with the rapid body reorientation possible on land results in the animal's visual sensorium increasing a million-fold [2,5]. All the opportunities and threats formerly seen a few body lengths ahead, often forcing high behavioral urgency, can be seen at a more comfortable distance and confers the possibility to use more extensive processing for lower-urgency behaviors. The emergence of planning, a time-consuming process that gives way to habit

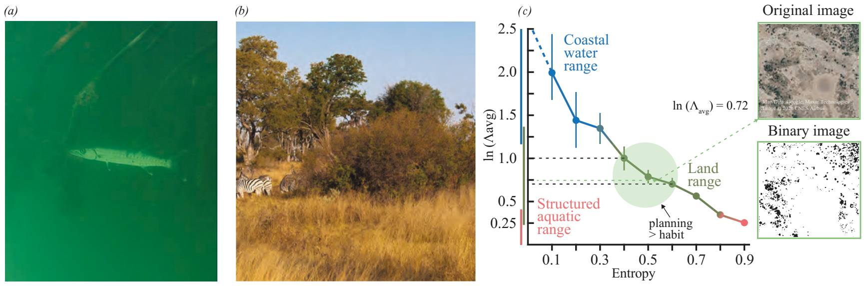

**Figure 3.** An aquatic visual scene *(a)* compared to a terrestrial visual scene *(b)*, and the different realms of lacunarity characterizing land versus underwater habitats *(c)*. The marine environment has ≈100 times less biomass than land despite occupying more than twice the area of land, and most of the biomass is accumulated in animals; in contrast, on land most of the biomass (≈95%) is in plants, primarily in their stems and trunks. Key sensory signals like light travel a far shorter distance through water than through air. Focusing on light, aquatic visual scenes are blurry, homogeneous and typically empty other than the occasional animal seen at close quarters *(a)*. In contrast, terrestrial visual scenes are dominated by biogenic and topographic structure, in a medium that enables sensing from a far greater distance *(b)*. (c) The mean lacunarity of land habitats is midway between the high lacunarity of coastal water zones and low lacunarity of structured aquatic zones. Here, we plot this against another measure of habitat structure, entropy, which has proven useful for generative models of different landscape types within the simulations of predator-prey dynamics discussed later. The inset shows a sample of a savannah-like habitat from the Okavango Delta, where there is a mix of open areas and closed areas. The green filled circle shows a region of environmental entropy/lacunarity where simulations show there is a selective benefit to plan-based action selection during evasion of a visually guided predator. Top-view images are converted to black and white images prior to the lacunarity calculation. Image *(a)* from [33] with permission from Elsevier; *(b)* from "Zebra and giraffe" by Caty T, used under CC BY 2.0 (cropped from original); *(c)* from [5], used under CC BY 4.0.

when time is short, likely depends on this additional time [24–26]. However, even with other possible long-range senses in water, as will be detailed later, the absence of much of the habitat structure found on land appears to reduce the utility of planning in water. An exception may occur where temporary structures are created by certain land mammals that have returned to the water and use echolocation, which has much greater range than vision in water. Examples of these include bubble nets, mud rings, and the use of multiple bodies to form walls and carousels during cooperative hunts of whales and dolphins [27].

**Paleontology of the water-land transition** A bony testament to the effect of the water-land transition on vision is the change in eye orbit size—a reliable proxy for eye size—when vertebrates came on to land over 300 million years ago (figure 2). Analysis of the variation in orbit size over pre-, mid- and post-transition shows eye orbit size triples [2]. Tripling eye size has almost no effect on underwater visual range, but produces a large payoff in aerial range, particularly for unimpeded sightlines over water (figure 1). The transitional tetrapods, some of which are believed to have been primarily aquatic such as *Tiktaalik*, already show this adaptation [28]. Given the flattening of the skull with eyes perched high (figure 2) and the use of biting for predation [29] in addition to the more common suction method found in aquatic animals, these animals appear to already be exploiting a greater visual range. What they used this for is less clear, but seeing distant prey over the water surface would have been possible, including terrestrial invertebrates (preceding vertebrates on to land by 50 Ma), other transitional tetrapods and air-breathing fish [30] that surfaced to breathe using ventilation holes just behind the eyes (spiracles, green; figure 2), or early amphibious taxa and stranded fish [2,21,31,32].

## (b) Components of the terrestrial tableau

Land, with a mean elevation above sea of 840 m, has many forms of structural complexity arising from plants spanning a wide spatial scale from grasses to large trees (figure 3), as well as arising from topographical features spanning ravines and hillocks to canyons and mountains. In addition, terra firma presents an interface varying from hard ground and other solids such as tree trunks to flowable, plastically deforming solids and granular media such as sand, mud, and leaf litter all at angles varying from horizontal to vertical [34]. The challenge of terradynamics for locomoting animals is in its much higher diversity of physics compared to the uniformity of hydrodynamics [8]. The diversity of land habitats contrasts with the relative homogeneity of marine habitats, whose mean depth of 3,700 m puts most of the ocean far outside the 200 m deep zone where enough light penetrates to support photosynthesis [35].

Land is a scaffold on which the prime directive of plant life—to intercept light—competes with the visual range of animals unleashed by the transparency of air, forming occlusions that make clues of adversary state cryptic. In very dense foliage visual range is contracted similar to the aquatic context. The effects of occlusions on land are manifold—for pursuit predators, it is hard to play hide and seek on a flat open plain; while for ambush predators, occlusions provide something to ambush from. Later we will provide evidence that between the extremes of dense vegetative or topographical barriers and flat open plains there is an intermediate level of sight-line interruption—such as savannah-like habitats—that provide high selective benefit to planning in predator-prey interactions [5]. Note that crypsis is hardly unique to the terrestrial condition, as it is a major theme of aquatic predator-prey dynamics as well [11]; however, aquatic animals have far less at their disposal—chiefly background matching, given the relative paucity of topographic or vegetative barriers. The octopus, the champion of underwater crypsis (and perhaps of underwater cognition besides aquatic mammals [36]) can use their flexibility to exploit very small hiding spots in the benthos and use millions of display and sensing elements to match arbitrary patterns to deceive foe and conspecific competitor alike [37–41].

The change in resources from water to land is shown through biomass data [1]. The total primary productivity—the amount of fixed carbon per unit time (mostly photosynthetic) across all of life—on land is similar to that of the ocean, despite land only being a third of the Earth's total surface [1]. However, the magnitude and distribution of the ensuing net biomass is markedly different between these two ecosystems [1]. Land biomass (≈470 gigatons of carbon, Gt C) is two orders of magnitude higher than marine biomass (≈6 Gt C) [1]. Ninty-five percent of this is plants; consumers such as animals are a relatively minor component. Oddly, this is flipped in the marine environment: the biomass of producers (mostly photosynthetic) is only 20% of the total. This is because the producers, primarily phytoplankton, turnover in a matter of days, while consumers such as fish turnover on a much slower time scale [1]. A surprising point worth noting for animals in terms of choosing food is that while not all of terrestrial biomass is equally easily acquired and digested for its energy (thus herbivores have digestive tracts three times the length of a carnivore's), it is similar in energy density per unit dry mass—around a factor of two from the lowest energy density to the highest [42].

Thus, in addition to the geological texture of land, there is a massive amount of biogenic structure growing on it that is for the most part absent from oceans but for coral reefs, kelp forests, and mangroves. Besides providing food and crypsis, this living scaffold provides a host of new biomechanical niches, including climbing on stems and trunks, jumping or brachiating between trees, and crawling, slithering, or burrowing through organic and inorganic material.

As important as land's carbon-hoarding tendencies is the way in which it is arrayed on the landscape. Lacunarity (from lacuna, a gap) is a measure of the variability of gaps in a landscape, such as grassland between trees, and is a useful measure in this regard [5,43–45]. Terrestrial landscapes inhabit a realm of mean lacunarity nesting between coastal seascapes and complex aquatic seascapes such as those provided by coral reefs [5]. In the center of the land lacunarity domain, habitats feature patches of dense vegetation interspersed by expanses of grassland (savannah-like). It is in this region (green circle, figure 3c) where simulation results we will discuss near the end show an advantage for planning over automatized action sequences.

## (c) Terradynamics and the need for multi-jointed limbs

Animals move by way of interaction forces emerging from muscles as they push the body against the external environment. From the standpoint of a vertebrate in water, the force situation on land is so different as to be like life on an alien planet. If you compute the force on a fish in water from gravity, it is only at most a few percent of the force on land, as fish approach neutral buoyancy (teleosts especially due to a swim bladder, and slightly less so for the cartilaginous fish which need to swim while oscillating a non-symmetric tail to fight gravity) [12,46,47]. For this reason, if you rotate an underwater vertebrate 180° around its long axis, you will be hard pressed to notice the difference from a distance due to the symmetry of the top and bottom halves of the body. Rotating limbed animals in this way breaks symmetry in an obvious way. The change in interaction forces bears on why the tetrapod body plan is marked by a high number of joints compared to the ancestral body, which in turn requires substantial neural innovation for coordinating between the multiplying limb-centered frames as will be detailed later. One example we will discuss is wrist flexion for movement, and another is the evolution of the neck.

Substrates around the water-land interface are often granular and yield upon interaction, such as wet or dry sand and mud [8,34]. In prior work examining movement over such substrates, using live and robotic sea turtles moving over sand, it was found that locomotor effectiveness was determined by an interaction between limb substrate intrusion, belly friction, degree of substrate disturbance, and wrist flexibility [9]. Without wrist flexion, the region of contact with the sand rotated with forward body movement, and this disturbance causes the sand around the limb contact area to now become soft and flowing [9]. As a result, the body sinks down into the disturbed sand, causing a large increase in the belly friction. In addition, the flowing sand at the limb intrusion point reduced the propulsive force that could be applied before exceeding its lower yield stress (at which point the limb slips back). To move effectively, then, the sea turtle has to use its limbs not only as propulsors, but also as manipulators, actuating joints of the limb to carefully control interaction with the ground and maintain forward movement.

Neck mobility initially appeared in the transitional tetrapod *Tiktaalik* 385 million years ago [23]. Its absence prior to that time may partially relate to drag or control challenges of underwater head rotations. Animals on land turn their head, and even at full speed, this incurs insignificant yaw or pitch destabilization due to the low drag force of air. However, another key factor is that above water, head rotation vastly expands the total visual sensory volume that can be inspected, while below water this is not true. Consider two animals: one animal with 3 meters of underwater visual range and another on land with 300 meters of visual range. If the fields of view of both animals expands to 360 degrees due to head mobility, the total sensory volume on land would be $100^3$ or a million-fold larger compared to the underwater sensory volume [2,48,49]. A signature of the yaw instability issue combined with the advantages of swiveling larger sensory volumes may be seen in mammalian underwater echolocators, with their much longer sensory range than is possible with underwater vision (order 100 m for prey-sized objects [50]). At low speeds, they use head rotations underwater during esonification of their targets [51] while at higher speeds they steer their beam internally over a more limited range without moving their head [52].

## (d) Limbs and avoidance of tipping over

Since being above water puts the full force of gravity on the body, and dragging the body incurs a large drag penalty or can cause movement to fail [9,53], attaining ground clearance and associated neural control was important for the early land vertebrate. Brains greatly increased in size in two key radiations (mammals and birds) and not in a third (reptiles), and as will be described later, most of that increase is in the telencephalon and in the cerebellum. Just as controlling the body from falling over when on land depends on the body's orientation to gravity, muscle activations to move a limb to a certain point in the egocentric frame are entirely different if that limb's initial orientation is parallel or transverse to gravity. Yet, this is a common need given movement over the variously flat, tilted, or vertical surfaces of land. Compensating for these variable control needs and reweighting sensory inputs according to body state seems part of the cerebellum's function [54] as discussed further below.

Focusing on avoidance of tipping over, the relevant abstraction is the support polygon—the points of contact on the ground—relative to the body's center of mass. When the center of mass is low and within a wide polygon (sprawled posture), there is no tipping; but if it is high, then only a slight body destabilization will bring the center of mass outside of the polygon and result in falling over without corrective maneuvers [55]. Indeed, one clinical sign of cerebeller damage is taking a wide stance [56], the bipedal equivalent of the sprawled stance that occurred in ancestral tetrapods and still used by amphibians and many reptiles. Unsurprisingly, aquatic therapy is a common modality for balance issues in humans [57], either directly related to cerebellum deficits, or to those of the basal ganglia to which it is highly coupled. Simply getting to a sprawled posture required a 40 million year-long "training-wheel" phase at the transition on to land in which partial submersion and body dragging was prominent [53,58,59], as well as a need for tail manipulation [60,61].

The issue of sprawled-stance versus the more upright stance found in more derived tetrapods such as mammals, with the feet directly under the body, has received considerable attention in the biomechanics and evolution literature [53,55,62–68] though less within neuroscience [69]. There appears to be a correlation between the upright stance found in mammals and their much higher speed and energy use, in comparison to lizards (all ecotherms measured at 35–40° for the following numbers, from [70]). The $\dot{V}O_{2max}$ of mammals is 6-fold that of lizards; at the $\dot{V}O_{2max}$ they have a maximal aerobic speed that is ≈7.4-fold higher. Their daily energy expenditure is ≈11.4-fold higher. The increase in daily energy expenditure relates not only to higher speeds, but also to their 10-fold larger relative brain mass over that of ectotherms [3].

These considerations point to an ecological stratification of niches along a dimension of power density [71]. High power density animals like birds and mammals go faster and have more rapid neural computation due to hotter, larger brains [3,72], while low power density animals like amphibians and lizards go slower and have slower neural computation in smaller brains, using strategies like sprawled posture. It is interesting, and seemingly not accidental, that the low power density animals on land have a number of features (e.g., small, cold brains) similar to the underwater vertebrates from which they evolved. These neuroecological considerations of the water to land transition provides background for understanding changes in the brain over the water to land transition. The issue of power density will return at the end, where we will argue that the water to land transition is paralled by a habit to plan transition in potential action control modes among mammals and birds—seemingly rare or nonexistant in the ectothermic land animals perhaps due to planning's high computational demands.

## 3. Approaches to the evolution of brains and brain function

Here, we begin to consider how vertebrate brains have evolved consequent to the new informational and mechanical ecology offered them by life on land. We will argue that the water-to-land transition offers potentially massive benefits to the possessors of brains capable of solving some very specific problems in gathering information and structuring decisions. The study of brain evolution has been active for more than a century, and now carries with it a host of broad and essentially unresolved questions, several of which we will touch on. Brain evolution research ranges from the broadest questions of the relation of brain mass to survival and longevity to the specifics of circuit redesign in sensorimotor specialists. The circuitry-intensive tasks of accurate integration of visual information over a moving eye, neck and body and the integration of multiple motor effectors, both of which demand plasticity over both phylogenetic and developmental time, come to depend in mammals on the neocortex. These functions are expanded and altered from their original predominantly "hardwired" midbrain organization, entailing a new computational architecture whose extended use for comparisons of new domains of information may be key to its retention in the neocortex.

## (a) Brain mass and behavioral complexity

### (i) Behavioral complexity

A taxon-general, positive relationship of brain mass to behavioral complexity has survived a contentious century of redefinition and refinement of the measures of both "complexity" and "mass" [73–76]. Behavioral complexity, variously identified ad hoc with the capacities of prey versus predator [73], bottom feeders versus more ambitious predators [77], folivores versus frugivores [78], or residence in low versus high environmental complexity [5,79] correlates with brain size. Behavioral inventories (including stringently-defined "behavioral innovations" in the wild), success in invasion of new niches after accidental introductions, and relative longevity also correlate with greater brain mass, often in interaction with sociality [80–82]. "Cognitive control", the ability to choose the best of competing responses accurately [83] or to delay reward for increasing lengths of time [84] correlate similarly. Finally, the endothermic branches of the terrestrial vertebrate invasion, birds and mammals, show a 10-fold increase in relative brain size, called a "grade shift", which is one of the most distinct in vertebrate history. What is this as-yet undefined brain mass? Neurons, glia, or connections? All of the brain, or parts (and which parts?), more generalized "computing power", memory, or specific classes of circuitry? The water-to-land transition generates an unusually well-defined list of behavioral necessities that allow some reinterpretations of the basic facts known about how brains change.

### (ii) Mass and neuron number

Overall mass, a crude measure indeed for any computing device, has successfully resisted more decomposition than would seem probable. Substitution of neuron number for mass, whether done by exhaustive stereological techniques or flow cytometry [85–88], produces generally similar rankings, and shows that between-taxon density differences are pervasive. Neuron number is usually thought to be the germinal element of change in brain volume, but in specific cases, alteration in the amount of connectivity can be the direct cause of a significant functional change.

For specific cases we will discuss, we draw your attention also to alterations in convergence of connectivity as a direct cause of significant volumetric and functional change. For example, in primate neocortex, while the prefrontal and parietal cortex are equal in their disproportionate volume increase in large brains, they stem from different causes. The increase in prefrontal volume is largely due to an increase in axodendritic volume that reflects extreme convergence of inputs to the frontal cortex [89]. The increase in parietal volume is due to increased neuron number [90]. The distinction between increased convergence in the frontal cortex—useful for action selection—and more computational elements in parietal cortex—useful for accurate integration of embedded visual circuits—may be essential to the tasks they perform.

### (iii) "Correcting" brain mass for body mass

How to separate the necessary costs of maintenance of a larger sensory and motor periphery and its visceral regulation from potentially increased computational power has been a perennial issue. While Jerison's measure of relative brain size, the "encephalization quotient" (EQ), [73], successfully identifies those species with relatively large brains for their bodies, its conceptual basis is problematic [91]. Encephalization measures very often do no better than absolute brain mass in predicting behavioral complexity, as in the cognitive control experiments described earlier [83]. Overall, the point of this section is to show that increase in brain mass, absolute or relative, can be one aspect of an adaptive response to the challenge of a new niche. Examining the phylogenetic path a species has taken to its present brain and body masses can be particularly informative about the significance of changes observed [92,93] to which we can add an ecological path. Overall, as apparent from the neuroecology section above, removing the requirements of body control from consideration in brain evolution seems poorly motivated. See the electronic supplementary material for other issues in comparing brains.

