9 Finding Minds: Evidence from Neuroanatomy

Where can minds be found? This question is crucial for establishing the replicability of Umweltian cognition and consciousness. Yet it is exceedingly difficult to answer. We cannot observe minds in the way that we can observe other features of organisms, such as morphologies, behaviors, and even proteins and genetic sequences with the aid of a sufficiently powerful microscope. Mind is not a substance that reflects light and bends gravity; nor are mental states identical to brain states, given their multiple neural realization: there is no reason to think that the same biochemical brain state will reflect the same mental state in the brains of different animals or extraterrestrials.[1]

The most sensible view is that mind is a functional realization of the organization of bodies, including but not necessarily limited to nervous systems. However, the nature of this functional realization remains contested.[2] Even if we managed to agree on the relevant functional relations and devised reliable ways of probing for them in the world, there is still the problem, discussed in the previous chapter, that minds, or at least the feelings that accompany them, cannot be accessed from the third-personal perspective and hence cannot be observed directly with any scientific apparatus. Thankfully, direct perception, whether naked or technologically enhanced, is not the only means by which to generate reliable inferences about the presence of entities that we cannot see, so long as these entities have causal powers. Much as physicists can detect the traces of subatomic particles by observing the aftermath of particle collisions in high-speed accelerators, so too can we detect the causal signatures of mind in the world.

This signature is composed of three mutually informing lines of evidence: neuroanatomy, behavior, and evolution. Precisely how these lines of evidence work together to establish the existence of minds of particular types will be explored in the next chapter. The task that will occupy us here is to review the evidence from neuroanatomy and explain how it can be used to construct a provisional phylogenetic distribution of mind from which inferences about its evolutionary replicability can be drawn.

1.   Convergent Bilaterian Brains

We saw in the previous chapter that minimal cognition is likely to be a cosmic feature of living worlds. Even if cognition is conceived in somewhat more demanding terms than bare information processing, such as in terms of sensorimotor mechanisms that produce faster information flows, cross-kingdom convergence on such mechanisms suggests that cognition has wide scope and is relatively easy to evolve from disparate developmental starting points. Yet cognition in this minimal sense does not rise to the level of what many would want to call "mind," at least not in anything like the rich Umweltian sense contemplated in the previous chapter. What we are in search of is the kind of mind that comes with the rich information-integrative capacities of *brains*. Brains are hierarchically organized centers of parallel processing that receive, interpret, and integrate information from sensory modalities and other peripheral modular systems, packaging complex representations and making them available for executive decision making and action. Can we glean anything from the way brains are distributed in the living world about whether and how intelligence is likely to arise elsewhere in the universe?

The nervous systems of extant animal groups can be divided into three basic categories: diffuse neural nets, cerebral ganglion, and brains. As with much else in the biological world, there is no clean dividing line between these grades of neural complexity, and there is considerable variation within them. At precisely what point, for example, cephalic ganglionic complexity rises to the level of a brain is essentially arbitrary. Notwithstanding this continuum in neural complexity, the above coarse-grained categories are useful: there are stark morphological and functional differences between full-blown central processing centers, on the one hand, and primitive cephalic ganglia, on the other. And as we shall see in chapter 10, these neural complexity grades map reasonably well onto the behavioral sophistication of lineages and the lifeways they lead.

The discussion that follows will pivot around the provocative claim made by Simon Conway Morris that centralized nervous systems are an inevitable outcome of evolution.[3] In order to answer this question, we need to know how many times centralized nervous systems evolved and what sorts of contingencies these iterations (if they exist) may have relied upon. But learning the distribution of neural complexity among extant animals does not, by itself, reveal how many times neural complexity grades evolved, so it tells us little about the evolutionary robustness of such outcomes. To shed light on this question, information about the existing distribution of neural complexity must be superimposed onto our scientific understanding of the relatedness of animal groups. In essence, resolving the evolutionary history of brains is the first step toward constructing a phylogeny of minds.

1.1   Observer Selection Effects and Contingency Credences

Let us say, for the sake of argument, that brains evolved only once in the history of life on Earth, and that this trait was transmitted continuously via descent from a common ancestor to all existing animals with brains. This single origin scenario for brains should increase our credence in the contingency hypothesis about mind because (1) the existence of minds depends on the existence of functional brains and (2) observer selection biases (see chapter 1) guarantee that brains will evolve in any history of life in which a species comes to ponder the prospects of intelligent life in the cosmos, no matter how radically contingent and infinitesimally rare such an evolutionary outcome might be. The alternative scenario is that brains evolved multiple times such that some of the animal brains we observe descend from separate origin points in the history of life on Earth. This multiple origins scenario should increase our credence in the robust replicability thesis as it applies to brains and, by a somewhat more tentative extension, to minds. For any intelligent observer posing these cosmic questions need not hail from a history of life in which brains and their attendant minds evolved multiple times. The multiple origins of brain/mind complexes gestures at law-like constraint, rather than cosmic accident.

If the multiple origins scenario is correct, then we have the beginnings of a case for the law-like expectability of mind—but only the beginning. Whether this pattern of iteration supports the the robust replicability thesis as it relates to brain–mind complexes would depend on three things. First, it would depend on what the relevant initial conditions are taken to be and how evolutionarily robust we think they are. For instance, does our question about the robustness of brain–mind complexes presuppose the origin of eukaryote-grade complexity, complex multicellularity, functional neurons, or none of these things? Second, it would depend on the extent to which the co-optation of conserved substrates, such as homologous cell types or gene regulatory networks, undermines the independence of specific brain iterations. Third, it would depend on whether we are licensed to make an inference from the existence of brains to the existence of minds. Before addressing these points, let us begin with the basic homology-convergence question first, which, as it turns out, is surprisingly difficult to answer.

1.2   How Many Times Have Brains Evolved?

To work out how many times brains have evolved in the history of life on Earth, we need an animal cladogram—a working reconstruction of evolutionary relationships among animal groups on which we can place the extant nodes of neural complexity. Animals are grouped into a number of clades that reflect high-level taxonomic categories in the Linnaean system of classification, like

phyla and superphyla. Whereas nervous systems of varying levels of complexity can be found in virtually all animal groups (save for a few basal clades, as we will discuss), true brains are only present in a handful of phyla. Specifically, centralized nervous systems are found in chordates, arthropods, annelids, and mollusks, which in turn span the two bilaterian superphyla known as *protostomes* and *deuterostomes*, respectively.

