Convergent minds: the evolution of cognitive complexity in nature

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Stephen Jay Gould [1,2] argued that replaying the ‘tape of life’ would result in radically different evolutionary outcomes. Gould’s ‘radical contingency thesis’ focused primarily on animal morphology, and in particular on the specific parameters of animal body plans, which, he argued, reflect but a small fraction of the larger set of equally functional morphological possibilities that for historically contingent reasons were never actualized. Were the tape replayed from different crucial junctures in the history of life, Gould contended, animal evolution would be channelled into radically different pathways, its topography would assume a markedly different shape, and many properties associated with extant animal life would never have arisen. Imagine how the history of animal life would have unfolded, for example, were it not for the improbable survival of ancestral chordates like *Pikaia*, which gave rise to all modern vertebrates, or for the fortuitous persistence of the lobe-finned fish that would eventually give rise to tetrapods, or for the asteroid-induced extinction of the non-avian dinosaurs whose emptied niches permitted the unlikely radiation and macro-faunal dominance of mammals. These examples suggest that the radical contingency thesis is best interpreted as a ‘modal’ thesis, that is, as a claim about the instability of certain evolutionary outcomes across possible evolutionary worlds. More precisely, it is a claim about the causal dependency of evolutionary outcomes on small changes in initial conditions, such as quirky survival, extinction or mutation events, particularly in the early stages of the evolution of higher taxa like phyla, classes and orders [3,4]. This sensitive dependency explains other features commonly attributed to the Gouldian view of macroevolution, such as unpredictability [5,6], stochasticity [7] and path-dependency [8].

Although the radical contingency thesis was aimed at the morphological features of life, it is particularly provocative for the implications it might have for the emergence of sophisticated forms of cognition. Is the evolution of mind a historical accident, unlikely to be replicated across alternative histories of life, much as Gould argued about animal body plans? Or do we have reason to think that mind and its associated cognitive competencies is a robustly replicable feature of the evolutionary process? Given that we are privy to only a single history of life, how can we even begin to adjudicate such questions? One promising avenue for investigating evolutionary contingency in general is to examine patterns of convergent evolution—the independent origination of similar biological forms and functions [5,6,9–11]. Under certain conditions, convergence may constitute natural experimental replications that provide evidence for the robustness of the iterated outcomes observed [4]. Although the term ‘convergence’ is typically reserved for descriptions of morphological character states, the concept can usefully be extended to functional properties such as cognition [12]. We may therefore investigate the replicability of cognitive capacities of varying degrees of complexity, as well as the developmental and ecological conditions under which particular cognitive forms are likely to arise, by establishing the extent and phylogenetic distribution of cognitive convergence [12,13].

If patterns of cognitive convergence are to serve as evidence for robust evolutionary replicability, however, it is critical that the iterated evolution of similar
cognitive capacities be demonstrated in taxonomically distant groups of animals. This is because the evolutionary distance of converging lineages serves as a natural experimental control for conserved (homologous) developmental variables that could potentially undermine the independence of iterations and thus restrict the generalizability of any regularities observed. If convergence is phylogenetically deep, then shared developmental constraints are unlikely to be responsible for the observed repetitions. For instance, if we observe certain complex cognitive properties in lineages whose common ancestor in all probability lacked complex brain structures or even a centralized nervous system—then this indicates the evolutionary replicability of these properties across temporally deep replays of the tape of life (e.g., across alternative histories of animal life), and in some cases could indicate their law-like necessity in any complex multicellular world.

Convergence across great taxonomic distances is also crucial for establishing the ecological causes and evolutionary consequences of cognitive evolution, as well as the developmental substrates that facilitate and constrain the emergence of complex cognitive forms. By controlling for many (though perhaps not all) phylogenetic constraints, the taxonomic breadth of convergent iteration increases our confidence that any regularities observed will hold up across disparate initial conditions and phylogenetic contexts. In essence, convergence can indicate that certain cognitive forms are less sensitive to boundary conditions, less path-dependent, and less unpredictable than the radical contingency thesis might have us believe. Do patterns of cognitive convergence support a ‘robust replicability thesis’ of mind?

It is crucial that any study of cognitive convergence that aims to draw broad lessons about the evolution of mind—not only about its replicability, but also about the specific developmental and ecological conditions under which it is likely (and unlikely) to occur—must look to convergence across higher taxa, both within chordates and between chordates and other phyla in Bilateria, especially arthropods and molluscs. On prevailing phylogenetic reconstructions, arthropods and molluscs share a common ancestor with vertebrates that in all probability did not possess a centralized nervous system or even vision, both of which are thought to have evolved independently in these groups after their divergence over 500 million years ago in the Cambrian (notwithstanding conserved genes and embryonic patterning mechanisms involved in the ontogeny and evolution of all known nervous systems) [14]; but see [15]. A growing body of comparative cognition research on molluscs (in particular, cephalopods; e.g. [16] and arthropods (especially insects and arachnids; e.g. [17–19]) suggests that complex cognition did not arise solely in the vertebrate clade—and thus, contra Gould, would not have gone un-actualized had Pikaia and its ilk been less fortunate. Similarly, certain bird and mammal clades, which share a common ancestor that lived over 300 million years ago in the Carboniferous, exhibit convergently enlarged brain structures [20] and a convergent cognitive tool kit that includes capacities such as causal reasoning, flexible problem solving and imagination [12,21,22]. Similar patterns of convergence can be seen at finer grains of taxonomic resolution, including between numerous mammalian lineages such as cetaceans, primates, elephants, and carnivores [23], indicating predictability and path-independency across shallower—though still quite substantial—replays of the tape of life.