## (b) Fractionating behavior and the brain

The search for better focus on the drives and mechanisms of brain evolution led researchers looking at the relationship of whole brain volume increases to aspects of real-world function—the allometric tradition—naturally desire to make a more detailed account. The next step was to attempt to find variable behavioral competencies that correlated with the volume of particular neural substrates. The first, and most dramatic evidence for different brains for different niches was the contrast between olfactory versus visual representation in nocturnal versus diurnal mammals. Those who are principally nocturnal have relatively larger olfactory bulbs and olfactory cortices while diurnal animals favor the remaining forebrain, specifically the neocortex in mammals. This contrast can be seen throughout the vertebrate lineage, in sharks and rays, teleosts, reptiles, birds, mammals, in characteristic changes from domestication, and in individual variation in humans [94–103]. Oddly, moving away from this particular axis of vertebrate brain organization to find other similarly-sized effects has proved difficult. The analytical problem facing researchers may be appreciated in figure 4 [104].

Although it is clear that the olfactory bulb is quite variable in volume, and many other interesting distinctions appear, the first message of figure 4 is covariation and high predictability. A principal component analysis of the mammals in this set shows that the first and second principal components explain 99% of the variance. All brain divisions load on the first principal component (Factor 1) which explains about 96% of the variance. Olfactory bulb, olfactory cortices, hippocampus and amygdala load on the second principal component (Factor 2), about 3%. The remaining 1% of variance must then subsume individual variation, variation by sex, experience effects, and simple error in addition to any niche or specialist variation in the "proper mass" of interest.

The second message of figure 4 is the overwhelming contribution of differential allometry, the different slopes of rate of increase of size of particular brain divisions with increase in brain size. This difference can be difficult to appreciate in the necessary log/log relationships plotted in the graphs, but can be seen in the two insets. Both the forebrain and the cerebellum have "positive allometry" with respect to the rest of the brain. In the bottom inset, we show a set of four vertebrates (goldfish, whale shark, cat and sheep) whose brains range up progressively in size but which are shown at the same magnification, with the goldfish boosted as indicated so that it can be seen. These brains show how the forebrain and cerebellum progressively and predictably come to dominate brain volume. In the side inset, a similar point is made about the positive allometry of the neocortex with respect to the rest of the forebrain for three marsupials, the dunnart (the "marsupial mouse"), the sugar glider and the gray kangaroo, chosen for a smooth progression in size and similar Factor 1 and 2 loadings. In this case, the coronal sections of each brain are printed at different magnifications, but are visually matched in size so that the regular expansion of the neocortex in the larger brains can be appreciated.

Unfortunately, the search for a relation between a specific behavioral ability and the volume of a particular brain division, area or nucleus has been unusually prone to premature conclusions because of the markedly different allometry of brain parts and the covariation between the elements of Factors 1 and 2. These two issues make defining a "base" rate of change exceptionally difficult. Interestingly, at least some cases of what would seem to be very species-specific adaptations in complexity, like differences in dexterity ranging from paws to hands are accompanied by more neural tissue dedicated to the appropriate limb, but which in turn is entirely accounted for by overall brain mass [109]. Most important, figure 4 and 5 together beg the question of just why the allometrically-privileged structures like the forebrain and cerebellum are so, and why the vision versus olfaction dimension of variability can make such a demand on brain organization, which other sensory specialists rarely show.

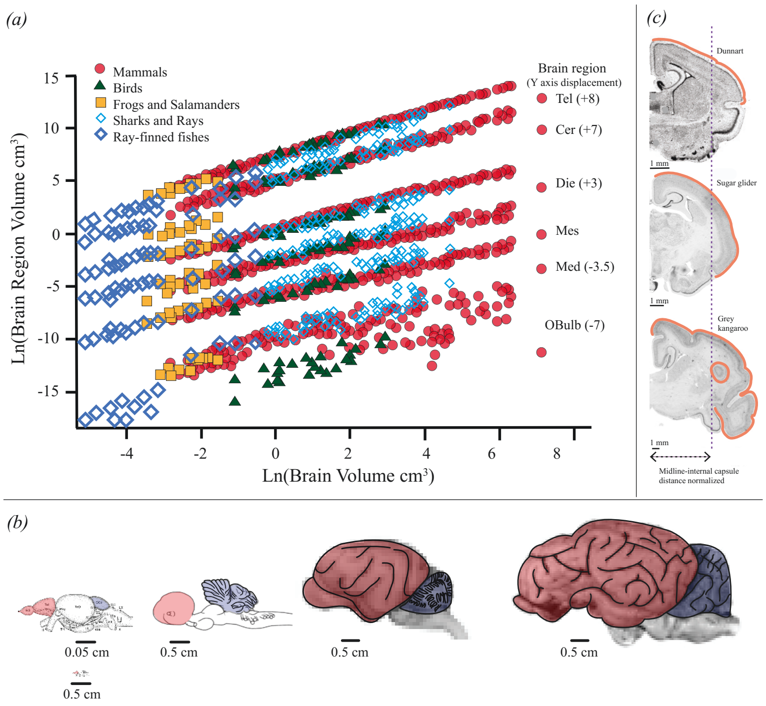

**Figure 4.** *(a)* The natural-logged values of brain region volumes are regressed against the natural-logged values of overall brain volume in ray-finned fishes, sharks and rays, amphibians and mammals. While simple regression is easiest to visually comprehend, and emphasizes the brains of smaller volumes central to the water-land transition, it has the fault of minimizing the apparent variability of the structures with the largest allometric slope in the largest brains (primates, large ungulates and carnivores), which should be kept in mind. Other representations with a variety of indexing and any form of general linear analysis corrected for overweighting of phylogenetic covariation will confirm the overall features we describe and can be found elsewhere [100,103,105]. Added species' brain divisions were drawn to match the original Stephan dataset conventions. Brain divisions are ordered from bottom to top in order of increasing slope. A constant was added to the brain region volume to separate brain region volumes on the Y axis and is listed adjacent to each named structure. *(b)* Lateral drawings of four vertebrate brains to show the effect of the high allometric slope of the telencephalon (red) and cerebellum (blue) relative to the remaining brain on their increasing contribution to total brain mass in four species. Left to right: a teleost, the goldfish (*Carassius auratus*) [106], a chondrichthyan, the whale shark (*Rhincodon typus*) [105], and two mammals, the domestic cat (*Felis catus*) and the domestic sheep (*Ovis aries domestica*) [107]. They are all shown to approximately the same rostro-caudal length, but notice the size of the scale bar, always 0.5 cm, under each but for the magnified fish brain at 0.05 cm. *(c)* As in the bottom inset, this time the increasing contribution of the neocortex to total brain volume, for three marsupials with brain size increasing from top to bottom. They are shown to approximately equilibrate the distance from midline to the lateral margin of the putamen (dotted line), and each is marked with a 1 mm scale bar. These marsupials were chosen because of their more intermediate values on the neocortex/olfactory-limbic axis (figure 5*c*). From top to bottom, the fat-tailed dunnart (≈16 g, *Sminthopsis crassicaudata*) [108], the sugar glider (≈120 g, *Petaurus breviceps*), and the grey kangaroo (≈45,000 g, *Macropus fuliginosus*). The latter two images are from the Comparative Mammalian Brain Collections, www.brainmuseum.org, property of the University of Wisconsin and Michigan State Comparative Mammalian Brain Collections funded by the National Science Foundation and the National Institutes of Health.

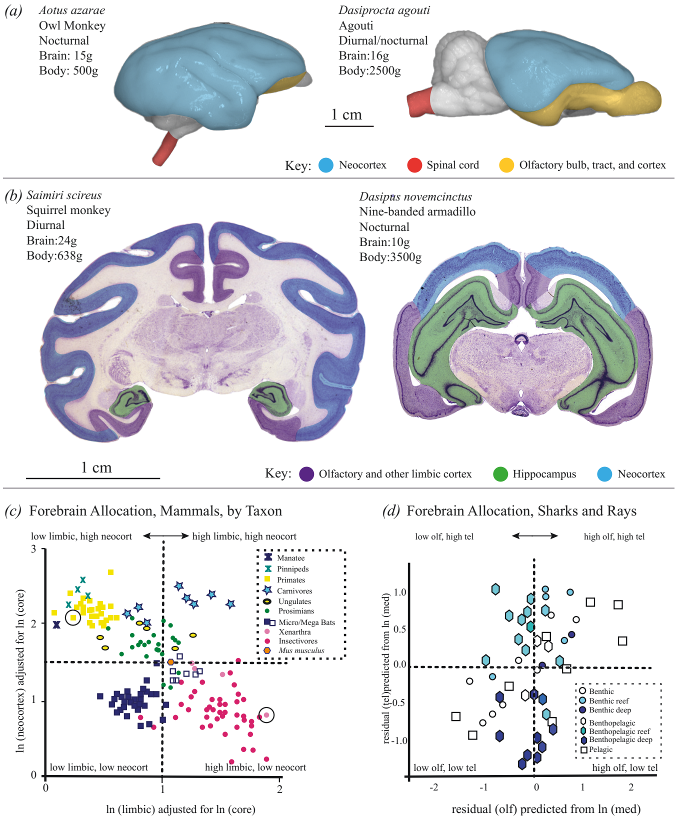

**Figure 5.** Allocation of forebrain volume to olfactory/limbic components versus neocortex or “other forebrain” in vertebrates. All vertebrate taxonomic groups examined to date show covariation of a set of olfactory and limbic structures which vary independently or negatively with respect to the volume of the rest of the brain or neocortex. The species chosen for illustration in panels *(a)* and *(b)* contrast the structural consequences of weighting on the olfactory/limbic factor, in the context of other covariates, brain and body mass and nocturnal and diurnal niche. *(a)* Contrast of the nocturnal owl monkey with the nocturnal/diurnal agouti, lateral view, rostral to the right. Their brains are quite similar in volume, while the agouti’s body mass is approximately 5 times the owl monkey’s, which can be appreciated by comparing the spinal cords (black arrows). In the owl monkey, the olfactory bulb and tract is a barely-visible thin ribbon on the inferior aspect of the rostral forebrain, while the agouti’s are robust. Primary olfactory cortex, piriform cortex, is visible below the dorsal neocortex. In the owl monkey, the size of the neocortex obscures all other brain components from view, including the cerebellum, equal in size to the agouti’s [110]. Magnification is equivalent for both brains. *(b)* A coronal section from a large-brained, small bodied squirrel monkey (Primata) is contrasted with that of a small-brained, larger-bodied armadillo (Xenarthra), which represent the extreme divisions of the graph in *(c)*. The section was chosen at the point of maximum cross-sectional volume of the hippocampus of each, which is quite small in the monkey, as is the olfactory cortex. In the armadillo, the hippocampus and olfactory bulb and cortices dominate the volume of the forebrain. Images are from the Comparative Mammalian Brain Collections, www.brainmuseum.org, property of the University of Wisconsin and Michigan State Comparative Mammalian Brain Collections, funded by the National Science Foundation and the National Institutes of Health. *(c)* The strong negative correlation within and across mammalian taxonomic groups of the relative volume of the olfactory/limbic principal component compared to neocortex volume, both normed with respect to core (medulla, mesencephalon, diencephalon, and striatum) [103]. Additional point for *Mus musculus* estimated from [111]. Black circle in the upper left quadrant is around the the squirrel monkey data point, while that in the lower right quadrant is the armadillo. Microbats are filled squares, while mega bats are open. *(d)* A comparable analysis of residual volumes of the olfactory bulb versus “rest of forebrain” predicted from medulla volume for sharks and rays. In this case, brain volumes show a relation to niche, with greater volume for “rest of forebrain” for reef denizens (turquoise symbols) and greater olfactory bulb volume for deep water denizens (dark blue), but the brain features vary independently, not negatively with respect to each other [94].

Before proceeding, one qualification is in order. To believe that that mosaic volume alterations are not part of the evolutionary palette would be incorrect. The forgoing discussion has principally referenced mammals, which were the only vertebrates with data available for analysis for some time. Demonstrated differences in allocation of neural tissue are often seen in small mammals with pronounced sensory specializations, like the star-nosed mole [112], or in allocation to specialized body parts within primary sensory areas in larger mammals [113]. The remaining vertebrate taxonomic groups, particularly birds [114,115] show considerably more variability in brain organization both between species, and across the lifetimes of individuals. Brain reorganizations may be seasonal or related to changing sex or social status (for example [116]). The source of such brain variation in non-mammalian vertebrates is partially from much more modifiable neurogenesis over their lifespans compared to mammals [117].

## (c) Deep dives into specialized behaviors and abilities: neuroethology

One alternative to the allometric study of very general traits over very many animals' brains in order to understand brain evolution has been the intensive study of easily-recognized, specialized traits in particular animals. The neuroethological approach offers the opportunity to study behaviors that are unambiguously the result of special selection, distinguish innate and learned contributions to behavior, and investigate the role of environmental context [118]. Conspecific recognition in amphibians [119], prey capture behavior in fish [120], echolocation in bats [121], electroreception in mormyrids [122], territorial displays in lizards [123] and food caching in birds [124] are some examples of this first approach. By now, though, the number of studies of diverse animals (even allowing for the dominating laboratory mouse) makes it impossible to draw a line around the domain of neuroethology [6]—it has become the field of systems neuroscience. For the most part, in accord with the discussion of fractionating the brain, most of the specialized systems of neuroethology can be seen as elaboration of existing subsystems rather than add-ons of new parts, compared to closely related species without the specialization. Even the "song system" of passerine birds, whose components were originally granted an entirely independent neuroanatomical nomenclature, has been progressively gathered back into the avian fold [125–127].

The idea that an entire behavioral capability could be dependent on a single brain part has gone progressively out of favor as neuroscience describes functional distribution more closely. Brain regions are more often viewed as the providers of a particular class of computations which multiple behaviors may utilize, which we will explore more deeply later in this paper. Focus has shifted toward identifying factors that can produce distributed recruitment of processing power across multiple brain regions, and those can include alteration in neuromodulators and neurohormones [128,129], "reservoirs of variability" in founder species [130], "evolutionary paths of least resistance" [131] or niche constructions large and small [132]. Unlike the relative scarcity of specialized volume differences related to function, these other sources of evolutionary change are ubiquitous. Via changes in these systems, "experience effects" are not late add-ons to brain structure but can be fundamental to the path of structural development [133,134]. Via changes in life history, evolution changes the opportunity for the environment to impact brain development and the brain's responsiveness to particular inputs [135].

The critical challenge is to find a principled way to integrate the general positive manifold of brain and behavioral complexity discussed above with the accounts of specific, adaptive behaviors of neuroethology and systems neuroscience. We will argue that a very specific example of this kind comes from the water to land transition. The computational challenge of the specific, but ubiquitous problem of how to integrate increasingly mobile spatial frames of eye, head, neck and limbs in terrestrial vertebrates is the explicit kind of behavioral adaptation favored in neuroethology, and indeed, the study of integration of auditory and visual information in the midbrain is one of its classic paradigms [136]. Adding a phylogenetic and neuroecological level to this account underlines an overlooked aspect of changed distribution of function in the terrestrial midbrain and forebrain.

# 4. The fundamental decisions: Orienting, approaching and avoiding

## (a) Simple approach in water becomes elaborated on land

While a fish striking at a swimming insect, a frog striking at a flying insect, or a human using a flyswatter might appear to be executing quite similar tasks, the motor and sensory computational requirements necessary to success in this minimal effort are much more complex on land. Given the depth and richness of the visual array and the need for more variable and nuanced interactions with land over water discussed above, virtually all land vertebrates have amplified various combinations of ocular motility, flexible necks and torsos, and scanning and searching procedures to exploit their visual resources. By comparison, fish principally use their oculomotor capabilities not to seek out nor avoid, but to stabilize their motion with respect to the visual environment, using saccades to recenter their eyes in orbit [137]. No fish is known to use smooth pursuit to keep prey in sight, though some do have saccade and variable aim abilities [138], and conjugate vergence of the eyes is used preceding the moment of attack, possibly as a mechanism of estimating strike distance [139,140]. When fish strike, the mouth is by far the organ of choice, but land animals quickly elaborate multiple-axis foveation, limb placement and grasp, and a reasonable percentage even develop tool use. No matter how rich a visual array, if it cannot be searched (either in real time or memory), and the results of that search accurately represented in ego-, paw- or hand-centered coordinates, it will not be useful. Just how and where this *sine qua non* is integrated into the terrestrial brain sheds new light on the nature of neocortex evolution.

## (b) The midbrain optic tectum

### (i) Approach

The midbrain tectum is highly conserved in its connectional structure across vertebrates. More than any other structure in the brain, it physically replicates the spatial relationships of the visual (and other sensory) scene to the body in the brain and thus lays out a solution of how to orient the mouth or body to a desired object or location of interest. The retinal surface, representing the visual world, is laid out topographically across the surface of the tectum, central visual field in rostral tectum, peripheral visual field in caudal tectum, upper visual field medially, lower visual field laterally. The next layer down brings in somatosensory, or auditory, or infrared (depending on which the species possesses and prefers), in spatial register with forward visual fields, whiskers and forward auditory receptive fields located in front and their corresponding opposites behind. Yet further down is the motor approach zone, with secondary or tertiary motoneurons, capable of orienting each animal toward the location of items of interest with a species-appropriate action: whether prey strike, head turn with ears pricked, or conjugate eye movements alone [141].