Many readers will recall being taught in high school biology that insects—arthropods nested within *Protostomia*—have decentralized ganglionic nervous systems. This view is outdated and now known to be wrong. Like the vertebrate brain, the *mushroom bodies* of arthropods (analogs of which can be found in polychaete annelids) are centralized neural structures characterized by reentrant pathways that permit an ongoing exchange of signals to and from all major brain areas and sensory systems, supporting attentional processes, learning, and the executive control of the body and its movements.[4] Insect mushroom bodies have significant dendritic ramifications and take inputs from all critical regions of the brain—a signature of higher-order information integration and, potentially, of sophisticated forms of cognition like learning and memory.[5]

Working out how many evolutionary origins of brains are reflected in the extant distribution of centralized nervous systems among bilaterian phyla requires that we accurately reconstruct the evolutionary relationships between major bilaterian groups. Unfortunately, resolving evolutionary relations among phyla has proved difficult—much more so than discerning the phyla themselves. This because bilaterian phyla arose in the geological eye-blink that was the Cambrian explosion, and they have remained morphologically stable ever since (see chapter 2). During this Big Bang of animal evolution, nearly all bilaterian clades split from their last common ancestor in as few as tens of millions of years—an incomprehensibly vast span of time from the human perspective, but too brief for evolutionary descent to leave an unmistakable trace in the geological and genomic records.

We face three possible scenarios for the evolution of bilaterian brains. In the first scenario, the last common ancestor to all bilaterians not only had a through-gut (a crucial animal innovation that allowed for the processing of ingested sediment) but also a complex head encasing a centralized nervous system with a tripartite organization (composed of a forebrain, midbrain, and hindbrain), which was transmitted continuously through common descent to all bilaterian lineages that have brains today. In the second scenario, the last common ancestor to all bilaterians had a through-gut and neural nets (and perhaps even neural ganglion), but true brains evolved from these homologous ancestral nervous systems at least three or four separate times in bilaterians. In the third

scenario, the last common ancestor to all bilaterians had no nervous system (and perhaps no gut) at all, with the implication being that neurons, ganglia, and central nervous systems all arose multiple times within *Bilateria*.

Which of these scenarios is most likely to be correct? The third scenario—the repeated evolution of neurons and basic nervous systems in *Bilateria*—may be the least plausible for two reasons. First, the fossil record of the late Ediacaran—which, it may be recalled, is the period immediately preceding the Cambrian explosion, characterized by an enigmatic multicellular fauna with opaque affinities to metazoans—shows trace fossils of burrowing and other avoidance behaviors, which indicate that basic sensory-motor systems predate and hence were probably present in the first bilaterians.

Second, cnidarians—the radially symmetric phylum that includes jellyfish, corals, sea anemones, hydrozoans, and cubozoans—have decentralized nerve nets of varying complexities. And cnidarians are widely thought to be the sister group to *Bilateria*, from which they are estimated to have split more than 700 million years ago—nearly 200 million years before the Cambrian explosion. If this is right, then a parsimonious reading suggests that the last common ancestor of cnidarians and bilaterians had a primitive nervous system that was transmitted to bilaterians.

The alternative, of course, is that cnidarians and bilaterians evolved neurons independently (or perhaps from a conserved genetic potential). But this flies in the face of a guiding epistemic assumption of cladistics—namely, that a hypothesis that postulates the single origin of a complex character state followed by ancestral transmission is more parsimonious (all else being equal), and hence a preferable explanation of observed data, than a hypothesis that postulates multiple origins.[6] Moreover, genetic and developmental affinities between cnidarian and bilaterian neurons and nervous systems generally (but not exclusively) corroborate a single origin.[7] This does not rule out the possibility that neurons as a functional cell type evolved more than once, as we shall see in the next section. But it does speak quite clearly in favor of the proposition that the last common ancestor of all bilaterians had ancestral neurons and a primitive nervous system.

Having dispensed with the third scenario, we are left to the trickier task of adjudicating the first two. Given the general theoretical preference for single-origin hypotheses, one might think that, all else being equal, the first scenario (brain homology) would be preferred over the second (brain convergence). But in fact a stronger cladistic case can be made for the multiple origins of brains given the sheer number of major character state changes that are entailed by the brain homology hypothesis. The crux of the matter boils down to which set of evolutionary outcomes is deemed more likely, given all of the available

evidence and background theory: a *small* number of brain/head/eye *gains* or a *very substantial* number of brain/head/eye losses.

The brain homology hypothesis entails losses across the board, with more than 75 percent of existing animal phyla having quite literally lost their heads and exhibiting secondarily degenerated nervous systems. In contrast, the convergence scenario does not require any brain/head/eye losses in the bilaterian phyla that lack these features, because in that hypothesis these groups never had them in the first place. Instead, the heavy lifting for the convergence hypothesis comes in through its remarkable postulation that brains originated from primeval nervous systems *at least three or four times within Bilateria*. Both the homology scenario and the convergence scenario seem improbable, and yet one of them must be true.

Given that both scenarios are consistent with the extant phylogenetic distribution of nervous systems, which hypothesis offers the better explanation of the observed data? The answer that one gives to this question will depend on whether one accords greater evidential weight to phylogenetic patterns of morphology or to the genetic factors that underlie the development of nervous systems in distant groups. In truth, this is an oversimplification because morphological and molecular evidence point to some extent in both directions. There is, in my view, a clear frontrunner, but the scientific jury is still deliberating and far from a verdict. We are therefore venturing into the frontiers of scientific knowledge.

1.3 Gains, Losses, and Evolutionary Parsimony

The question before us is whether the brains observed in distant bilaterians represent phylogenetically primitive or convergently derived character states of nervous systems. Any answer to this question will turn on the features of the last common ancestor of *Bilateria*, about which little is currently known. The received view, at least among paleobiologists, is that the last common bilaterian ancestor was comparably simple: an eyeless, headless, and brainless animal with very limited motor capabilities.[8] Not all biologists agree with this assessment, however, for reasons that will soon be clear.

On standard approaches, "out-group analysis" is used to determine the "polarity" of a character in a cladogram—that is, to determine which character state is likely to be ancestral and which is likely to be derived among the alternative character states exhibited by a given set of taxa (the "in-group"). Out-group comparison looks at the character state in an "out-group" (typically a sister taxon to minimize evolutionary distance); if there is only one out-group (or if all out-groups exhibit the same character state), then the character state of the out-group is taken to be the most likely ancestral condition. Once trait polarity

is determined, the most likely evolutionary reconstruction of the trait is deemed to be the one with the fewest character state changes. Unlikely events do occur, of course, and so the findings of out-group analysis are to be taken as *prima facie* but defeasible evidence for a particular evolutionary hypothesis.

If we use out-group analysis to map nervous system character states—broadly partitioned into neural nets, ganglia, and brains—onto our best current reconstructions of metazoan evolutionary relationships, we find that brains are likely to have evolved multiple times in *Bilateria*. Figure 9.1 illustrates current scientific thinking about the evolutionary relations among metazoans in light of both fossil and molecular data, together with what is arguably the most parsimonious evolutionary history of nervous systems in light of these clade relations.

Not surprisingly, there are some important wrinkles and fluid elements in these reconstructions that we will consider below. But if we assume that sponges (which lack neurons, digestive tracks, and circulatory systems) are the most basal animal clade, then the presence of neural nets but not true brains in nonbilaterian animals like cnidarians and ctenophores, which branched off after the divergence of sponges but before the origins of *Bilateria*, suggests that neural nets are the ancestral character state of bilaterian nervous systems and brains are the derived state. And if this is so, then it implies that brains arose several times in *Bilateria*. Lending further weight to the multiple origins scenario are more taxonomically fine-grained out-group analyses that indicate convergence on varying degrees of nervous system centralization *within* phyla, such as within mollusks. The hypothesis that the ancestral mollusk had a complex brain that was repeatedly lost within the clade entails many more character state changes than does the intra-clade convergence scenario.

Having said all this, there is a large phylogenetic gulf between cnidarians and bilaterians. Were we to discover an extinct taxon in between whose nervous system structure could be ascertained, this would substantially affect our credence in the previous analysis of trait polarity. Another thing to take into account is that losses may be evolutionarily more accessible than gains when it comes to complex characters like brains; if so, then we should not assume that a tree entailing fewer character state changes but more brain gains is more likely than one entailing more character states changes but fewer brain grains. Still, there are sound reasons to prefer the convergence hypothesis beyond an epistemic preference for fewer character state changes.

If the bilaterian brain homology hypothesis is true—that is, if arthropods, vertebrates, mollusks, and annelids all have robust centralized nervous systems because they descend from a common ancestor that had a similarly complex nervous system—this would entail the loss of brains and a massive reduction
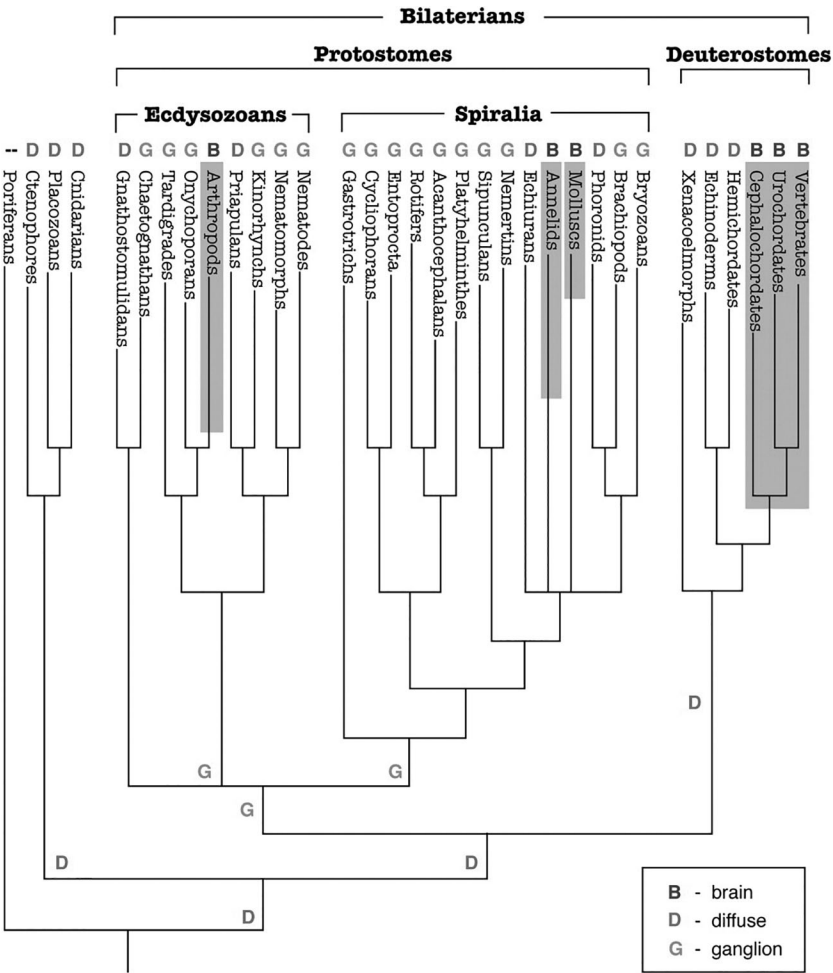
Figure 9.1
Out-group analysis of nervous system phylogeny across extant metazoans indicating that brains independently evolved at least four times in bilaterians. From R. G. Northcutt, "Evolution of Centralized Nervous Systems: Two Schools of Evolutionary Thought," *Proceedings of the National Academy of Sciences of the United States of America* 109, Suppl. 1 (2012): 10626–10633.

of nervous systems in more than a dozen bilaterian phyla quite rapidly in the early Phanerozoic, with the implication that twenty-three of the thirty existing animal phyla have secondarily degenerated brains and entirely vanished heads.[9] In fact, the situation is even worse for the bilaterian brain homology hypothesis because there is substantial nervous system variation *within* phyla that would (*ex hypothesi*) have retained the ancestral executive brain, such as within the mollusk and annelid clades. Taking into account this intra-clade

variation would imply an even greater total number of brain and head losses—such as in bivalves, chitons, and snails within *Mollusca*; and in earthworms and clitellates within *Annelida*.

We are right to be wary of progressivist penchants that might cause us to downplay the likelihood of reductions and simplifications in macroevolution. Still, the loss of heads/brains/eyes in 75 percent of bilaterian phyla as well as the radical functional and ecological reorganization of the same proportion of bilaterian body plans seems on its face to be implausible, particularly given the developmental stability of animal body plans for the duration of the Phanerozoic.

It is true that neural tissue imposes significant metabolic demands on organisms that natural selection will tend to shed if doing so is beneficial. It is also true that brain *size* has been reduced in many animal lineages for whom the metabolic costs of cognitive substrate outweigh the benefits of enhanced cognition. This is poignantly illustrated by secondarily herbivorous vertebrates (like pandas) whose calorie-frugal diet can no longer sustain their carnivorous clade's historical brain tissue expenditures. It is the case as well for lineages whose ecology calls for the reduction of neurologically demanding somatosensory functions, such as "cavefish"—several groups of freshwater fish adapted to lightless underground habitats that have repeatedly lost portions of the cortex dedicated to visual processing. The loss of a complex head is thus not totally inconceivable.