One basic role of the midbrain optic tectum is quite easy to assess: orienting toward food (the term "optic tectum" will be used for all vertebrates). The behavior of orienting toward species-appropriate food items in bony fish, amphibians, birds and mammals, either completely dependent or partly on the optic tectum, is so reliable that it is the basic assay for the normal and abnormal development of the visuotopic map in the tectum representation [142–145]. These motions are not automatic or reflexive: species-typical criteria are wired into the response properties of the visual neurons, and motivational and physiological states help gate movements by their interactions with basal forebrain and diencephalon. The optic tectum is often cited as an example of plasticity, because if the optic nerve is severed in goldfish and some amphibians, it will regrow and reconnect appropriately [142]. If one sensory surface is developmentally displaced with respect to another, they will align to bring themselves into register during a critical period [136], and in some mammals receptive field location will be altered dynamically to correct for eye movements of limited range [146]. However, this structure has the basic vertebrate body (the fish body) patently wired into it. Looking back over one's shoulder toward an interesting sound would throw its visual, somatosensory, auditory and motor representations unusably, and perhaps fatally out of register. In teleosts, as reviewed earlier, the tectum also participates in an optomotor reflex whereby the animal stabilizes its position if the distal visual environment moves (that is, in the lab, an experimenter moves stripes in an aquarium wall) [145] The goal of this "reflex" is functionally analogous to how a human swimmer might key on a shore landmark to keep their position against an ocean current. In the mammals that have been closely studied, optomotor responses do not involve the tectum (reviewed in [147]). Instead, a variety of interacting, often mutually overriding mechanisms for stabilization of eyes, body and posture are added to its neural control systems, especially when the species in question is in command of a large repertoire of eye movements [137,148,149]. These new mechanisms come to depend principally on the vestibulocerebellum and subcortical optic nuclei, and the forebrain as well.

Interestingly, birds appear to have a hybrid system at multiple levels, exploiting increased ability to use visual information while under "aquatic" constraints [150]. In flight, their aerodynamic constraints are similar to the hydrodynamic constraints of fish (and dolphins, as described earlier). In tandem, the range of bird eye movements, in the relatively few species studied, are reduced or altogether eliminated. As in fish, the essential information about whole field movement, as might be experienced in an air current (described below) is conveyed to the optic tectum whose volume is relatively large in birds [151] ("Mes" regression line in figure 4*a*; note that bird values (green triangles) lie above mammal values (red circles), closer to sharks and rays (blue triangles)). While, like fish, the relative movement of bird sensory surfaces with respect to each other is constrained, the visual acuity and pattern and object recognition of some birds exceeds most land vertebrates. Their eyes may be multifoveate with specialized tracking and scanning abilities—for example, a high-acuity region of the retina may be preferentially used to guide cruising, and a second retinal area for prey capture [114,152]). In general, while mammals directly trade off central visual field acuity for peripheral acuity [153], birds can maintain high peripheral acuity while developing even higher central specializations for acuity, all with higher temporal resolution as well [154]. The interleaving machinery of navigational and pattern-recognition abilities employs multiple subcortical nuclei, the vestibulocerebellum and major components of the forebrain.

Why would the medium, whether water, land or air affect the relative use of midbrain vs. forebrain in teleosts, birds and mammals (including bats)? In aquatic environments, movement of the distal visual field either arises from movement of the animal by water currents, which the fish must counter to remain stable, or from self-initiated movement which must be discounted. Therefore, compensation for this omnipresent, large-magnitude external cause of self-motion must be always available to modulate approach, avoidance or any other visual calculation of importance, likely accounting for its residence in the optic tectum. On land, it is unusual for the surrounding medium, air, to be moving at such a speed as to directly move an organism, contrasted with its role as a moment-by-moment problem to be countered or exploited in water, or in flight in air. In land animals, if the animal has not initiated movement itself (which typically predicts and thereby "cancels" the sensation of visual field motion), movement of the distal visual environment instead signifies potential catastrophic failure of postural stabilization (so well calibrated is this system that numerous mammals, including ourselves, use any signal from it as a signal of poisoning, particularly alcohol poisoning, hence carsickness and some hangover prevention). In terrestrial environments, the principal use of oculomotor information becomes optimization of visual information processing [155,156], keeping the eye stable with respect to the visual surround. Basic ocular stabilizing mechanisms are overlaid with overrides that permit saccades and visual pursuit, which are distributed in the brain and normally involve the cerebellum as well as numerous subcortical pathways, as mentioned earlier. Avian vision must hybridize the aquatic stabilizing mechanisms with the high-acuity requirements of terrestrial vision.

Birds have, in part, a second fish-like feature relevant to neural organization (interestingly, bats have evidence of the same midbrain dependence; figure 5). The use of wings for flight rather than for grasping or navigating terrain makes birds more fishlike in the kinds of orientation and approach to be controlled in a substantial part of their ecology. Limb control is obviously not a feature of fish, and the neural locus organizing limb movement for the most part ends up outside the brainstem and midbrain in terrestrial animals, particularly for grasp. What about perching birds, and even more, birds like parrots with good manipulation capabilities in their feet? Any answer to this question would be quite interesting, but has spurred virtually no research (excepting lateralization of foot preference in relation to song, by analogy to human language lateralization and handedness [157]). Finally, a much-researched third type of mammal can be added to those having the design features of passive movement and absence of functional limbs. Human infants have been shown to be highly dependent on the midbrain for visual orientation in the first three months, but over the first year, the cortex becomes dominant in visuomotor control [158,159]. Typically, this is interpreted as the large cortex overtaking or subsuming midbrain control [160]. The changing neuroecology of the infant might be a better way to understand a problematic "ontogeny recapitulates phylogeny" interpretation: an infant makes the neural transition from a limbless creature subject to passive movement to a fully terrestrial one by the end of the first year.

### (ii) Avoid, scan, traverse

In almost all species, avoidance movements to visual events also depend upon the tectum, from dorsiflexion to overhead shadows in fish [145], to a 180 degree leap or scramble away from a threat in birds, amphibians and small mammals [161,162]. While organization of approach resides in the dorsal tectal layers, organization of avoidance depends on the more ventral layers, with those in close apposition to the dorsal periaqueductal gray, an organizing region for avoidance generated by negative somatic and visceral events [163]. Additional approach-avoid behavior can also be dependent on the midbrain, such as initiation of visual exploration of the environment—scanning on entry to new arenas—and avoidance of obstacles in the terrain for desired orienting movements in either approach or escape [162]. Some form of coding of species-relevant identification of the objects of desire or avoidance may also be part of optic tectum single-unit electrophysiology, but the scattering of this research over decades, theorists and species makes a phylogenetic summary of this research approach close to impossible.

## (c) Posterior parietal cortex, the integration of reference frames, and the multiplication of end-organs for grasp

The computational demands of the terrestrial vertebrate body radically expand those of the minimal aquatic body. The addition of four limbs, which even if not employed directly for grasp, must minimally be added to the description of "an egocentric frame of reference" from visually directed footfalls or locomotoric grasping, as in tree climbing or branch swinging. Greater ranges of relative eye, neck and torso movements further complicate the rendering of a body "main axis" even for simple approach. The much-studied partial separation of the two routes of visual information to the forebrain in terrestrial vertebrates, the tecto-pulvinar-cortical versus geniculocortical pathways [166], or alternately, the dorsal versus ventral visual streams in mammalian cortex [167], probably have their functional roots in this essential added-on computation.

Within the neocortex, the posterior parietal cortex has a positive allometry equal to frontal cortex. That is, as the neocortex increases in absolute size, the frontal and parietal show the relatively largest increases (every brain subdivision has an allometric relationship with respect to the division it is in, such as cortical areas or regions with respect to whole neocortex, thalamic nuclei with respect to whole thalamus and so on). Functionally, both participate in the general, spatially-organized egocentric topography of the lateral neocortical convexity (figure 6). That

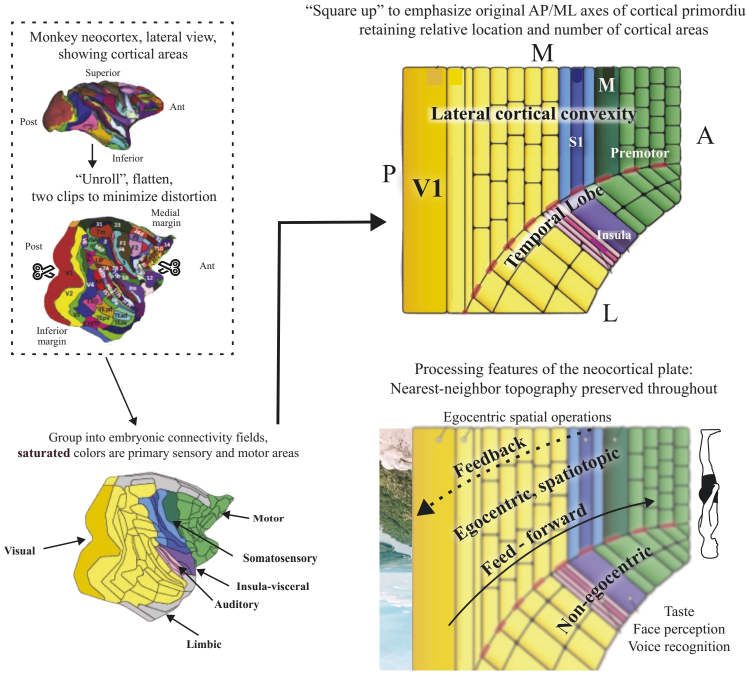

**Figure 6.** Schematic demonstrating the egocentric topography of the lateral cortical convexity, and the non-egocentric, but nearest-neighbor topology of the temporal lobe. For this representation, the current arealization of the lateral convexity of the neocortex in an individual macaque (*Macaca fascicularis*), with the procedures of the same authors for unrolling and "flattening" the cortex [89] is used as the basic template (Dotted line box, top left) used with permission as described in [90]. The flattened map in in the bottom left groups the same map into compartments of embryonic thalamocortical topographic continuity [164,165] each associated with a unique primary sensory or motor area, as labeled on this map and also as described in [90]. In the top right, the flattened schematization, now omitting limbic cortex, is squared up to correspond to the medial-to-lateral and the anterior-to-posterior location of these fields in the embryonic cortical plate with emphasis placed on longitudinal stripes of cortical areas extending along the mediolateral axis of the unrolled cortex, always maintaining nearest-neighbor relationships. The number of non-primary cortical areas, each represented by a rectangle in this figure, corresponds to the macaque cortex from which it was drawn, but would vary by species, with fewer areas in smaller-brained mammals, and more areas in larger ones. Finally (bottom right), functional mappings of interest are overlaid on this representation, the visual and somatomotor egocentric representational axes indicated by the visual scene and human figure to the left and right of the cortex, as well as the feedforward/feedback pathways described by Markov and colleagues [89]. In the temporal lobe, three examples of the several non-egocentric functional maps (which still maintain nearest-neighbor thalamocortical projection relationships) represented in that region are given. Elements from [90] are redrawn and rearranged, containing new material.

is, the lower visual field, sounds from the floor and the sensations and actions of feet position themselves in the medial superior margin of the cortex, while upper regions of multimodal and motoric space abut the temporal lobe [90]. In order to participate in this organizing egocentric topography for action, the position of eyes-in-head, head on neck and torso rotations must be integrated to allow the head to turn or the hand to reach toward a desired goal. To the surprise of most of the original researchers in this area, the posterior parietal cortex does not accomplish this by generating a sequential, embedded hierarchy of maps of visual-stimulus-in-retina, then retina-in-head, and then head-on-body explicit in successive parietal cortical areas. Rather a non-hierarchical recombination of subsets of retinal, eye, and head positions in different parietal areas produces a standing combinatorial array of a retinal target position weighted by eye-in-head, head-on-neck, and arm positions—all of these in the very general egocentric frame of the whole lateral cortex. Any particular motion is represented by a weighted combination of outputs from this array relayed directly to effectors, to the striatum and hippocampus, and to the frontal lobe [168–171]. This organization is quite distinct from the orderly superposition of sensory and motor maps in the optic tectum, but has extreme modifiability—or "evolvability"—in both individual development and in evolutionary time to accommodate new body arrangements and abilities.

The parallel terrestrial multiplication of types of "grasp"—"foveation", bringing items to mouth, independent grasps by either hand, whole-body tackles, and catches and kicks of any object—appear to have found a similar solution to the egocentric axis integration problem just described. Potential points of contact with the world are not represented as explicit locations on the body on a general egocentric map. Rather a series of overlaid maps are described, some representing distance with respect to the mouth, or either hand, or the midline, or created ad hoc [172–175]. The formerly perplexing study of 23 mammals varying in "dexterity" from the slow loris and rabbit to the marmoset and macaque [109], concerning the measured volume of cortex contributing corticospinal neurons to upper limbs, can now be put in context. Direct-projection cortical volume did in fact correlate with dexterity, but that volume in turn was entirely accounted for by total cortical volume. Considering the sequence of body, hand, eye and mouth spatial registrations required for a monkey to request social foraging for an insect in the pelt of another monkey, catch the insect with a pincer grip, visually inspect it, and bring it to its own mouth, the need for cortical volume in excess of the neurons generating the immediate volume of the corticospinal tract origin is no longer mysterious.

As to functional homology of these functions across aquatic to terrestrial environments, by their simple description, they cannot be homologous—fish are not required to recalibrate relative map positions of shifting sensory frames and localize limbs. Some recalibration of reference frames does occur in the vertebrate optic tectum, recentering the egocentric map after eye movements, though the computational job is slight compared to the large range of parietal computations. A neuroanatomical substrate for a potential elaborated map in the forebrain can be found in ascending projections from midbrain to forebrain in most vertebrates, Butler's [166] "collothalamic" projections, though a convincing "thalamocortical" homologue cannot be found in fish [6]. The ability to initiate approach movements is quite distributed in the spinal cord, midbrain and forebrain in mammals, but the ability to control single limbs, digits, and rapid movements of the mouth and face depends on the cortex.

## 5. Egocentric versus allocentric maps: understanding the forebrain through the water-to land transition

### (a) Characterizing sensory systems and the animals using them

Considering the transition from water to land from the brain's perspective can be understood on first pass as a change in the relative usefulness of different classes of sensory information coupled with marked and variable new motor capabilities. For example, in water, chemosensory information can be used as a kind of distance sense with a range greater than vision, and is particularly useful for "object" or source identification, whether that be the olfactory signature of a location, or a potential mate or prey. Terrestrial olfaction does not lose these functions, but becomes supplanted, in part, by the greater usefulness of vision, except for those cases where useful chemical information might have no visual correlate, such as the presence of a poison or the reproductive state of a conspecific.

Both folk and academic beliefs about sensory systems color beliefs about the internal states and capacities of those thought to be sensory specialists. Sharks, for example, had been characterized as "swimming noses", with olfactory information dominating the forebrain, by the pioneer comparative neuroanatomists [176], as reviewed in [177]. A revisionist period followed, showing that multiple sensory modalities also had access to the aquatic forebrain [77], but of late, the pendulum has swung back to acknowledge that yes, olfaction appears to dominate, though not as completely as the first claims pronounced [178–181]. For vision, particularly considering mammals, it is instructive to notice just how much of the cortical surface is captured by primary visual cortex and extrastriate visual representations in even nocturnal animals like rats and mice. The relative representation of vision in "non-visual" mammals such as these exceeds that of diurnal, shore-dwelling sharks and rays [94,182]—perhaps not surprising given that estimated nighttime visual ranges on land exceed daytime ranges in water [2]. The diurnal, high-visual-acuity terrestrial mammal does not have an aquatic counterpart.

The distance information available to an animal will also likely privilege different memory and decision-making strategies. Consider a diurnal marmot-sized mammal entering a large, fairly open field in a woodland that it has entered before, compared to a trout viewing the extended riverbank before it. The marmot has had the opportunity to "tag" the multiple distant but recognizable features it sees as represented egocentrically, each with its reinforcement history, and its motoric affordances. For decisions of where to proceed, the marmot can neglect an allocentric representation of its relation to unseen landscapes, to a degree. So scanning, left to right: "water"; "potential danger"; "berries depleted"; "possible berries", "good hiding location". This kind of visual array maps easily onto what is understood about the egocentric cortical surface, for sensory representations of useful objects and routes, and their evaluation via its reinforcement history, as realized in the frontal/prefrontal cortex to basal ganglia connections [183–185]. The larger the mammalian brain, the relatively more mass is allocated to this egocentrically- and hierarchically-organized prefrontal/ frontal cortex, supporting such decision arrays, then decision trees, and onto variable strategies [186] such as planning, which we will discuss shortly. The trout will generally view no such differentiated array at effective visual infinity (figure 3b). Conceivably, the trout might have instead evolved an unusually good memorized allocentric representation system to use in lieu of a directly perceptible, tagged array [187]. It would be interesting to compare capacities for allocentric route memorization versus static spatial arrays in aquatic and terrestrial foragers, though a memorized allocentric summary could not fully compensate for an immediately perceived array [188] particularly in fast-changing scenes [5].

### (b) The olfactory-limbic complex: a sensory specialization or fundamental computational division?

The "olfactory" versus "visual" distinction is so striking in vertebrate brains that it can be seen in whole brains (figure 5*a*–*b*). The large brain volume devoted to olfactory processing in olfactory specialists generated Jerison's term "proper mass" in his first allometric investigations of the vertebrate brain (1973). Figure 5*a* shows a lateral view of the identically-sized brains of an owl monkey and versus an agouti—a primarily diurnal rodent—showing the large volume of neocortex in the primate, completely hiding the cerebellum. Figure 5*b* shows a coronal section of the forebrain at the level of posterior thalamus in a squirrel monkey (one of the yellow dots in the upper left quadrant in figure 5*c*), and a similar section in the nine-banded armadillo (one of the red dots, Xenarthra, in the bottom right quadrant of figure 5*c*). Comparing the two, the relatively greater extent of the neocortex in the squirrel monkey compared to the greater extent of the olfactory cortices in the armadillo is as expected, but the extreme volume of its hippocampus compared to the squirrel monkey is startling. While the hippocampus gets olfactory input, it is not the majority input even in an olfactory specialist, which the multiple descriptions of hippocampal "place cells" support [189].