However, as evolutionary neuroscientist Leonid Moroz and his collaborators note, apart from parasites, there are no instances of major clades radically altering their lifeways—for example, switching from active predation to sessile filter-feeding—and, we might note, losing their heads and brains in the process. Even barnacles—arthropod crustacean filter-feeders with sessile, parasitic lifestyles—have retained minimal brains and compound eyes. The same is true of tiny copepod crustaceans and other meiofauna (minute interstitial animals that live in marine and terrestrial sediments), some of which are parasitic and lack circulatory systems but nevertheless have retained centralized nervous systems and eyes.

It is possible that there were weaker developmental constraints on early animals before bilaterian anatomies and lifeways congealed. Perhaps, for instance, there was less prohibitive pleiotropy, and hence more "quasi-independence," in upstream components of the bilaterian developmental plan before it evolved into the highly specialized forms that are reflected in modern phyla. The trouble with this is that, as we have seen, the brain homology hypothesis requires that the last common ancestor of *Bilateria* was equipped with a highly complex body, brain, and visual system, presumably with an active lifestyle to match—precisely the

sort of body plan that we would expect to be entrenched due to the causal topography of development (described in chapter 2).

Without being able to point to a single clear example of total brain/head/eye reduction in a nonparasitic lineage in the history of life on Earth, we should be loath to believe that it occurred on more (and perhaps many more) than a dozen occasions in the base of the Cambrian. The bilaterian brain homology hypothesis thus paints a decidedly unlikely picture of the evolution of bilaterian body plans. We would therefore need overwhelming evidence from other biological sources before it could be accepted. Enter developmental genetics.

1.4   When *Ceteris* Is Not *Paribus*

One reason why the question of brain convergence remains unresolved is that there is an apparent conflict between phylogenetic (out-group) analysis and molecular-developmental data. In particular, there are compelling structural similarities between arthropod and vertebrate brains, as well as orthologous genes and neural patterning mechanisms shared between these groups, that appear to support the brain homology hypothesis over the convergence hypothesis.

For instance, some of the genes that are implicated in the patterning of the nervous system into forebrain, midbrain, and hindbrain are shared between arthropods and vertebrates. This deep nervous system homology has been established in much the same way that deep homology in eye morphogenesis has been established, namely by swapping genes involved in the construction of brains between arthropods (drosophila) and vertebrates (mice) and showing that this fails to derail or otherwise affect healthy nervous system development in these groups.[10] In addition, gene knockout studies in drosophila and mice that deliberately interfere with the expression of molecules involved in memory and learning (such as protein kinase A) suggest that similar gene-regulatory networks underlie brain development in these disparate phyla.[11]

Nevertheless, there are several reasons to be cautious about the genetic-developmental data as they pertain to the brain homology-convergence question. First, to reiterate a point made earlier, the loss of the head/brain/eye complex and radical body plan reorganization in at least a dozen major animal phyla and many more classes within phyla is a difficult phylogenetic pill to swallow—though this goes to how we should balance conflicting sources of evidence, not to the merits of the evidence itself. Second, and more to the point, the fact that there are conserved genes and regulatory networks that underwrite the development of nervous systems across brained bilaterians does not imply that those genes functioned similarly in the last common ancestor and hence that they lost their function in most animal phyla.

Some have argued that the presence of conserved genes and homologous cell types in the development of eyes in distant phyla indicates that the last common ancestor of eye-bearing bilaterians possessed vision, and hence that the visual adaptation is homologous (monophyletic) rather than convergent (polyphyletic). But as we saw in chapter 6, this inference is problematic for a number of reasons that carry over into ruminations on the deep homology of nervous systems. The lesson there was that although the deep homolog *Pax6* is involved in the development of all known eyes, it is also present in non-eye-bearing phyla, such as echinoderms, that do not have eyes or photoreceptor cells of any kind; moreover, *Pax6* does not direct the specific contours of eye morphogenesis—instead it acts more like an on-off switch. This suggests that *Pax6* was repeatedly co-opted in the convergent construction of eyes, not that eyes are monophyletic *at the level of macroscopic organization*. When viewed in the light of out-group analysis, this speaks in favor of the convergent cooptation of *Pax6* for visual functions.

The same lessons can be brought to bear on the evolution of heads and nervous systems. We should not assume from the presence of deep homologs in the patterning of vertebrate and arthropod nervous systems that this is reflective of the ancestral function of the underlying orthologous genes—particularly when these genes are responsible for very coarse-grained neuroanatomical outcomes, rather than specifying the particular contours of brain development. The fact that the head-to-tail patterning of animals is directed by homologous transcription switches does not make arthropod, vertebrate, and cephalopod heads and mouth parts homologous. As zoologist Thomas Cavalier-Smith has aptly put it, "thinking human and grasshopper heads structurally homologous is as bad as calling a vacuum cleaner and light bulb homologous, because identical switches can turn both on."[12]

This brings us to the evidence of gross structural homology. It has long been recognized that the mushroom bodies of insects and stomatopod crustaceans—the centralized processing lobes responsible for learning, memory, and spatial cognition in these groups—appear to have organizational similarities to the mammalian hippocampus. For instance, brain regions associated with specific behaviors in vertebrates and arthropods, such as locomotion, are located in the same relative position with respect to other neural subsystems, such as those associated with light sensing. Why should this be so, if not a contingent quirk of history transmitted faithfully through common ancestry? Other structural similarities between arthropod and vertebrate brains include the parallel arrangement of neuronal fibers recently reported by Wolff and Strausfeld,[13] as well as reentrant connections that produce a bidirectional flow of information to and from disparate regions of the brain, allowing for the integration of sensory data and the executive control of bodily movement.

To bear the clear stamp of history, however, it is crucial that the organizational similarities identified between arthropod and vertebrate brains are not functionally constrained features of nervous systems in general, lest similarities due to convergence be mistaken for similarities due to common ancestry. The key question, therefore, is whether the structural resemblances that have been identified in the ground plan of insect mushroom bodies and the vertebrate hippocampus reflect the quirks of common ancestry or broad external constraints on nervous system form.

Some "vertebrate-like" features of invertebrate nervous systems—especially in the mushroom bodies of insects and the vertical lobe of coleoids—are probably due to the convergent evolution of cognitive functions that support activity-dependent and long-term plasticity mechanisms that underwrite memory, associative learning, categorization, and the flexible behavior these capacities underwrite.[14] Thus, at least some of the neuroanatomical similarities across brain-bearing phyla could indicate functional constraints rather than a single macro-morphological origin of the brain.

In focusing on the compelling organizational similarities between vertebrate and arthropod brains, it is easy to overlook the fact that the complex brains of coleoid cephalopod mollusks do not share any of these features, which in turn suggests that it evolved independently. Mollusk brains thus represent an important anomaly facing the bilaterian brain homology hypothesis. Let us now examine this anomaly more closely.

1.5   The Curious Case of the Coleoids

Even if one takes developmental similarities to be more probative than outgroup analyses in determining the polarity of a trait, a further wrench is thrown into the bilaterian brain homology hypothesis by the complex brains of coleoid mollusks, which do not fit neatly into the homology picture. Coleoids are a subclass of cephalopod mollusks whose extant members include octopuses, squid, and cuttlefish, and whose extinct members include the belemnoids (whose conical calcite guards pervade Mesozoic marine rocks). Coleoids are closely related to other cephalopods, such as the extinct ammonites and the living nautilids; and as mollusks, they are more closely related to all brainless bivalves and ganglionated snails than they are to other animal phyla with executive brains, such as vertebrates and arthropods. We saw in chapter 7 that the convergent camera eye of coleoids is strikingly similar to the vertebrate eye in terms of its gross morphology and functionality. If complex eyes are the evolutionary gateway to the mind, then we should expect to find the high-resolution, focus-capable eyes of coleoids connected to a coevolved neuronal mass that rises to the level of a brain.

The coleoid camera eye is indeed complimented by a behemoth brain—one that is stunningly complex by molluscan standards, but also not too shabby by vertebrate standards, weighing in at 140 million neurons (which is significantly larger than the brain of a mouse). This massive expansion of the ancestral mollusk nervous system includes not only formidable optic lobes to process visual information, but also the vertical lobes: centers of higher-order integration that are associated with memory and learning (though long-term storage occurs in a different area of the coleoid brain).[15] Octopod nervous systems are more distributed than those of vertebrates and arthropods, however, with nearly three-fifths of their neuronal mass dedicated to the operation of semi-autonomous sucker-lined arms and chromotaphores (color pigment cells used in crypsis, mimicry, and hunting displays), both of which are capable of autonomous activity. The extent of executive autonomy in octopuses, and in coleoids more generally, remains an area of active research.[16] Nevertheless, we know from coleoid lesioning studies—in which researchers execute carefully controlled damage to the vertical lobe and then infer from behavioral observations of the lesioned animal that certain cognitive changes have occurred—that visual, chemosensory, tactile, and proprioceptive system inputs are integrated, complex representations are formed, and behaviors are executively controlled by the coleoid central nervous system.

Whereas all vertebrates have executive brains that are presumably descended from a single common vertebrate ancestor, mollusks show tremendous diversity in their nervous system organization. If the last common ancestor to *Bilateria* had a complex centralized nervous system, this would imply (among other things) that noncephalopod mollusks, such as bivalves, snails, and chitons, lost (or massively reduced) the ancestral bilaterian brain. As noted earlier, this significantly multiplies the number of brain losses and body plan reconfigurations that are entailed by the bilaterian brain homology hypothesis.

The brains of some coleoid mollusks, such as the common octopus, are encased in a cartilaginous cranium between the eyes and contain far more neurons than many mammals. Yet they are organized in a fundamentally different way than the brains of vertebrates and arthropods. There is currently no evidence that the vertical lobe of coleoid mollusks is homologous to the vertebrate hippocampus or to the arthropodian mushroom bodies, even if it is similar at a cellular and functional level, including the reentrant pathways and long-term potentiation capacities that are characteristic of an integrative and associative brain structure.

The alien nature of coleoid brain anatomy is complemented by the unique developmental patterning of coleoid nervous systems. The molecular and developmental signatures of brain homology that have been identified for arthropods and vertebrates also appear to be lacking in coleoids.[17] For instance,

the deep homologs that are implicated in the development of vertebrate and arthropodian nervous systems do not appear to have similar functions in the development of coleoid mollusk brains. Furthermore, although cephalopod neurons are similar to those of vertebrates, the molecular basis of learning and neuromodulation in cephalopods draws upon a family of proteins that are uniquely conserved in mollusks.[18] Finally, analyses of octopod genomes show massive parallel expansions in gene families associated with the specification of nervous systems in vertebrates, which indicates multilevel convergence on enhanced cognitive functions via the repeated modifications of conserved genes.[19] In short, the developmental data bolster out-group analyses that indicate a separate origin of brains in mollusks, with some convergent co-optation of conserved molecules. This, in turn, bolsters the out-group analysis of brain evolution in bilaterians more broadly.

How can the bilaterian brain homology hypothesis make sense of the coleoid case? One response would be to propose that vertebrates and arthropods share a common brainy ancestor that mollusks do not also share. But this would entail a massive overhaul of bilaterian phylogeny, requiring that we reject the protostome-deuterostome division—a grouping that few would dispute and that is itself premised on the profound developmental differences between these clades (which are distinguished in part by whether the mouth is generated from earlier or later invaginations in embryonic development).

A second, more plausible response is to propose that the ancestral bilaterian head/brain/eye complex was lost in early mollusks but then regained in cephalopods. In that case, however, there would be at least two origins of brains, which refutes the bilaterian brain homology hypothesis. Moreover, the loss-followed-by-gain scenario in mollusks proposes two fairly complex character state changes, which is less parsimonious than the convergence hypothesis, which proposes only one. Even if one thinks that brain losses are more probable than gains, this is of little help here because a gain is presupposed in addition to a loss, though this burden would even out if arthropod and vertebrate brains were deemed homologous. In short, there are no clear advantages to this hypothesis although, of course, it could still be true.

There is a meaningful sense in which coleoids are "intelligent aliens on Earth." That phrase is not meant to be taken literally to imply that coleoids originated on another planet and were transported to Earth on a soft-landing meteor (though at least one scientific paper makes that eccentric argument![20]). Rather, it is to say that coleoids are among the best approximations we have of intelligent extraterrestrial life because they represent a clearly separate origin of brains boasting mammalian levels of neural complexity, giving us a rare window into the possibility space of alien minds.

1.6   The Gateway Revisited

Let us consider one final piece of the puzzle that comes on the heels of the foregoing discussion of eyes and brains. The "evolutionary gateway" argument, laid out in previous chapters, contends that image-forming sensory modalities, especially vision, are not only robustly replicable in their own right but also tied to the evolution of sophisticated cognition and behavior through a coevolutionary feedback process that resulted in neural-motor-proprioceptive complexification in several bilaterian phyla. Once the Umwelt platform was established and organisms found their place in the world, more complex cognitive functions, such as flexible learning capacities, could then be folded in.