Not all of the set of structures we term the "olfactory-limbic complex" on the basis of their volumetric covariation in mammals can be seen in figure 5*a*–*b*, and they include the olfactory bulbs, olfactory cortex, perirhinal cortex, hippocampus, amygdala and septum [103]. In mammals, there is a robust negative correlation of neocortex volume and the volume of the olfactory-limbic complex, both within and across taxonomic groups (figure 5*c*). Those mammals with a high weighting of the olfactory-limbic complex are quite often nocturnal, or locate their food non-visually, as anteaters do. The species that are high on both factors, for example, the large carnivores (figure 5*c* blue stars), or low on both, like microbats (figure 5*c* blue-filled squares) would be good targets for greater investigation. Interestingly, the same covariation pattern often can be seen in individual variation of a number of domesticated species [111] and in human volumetric variation [98], suggesting genetic or stable developmental control of the covariation.

Do components of this covariation appear outside mammals? In figure 5*d* the relative masses of the olfactory bulb versus the remaining telencephalon are compared for deep-water sharks and rays versus their pelagic and shallow water counterparts. Olfactory bulb size is increased in the deep-water chondrichthyans, but rest-of-forebrain is independent of it [94]. That is, olfactory bulb increase does not entail smaller rest-of brain. Similarly, reef dwellers have relatively greater mass in the “rest of telencephalon”. This evidence provides some support for a strategic allocation of neural tissue on the basis of preferred sensory modality, but no elaborate factor structure. The actual or potential dorsal pallium, the structure giving rise to most of the neocortex in mammals, is quite variable in the several fish lineages, ranging from a few cells with principally olfactory input in ray-finned fishes [181] to a central pallial nucleus in sharks that receives visual input and is involved in visual behavior [190]. Functional homologies in fish behavior based on medial, dorsal and lateral pallial origins in several fish lineages have been described [191]. Given this variability, perhaps the most interesting question is to determine what it is about the forebrain that produces its consistent allometric predominance when brains enlarge (figure 4).

Returning to the olfactory-limbic complex, the sensory account (that is, olfactory-versus-visual) of the enduring distinction of allocation of resources between limbic and neocortical forebrain in the vertebrate brain reveals multiple problems, and eventually disintegrates. Historically, the term “limbic system” was coined to describe the interconnected cortical areas including olfactory, perirhinal, entorhinal, hippocampal and cingulate cortices that are located along the outer edge, the limbus, of the collected forebrain cortices. The olfactory bulb itself was not seen as integral to the grouping. To the perpetual confusion of the popular understanding of the brain, the limbic regions were fancifully termed the “primitive” or “emotional” brain [192], though none of these regions are more primitive than other forebrain nor exclusively involved with either emotion or olfaction, excepting primary olfactory cortex [193]. “Neocortex” or worse still, “rest-of-brain” is not a sensory category at all. Similarly, in terrestrial vertebrates generally and in diurnal mammals particularly, excepting the olfactory bulb and cortex, none of the listed structures are devoted to olfaction alone, and in primates, the hippocampus has the largest volume of the limbic-olfactory complex, while olfaction as a fraction of its input is tiny [103]. In marine mammals, the olfactory bulbs become vestigial (5C), and the immediately connected cortices are reduced, but the hippocampus is relatively little changed. Still, whatever category these collections of brain structures represent, development keeps them distinct, both in their germinal zones [194] and in the later expression of transcription factors [195]. The “limbic factor” does not permit the dorsal thalamus, the structure relaying visual, somatic and auditory input to the neocortex, to enter limbic cortex [196]. Such reticence in mixing “modalities” or more neutrally, the connectivity of the products of designated embryonic zones at any other level of the brainstem, midbrain or other forebrain is quite unusual. A further interesting hint is that the same sequestration and reciprocal covariation has been observed in *Drosophila*, and possibly, several other insect nervous systems [197].

## (c) The distinction between the olfactory-limbic complex and the neocortex is computational

We suggest that above and beyond a distinction between olfaction and vision sensory modalities, there is a more fundamental distinction between the basic wiring of the structures of the olfactory-limbic complex and the neocortex. This wiring principle discriminates basic olfactory and basic visual processing, but is not confined to them. We have already discussed that the lateral convexity of the neocortex has a cross-modal, loose egocentric topography, which arises from the alignment of the spatial up-to-down axes of the primary visual and somatomotor surfaces [90].

This cross-modal overall mapping relies on point-to-point mapping of each modality separately. For vision, neighboring areas in the visual field represent neighboring areas in the retina, and so forth in the thalamus and cortex. For somesthesis, the same is true for the relationship between the skin surface and their neural representations, and more generally for peripheral musculature, as the sensory and motor homunculi of the cortex testify. The mapping principle that characterizes the entire neocortex is not egocentric topographic mapping, however, but is the maintenance of nearest neighbor relationships of the sensory surface as they project via thalamus into the cortex, in the motor areas it projects to, and in the connections between cortical areas. This clarifying distinction may be understood by considering the cortical representation of audition. In the case of audition, the transduction process of the cochlea produces a tonotopic map of sound, where nearest neighbors on the cochlea represent close frequencies, but nothing about the external location of the sound in egocentric space. The primary auditory cortex represents this tonotopic map. No separate map of auditory space is to be found in the cortex, though appropriate spatial auditory responses appear in the multisensory neurons of egocentric parietal cortex [170]). Other cortical areas of the temporal cortex have reduced or absent egocentric maps—for example, the relative lack of topographic order in gustatory and visceral representations in the insula. In “face” or “scene” areas, detailed nearest-neighbor order of scenes and faces is preserved, with only the preference for an upright position in both cases showing egocentricity. In the hierarchical, back-to-front convergence of information between cortical areas across the entire neocortex, the “grain” of the nearest-neighbor array-to-array mapping, whether representing spatial location or any other dimension, grows larger, but the organization principle is maintained [90].

That nearest-neighbor topography characterizes the neocortex has been known for some time, but that the olfactory cortices and hippocampus share a different organizing principle has been clarified more recently, particularly as the understanding of olfactory coding has progressed. In both of these structures, their input does not preserve nearest-neighbor relationships in the connections of the input array to the target array. Connectivity is diffuse and correlated information in the input is recognized by temporal co-occurrence [198]. This might be the simultaneous activation of receptors distributed across the olfactory bulb identifying an odorant [199,200], or the simultaneous, sensory, motor, motivational and visceral activations that specify either a scene or event in the hippocampus [201]. Sequences can be assembled to specify an item, as in homing in on an identifiable complex odorant via a concentration gradient [198], or connecting consecutive scenes to construct allocentric space or an autobiographical memory. Finally, a strikingly similar non-cohabitation rule for hippocampus and cortex, completely independent of sensory modalities, was proposed in McClelland, McNaughton and O’Reilly’s classic paper (1995) [202] to prevent catastrophic overwriting of long-term memory.

The connectivity rules for axons are also distinct in development for these structures, which suggests that it may be impossible or perhaps simply inefficient for neurons to attempt to organize themselves on different Hebbian grouping rules simultaneously, one spatial, one temporal. For early vision, reliance on nearest-spatial-neighbor correlations is optimal for data sparsification of the visual world, for both features of reducing redundancies in representation and identifying useful conjunctions [203]. Similar analyses have rarely been done for olfaction and allocentric spatial memory. Considerations of how the transition from an aquatic to a terrestrial environment might alter olfactory processing have been offered that reflect some of these ideas [204]. A more recent claim is that the hippocampus’ computational role is the creation of task-specific low-dimensional manifolds that contain a geometric representation of learned knowledge through sequences of hippocampal cell activations [205].

Whether the mature derivatives of the medial pallium and hypothetical dorsal pallium in fish have the same general properties in axonal projections and integration principles seen in mammals is yet to be determined, but it seems reasonably certain that the set of modalities represented in the mammalian cortex do not claim a sequestered space in the aquatic forebrain [179,180,206]. For the purposes of this paper, the central point is that consideration of the information available in aquatic versus terrestrial ecologies produces more powerful insights for the evolution of computational processes in the brain than whether a species is more "olfactory" or "visual". Perhaps, the immense computational necessities of registration of spatial reference frames and integration of limbs for egocentric operations in the water-to-land transition pressed the minimal sensory segregation seen in teleosts toward the computational independence seen in mammals.

## 6. The variable terrestrial body, contextualized decisions and predictions

So far, following the demonstrations of the richness of the terrestrial visual ecology for guiding behavior, the computational necessities of the new structures gathering this information, and the comparable problems of new limbs and other end-organs were described. To begin, this information integration was related to the fundamental approach/avoid decision structure of the midbrain, but it is clear that the machinery of decision-making is also quite altered in the terrestrial world, allowing more planning and prediction [5,26]. The optic tectum is more a reactive than a predictive device for egocentric operations, in keeping with the visual affordances of the marine world described in the section on neuroecology. The changed forebrain apparatus for motor decisions in the terrestrial world maintains a similar relationship to the conserved dopaminergic evaluative circuitry of the basal forebrain and diencephalon that the midbrain maintains [163,207]. The frontal and prefrontal cortex, now focusing on mammals, embed decisions in several extended contexts, all with a similar looped organization, which we will sketch briefly.

Motor commands from the motor cortex, itself embedded in a hierarchical cortical structure of prefrontal cortex which also increases in size disproportionately with brain size [208], encompassing larger and larger time windows, go directly to effectors of all kinds, including motor neurons directly, and secondary and tertiary motor regions of the midbrain and medulla. These commands are also accompanied by corollary discharge of four different kinds, all of which can return modification or cancellation of the intended acts through the thalamus, thus looped back to the motor cortices [183]. The first is corollary discharge to the basal ganglia, where its history of reinforcement success, including its habit status, may be modified by the current context, as represented by the array-to-array mapping of neocortex to the basal ganglia, and canceled or delayed via a thalamic loop [184,209–211]. Second, the current state of the body and all its relevant sensory systems are represented to the motor and premotor cortex directly through the hierarchical ascending projections of the neocortex [212], as well as the route via the basal ganglia. This loop updates the intended results of the motion for sensory surfaces and limb positions as well. Third, the cerebellum in mammals has been repurposed from its marine role in sensory predictions, such as filtering the effects of water turbulence caused by respiration through gills on the body surface [213] and calibrating the effects of unexpected vestibular challenges on upcoming visual and somatosensory input [214]. Massive input from the motor and premotor cortex, and in fact most of the cortex, via the pons and deep cerebellar nuclei, registers the proposed movement and corrects it for the altered load of variable limb positions, and the body state (for example, fatigue, damage or pain) [215]. These computed updates are conveyed back to the motor thalamus via an entirely new tract in mammals, the superior cerebellar peduncle. Finally, the hippocampus receives a processed version of the ongoing cortical state via the entorhinal cortex, as part of the recording of successive scenes generating an autobiographical timeline, and linking successive scenes to generate an allocentric space, or generate a trajectory of a planned movement through a previously generated space [183,201,216]. The word "context" hardly does this wealth of information justice, and it is important to remember the range it can cover from the smallest to the largest brains. Action plans can range from the simple execution and contextual endorsement of an ingrained habit (enter this burrow, where it will be dark), to actions evaluated probabilistically for outcome values in extended frames (will hitting the policeman with a flagpole be effective to clear a path up the stairs, in light of the decline and fall of the Roman Empire?).

While we can clearly identify the simple end of these action control possibilities in all animals, it seems that the more complex control possibilities—namely using a predictive model to plan a future trajectory and enact it—while present in at least some mammals and birds, is rare among aquatic animals excepting land mammals that have returned to an aquatic existence. Perhaps, then, the ecological water to land transition included a cognitive "habit to plan" transition in possible ways to control behavior. We will examine this hypothesis next.

## 7. A habit to plan transition

Planning involves some form of imagining of future state and evaluation prior to behavioral execution [26]. If it occurs at all in aquatic animals—other than former land animals like dolphins and whales—it seems to be less common than among the two radiations of land vertebrates this review has focused on, mammals and birds [5]. Can any of the previously discussed neuroecological or brain evolution changes provide insight into this apparent disparity? In water, the short range of most interactions means that the previously discussed fast and stereotyped action selection mechanisms of the tectum are favored [217–219]. On land, computational results suggest that spatial planning is advantaged in a certain type of terrestrial habitat, one where clusters of sight line-blocking vegetation (conferring places for hiding and stealth) are separated by large open areas (conferring detection of distant opportunities and the time to plan to attain them) [5]. As we will describe, planning enables zero-shot learning where animals can effectively learn from hypothetical experience prior to enacting one of the multiple futures considered [220]. While planning provides strategic choice between a set of rewards, where it has the largest impact is when irreversible outcomes are present among choices, such as choices made in escaping from a predator [5,221].

### (a) Under water vs above water decision making

As described earlier, fish see one to several body lengths ahead [2,10]. Upon sensing a predator, a rapid escape maneuver occurs, often aided by a ten millisecond reduction in the delay between detection of an attack and initiation of an escape through activation of a giant command neuron called the Mauthner cell found in aquatic vertebrates [218,219,222] (figure 7*a*). An example is the ambush predation of larval zebrafish by dragonfly nymphs, which use a hydraulically-powered grasping appendage (mask) to capture prey ( [219], figure 7*b*). Experiments show that a gap of only 15 milliseconds in the arrival time of the predator separates a high likelihood of survival from a low likelihood [219]. Theory and modeling indicate that a key abstraction that predicts outcome is the "motor volume," defined as where the predator or prey can reach over a specified duration given any feasible input to its musculoskeletal system [219] (figure 7*c*). If the motor volume of the predator largely encompasses that of the prey over the time period from initiation of attack until the predator reaches the prey, then the chance of survival is low (figure 7*d*), while if it only intersects a small portion of the motor volume of the prey, survival is probable [219]. One way for the overlap to be low is if the sensory volume of the prey—the volume within which the prey senses the predator—is large enough to provide for more time to initiate escape. Another is for the prey to initiate movement sooner after detecting the predator by decreasing neural processing delays. This is the strategy of activating the Mauthner cell. Escape for the fish, either way, is a decision under temporal duress. Delays on the order of conduction times of signals along neurons make the difference between survival and death. Clearly, there is no time for planning, and when there is no time for planning there is reliance on habits [24,25].

As detailed in the section on light above, the situation is entirely different for behavior on land, since in some situations at least a predator can be sensed with more time until capture (figure 7*e*). To test the intuition that planning can be more advantaged in such a scenario, a prior study examined how escape from a stalking predator is affected by a host of factors [5]. These

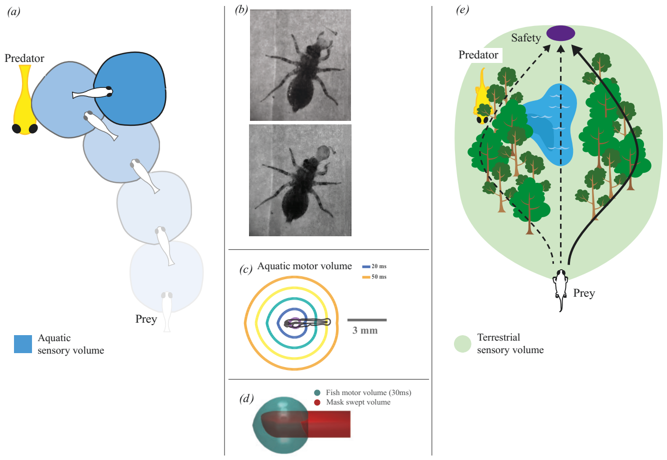

**Figure 7.** Variation in sensory and motor volume overlap during predator-prey interactions in water and in air. *(a)* The aquatic visual sensory volume is small, and the fish sees the predator just in time to attempt an escape maneuver. *(b)* Snapshots of an aquatic dragonfly nymph attacking a larval zebrafish (4 mm long) by rapidly extending its prehensile mask. *(c)* Side view of several isochrones of the estimated motor volume of the fish—showing where its center of mass can reach at the corresponding time given maximal activation of the body musculature. *(d)* The 30 ms motor volume of the fish (blue) is shown against the swept volume of the prehensile mask seen in *(b)* (red). In this example where the mask has reached the fish in 30 ms, as much of the fish's motor volume at 30 ms is within the mask's 30 ms motor volume, the probability of survival is low. *(e)* On land, the sensory volume is a million-fold larger due to the ≈100x increase in visual range. Several future trajectories to a safety point can be inspected while hiding from a predator: one (far left) going too near the predator, one (middle) requiring a risky swim through a water body, and one (far right) that avoids being revealed by stalking along a line of vegetation. The prey gets to safety by skirting both the sensory volume of the predator, and the predator's near-term motor volume. Panels *(a)* and *(e)* from [5]; panel *(b)* unpublished images from MacIver, panels *(c)*–*(d)* from [219].

include how densely cluttered the environment was, the range at which a predator was detected, and whether the prey was using habits or planning. In the planning condition, the study varied the amount of planning the prey was allowed to do before taking action. The predator in these computational experiments was controlled through a simple reactive policy: if the prey is in view, pursue it until captured (details: [5]).

The study found that in the condition designed to represent the aquatic scenario (open space, short sensing range), planning conferred no advantage over habits. In the land condition (space with barriers to vision, extended sensing range), planning led to higher survival rates on land compared to habits, but not in all terrestrial conditions (figure 8). In conditions where there were few barriers to vision (similar to an open plain), results matched the aquatic condition: no advantage to planning, despite the much higher range to detect predators. In conditions where there were many barriers (similar to a rain forest), again there was no advantage to planning—a high density of barriers is just like having the short visual range present in the aquatic scenario. In between these two regions there is an intermediate level of openness, with lacunarity values comparable to savannah habitats—figure 3—in which there is clusters of vegetation interspersed with open areas. If we look at the expected value function, which discloses the expected reward to the prey as different paths are considered during the planning process, a unique feature of the interaction between sensing range, occlusions, and moving prey and predator is high variability of the expected reward over time. This corresponds to the high variability of successful paths through the space (figure 8*b*). In this region, using habits fails to be adaptive because these are learned previously and—without radically intractable compute times due to the combinatorial growth of possibilities—have to be poorly matched to the volatile environment.