If this story is right, then the prospect of bilaterian brain homology hinges on the prospect of bilaterian eye homology—and the latter scenario, as we saw in earlier chapters, is implausible (though not impossible). The ontogeny of the camera eye in cephalopod mollusks is completely different than that of the vertebrate camera eye, resulting in a blind spot in the latter but not in the former. The cephalopod camera eye also employs radically different mechanisms of focus: cephalopod eyes focus by moving the lens closer to or further from the retina, whereas vertebrate eyes focus by changing the shape of the lens itself. Cephalopod camera eyes do not seem to be merely arthropod compound eyes that have been reduced to a single chamber and afforded a few bells and whistles. Consistent with the profound developmental and structural differences between arthropod, vertebrate, and cephalopod eyes, there are no known genes that direct the specific gross morphological arrangements of all eye types. Eyes are thus likely to be polyphyletic both at the phenotypic level and at the level of genes. This, in turn, suggests that brains are probably polyphyletic as well.

Fossil evidence bolsters this conclusion. Proto-vertebrates found among the early Cambrian fauna, such as *Pikaia* (the critter we encountered in chapter 2), lack true eyes and a brain. It is hard not to interpret such animals as basal or "stem" vertebrates that branched off before the vertebrate lineage had developed complex eyes and cranium-encased central nervous systems. One strains to see *Pikaia* and its early vertebrate ilk as a secondarily reduced vertebrate condition, which despite a pelagic swimming ecology, lost all of the major neurological and optical accoutrements of its ghostly bilaterian ancestor.

Moreover, cephalopod brains clearly postdate the Cambrian explosion, perhaps by tens of millions of years; the same may be true, though to a lesser extent, of vertebrate brains (see discussion of Cambrian craniates in

chapter 2). All this suggests that image-forming eyes—and with them, heads, brains, and mobile bodies—either were absent in the last bilaterian ancestor (the more parsimonious reading) or else were present in the last bilaterian ancestor but were completely lost and then regained in cephalopods and vertebrates (the less parsimonious reading). Either way, we are looking at the multiple origins of eyes, cephalic brains, and the active lifestyles these structures support.

In sum, the totality of the evidence at present speaks to the multiple origins of brains via the repeated cooptation of conserved genetic, regulatory, and cellular elements. Even if brains were constructed out of homologous cell types, patterning mechanisms, and secretory signaling molecules, their information-integrative functions would have been realized independently in several bilaterian lineages. Central nervous systems are thus likely to be robustly replicable outcomes, at least given the origins of neurons and synapses—a problem to which we now turn.

2.   The Perplexing Phylogeny of the Neuron

If the evolutionary history of animal brains is uncertain, the phylogeny of the neuron and synaptic signaling systems is shrouded in even greater mystery. As with brains, the evidence for neuron cell type homology is mixed. There are currently no known genes or regulatory networks that produce neurons in all groups of animals that have them, which is contrary to what we should expect if the metazoan neuron homology hypothesis were true. And just as importantly, neurons do not arise from the same germ layer in embryonic development in all animals that have nervous systems. In some animals, such as vertebrates and arthropods, neurons arise from the ectoderm (the outer embryonic layer) while in others, such as cnidarians, neurons arise from the endoderm (the middle embryonic germ layer). These differences in development could imply separate epigenetic origins of nervous tissue in metazoans, leading some neuroevolutionary biologists to treat the neuron cell type as a de facto functional kind so as to leave open the question of common ancestry.[21]

Arthropods and vertebrates have similar electrical synaptic connections and use the same low-weight neurotransmitters to regulate voltage-gated ion channels between neurons; but the gap junctions that establish these intercellular channels are formed by entirely different molecules in each phylum.[22] Although there are molecules involved in synaptic signaling in most animal neurons (but see the discussion of ctenophores in the next section), these molecules are also used in non-neuronal cells and are present in unicellular eukaryotes and

prokaryotes—and thus could easily have been co-opted on separate occasions for neuronal functions.[23] But just as genetic and developmental similarities do not necessarily indicate homology, neither are genetic and developmental differences dispositive on the issue of convergence. Perhaps neurons and synaptic structures originated once but were genetically and developmentally reorganized in early metazoan evolution. Out-group comparisons add the much-needed paleontological context in which to interpret the comparative genetics and development of nervous systems.
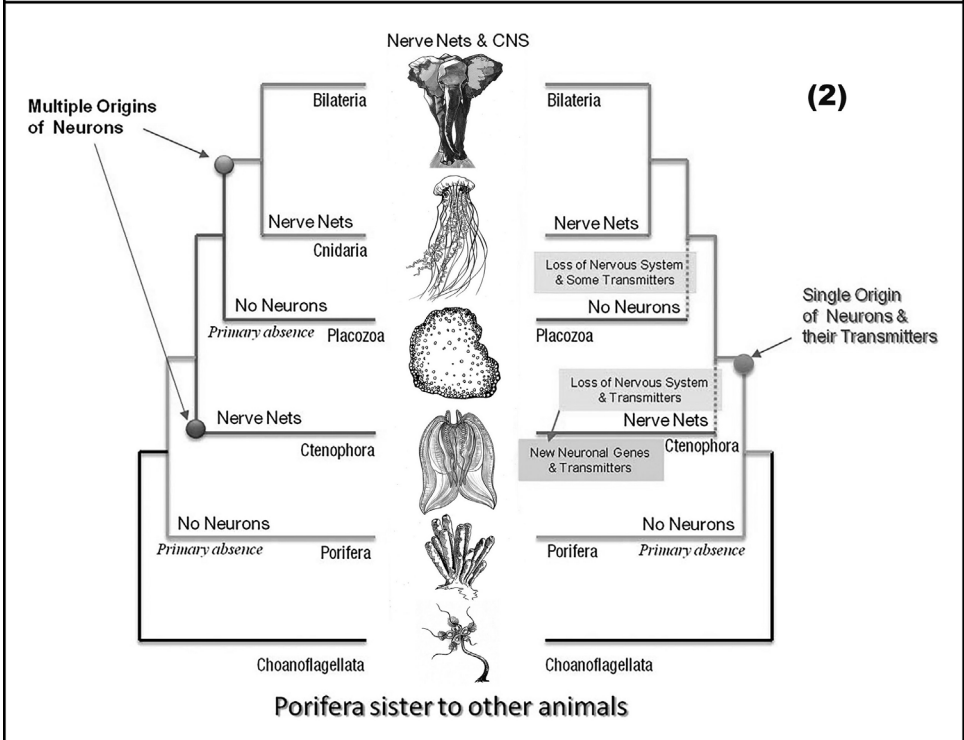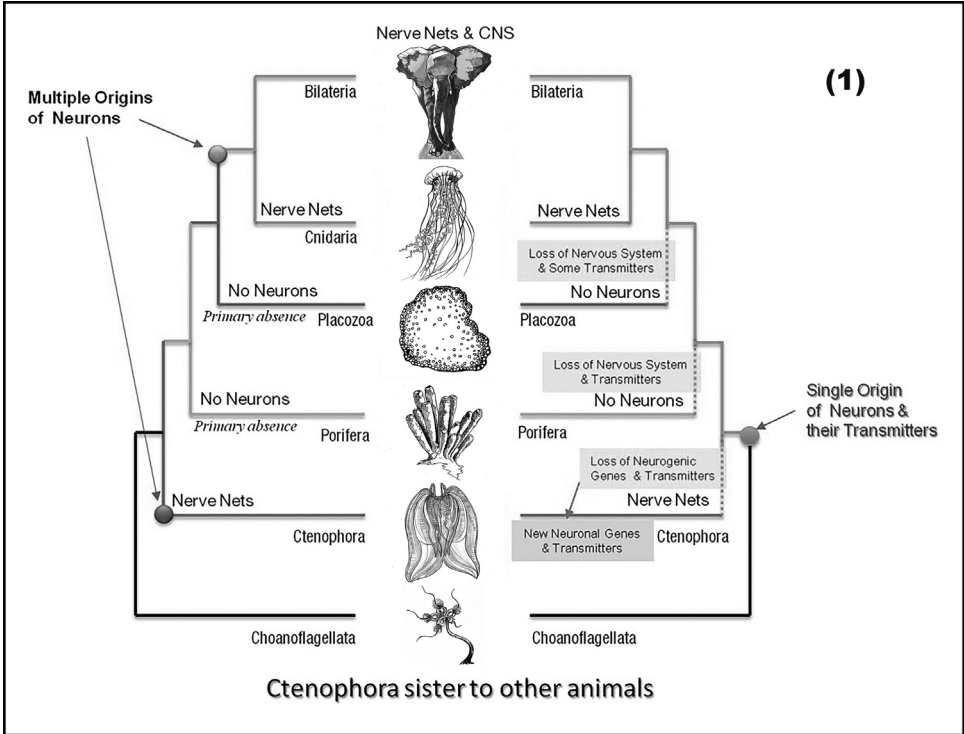
2.1 A View from the Abyss