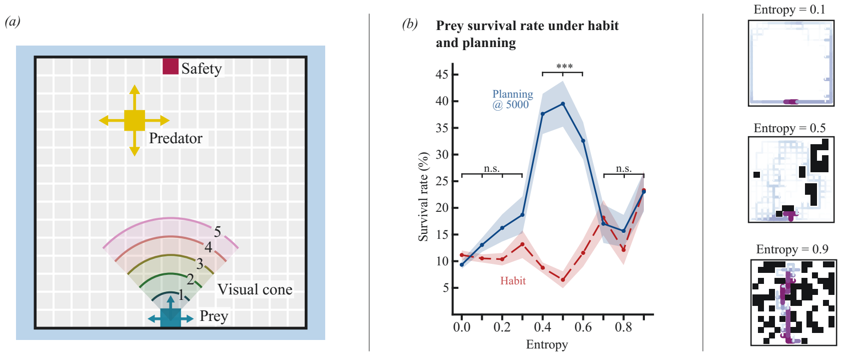

**Figure 8.** *(a)* Predator-prey simulations were performed in which the prey needed to reach the safety point without capture (details: [5]). These occurred in a grid world as the prey's action selection method varied between habit and planning (the faster predator was always under a reactive controller to chase prey when seen, and search when not), visual range varied from short to unlimited, and obstacle density as quantified by entropy (black squares in panel b) varied from zero to high. *(b)* Mid-entropy environments had the highest survival rates at the maximal degree of planning simulated. Low- and high-entropy environments performed no better under plan-based action selection than habit-based. On the right, occupancy frequency heat maps show that successful paths were stereotyped for low entropy and high entropy. In mid entropy there was a high diversity of successful paths. Modified from [5].

In savanna-like habitats, the paths taken by prey suggest the use of occlusions to deceive the predator. Video 1 and Video 2 of the electronic supplementary materials show how, as the amount of planning that the prey performs increases from a baseline to 100 times the baseline, so too does 1) its margin of safety from being captured and 2) its use of tactics like waiting behind occlusions in critical spots where moving forward would have disclosed its position to the predator (the "battle of waits" [223]).

These results suggest that the selective benefit for planning underwater may be low, which is not to say that once it has evolved on land in big-brained and warm-blooded animals, it may be maintained for its advantages as appears to be true in dolphins and whales. This may be through the creation of ephemeral structures within the open space of water over which planning can work—mud rings, bubble nets and so on, as mentioned above [27]. As detailed elsewhere, however, planning is a complex process which requires considerable computation with current models [5]. While these models may not be representative of the way brains actually do planning, all models thus far posited are far more intensive to compute than retrieval of previously learned or innate habits [5].

## (b) Planning as high efficiency virtualized learning

While the simulation results indicate that planning can increase survival rate, it is also costly in terms of time and computation. How can we understand this trade off space? Modeling work in reinforcement learning can provide insights. In this domain, planning is called a model-based method, since a model of action-outcome relationships is needed, whereas learning a strategy for subsequent reuse, called a habit above, is termed a model-free method [224].

The artificial intelligence (AI) called AlphaGo is a primarily model-free method that required the equivalent of 7.8 million matches from human games and self-play to beat the world champion of Go, Lee Sedol, by 4 games to 1 [225]. Even if Sedol had played 3 games every day of his 36 years alive, 7.8 million games would require 200 lifetimes. The power differential is even larger, with 20 watts needed for Lee's brain versus 1,000,000 watts estimated for AlphaGo. The gap between the number of trials that machines require compared to animals is called the "sample efficiency" problem of reinforcement learning methods. The space of learnable strategies is enormous, and model-free methods are searching and sampling from this space, but seemingly not as efficiently as brains can.

The current champion of the series of AIs that started with AlphaGo is MuZero [226], which combines elements of planning with the model-free reinforcement methods used in AlphaGo. An analysis of why planning helps for this AI suggests that planning improves the sample efficiency of learning [227], as also suggested by earlier work [228]. The use of the word "learning" in this context can be confusing, since the learning typically denotes changes arising from experience [229]. In this case, learning denotes a virtualized analog that precedes action in the world: there is no experience happening in the world, simply the same internal search and simulation process that is core to all current models of planning [26]. For example, in thinking through a map to work, you might think of a new method to go home you had never thought of before—or you could say you learned a new way home, even though all you were doing was forward simulating and searching your internal representations. The alternative in a model-free context might be to try all possible paths home (in the physical world), an extremely large number of paths, leading to the low sampling efficiency problem and therefore very slow learning. The planning mechanism, however, has ways of cutting through the massive possible solution space to consider only a few paths with higher likelihoods of being a useful shortcut. One way our planning system may do that is by focusing on regions where there are transitions from open space to closed space (meaning near occlusions, good to move to for hiding), or closed space to open space (good to get to for rapid movement or intentionally disclosing position to the adversary) [5]. Transitions in the connectedness of space can be easily computed given enough visual range. In non-spatial planning problems such as who you should groom next in a troop of primates, such transitions translate to changes in the degree of connectedness of nodes of a network representation of social/kinship relations [230] rather than literal space.

## 8. Future Directions and Conclusion

### (a) Lacunae in knowledge: Small and large, transitory and persisting

A paper such as this, covering a wide range of disparate topics, will directly reveal where information is lacking, at many levels. First, there are gaps immediately pertinent to the paper, such as any holes in the authors' own knowledge, particularly those that interfere with proper understanding and resolution of controversies, or gaps in empirical knowledge that require assumptions or speculations at key points in an evolutionary argument. Second, a state that will be familiar to any researcher assembling a database or meta-analysis, the coverage of knowledge that is assumed to be well-known is often dismayingly overestimated, often accompanied by the absence of key details that would allow large databases to be integrated. Finally, only data that can be gathered is gathered—analysis of the single-unit neurophysiology at global navigation decision points in great white sharks is far off. Less dramatically, for anything other than gross morphology or large-scale behavior patterns, the generally smaller, more tractable and cheaper lab animals overwhelm the available information, from demonstration of gene and gene-product expression, to electrophysiology, to analytical approaches to behavior. These animals are far from a fair sample of existing taxa, emphasizing the small-brained, the predated-upon and the promiscuous. All of these influence the fundamental inferential problem of constructing the process of evolution from forever-incomplete knowledge.

One assumption, perhaps best characterized as a studied agnosticism, should be laid out. In the case of tracing the homologies of whole brain structures, from the first vertebrates, through the branches of their aquatic descendants, to their terrestrial descendants, conclusions vary considerably. One end of the range is defined by the claim of close conservation of all major brain components from the earliest lampreys to all extant vertebrates [207,231,232]. For two sister groups of the three-branch aquatic radiation, cartilaginous and ray-finned fishes (the remaining lobe-finned fishes making the transition to land), there is general consensus on the conservation and predictable scaling of major brain components [77,94], with a variety of views on the best characterization of the forebrain. Principal forebrain issues for these two groups are its relative domination by olfaction compared to multisensory integration and to what extent the embryonic dorsal pallium of the forebrain gives rise to connectivity or internal structure shared across vertebrates, or has specific features shared with the neocortex in mammals [233]. Variability from a tissue dominated by olfaction to integrative multisensory, dependent on niche, is emphasized for chondrichthyans (sharks and rays) [178,234]. A general absence of conserved structure in the pallial aspect of the forebrain of teleosts is claimed, the most species-numerous of the radiations [6], though not without controversy [179,180]. Differences arise from the information sources individual researchers view as most critical, which range from whole-brain morphology, connectional architecture, identification of regional identity via genomic and other neurochemical identification [194,235], and whether the whole brain or the forebrain is the subject of the most scrutiny. For birds versus mammals a comparable controversy has persisted for decades about the homologies of forebrain regions [236,237]. In both cases, we have avoided any argument about the emergence of land vertebrates that depends on the connectional and functional anatomy of an identified forebrain neuron class, with the limited exceptions of the assumption of conservation of the basal ganglia/nucleus accumbens reinforcement circuitry, which appears to have reasonable acceptance, and the medial pallium, the hippocampus in adult mammals, which is persistently identified with multimodal spatial and learning functions when investigated.

At this point we should firmly acknowledge a deficiency in our reportage of empirical information about the water to-land transition, the result of a lack of behavioral work combined with neurophysiology in reptiles in most of their diverse radiations (but see [238]). Recall that salamanders, lizards, and crocodilians retain their sprawling posture, sparing themselves some of the problems of degrees of freedom in multi-jointed limbs and postural control, which might provide an avenue to understand where in the brain the first new control paths might have been established [69,70]. Particularly in visuomotor systems, behavior and many neurophysiological mechanisms can be compared with reasonable certainty across teleosts, amphibians, birds, and small and large mammals, but possible transitional states of the smaller-brained reptile ectotherm are missing from our discussion. The large predators who are ectotherms, from great white sharks to Komodo dragons [239,240], are especially interesting. The necessity to leap from information sources about teleost organization to primates and birds might produce the impression that there was, or that the authors of this paper believe there was a massive, stepwise increase in complexity of eyes, limbs and brains when vertebrates first stepped on land. Foremost, examining what visuomotor integration problems the various reptile taxa faced, and what forebrain brain regions were brought in would be exceptionally useful. Using available information in a neuroecological light might be useful in finding continutity in visuomotor evolution—that is, by viewing the small nocturnal rodent or shrew as a fish, with similar strong limitations on the visual information they can use. Target acquisition in mice is primarily done by head/body orientation, though there are some eye movements. Their compact head and limb structure (contrast ungulates, or diurnal carnivores) may allow adequate remapping within the fixed tectal structure, and in fact, the midbrain tectum remains comparatively large in this group.

Finally, the general availability of comparative information should be noted. With the proliferation of corpora of genetic, morphological and neurochemical descriptions of model systems "from fish to man", including the exhaustive cataloguing of every connection and cell class in the mouse basal ganglia, or mammalian motor cortex [241,242], and the expansion of the number of databases of brain anatomy, from the Digital Fish Library (http://www.digitalfishlibrary.org), to primate databases that have more than doubled in species covered [78], readers not in these fields might be forgiven for assuming that more is known than there is. Integration of databases in different domains is often possible only at the juncture of the crudest measurement in each. As behavioral ecology was finding its feet, while comparative psychology began restricting itself to the laboratory, an attempt was made to begin building "ethograms", behavioral inventories which ran afoul of disagreement about behavioral taxonomies, e.g. whether small amplitude, rapid forward motion in fish, body-inflated, should have the additional interpretive descriptor of "territorial defense". Meanwhile, a reasonably substantial literature in behavior has grown in several fields separately, which, at least according to citation patterns, appears to be opaque or unusable to each other [243]. Some potential ways forward are appealing, for example, the generation of basic movement taxonomies by AI categorization of unrestrained, if not fully "natural" behavior [244], or attempts to match behavioral innovations to genetic alterations in closely related species [245]. Additionally, the ability to compare new or conserved genetic mechanisms in neuronal morphologies or other cell biology with new or conserved computational or behavioral phenotypes is particularly exciting [246].

### (b) Potential computational models for changed behavior at the water-land transition, particularly foraging and predator avoidance

This article has attempted to lay out the differences in the amount and layout of information, visual information in particular, between air and water. This limitation, a limitation of both information availability and pages, will hopefully be resolved in due course, particularly in the olfactory domain. A second factor that emerged was the importance of sub-habitats in vision, where and when animals chance the unobstructed sightlines of their predators. The reverse transition from land to water, as seen in multiple marine mammals is a very interesting source of information about alteration of paths of evolution depending on the initial state of an animal's nervous system on entering new environments. Large mammals are literally the most visible, but there is a substantial cohort of marine "rodents" that is largely unstudied (the exact classification of many small mammals remains in flux) [162]. Since for mammals breathing to smell underwater would result in drowning, olfaction is sacrificed to respiration in this group [103]. Vision must lose dominance, while echolocation arises numerous times, though rather little is known about the neural substrates of marine mammal echolocation. The ability for dexterous manipulation is often lost in favor of streamlining, even though the ability to stow such useful appendages during rapid motion would not appear to require extensive modification of either, as various otters testify.

The stabilization of the push-pull relationship of the embryonic separation and adult contrast of computational abilities in the neocortex versus the olfactory-hippocampal system described here clearly requires much more scrutiny. We have advanced the hypothesis that the embryonic and early developmental establishment of both systems—neocortex requiring rough simultaneity in physically-neighboring neurons to reach its basic structure of iterated egocentric or other topographic maps, and the olfactory-hippocampal system requiring more precise simultaneity to connect distributed neurons together—is the reason they are sequestered from each other in large degree in early development [247]. Further, we argued that the grouping of olfactory bulb and olfactory cortex, and hippocampus together was one of computational similarity, not of "subject"—odorant in the first case, event in the other.

At least in Chondrichthyes, adaptive variation in olfaction versus visual dependence is plain, though assessing the variation in the derivatives of medial pallium in the adult is not yet possible. This variation is amplified in the relative development of both systems in avian and in mammalian brains, now including hippocampus and associated limbic cortices along with olfactory structures. The variation is so pronounced, as in the extent of the hippocampus of the armadillo in figure 5, that it seems entirely possible that completely different strategies for common needs might have developed independently. For example, a nocturnal olfactory specialist might develop a fully-memorized allocentric environmental representation for avoidance of and escape from predators and for foraging, while a neocortex-dependent animal might use the cued-array map described earlier, augmented by sequence information contributed by its hippocampal formation. The fact that the largest mammalian predators in our sample have the largest, and most symmetric representation of both subcomponents is highly interesting. Balanced or asymmetric, the information sources of these two anatomical entities must be integrated in some way, and the nature of information integration in intervening structures in the animals with the most distinct lifestyle and structural differences, for example, entorhinal cortex or the amygdala, would be very informative about how such information-integration problems are solved in evolutionary time.

## (c) Prediction and planning

The burgeoning of interest in predictive coding as a ubiquitous process in neural computation has immediate relevance for how to view the evolutionary account of the emergence of planning as a useful component of the behavior of relevant land vertebrates. “Predictive coding” is presently the catch-all term for any use of memory (genetic or computed) to inform or supplement a present sensory or motor representation, or predict the sensory, motor or value consequences of decisions on limited data in any realm. The range of potential examples is wide: lateral inhibition predicts that neighboring neurons in topographic maps will be correlated, reducing the cost of duplication of correlated information [248]; prediction “fills in” scotomata or areas of reduced sensory input such as the visual periphery with their probable contents [249]; in fish, the cerebellum discounts the expected effects of turbulence of gill respiration on somatosensory input. Earlier, we described the necessity of integrating the sensory consequences of a whole body, sensory surface or limb movement, as well as its motor consequences, but might better have described it as a component of prediction, used to generate an intended body position as the stage for the next movement. Investigation of the prevalence of predictive coding by brain size or by taxon is minimal as yet, though it is widely assumed that the amount and duration of memory will be related to brain size [250]. The present paper marks one first foray into the environmental affordances of planning, and the costs of its computation in an evolutionary framework.

The feed-forward, feed-back circuit of the mammalian motor and premotor cortex through the basal ganglia returning via the thalamus to the original generator is the computational structure most relevant to the planning described in this paper, though at this point a healthy agnosticism should be retained about where and how similar circuitry might emerge. Motor commands are usually conceived in this circuit as one-shots, stop/go, left/right, where the motor command is fitted with its immediate sensory context, event sequences or other hippocampal contexts in which it is embedded, and evaluated for success or reinforcement expectations by the history of such actions in the basal ganglia. By virtue of downstream or recurrent projections to the thalamus, the action may thereby be aborted, modified or executed, and in time elevated to habit [184,209]. “Hierarchical reinforcement learning” may introduce levels of execution to such a command, which may integrate sequences. “Planning” as discussed in this paper involves computation of the virtual consequences of any one, or a set of independent decisions, extending in a branching tree-like fashion to several expected outcomes. We suggested, with minimal elaboration, that the combinatorial procedure used to compute an egocentric location, or a limb position as described by Andersen, Colby and colleagues previously—if reimagined as decision consequences strung out over time—might support sequential planning. Many other solutions are possible, of course, even likely—hybrid decisions involving multiple structures and decision classes for example [251].

We briefly mentioned the interesting clue from follow ups on the success of the latest offspring of AlphaGo, MuZero, on why adding model-based planning can lead to efficiencies in learning compared to model-free reinforcement learning with massive training. Planning may act to prune an infinite range of possible sequences into the future into a more informative set for efficient learning, particularly useful in volatile environments where the shelf life of canned solutions is short. But why is it enriched in some animals and less so in others? We have hypothesized that a certain structure of partial information, provided by savanna-like habitats similar to those invaded by the first hominins [5], maximizes its value. But there is likely more to it. One idea that may merit examination has to do with more and less costly ways for a species to sample the adaptive landscape that is continuously evolving at all timescales. These sample methods are essentially the r and K reproductive strategies. The r strategy of many samples with low investment is like a Monte Carlo simulation, while the K strategy of fewer samples with more investment calls for more robust decision making. Indeed bigger brained animals live longer [80], with fewer offspring and larger parental investment. As detailed above, the biomass of land is two orders of magnitude higher than that of the oceans, making the aquatic context harder to support an energy intensive investment in bigger brains or longer parental period. But even for terrestrial ectotherms that have access to this bounty, it is seemingly harder to attain without the energy intensive lifestyle of birds and mammals, with the latter expending an order of magnitude more energy per day than terrestrial ectotherms [70]. So far, we have discussed predation and escape as our principle examples of planning, but a further consideration of large mammals, above and below water, suggests a larger context for it. Where planning may be most useful is for those organisms whose own energy investment and that of their parents means death is especially costly, and successful decision-making around possibly mortal outcomes becomes key.