A lynchpin to the neuron evolution debate is the phylogenetic position of a group of animals called "ctenophores." Ctenophores are beautiful, active predators that superficially resemble jellyfish; they have surprisingly complex sensorimotor systems (including high neural concentrations and true muscular systems), which underwrite a range of hunting behaviors that have been compared in their diversity to the predatory repertoire of spiders. The deep-sea "aliens" of James Cameron's film *The Abyss* (1989) seem to have been loosely—and, in hindsight, serendipitously—modeled on ctenophores, though they still bear the scars of the humanoid epidemic.

Ctenophore nervous and muscular systems are produced by nonhomologous genes and germ layers and deploy synaptic signaling mechanisms that differ from those of other metazoans. It is true that homology in a trait can be maintained despite a significant turnover in its genetic underpinnings.[24] However, the sheer turnover that is contemplated for the evolution of ctenophore nervous systems is so comprehensive, and on so many levels, that a homology-preserving transition seems on its face unlikely.

This leaves us with two options: either (1) the genes and low-molecular-weight signaling mechanisms (such as serotonin, dopamine, adrenaline, acetylcholine, and histamine) associated with nervous system ontogeny and function have been entirely lost and replaced in ctenophores, despite being deeply conserved in cnidarians/bilaterians and despite ctenophores maintaining an active predatory (rather than sessile or parasitic) lifestyle; or (2) functional neurons and nervous systems arose at least twice in metazoans.

Which of these scenarios is likely to be correct depends, in no small part, on the phylogenetic position of ctenophores. If ctenophores are the sister taxa to all other animals and hence more basal than sponges, as some recent research suggests,[25] then this militates in favor of the multiple origins scenario, especially when taken in conjunction with the molecular-developmental data. Alternatively, if sponges, which are sessile and have no neurons or nervous systems, are the most basal animal group—which has long been suspected to

(1)

Multiple Origins of Neurons

Nerve Nets & CNS

Bilateria

Bilateria

Nerve Nets

Nerve Nets

Cnidaria

Loss of Nervous System & Some Transmitters

No Neurons

No Neurons

Primary absence Placozoa

Placozoa

Loss of Nervous System & Transmitters

No Neurons

No Neurons

Primary absence Porifera

Porifera

Single Origin of Neurons & their Transmitters

Loss of Neurogenic Genes & Transmitters

Nerve Nets

Nerve Nets

New Neuronal Genes & Transmitters

Ctenophora

Ctenophora

Choanoflagellata

Choanoflagellata

Ctenophora sister to other animals

(2)

Multiple Origins of Neurons

Nerve Nets & CNS

Bilateria

Bilateria

Nerve Nets

Nerve Nets

Cnidaria

Loss of Nervous System & Some Transmitters

No Neurons

No Neurons

Primary absence Placozoa

Placozoa

Loss of Nervous System & Transmitters

Nerve Nets

Nerve Nets

Single Origin of Neurons & their Transmitters

New Neuronal Genes & Transmitters

Ctenophora

Ctenophora

No Neurons

No Neurons

Primary absence Porifera

Porifera *Primary absence*

Choanoflagellata

Choanoflagellata

Porifera sister to other animals

be the case and also garners recent support[26]—then this militates in favor of the comprehensive neuronal loss/replacement scenario in ctenophores. Within that picture, two possible scenarios emerge: (1) nervous systems were maintained in ctenophores through an unbroken chain of common decent despite a comprehensive turnover in the molecular and genetic mechanisms underlying them; or (2) nervous systems were lost and then regained in cteno-phores, an event that would effectively constitute a novel origin.

As Moroz and colleagues point out,[27] however, even if sponges turn out to be the most basal animal, this is consistent with a multiple origins scenario for neurons, synaptic morphology, and primitive nervous systems, so long as ctenophores are the second lineage to branch off from sponges, followed by placozoans (the simplest known nonparasitic animal, but according to molecular analysis not the most basal), cnidarians, and bilaterians, respec-tively (see figure 9.2). Alternatively, in the single-origin scenario, neurons could have been present in the last common ancestor of ctenophores/cnidar-ians/placozoans but subsequently lost in placozoans and completely turned over in ctenophores. It is not clear which of these scenarios is most probable.

In short, the same dilemmas that impede the evolutionary reconstruction of bilaterian brains—such as how we ought to weigh the relative probabilities of character state gains and losses, the prospects of developmental co-optations and turnovers, the relative weight accorded to out-group versus developmental analyses, and so forth—also encumber the phylogenetic construction of the *building blocks* of brains. If the neuron cell type did turn out to be an iterated functional kind, this might explain some of the genuinely perplexing aspects of neuron phylogeny. As biologist William Kristan concludes in reviewing the current scientific picture of neuronal evolution, "the multiple origins of neurons may, in fact, be why defining 'neuron' is so difficult, and why defining the origin of neurons is so complex."[28]

Figure 9.2

Two scenarios for the evolution of neurons. In the first scenario (*top*), ctenophores are taken to be the most basal animal, and neurons either arose twice (once in ctenophores and once in the last common ancestor of cnidarians and bilaterians—see left side); or else they arose once (in the common metazoan ancestor), neuronal genes and neurotransmitters were completely turned over in ctenophores, and nervous systems and neurotransmitters were entirely lost in sponges and placozoans (see right side). In the second scenario (*bottom*), sponges are taken to be the most basal animal, and neurons either arose twice—once in ctenophores and once in the last common ancestor of cnidarians and bilaterians, so long as ctenophores are more basal than placozoans (see left side); or neurons arose once and neuronal genes, neurotransmitters were completely turned over in ctenophores, and nervous systems were lost in placozoans (assuming, again, that ctenophores are more basal than placozoans). Redrawn from L. L. Moroz, "The Genealogy of Genealogy of Neurons," *Communicative and Integrative Biology* 7, no. 6 (2014): e993269.

2.2   The Evolvability of Functional Neurons

There appears to be no shortage of ways to realize neuron-like potentials in complex multicellular organisms. Many animal cells other than neurons are capable of generating action potentials that facilitate communication across cell populations, so it is not difficult to imagine secretory cells being repeatedly co-opted for neuron-like functions. Neurons can be created in vitro by modifying the epigenesis of cnidarian epithelial cells, which suggests that the repeated evolution of functional neurons from non-neuronal cell lines cannot be too difficult to achieve. The evolvability of functional neurons is further supported by convergence on action potentials and information-transfer mechanisms in lineages for whom rapid sensory-motor mechanisms are either inaccessible or not required.

For instance, action potentials have evolved in the first major origin of complex multicellularity: the green plants, some of whom, such as the carnivorous Venus flytrap, are capable of limited rapid movements. Such "real-time" plant behaviors are made possible by action potentials that are analogous in certain ways to animal nervous systems. Mechanosensory stimuli trigger sensory hairs, which then generate a propagating action potential that initiates a rapid motor response—such as the snapping shut of two leaf lobes, resulting in the imprisonment of hapless insect prey. Though the precise biochemical mechanisms of this snapping mechanism are poorly understood,[29] it is likely achieved by gated ion channels, which produce a flow of water or acid molecules that cause cells in the lobes to change shape, causing the lobes, which are held under tension, to snap shut. A basic memory system is also employed: to avoid snapping shut due to noise (such as raindrops), the snapping mechanism is only initiated when two stimuli separated in time by a few seconds are detected.

Even plants that lack action potentials have cognition-like links between stimulus and behavior, albeit on a timescale that is not intuitively obvious to humans. Like sessile animals, most plants have lifestyles that do not require active movement. As a result, they can afford to rely on more sluggish, protein-based molecular signaling mechanisms that have "on-off" (Boolean) switch-like capabilities and exhibit feedback and frequency modulation effects. These complex and poorly understood metabolic transduction networks, which are functionally analogous in certain ways to neural nets, enable plants to learn, remember, navigate stimulus fields and behave "intelligently" to vagaries of the external environment.[30]

Hundreds of intercellular signaling molecules are probably deployed by these systems, including but not limited to hormones. The information integrational capacities of hormone-style signaling systems may have outer limits.

For example, due to their low signaling speed, such systems are probably unable to achieve the synchrony and reentry necessary for stimulus binding, which may preclude plant consciousness—or at least consciousness in the rich Umweltian sense discussed in previous chapters. The point, however, is that the evolution of proto-neural functions in plants—a clade that lacks motor systems and relies almost entirely on growth for movement—indicates the deep replicability of the action potentials, logical switching mechanisms, and molecular signaling networks that support sophisticated behavior.

In sum, it is highly possible that functional neurons originated more than once in the evolution of animal epigenesis, likely from multiple germ layers, by co-opting the basic signaling functions of secretory cells and recruiting low-weight molecules as neurotransmitters. If we conceive of nervous systems even more broadly to include molecular transduction networks that are designed to transmit information, such as those found in green plants, then the outcome is even more evolutionarily robust. Even if a homologous cell type—such as a monophyletic neuron—were implicated in the construction of nervous systems in all animal groups, this would not convert brain convergences into "Gouldian repetitions" (see chapter 5); for if there are broad constraints on the structure of bilaterian nervous systems, there is no reason to think they stem from any radically contingent properties of neurons themselves.

At the very minimum, then, we can say that the evolution of brains is likely robust if we presuppose the evolution of neurons and synaptic signaling mechanisms among the initial conditions of the replay. Whether brains are cosmically projectible, and if so, with what sort of frequency, depends on the evolutionary robustness of functional neurons as well as other major developmental and metabolic innovations that resulted in animal-grade complexity, which at present are not well understood. Of course, future findings may call all of this into question—that is the beauty of science. But for now, we have to make the most of our view from the frontier.

2.3 From Brains to Minds

Even if centralized nervous systems have evolved repeatedly and independently, this does not show that mind is a robustly replicable feature of the evolutionary process. This is because the existence of brains does not decisively establish the existence of Umweltian minds. We can be reasonably certain that the distributed nervous systems of cnidarians and echinoderms, and the primitive ganglion of bryozoans and nematodes, even if they accomplish some levels of information integration, do not engage in stimulus binding or give rise to a unified consciousness. But we are on more uncertain grounds

when it comes to the centralized brains of arthropods and mollusks and the cognitive mechanisms they might support. Not all information processing and integration results in stimulus and semantic binding, mental representations of the body in space, attention, concepts, subjectivity, emotions, and so on. Because the inference from brains to minds is imperfect, the neuroanatomical evidence must be corroborated by observations of animal behavior. In the next chapter, we explore this critical source of evidence.

This is a section of

Contingency and Convergence
Toward a Cosmic Biology of Body and Mind

By: Russell Powell

Citation:

The MIT Press