In the prior paragraph, we pointed at interesting research in AI demonstrating the gains that can be made in solving learning and performance in games by adding aspects of model-based planning, but with the important qualification of its usefulness in volatile environments where learning times are short. This interaction of learning style with environmental affordances is central to a neuroecological approach. In current cognitive science, a similar interaction of computational tools and a learning/action environment is emerging. For example, the capacity of working memory, as a property of the computing power of an individual, is often laid out as a fundamental constraint on the nature of possible communication systems, motor capacities and so forth. In human language, Christiansen and Chater [252] have argued that 3–4 sequential units of speech must be chunked into a lexical or semantic decision. This amounts to a “now-or-never bottleneck” for human language comprehension, arising from an interaction of memory constraints over a limited time window with the possible speed of language comprehension. They have argued that language itself evolves to match this computing constraint of the human nervous system. Another aspect to this limit of four items in working memory has now been suggested, that it is an optimization of the number of steps into the future that provide useful results prior to combinatorial explosion [253]. In both cases, the ecology, language or landscape, together with the computing device generate the required computation.

**Data Accessibility.** All data available in cited literature.

**Authors’ Contributions.** M.A.M. and B.L.F. wrote the manuscript.

**Competing Interests.** We declare we have no competing interests

**Funding.** M.A.M. was supported by the NSF Brain Initiative under ECCS-1835389 and NSF IIS-2123725.

**Acknowledgements.** We thank Daniel I. Goldman for helpful discussions.

## References

1. Bar-On YM, Phillips R, Milo R. 2018 The biomass distribution on Earth. *Proceedings of the National Academy of Sciences* **115**, 6506–6511. Publisher: National Academy of Sciences Section: Biological Sciences.
2. MacIver MA, Schmitz L, Mugan U, Murphey TD, Mobley CD. 2017 Massive increase in visual range preceded the origin of terrestrial vertebrates. *Proc. Natl. Acad. Sci. U.S.A* **114**, E2375–E2384.
3. Yu Y, Karbowski J, Sachdev RN, Feng J. 2014 Effect of temperature and glia in brain size enlargement and origin of allometric body-brain size scaling in vertebrates. *BMC Evol. Bio* **14**, 178.
4. Vermeij GJ. 2017 How the land became the locus of major evolutionary innovations. *Current Biology* **27**, 3178–3182.
5. Mugan U, MacIver MA. 2020 Spatial planning with long visual range benefits escape from visual predators in complex naturalistic environments. *Nature Communications* **11**, 3057. Number: 1 Publisher: Nature Publishing Group.
6. Striedter GF, Northcutt RG. 2020 *Brains through time: a natural history of vertebrates*. Oxford University Press. OCLC: 1162849672.
7. Rossi GS, Wright PA. 2021 Does leaving water make fish smarter? Terrestrial exposure and exercise improve spatial learning in an amphibious fish. *Proceedings. Biological Sciences* **288**,

20210603.

8. Li C, Zhang T, Goldman DI. 2013 A Terradynamics of Legged Locomotion on Granular Media. *Science* **339**, 1408–1412. Publisher: American Association for the Advancement of Science _eprint: https://science.sciencemag.org/content/339/6126/1408.full.pdf.
9. Mazouchova N, Umbanhowar PB, Goldman DI. 2013 Flipper-driven terrestrial locomotion of a sea turtle-inspired robot. *Bioinspiration & Biomimetics* **8**, 026007. Publisher: IOP Publishing.
10. Nilsson DE, Warrant E, Johnsen S. 2014 Computational visual ecology in the pelagic realm. *Phil. Trans. R. Soc. B* **369**.
11. Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. 2014 *Visual ecology*. Princeton, N.J.: Princeton University Press.
12. Denny MW, American Society of Zoologists, Meeting. 1993 *Air and water: the biology and physics of life's media*. Princeton, N.J.: Princeton University Press. OCLC: 26094823.
13. Mobley CD. 1995 The Optical Properties of Water. In Bass M, editor, *Handbook of optics* vol. 1 pp. 43.3–43.56. New York: McGraw-Hill 2nd edition.
14. Johnsen S, Widder EA, Mobley CD. 2004 Propagation and Perception of Bioluminescence: Factors Affecting Counterillumination as a Cryptic Strategy. *The Biological Bulletin* **207**, 1–16.
15. Davies-Colley RJ, Nagels JW. 2008 Predicting light penetration into river waters. *Journal of Geophysical Research: Biogeosciences* **113**, 1–9.
16. Davies-Colley RJ. 1988 Measuring water clarity with a black disk. *Limnology and Oceanography* **33**, 616–623.
17. Koenings J, Edmundson J. 1991 Secchi disk and photometer estimates of light regimes in Alaskan lakes: Effects of yellow color and turbidity. *Limnology and Oceanography* **36**, 91–105.
18. Killinger D, Churnside J, Rothman L. 1995 Atmospheric Optics. In Bass M, of America. OS, editors, *Handbook of optics* vol. 1 pp. 44.1–44.49. New York: McGraw-Hill 2nd edition.
19. Middleton WEK. 1952 *Vision through the atmosphere*. Toronto: University of Toronto Press.
20. McFarlan D. 1991 *Guinness Book of World Records*. New York, New York: Fact On File. OCLC: 733637579.
21. Beznosov PA, Clack JA, Lukševičs E, Ruta M, Ahlberg PE. 2019 Morphology of the earliest reconstructable tetrapod Parmastega aelidae. *Nature* **574**, 527–531. Number: 7779 Publisher: Nature Publishing Group.
22. Land MF. 2015 Eye movements of vertebrates and their relation to eye form and function. *Journal of Comparative Physiology A* **201**, 195–214.
23. Downs JP, Daeschler EB, Jenkins FA, Shubin NH. 2008 The cranial endoskeleton of Tiktaalik roseae. *Nature* **455**, 925–929. Number: 7215 Publisher: Nature Publishing Group.
24. Keramati M, Smittenaar P, Dolan RJ, Dayan P. 2016 Adaptive integration of habits into depth-limited planning defines a habitual-goal–directed spectrum. *Proc. Natl. Acad. Sci. U.S.A* **113**, 12868–12873.
25. Qi S, Hassabis D, Sun J, Guo F, Daw N, Mobbs D. 2018 How cognitive and reactive fear circuits optimize escape decisions in humans. *Proceedings of the National Academy of Sciences* **115**, 3186–3191. Publisher: National Academy of Sciences _eprint: https://www.pnas.org/content/115/12/3186.full.pdf.
26. Hunt LT, Daw ND, Kaanders P, MacIver MA, Mugan U, Procyk E, Redish AD, Russo E, Scholl J, Stachenfeld K, Wilson CRE, Kolling N. 2021 Formalizing planning and information search in naturalistic decision-making. *Nature Neuroscience* pp. 1–14. Bandiera_abtest: a Cg_type: Nature Research Journals Primary_atype: Reviews Publisher: Nature Publishing Group Subject_term: Decision;Learning algorithms;Motivation;Psychology;Reward Subject_term_id: decision;learning-algorithms;motivation;psychology;reward.
27. Haque M, Rahmani A, Egerstedt M. 2009 A Hybrid, Multi-Agent Model of Foraging Bottlenose Dolphins. *IFAC Proceedings Volumes* **42**, 262–267. 3rd IFAC Conference on Analysis and Design of Hybrid Systems.
28. Clack JA. 2012 *Gaining ground : The origin and evolution of tetrapods*. Bloomington: Indiana University Press.
29. Lemberg JB, Daeschler EB, Shubin NH. 2021 The feeding system of Tiktaalik roseae: an intermediate between suction feeding and biting. *Proceedings of the National Academy of Sciences* **118**. ISBN: 9782016421116 Publisher: National Academy of Sciences Section: Biological Sciences.
30. Graham JB, Wegner NC, Miller LA, Jew CJ, Lai NC, Berquist RM, Frank LR, Long JA. 2014 Spiracular air breathing in polypterid fishes and its implications for aerial respiration in stem tetrapods. *Nature Communications* **5**, 3022. Number: 1 Publisher: Nature Publishing Group.

31. Fröbisch NB, Witzmann F. 2019 Early tetrapods had an eye on the land. *Nature* **574**, 494–495. Number: 7779 Publisher: Nature Publishing Group.
32. Niedźwiedzki G, Szrek P, Narkiewicz K, Narkiewicz M, Ahlberg PE. 2010 Tetrapod trackways from the early Middle Devonian period of Poland. *Nature* **463**, 43–48. Number: 7277 Publisher: Nature Publishing Group.
33. Nilsson DE. 2017 Evolution: An Irresistibly Clear View of Land. *Curr. Biol.* **27**, R715–R717.
34. Astley HC, Mendelson JR, Dai J, Gong C, Chong B, Rieser JM, Schiebel PE, Sharpe SS, Hatton RL, Choset H, Goldman DI. 2020 Surprising simplicities and syntheses in limbless self-propulsion in sand. *The Journal of Experimental Biology* **223**, jeb103564.
35. Yamakita T, Miyashita T. 2014 Landscape Mosaicness in the Ocean: Its Significance for Biodiversity Patterns in Benthic Organisms and Fish. In *Integrative Observations and Assessments* Ecological Research Monographs pp. 131–148. Tokyo: Springer Japan.
36. Mather JA, Dickel L. 2017 Cephalopod complex cognition. *Curr. Opin. Behav. Sci* **16**, 131 – 137. Comparative cognition.
37. Messenger JB. 2001 Cephalopod chromatophores: neurobiology and natural history. *Biological Reviews of the Cambridge Philosophical Society* **76**, 473–528.
38. Ramirez MD, Oakley TH. 2015 Eye-independent, light-activated chromatophore expansion (LACE) and expression of phototransduction genes in the skin of Octopus bimaculoides. *J. Exp. Biol.* **218**, 1513–1520.
39. Kingston ACN, Kuzirian AM, Hanlon RT, Cronin TW. 2015 Visual phototransduction components in cephalopod chromatophores suggest dermal photoreception. *J. Exp. Biol.* **218**, 1596–1602.
40. Brown C, Garwood MP, Williamson JE. 2012 It pays to cheat: tactical deception in a cephalopod social signalling system. *Biol. Letters* **8**, 729–732.
41. Hanlon RT, Messenger JB. 2018 Cephalopod behaviour. .
42. Brown JH, Hall CAS, Sibly RM. 2018 Equal fitness paradigm explained by a trade-off between generation time and energy production rate. *Nature Ecology & Evolution* **2**, 262–268. Number: 2 Publisher: Nature Publishing Group.
43. Barbosa P, Castellanos I. 2005 *Ecology of predator-prey interactions*. Oxford University Press.
44. King AW et al.. 1999 Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landsc. Ecol.* **14**, 73–82.
45. Plotnick RE, Gardner RH, O'Neill RV. 1993 Lacunarity indices as measures of landscape texture. *Landsc. Ecol.* **8**, 201–211.
46. Pelster B. 2009 Buoyancy Control in Aquatic Vertebrates. In Glass M, Wood S, editors, *Cardio-Respiratory Control in Vertebrates: Comparative and Evolutionary Aspects* pp. 65–98. Berlin, Heidelberg: Springer Berlin Heidelberg.
47. Harris JE. 1936 The role of the fins in the equilibrium of the swimming fish. I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchill). *J. Exp. Biol.* **13**, 476–493.
48. Snyder JB, Nelson ME, Burdick JW, MacIver MA. 2007 Omnidirectional sensory and motor volumes in an electric fish. *PLoS Biology* **5**, 2671–2683.
49. MacIver MA, Shirgaonkar AA, Patankar NA. 2010 Energy-information trade-offs between movement and sensing. *PLoS Computational Biology*.
50. Nelson ME, MacIver MA. 2006 Sensory acquisition in active sensing systems. *J. Comp. Physiol. A* **192**, 573–586.
51. Herzing DL. 2004 Social and nonsocial uses of echolocation in free-ranging *Stenella frontalis* and *Tursiops truncatus*. In Thomas JA, Moss CF, Vater M, editors, *Echolocation in Bats and Dolphins* pp. 404–410. Chicago: Univ. of Chicago Press.
52. Moore PW, Dankiewicz LA, Houser DS. 2008 Beamwidth control and angular target detection in an echolocating bottlenose dolphin (Tursiops truncatus). *The Journal of the Acoustical Society of America* **124**, 3324–3332. Publisher: Acoustical Society of America.
53. Nyakatura JA, Andrada E, Curth S, Fischer MS. 2014 Bridging "Romer's Gap": Limb Mechanics of an Extant Belly-Dragging Lizard Inform Debate on Tetrapod Locomotion During the Early Carboniferous. *Evolutionary Biology* **41**, 175–190. Place: New York Publisher: Springer WOS:000336327800001.
54. Morton SM, Bastian AJ. 2003 Relative Contributions of Balance and Voluntary Leg-Coordination Deficits to Cerebellar Gait Ataxia. *Journal of Neurophysiology* **89**, 1844–1856.
55. Ijspeert AJ. 2020 Amphibious and Sprawling Locomotion: From Biology to Robotics and Back. *Annual Review of Control, Robotics, and Autonomous Systems* **3**, 173–193. _eprint: https://doi.org/10.1146/annurev-control-091919-095731.

56. Pirker W, Katzenschlager R. 2017 Gait disorders in adults and the elderly. *Wiener Klinische Wochenschrift* **129**, 81–95.
57. Palamara G, Gotti F, Maestri R, Bera R, Gargantini R, Bossio F, Zivi I, Volpe D, Ferrazzoli D, Frazzitta G. 2017 Land Plus Aquatic Therapy Versus Land-Based Rehabilitation Alone for the Treatment of Balance Dysfunction in Parkinson Disease: A Randomized Controlled Study With 6-Month Follow-Up. *Archives of Physical Medicine and Rehabilitation* **98**, 1077–1085.
58. Dickson BV, Clack JA, Smithson TR, Pierce SE. 2021 Functional adaptive landscapes predict terrestrial capacity at the origin of limbs. *Nature* **589**, 242–245. Number: 7841 Publisher: Nature Publishing Group.
59. Molnar JL, Hutchinson JR, Diogo R, Clack JA, Pierce SE. 2021 Evolution of forelimb musculoskeletal function across the fish-to-tetrapod transition. *Science Advances* **7**, eabd7457. Publisher: American Association for the Advancement of Science Section: Research Article.
60. Kawano SM, Blob RW. 2013 Propulsive Forces of Mudskipper Fins and Salamander Limbs during Terrestrial Locomotion: Implications for the Invasion of Land. *Integrative and Comparative Biology* **53**, 283–294.
61. McInroe B, Astley HC, Gong C, Kawano SM, Schiebel PE, Rieser JM, Choset H, Blob RW, Goldman DI. 2016 Tail use improves performance on soft substrates in models of early vertebrate land locomotors. *Science* **353**, 154–158.
62. Reilly S, Elias J. 1998 Locomotion in alligator mississippiensis: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. *Journal of Experimental Biology* **201**, 2559–2574.
63. Chen JJ, Peattie AM, Autumn K, Full RJ. 2006 Differential leg function in a sprawled-posture quadrupedal trotter. *Journal of Experimental Biology* **209**, 249–259.
64. Full RJ, Kubow T, Schmitt J, Holmes P, Koditschek D. 2002 Quantifying Dynamic Stability and Maneuverability in Legged Locomotion1. *Integrative and Comparative Biology* **42**, 149–157.
65. Fischer MS, Blickhan R. 2006 The tri-segmented limbs of therian mammals: kinematics, dynamics, and self-stabilization-a review. *Journal of Experimental Zoology Part A: Comparative Experimental Biology* **305A**, 935–952.
66. Kubow TM, Full RJ. 1999 The role of the mechanical system in control: a hypothesis of self-stabilization in hexapedal runners. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **354**, 849–861. Publisher: Royal Society.
67. Full RJ, Koditschek DE. 1999 Templates and anchors: Neuromechanical hypotheses of legged locomotion on land. *J. Exp. Biol.* **202**, 3325–3332.
68. Lovegrove BG. 2017 A phenology of the evolution of endothermy in birds and mammals. *Biological Reviews* **92**, 1213–1240. Place: Hoboken Publisher: Wiley WOS:000398567200033.
69. Ryczko D, Simon A, Ijspeert AJ. 2020 Walking with Salamanders: From Molecules to Biorobotics. *Trends in Neurosciences* **43**, 916–930. Publisher: Elsevier.
70. Garland, Jr. T, Albuquerque RL. 2017 Locomotion, Energetics, Performance, and Behavior: A Mammalian Perspective on Lizards, and Vice Versa. *Integrative and Comparative Biology* **57**, 252–266.
71. Vermeij GJ. 2019 Power, competition, and the nature of history. *Paleobiology* **45**, 517–530. Publisher: The Paleontological Society.
72. Goldin MA, Mindlin GB. 2017 Temperature manipulation of neuronal dynamics in a forebrain motor control nucleus. *PLoS Comput. Biol.* **13**, e1005699.
73. Jerison H. 1973 *Evolution of the Brain and Intelligence*. New York: Academic Press.
74. Gould SJ. 1975 Allometry in primates, with emphasis on scaling and the evolution of the brain. In Szalay, editor, *Approaches to Primate Paleobiology* vol. 5 pp. 244–292. Basel: Karger.
75. Stephan H, Baron G, Frahm H. 1988 pp. 1–38. In *Comparative size of brain and brain components*, vol. 4, pp. 1–38. Alan R. Liss.
76. Street SE, Navarrete AF, Reader SM, Laland KN. 2017 Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of the National Academy of Sciences* **114**, 7908–7914.
77. Northcutt R. 1981 The evolution of the telencephalon in nonmammals. *Annual Review of Neuroscience* **4**, 301–350.
78. DeCasien AR, Williams SA, Higham JP. 2017 Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution* **1**, 0112.
79. Shumway C. 2008 Habitat complexity, brain and behavior.. *Brain, Behavior and Evolution* **72**, 123–134.

80. Gonzalez-Lagos C, Sol D, Reader SM. 2010 Large-brained mammals live longer. *Journal of Evolutionary Biology* **23**, 1064–1074.
81. Lefebvre L. 2013 Brains, innovations, tools and cultural transmission in birds, non-human primates, and fossil hominins. *Frontiers in Human Neuroscience* **7**.
82. Lefebvre L, Reader SM, Sol D. 2013 Innovating innovation rate and its relationship with brains, ecology and general intelligence. *Brain, Behavior and Evolution* **81**, 143–145.
83. MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, Aureli F, Baker JM, Bania AE, Barnard AM, Boogert NJ, Brannon EM, Bray EE, Bray J, Brent LJN, Burkart JM, Call J, Cantlon JF, Cheke LG, Clayton NS, Delgado MM, DiVincenti LJ, Fujita K, Herrmann E, Hiramatsu C, Jacobs LF, Jordan KE, Laude JR, Leimgruber KL, Messer EJE, de A. Moura AC, Ostojić L, Picard A, Platt ML, Plotnik JM, Range F, Reader SM, Reddy RB, Sandel AA, Santos LR, Schumann K, Seed AM, Sewall KB, Shaw RC, Slocombe KE, Su Y, Takimoto A, Tan J, Tao R, van Schaik CP, Virányi Z, Visalberghi E, Wade JC, Watanabe A, Widness J, Young JK, Zentall TR, Zhao Y. 2014 The evolution of self-control. *Proc. Natl. Acad. Sci. U.S.A* **111**, E2140–E2148.
84. Stevens JR. 2014 Evolutionary pressures on primate intertemporal choice. *Proceedings of the Royal Society B: Biological Sciences* **281**.
85. Andersen BB, Korbo L, Pakkenberg B. 1992 A quantitative study of the human cerebellum with unbiased stereological techniques. *Journal of Comparative Neurology* **326**, 549–560.
86. Walloe S, Pakkenberg B, Fabricius K. 2014 Stereological estimation of total cell numbers in the human cerebral and cerebellar cortex. *Frontiers in Human Neuroscience* **8**.
87. Herculano-Houzel S, Lent R. 2005 Isotropic fractionator: A simple, rapid method for the quantification of total cell and neuron numbers in the brain.. *Journal of Neuroscience*.
88. Herculano-Houzel S, Catania K, Manger PR, Kaas JH. 2015 Mammalian brains are made of these: A dataset of the numbers and densities of neuronal and nonneuronal cells in the brain of glires, primates, scandentia, eulipotyphlans, afrotherians and artiodactyls, and their relationship with body mass. *Brain, Behavior and Evolution* **86**, 145–163.
89. Markov NT, Ercsey-Ravasz M, Lamy C, Ribeiro Gomes AR, Magrou L, Misery P, Giroud P, Barone P, Dehay C, Toroczkai Z, Knoblauch K, Van Essen DC, Kennedy H. 2013 The role of long-range connections on the specificity of the macaque interareal cortical network. *Proc Natl Acad Sci U S A* **110**, 5187–92.
90. Finlay BL, Uchiyama R. 2015 Developmental mechanisms channeling cortical evolution. *Trends in Neurosciences* **38**, 69–76.
91. van Schaik CP, Triki Z, Bshary R, Heldstab S. 2021 A farewell to EQ: A new brain size measure for comparative primate cognition. *Brain, Behavior & Evolution* **In press.**
92. Smaers JB, Dechmann DKN, Goswami A, Soligo C, Safi K. 2012 Comparative analyses of evolutionary rates reveal different pathways to encephalization in bats, carnivorans, and primates. *Proceedings of the National Academy of Sciences* **109**, 18006–18011.
93. Smaers JB, Soligo C. 2013 Brain reorganization, not relative brain size, primarily characterizes anthropoid brain evolution. *Proceedings of the Royal Society B: Biological Sciences* **280**.
94. Yopak KE, Lisney TJ, Darlington RB, Collin SP, Montgomery JC, Finlay BL. 2010 A conserved pattern of brain scaling from sharks to primates. *Proceedings of the National Academy of Sciences* **107**, 12946–12951.
95. Platel R. 1976 Comparative volumetric analysis of the principal brain subdivisions in saurian repriles.. *J. Hirnforsch.* **17**, 513–517.
96. Jolicoeur P, Pirlot P, Baron G, Stephan H. 1984 Brain structure and correlation patterns in insectivora, chiroptera and primates. *Systematic Zoology* **33**, 14–29.
97. Iwaniuk A, Hurd P. 2005 The evolution of cerebrotypes in birds. *Brain, Behavior and Evolution* **65**, 215–230.
98. Charvet CJ, Darlington RB, Finlay BL. 2013 Variation in human brains may facilitate evolutionary change toward a limited range of phenotypes. *Brain, Behavior and Evolution* **81**, 74–85.
99. DeCasien AR, Higham JP. 2019 Primate mosaic brain evolution reflects selection on sensory and cognitive specialization. *Nature Ecology & Evolution* **3**, 1483–1493.
100. Stephan H, Frahm H, Baron G. 1981 New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol.* **35**, 1–29.
101. Kruska D. 1988 Mammalian domestication and its effect on brain structure and behavior. In Jerison H, Jerison I, editors, *Intelligence and Evolutionary Biology* vol. G17*NATO ASI series*. Berlin Heidelberg: Springer-Verlag.

102. Finlay B, Darlington R. 1995 Linked regularities in the development and evolution of mammalian brains. *Science* **268**, 1578–1584.

103. Reep R, Finlay B, Darlington R. 2007 The limbic system in mammalian brain evolution. *Brain Behav. Evol.* **70**, 57–70.

104. Charvet C, Finlay B. 2016 Evolving the developing cortex: conserved gradients of neurogenesis gracefully scale and channel new functions to their cortical representations in primates:. In Boughner C, Rolian C, editors, *Evolutionary Developmental Anthropology: A Postgenomic Approach to Understanding Primate and Human Evolution* pp. 231–260. New York: J. Wiley and Sons.

105. Yopak KE, Frank LR. 2009 Brain size and brain organization of the whale shark, Rhincodon typus, using magnetic resonance imaging. *Brain Behav Evol* **74**, 121–42.

106. Rupp B, Reichert H, Wullimann MF. 1996 The zebrafish brain: a neuroanatomical comparison with the goldfish. *Anatomy and embryology* **194**, 187–203.

107. Sorby-Adams AJ, Vink R, Turner RJ. 2018 Large animal models of stroke and traumatic brain injury as translational tools. *Am J Physiol Regul Integr Comp Physiol* **315**, R165–R190.

108. Suárez R, Paolino A, Kozulin P, Fenlon LR, Morcom LR, Englebright R, O'Hara PJ, Murray PJ, Richards LJ. 2017 Development of body, head and brain features in the Australian fat-tailed dunnart (Sminthopsis crassicaudata; Marsupialia: Dasyuridae); A postnatal model of forebrain formation. *PLOS ONE* **12**, e0184450.

109. Nudo R, Masteron R. 1990 Descending pathways to the spinal cord, IV: Some factors related to the amount of cortex devoted to the corticospinal tract.. *Journal of Comparative Neurology* **296**, 584–597.

110. Finlay BL, Hersman MN, Darlington RB. 1998 Patterns of vertebrate neurogenesis and the paths of vertebrate evolution. *Brain Behav Evol* **52**, 232–42.

111. Finlay B, Hinz F, R.B. D. 2011 Mapping behavioral evolution onto brain evolution: The strategic roles of conserved organization in individuals and species.. *Philosophical Transactions of the Royal Society, Series B*.

112. Catania K, Kaas J. 1995 Organization of the somatosensory cortex of the star-nosed mole. *Journal of Comparative Neurology* **351**, 549–567.

113. Krubitzer L, Huffman KJ. 2000 Arealization of the neocortex in mammals: Genetic and epigenetic contributions to the phenotype. *Brain ,Behavior and Evolution* **55**, 322–335.

114. Moore BA, Tyrrell LP, Pita D, Bininda-Emonds ORP, Fernández-Juricic E. 2017 Does retinal configuration make the head and eyes of foveate birds move?. *Scientific Reports* **7**, 38406.

115. Iwaniuk AN, Dean KM, Nelson JE. 2004 A mosaic pattern characterizes the evolution of the avian brain. *Proceedings of the Royal Society of London B* **271 Suppl 4**, S148–51.

116. Fernald RD. 2012 Social control of the brain. *Annual Review of Neuroscience* **35**, 133–151.

117. Kaslin J, Ganz J, Brand M. 2008 Proliferation, neurogenesis and regeneration in the non-mammalian vertebrate brain. *Philosophical Transactions of the Royal Society B* **363**, 101–122.

118. Hoyle G. 1984 The scope of neuroethology. *Behavioral and Brain Sciences* **7**, 367–381.

119. Capranica RR, Rose G. 1983 Frequency and Temporal Processing in the Auditory System of Anurans. In Huber F, Markl H, editors, *Neuroethology and Behavioral Physiology* pp. 136–152. Springer Berlin Heidelberg.

120. MacIver MA, Sharabash NM, Nelson ME. 2001 Prey-capture behavior in gymnotid electric fish: Motion analysis and effects of water conductivity. *J. Exp. Biol.* **204**, 543–557.

121. Suga N. 1989 Principles of auditory information-processing derived from neuroethology. *Journal of Experimental Biology* **146**, 277–286.

122. Hopkins CD. 1980 Evolution of electric communication channels of mormyrids. *Behavioral Ecology and Sociobiology* **7**, 1–13.

123. Fleishman LJ, Pallus AC. 2010 Motion perception and visual signal design in Anolis lizards. *Proceedings of the Royal Society B: Biological Sciences* **277**, 3547–3554.

124. Shettleworth S. 1990 Spatial memory in food-storing birds. *Philosophical Transactions of the Royal Society of London (B)* **329**, 143–151.

125. Nottebohm F, Stokes T, Leonard C. 1976 Central control of song in the canary, Serinus canarius. *Journal of Comparative Neurology* **165**, 457–486.

126. Vates GE, Broome BM, Mello CV, Nottebohm F. 1996 Auditory pathways of caudal telencephalon and their relation to the song system of adult male zebra finches (Taenopygia guttata). *J Comp Neurol* **366**, 613–642.

127. Chen R, Goldberg JH. 2020 Actor-critic reinforcement learning in the songbird. *Current Opinion in Neurobiology* **65**, 1–9.

128. Hofmann HA, Beery AK, Blumstein DT, Couzin ID, Earley RL, Hayes LD, Hurd PL, Lacey EA, Phelps SM, Solomon NG. 2014 An evolutionary framework for studying mechanisms of social behavior. *Trends in ecology & evolution* **29**, 581–589.
129. Ophir AG. 2017 Navigating monogamy: nonapeptide sensitivity in a memory neural circuit may shape social behavior and mating decisions. *Frontiers in Neuroscience* **11**, 397.
130. Joyce DA, Lunt DH, Genner MJ, Turner GF, Bills R, Seehausen O. 2011 Repeated colonization and hybridization in Lake Malawi cichlids. *Current Biology* **21**, R108–R109.
131. Schluter D, Marchinko KB, Barrett RDH, Rogers SM. 2010 Natural selection and the genetics of adaptation in threespine stickleback. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2479–2486.
132. Flynn EG, Laland KN, Kendal RL, Kendal JR. 2013 Developmental niche construction. *Developmental Science* **16**, 296–313.
133. Krubitzer LA, Prescott TJ. 2018 The combinatorial creature: Cortical phenotypes within and across lifetimes. *Trends in Neurosciences* **41**, 744–762.
134. Krubitzer LA, Seelke AMH. 2012 Cortical evolution in mammals: The bane and beauty of phenotypic variability. *Proceedings of the National Academy of Sciences* **109**, 10647–10654.
135. Hawkes K, Finlay BL. 2018 Mammalian brain development and our grandmothering life history. *Physiology & Behavior*.
136. Knudsen E, Brainard M. 1995 Creating a unified representation of visual and auditory space in the brain. In Cowan W, Shooter E, Stevens C, Thompson R, editors, *Annual Reviews of Neuroscience* vol. 18 pp. 19–44. Palo Alto: Annual Reviews Inc.
137. Land MF. 2019 The evolution of gaze shifting eye movements. In Hodgson T, editor, *Processes of Visuospatial Attention and Working Memory* pp. 3–11. Cham: Springer International Publishing.
138. Ben-Simon A, Ben-Shahar O, Vasserman G, Segev R. 2012 Predictive saccade in the absence of smooth pursuit: interception of moving targets in the archer fish. *Journal of Experimental Biology* **215**, 4248–4254.
139. Bianco I, Kampff A, Engert F. 2011 Prey Capture Behavior Evoked by Simple Visual Stimuli in Larval Zebrafish. *Frontiers in Systems Neuroscience* **5**, 101.
140. Patterson B, Abraham A, MacIver MA, McLean D. 2013 Visually guided gradation of prey capture movements in larval zebrafish. *The Journal of Experimental Biology* **16**, 3071–3083.
141. Basso MA, May PJ. 2017 Circuits for Action and Cognition: A View from the Superior Colliculus. *Annual Review of Vision Science* **3**, 197–226.
142. Sperry R. 1963 Chemoaffinity in the orderly growth of nerve fiber patterns and their connections. *Proceedings of the National Academy of Sciences (USA)* **50**.
143. Springer AD, Easter SS, Agranoff BW. 1977 The role of the optic tectum in various visually mediated behaviors of goldfish. *Brain Research* **128**, 393–404.
144. Finlay B, Schneps S, Schneider G. 1979 Orderly compression of the retinotectal projection following partial tectal ablation in the newborn hamster. *Nature* **280**, 153–154.
145. Northmore DPM. 2017 Holding visual attention for 400 million years: A model of tectum and torus longitudinalis in teleost fishes. *Vision Research* **131**, 44–56.
146. Jay MF, Sparks DL. 1984 Auditory receptive fields in primate superior colliculus shift with changes in eye position. *Nature* **309**.
147. Huberman AD, Niell CM. 2011 What can mice tell us about how vision works?. *Trends in Neurosciences* **34**, 464–473.
148. Büttner-Ennever JA, Horn AKE. 1997 Anatomical substrates of oculomotor control. *Current Opinion in Neurobiology* **7**, 872–879.
149. Lappi O. 2016 Eye movements in the wild: Oculomotor control, gaze behavior & frames of reference. *Neuroscience & Biobehavioral Reviews* **69**, 49–68.
150. Hodos B. 1995 The visual capabilites of birds. In Zeigler H, Bischof H, editors, *Vision, Brain and Behavior in Birds* pp. 63–76. Cambridge, Ma: MIT Press.
151. Knox PC, Donaldson I. 1995 The effect of afferent signals from extraocular muscles on visual responses of cells in the optic tectum of the pigeon. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **259**, 285–291.
152. Potier S, Mitkus M, Bonadonna F, Duriez O, Isard PF, Dulaurent T, Mentek M, Kelber A. 2017 Eye size, fovea, and foraging ecology in Accipitriform raptors. *Brain, Behavior and Evolution* **90**, 232–242.
153. Finlay B, Silveira LC, Reichenbach A. 2006 Comparative Aspects of Visual System

Development. In Kremers J, editor, *The Primate Visual System: A Comparative Approach* pp. 37–72. John Wiley and Sons.

154. Boström JE, Dimitrova M, Canton C, Håstad O, Qvarnström A, Ödeen A. 2016 Ultra-Rapid Vision in Birds. *PLOS ONE* **11**, 1–7.
155. Nilsson DE. 2009 The evolution of eyes and visually guided behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 2833–2847.
156. Rucci M, Victor JD. 2015 The unsteady eye: an information-processing stage, not a bug. *Trends Neurosci.* **38**, 195–206.
157. Brown C, Magat M. 2011 The evolution of lateralized foot use in parrots: a phylogenetic approach. *Behavioral Ecology* **22**, 1201–1208.
158. Braddick O, Atkinson J. 2011 Development of human visual function. *Vision Research* **51**, 1588–1609.
159. Johnson MH, Mareschal D. 2001 Cognitive and perceptual development during infancy. *Current Opinion in Neurobiology* **11**, 213–218.
160. Striedter G. 2005 *Principles of Brain Evolution*. New York: Sinauer.
161. Ingle DJ. 1990 Visually elicited evasive behavior in frogs. *BioScience* **40**, 284–291.
162. Finlay BL, Sengelaub DR. 1981 Toward a neuroethology of mammalian vision: ecology and anatomy of rodent visuomotor behavior. *Behavioural brain research* **3**, 133–149.
163. Merker B. 2007 Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences* **30**, 63–81.
164. Caviness, V. S. J, Frost DO. 1980 Tangential organization of thalamic projections to the neocortex in the mouse. *J Comp Neurol* **194**, 335–67.
165. Frost DO, Caviness, V. S. J. 1980 Radial organization of thalamic projections to the neocortex in the mouse. *J Comp Neurol* **194**, 369–93.
166. Butler A. 1994 The evolution of the dorsal thalamus of jawed vertebrates, including mammals - cladistic analysis and a new hypothesis. *Brain Research Reviews* **19**, 29–65.
167. Goodale MA. 2014 How (and why) the visual control of action differs from visual perception. *Proceedings of the Royal Society B: Biological Sciences* **281**.
168. Zipser D, Andersen R. 1988 A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* **331**, 679–684.
169. Stricanne B, Andersen RA, Mazzoni P. 1996 Eye-centered, head-centered, and intermediate coding of remembered sound locations in area LIP. *J Neurophysiol* **76**, 2071–2076.
170. Xing J, Andersen RA. 2000 Models of the posterior parietal cortex which perform multimodal integration and represent space in several coordinate frames. *Journal of Cognitive Neuroscience* **12**, 601–614.
171. Zhang CY, Aflalo T, Revechkis B, Rosario ER, Ouellette D, Pouratian N, Andersen RA. 2017 Partially mixed selectivity in human posterior parietal association cortex. *Neuron* **95**, 697–708.e4.
172. Colby CL, Duhamel JR. 1996 Spatial representations for action in parietal cortex. *Cognitive Brain Research* **5**, 105–115.
173. Colby CL, Duhamel J, Goldberg M. 1996 Multiple parietal representations of space. In Aertsen A, Braitenberg V, editors, *Brain Theory: Biological Basis and Computational Principles* pp. 37–52. Elseview.
174. Merriam EP, Genovese CR, Colby CL. 2003 Spatial updating in human parietal cortex. *Neuron* **39**, 361–73.
175. Groman SM, Keistler C, Keip AJ, Hammarlund E, DiLeone RJ, Pittenger C, Lee D, Taylor JR. 2019 Orbitofrontal circuits control multiple reinforcement-learning processes. *Neuron* **103**, 734–746.e3.
176. Ariens Kappers CU, Huber GC, Crosby ECN, Hafner. Y. 1936 *The Comparative Anatomy of the Nervous System of Vertebrates, Including Man.* New York: Hafner.
177. Romer AS, Parsons TS. 1977 The Vertebrate Body. *Philadelphia: Saunders*.
178. Hofmann MH, Northcutt RG. 2012 Forebrain organization in elasmobranchs. *Brain, Behavior and Evolution* **80**, 142–151.
179. Mueller T, Dong Z, Berberoglu M, Guo S. 2011 The dorsal pallium in zebrafish, Danio rerio (Cyprinidae, Teleostei). *Brain Research* **1381**, 95–105.
180. Mueller T. 2012 What is the thalamus in zebrafish?. *Frontiers in Neuroscience* **6**.
181. Striedter GF, Northcutt RG. 2021 The independent evolution of dorsal pallia in multiple vertebrate lineages. *Brain Behav Evol* pp. 1–12.

182. Kaskan P, Franco C, Yamada E, Silveira L, Darlington R, Finlay B. 2005 Peripheral variability and central constancy in mammalian visual system evolution. *Proceedings of the Royal Society: Biological Sciences* **272**, 91–100.
183. Atallah HE, Frank MJ, O'Reilly RC. 2004 Hippocampus, cortex, and basal ganglia: Insights from computational models of complementary learning systems. *Neurobiology of Learning and Memory* **82**, 253–267.
184. Graybiel AM. 2008 Habits, rituals, and the evaluative brain. *Annual Review of Neuroscience* **31**, 359–387.
185. O'Reilly JX, Jbabdi S, Rushworth MFS, Behrens TEJ. 2013 Brain systems for probabilistic and dynamic prediction: Computational specificity and integration. *PLOS Biology* **11**, e1001662.
186. Patai EZ, Spiers HJ. 2021 The versatile wayfinder: Prefrontal contributions to spatial navigation. *Trends in Cognitive Sciences* **25**, 520–533.
187. Wallach A, Harvey-Girard E, Jun JJ, Longtin A, Maler L. 2018 A time-stamp mechanism may provide temporal information necessary for egocentric to allocentric spatial transformations. *ELife* **7**.
188. Spiers HJ. 2020 The hippocampal cognitive map: One space or many?. *Trends in Cognitive Sciences* **24**, 168–170.
189. Poucet B, Save E, Lenck-Santini P. 2000 Sensory and memory properties of hippocampal place cells. *Reviews in the Neurosciences* **11**, 95–112.
190. Northcutt RG. 1995 The forebrain of gnathostomes: In search of a morphotype. *Brain, Behavior and Evolution* **46**, 304–318.
191. Broglio C, Gómez A, Durán E, Ocana FM, Jiménez-Moya F, Rodríguez F, Salas C. 2005 Hallmarks of a common forebrain vertebrate plan: specialized pallial areas for spatial, temporal and emotional memory in actinopterygian fish. *Brain Research Bulletin* **66**, 277–281.
192. MacLean PD. 1958 Contrasting functions of limbic and neocortical systems of the brain and their relevance to psychophysiological aspects of medicine. *The American Journal of Medicine* **25**, 611–626.
193. Cesario J, Johnson DJ, Eisthen HL. 2020 Your brain is not an onion with a tiny reptile inside. *Current Directions in Psychological Science* **29**, 255–260.
194. Nieuwenhuys R, Puelles L. 2015 *Towards a new neuromorphology*. Springer.
195. Levitt P. 1984 A monoclonal antibody to limbic system neurons. *Science* **223**, 299–301.
196. Levitt P, Barbe MF, Eagleson KL. 1997 Patterning and specification of the cerebral cortex. *Annual Review of Neuroscience* **20**, 1–24.
197. Keesey IW, Grabe V, Gruber L, Koerte S, Obiero GF, Bolton G, Khallaf MA, Kunert G, Lavista-Llanos S, Valenzano DR, Rybak J, Barrett BA, Knaden M, Hansson BS. 2019 Inverse resource allocation between vision and olfaction across the genus Drosophila. *Nat. Commun.* **10**, 1162.
198. Cleland TA, Borthakur A. 2020 A systematic framework for olfactory bulb signal transformations. *Frontiers in computational neuroscience* **14**.
199. Rubin BD, Katz LC. 1999 Optical imaging of odorant representations in the mammalian olfactory bulb. *Neuron* **23**, 499–511.
200. Ghosh S, Larson SD, Hefzi H, Marnoy Z, Cutforth T, Dokka K, Baldwin KK. 2011 Sensory maps in the olfactory cortex defined by long-range viral tracing of single neurons. *Nature* **472**, 217–220.
201. Eichenbaum H. 2017 On the integration of space, time, and memory. *Neuron* **95**, 1007–1018.
202. McClelland J, McNaughton BL, O'Reilly R. 1995 Why there are complementary learning systems in the hippocampus and neocortex: insights from successes and failures of connectionist models of learning and memory. *Psychological Bulletin* **102**, 419–457.
203. Olshausen BA, Field DJ. 1996 Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature* **381**, 607–609.
204. Jacobs LF. 2012 From chemotaxis to the cognitive map: The function of olfaction. *Proc. Natl. Acad. Sci. U.S.A* **109**, 10693–10700.
205. Nieh EH, Schottdorf M, Freeman NW, Low RJ, Lewallen S, Koay SA, Pinto L, Gauthier JL, Brody CD, Tank DW. 2021 Geometry of abstract learned knowledge in the hippocampus. *Nature* **595**.
206. Striedter GF. 2019 Variation across species and levels: Implications for model species research. *Brain, Behavior and Evolution* **93**, 57–69.
207. Pérez-Fernández J, Stephenson-Jones M, Suryanarayana SM, Robertson B, Grillner S. 2014 Evolutionarily conserved organization of the dopaminergic system in lamprey: SNc/VTA

afferent and efferent connectivity and D2 receptor expression. *Journal of Comparative Neurology* **522**, Spc1–Spc1.

208. Badre D, Nee DE. 2018 Frontal cortex and the hierarchical control of behavior. *Trends in Cognitive Sciences* **22**, 170–188.
209. Ito M, Doya K. 2011 Multiple representations and algorithms for reinforcement learning in the cortico-basal ganglia circuit. *Curr. Opin. Neurobiol.* **21**, 368–373.
210. Wolpert DM, Landy MS. 2012 Motor control is decision-making. *Current Opinion in Neurobiology* **22**, 996–1003.
211. Sheahan HR, Franklin DW, Wolpert DM. 2016 Motor planning, not execution, separates motor memories. *Neuron* **92**, 773–779.
212. Nakamura H, Kuroda T, Wakita M, Kusunoki M, Kato A, Mikami A, Sakata H, Itoh K. 2001 From three-dimensional space vision to prehensile hand movements: The lateral intraparietal area links the area V3A and the anterior intraparietal area in macaques. *Journal of Neuroscience* **21**, 8174–8187.
213. Warren R, Sawtell NB. 2016 A comparative approach to cerebellar function: insights from electrosensory systems. *Current Opinion in Neurobiology* **41**, 31–37.
214. Hashimoto M, Hibi M. 2012 Development and evolution of cerebellar neural circuits. *Development, growth & differentiation* **54**, 373–389.
215. Ito M. 2008 Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience* **9**, 304–313.
216. Eichenbaum H. 2017 The role of the hippocampus in navigation is memory. *Journal of neurophysiology* **117**, 1785–1796.
217. Dunn TW, Gebhardt C, Naumann EA, Riegler C, Ahrens MB, Engert F, Del Bene F. 2016 Neural Circuits Underlying Visually Evoked Escapes in Larval Zebrafish. *Neuron* **89**, 613–628.
218. Bhattacharyya K, McLean DL, MacIver MA. 2017 Visual Threat Assessment and Reticulospinal Encoding of Calibrated Responses in Larval Zebrafish. *Curr. Biol.* **27**, 2751–2762.
219. Bhattacharyya K, McLean DL, MacIver MA. 2021 Intersection of motor volumes predicts the outcome of ambush predation of larval zebrafish. *In press: Journal of Experimental Biology*.
220. Sutton RS. 1990 Integrated Architectures for Learning, Planning, and Reacting Based on Approximating Dynamic Programming. In Porter B, Mooney R, editors, *Machine Learning Proceedings 1990* pp. 216–224. San Francisco (CA): Morgan Kaufmann.
221. Racanière S, Weber T, Reichert D, Buesing L, Guez A, Rezende DJ, Badia AP, Vinyals O, Heess N, Li Y et al.. 2017 Imagination-augmented agents for deep reinforcement learning. In *Adv. Neur. In.* pp. 5690–5701.
222. Sillar KT, Picton LD, Heitler WJ. 2016 *The Neuroethology of Predation and Escape*. Wiley.
223. Hugie DM. 2003 The waiting game: a "battle of waits" between predator and prey. *Behavioral Ecology* **14**, 807–817. Publisher: International Society for Behavioral Ecology.
224. Daw ND, Niv Y, Dayan P. 2005 Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nat. Neurosci.* **8**, 1704–1711.
225. Silver D, Huang A, Maddison CJ, Guez A, Sifre L, Van Den Driessche G, Schrittwieser J, Antonoglou I, Panneershelvam V, Lanctot M et al.. 2016 Mastering the game of Go with deep neural networks and tree search. *nature* **529**, 484–489.
226. Schrittwieser J, Antonoglou I, Hubert T, Simonyan K, Sifre L, Schmitt S, Guez A, Lockhart E, Hassabis D, Graepel T, Lillicrap T, Silver D. 2020 Mastering Atari, Go, chess and shogi by planning with a learned model. *Nature* **588**, 604–609. Number: 7839 Publisher: Nature Publishing Group.
227. Hamrick JB, Friesen AL, Behbahani F, Guez A, Viola F, Witherspoon S, Anthony T, Buesing L, Veličković P, Weber T. 2021 On the role of planning in model-based deep reinforcement learning. *arXiv:2011.04021 [cs]*. arXiv: 2011.04021.
228. Lengyel M, Dayan P. 2007 Hippocampal Contributions to Control: The Third Way. In *Adv. Neur. In.* NIPS'07 pp. 889–896 USA. Curran Associates Inc.
229. Gershman SJ, Balbi PE, Gallistel CR, Gunawardena J. 2021 Reconsidering the evidence for learning in single cells. *eLife* **10**, e61907. Publisher: eLife Sciences Publications, Ltd.
230. Rodrigues MA, Boeving ER. 2019 Comparative social grooming networks in captive chimpanzees and bonobos. *Primates* **60**, 191–202.
231. Isa T, Marquez-Legorreta E, Grillner S, Scott EK. 2021 The tectum/superior colliculus as the vertebrate solution for spatial sensory integration and action. *Current Biology* **31**, R741–R762.

232. Suryanarayana SM, Pérez-Fernández J, Robertson B, Grillner S. 2021 The lamprey forebrain – evolutionary implications. *Brain, Behavior and Evolution*.
233. Northcutt R. 2011 Do teleost fishes possess a homologue of mammalian neocortex. *Brain, Behavior and Evolution* **78**, 136–138.
234. Yopak KE, Lisney TJ, Collin SP. 2015 Not all sharks are “swimming noses”: variation in olfactory bulb size in cartilaginous fishes. *Brain Structure and Function* **220**, 1127–1143.
235. Puelles L, Harrison M, Paxinos G, Watson C. 2013 A developmental ontology for the mammalian brain based on the prosomeric model. *Trends in Neurosciences* **36**, 570–578.
236. Jarvis ED, Gunturkun O, Bruce L, Csillag A, Karten H, Kuenzel W, Medina L, Paxinos G, Perkel DJ, Shimizu T, Striedter G, Wild JM, Ball GF, Dugas-Ford J, Durand SE, Hough GE, Husband S, Kubikova L, Lee DW, Mello CV, Powers A, Siang C, Smulders TV, Wada K, White SA, Yamamoto K, Yu J, Reiner A, Butler AB. 2005 Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* **6**, 151–9.
237. Montiel JF, Vasistha NA, Garcia-Moreno F, Molnár Z. 2016 From sauropsids to mammals and back: New approaches to comparative cortical development. *Journal of Comparative Neurology* **524**, 630–645.
238. Bels V, Russell A. 2019 *Behavior of lizards: evolutionary and mechanistic perspectives*. CRC Press.
239. Pianka ER, King D, King RA. 2004 *Varanoid lizards of the world*. Bloomington: Indiana University Press. OCLC: 1105390904.
240. Northcutt RG. 2013 Variation in Reptilian Brains and Cognition. *Brain, Behavior and Evolution* **82**, 45–54. Publisher: Karger Publishers.
241. Callaway EM, Dong HW, Ecker JR, Hawrylycz MJ, Huang ZJ, Lein ES, Ngai J, Osten P, Ren B, Tolias AS, White O, Zeng H, Zhuang X, Ascoli GA, Behrens MM, Chun J, Feng G, Gee JC, Ghosh SS, Halchenko YO, Hertzano R, Lim BK, Martone ME, Ng L, Pachter L, Ropelewski AJ, Tickle TL, Yang XW, Zhang K, Bakken TE, Berens P, Daigle TL, Harris JA, Jorstad NL, Kalmbach BE, Kobak D, Li YE, Liu H, Matho KS, Mukamel EA, Naeemi M, Scala F, Tan P, Ting JT, Xie F, Zhang M, Zhang Z, Zhou J, Zingg B, Armand E, Yao Z, Bertagnolli D, Casper T, Crichton K, Dee N, Diep D, Ding SL, Dong W, Dougherty EL, Fong O, Goldman M, Goldy J, Hodge RD, Hu L, Keene CD, Krienen FM, Kroll M, Lake BB, Lathia K, Linnarsson S, Liu CS, Macosko EZ, McCarroll SA, McMillen D, Nadaf NM, Nguyen TN, Palmer CR, Pham T, Plongthongkum N, Reed NM, Regev A, Rimorin C, Romanow WJ, Savoia S, Siletti K, Smith K, Sulc J, Tasic B, Tieu M, Torkelson A, Tung H, van Velthoven CTJ, Vanderburg CR, Yanny AM, Fang R, Hou X, Lucero JD, Osteen JK, Pinto-Duarte A, Poirion O et al.. 2021 A multimodal cell census and atlas of the mammalian primary motor cortex. *Nature* **598**, 86–102.
242. Foster NN, Barry J, Korobkova L, Garcia L, Gao L, Becerra M, Sherafat Y, Peng B, Li X, Choi JH, Gou L, Zingg B, Azam S, Lo D, Khanjani N, Zhang B, Stanis J, Bowman I, Cotter K, Cao C, Yamashita S, Tugangui A, Li A, Jiang T, Jia X, Feng Z, Aquino S, Mun HS, Zhu M, Santarelli A, Benavidez NL, Song M, Dan G, Fayzullina M, Ustrell S, Boesen T, Johnson DL, Xu H, Bienkowski MS, Yang XW, Gong H, Levine MS, Wickersham I, Luo Q, Hahn JD, Lim BK, Zhang LI, Cepeda C, Hintiryan H, Dong HW. 2021 The mouse cortico–basal ganglia–thalamic network. *Nature* **598**, 188–194.
243. Feldman Barrett L, Finlay BL. 2018 Concepts, goals and the control of survival-related behaviors. *Current Opinion in Behavioral Sciences* **24**, 172–179.
244. Datta SR, Anderson DJ, Branson K, Perona P, Leifer A. 2019 Computational Neuroethology: A Call to Action. *Neuron* **104**, 11–24.
245. Patil C, Sylvester JB, Abdilleh K, Norsworthy MW, Pottin K, Malinsky M, Bloomquist RF, Johnson ZV, McGrath PT, Streelman JT. 2021 Genome-enabled discovery of evolutionary divergence in brains and behavior. *Scientific Reports* **11**, 13016.
246. Tosches MA. 2021 From Cell Types to an Integrated Understanding of Brain Evolution: The Case of the Cerebral Cortex. *Annual Review of Cell and Developmental Biology* **37**, 495–517. PMID: 34416113.
247. Imam N, Finlay BL. 2020 Self-organization of cortical areas in the development and evolution of neocortex. *Proceedings of the National Academy of Sciences* p. 202011724.
248. Clarke SE, Naud R, Longtin A, Maler L. 2013 Speed-invariant encoding of looming object distance requires power law spike rate adaptation. *Proceedings of the National Academy of Sciences* **110**, 13624–13629.
249. Walsh KS, McGovern DP, Clark A, O’Connell RG. 2020 Evaluating the neurophysiological evidence for predictive processing as a model of perception. *Annals of the New York Academy of Sciences* **1464**, 242–268.

250. Finlay BL, Huang K. 2020 Developmental duration as an organizer of the evolving mammalian brain: scaling, adaptations, and exceptions. *Evolution & Development* **22**, 181–195.
251. Daw ND. 2018 Are we of two minds?. *Nature Neuroscience* **21**, 1497–1499.
252. Christiansen MH, Chater N. 2016 The now-or-never bottleneck: A fundamental constraint on language. *Behavioral and brain sciences* **39**.
253. Trapp S, Parr T, Friston K, Schröger E. 2021 The predictive brain must have a limitation in short-term memory capacity. *Current Directions in Psychological Science* **0**, 09637214211029977.