The independent evolution of complex cognition in the many millions of years since these groups separated from a cognitively simpler common ancestor is putative evidence of the power of natural selection to drive convergent cognitive evolution from highly disparate initial conditions [24], and thus provides a forceful counterexample to the radical contingency thesis as it relates to some complex forms of cognition. Some have argued that certain types of cognition are uniquely human, such as shared intentionality, moral norm acquisition, and other cognitive abilities that underpin ultra-cooperation [25] and cumulative cultural transmission [26] in humans—which, if truly singular, could indicate the highly contingent origins of these cognitive forms. Gould himself made a case for the radical contingency of human-specific cognition, while withholding judgement on the evolutionary replicability of more general forms of intelligence [27]. Yet the fact that there is currently little evidence of these particular cognitive abilities in nonhuman animals does not indicate that they are entirely absent in nonhuman clades, since very little testing has been conducted and the efficacy of experimental probes has been limited. In addition, the interplay of biology and culture in the development of such capacities is unclear, and the extent of culture in nonhuman animals is itself the subject of intensive investigation [28]. We must therefore keep an open mind in asking: What do patterns of convergence in the history of life on Earth tell us about the nature of mind, its evolution and its place in the universe?

This themed issue brings together an international group of leading researchers and theorists from across the natural sciences and from the philosophy of biological and cognitive science to explore the iterated evolution of cognitive complexity. Conceptual problems loom large in this discussion. For starters, what counts as evidence for the evolutionary replicability of mind will depend on how we define the relevant explanandum (or ‘reference class’). This poses a particular challenge in the case of cognition, a phenomenon about which there is no widespread agreement regarding its definition, its typology, or in virtue of which properties some types of cognition may be said to be more complex than others. On ‘big-tent’ accounts of cognition, such as information processing accounts, minimal cognitive processes are present in nearly all forms of life including prokaryotes and other unicellular organisms, with cognitive processes greying into metabolic ones [29]. Other more restrictive but still biologically broad-based accounts of cognition hold that minimal cognition consists in sensorimotor mechanisms that are organizationally decoupled from metabolic processes and thus support faster sensorimotor information flows—a function paradigmatically realized by nervous systems. Yet there are functionally analogous sensorimotor systems in plants, in unicellular eukaryotes, and even in bacteria—all of which exhibit functional memory and flexible stimulus–response pairing mechanisms that are distinct from metabolic processes [30]. Both bacteria and plants have been shown to exhibit complex behavioural repertoires with a degree of flexibility that was long presumed to require a functional nervous system. According to ‘bottom-up’ accounts of cognition, whether glossed in terms of general information processing or more specific sensorimotor information flows, cognition is not restricted to complex nervous systems or even to nervous systems at all—and thus it can be expected to be a universal feature of life wherever it evolves.
This bottom-up approach is championed by Keijer [31] who argues that the nature of cognition is to be discovered by examining the biological world, rather than decided a priori by appealing to anthropocentric intuitions. Drawing on recent findings demonstrating the complex behavioural repertoires of protists, plants, and fungi, Keijer proposes a notion of ‘biologically embodied cognition’, which combines biology’s bottom-up approach to cognition with an embodied, rather than a computational-representational and brain-bound, view. Van Duijn [32] does not take a stand on whether cognition is essentially computational or embodied, but he too draws on evidence from both unicellular and multicellular aneural organisms to challenge what he sees as the ‘cerebro-centrism’ of cognitive science and, by extension, comparative psychology. Evidence suggests that these aneural organisms exhibit basic forms of learning and possess complex molecular mechanisms of information transfer, which undermines the assumption that cognition requires nervous systems, let alone brains. Trewavas [33] a leading authority on plant cognition, offers a wide-ranging exploration of the mechanisms of information transfer that underwrite ‘intelligent’ behaviour in plants. He concludes that all organisms whose survival depends on coping with a complex environment must evolve ‘intelligence’, by which he means a set of sophisticated cognitive capacities that underwrite flexible responses to environmental contingencies. Cognition, on each of these ‘bottom-up’ accounts, can be expected to be biologically ubiquitous and modally robust (i.e. stable across alternative evolutionary histories).

Other cognition theorists opt for a ‘top-down’ approach that conceives of the replicability of mind more narrowly to refer to the robustness not simply of cognition, but of cognitive capacities that are canonically deemed complex—such as planning, insight, imagination, causal reasoning, meta-cognition, intentionality, self-recognition, consciousness, and the like—capacities that are not present, even in rudimentary forms, in the vast majority of organisms on Earth (only a tiny fraction of which are multicellular organisms). With a top-down approach, questions regarding the contingency and predictability of mind become in a sense more interesting and more pertinent, but also more difficult to evaluate. Research in the expanding field of comparative cognition purports to identify numerous instances of convergence on these more demanding cognitive properties.

A number of researchers from disparate disciplines have contributed to this theme issue on convergent minds, and several of these authors follow this top-down tradition in probing for the presence of sophisticated cognitive capacities such as imagination, proto-linguistic communication, and counting abilities in lineages as phylogenetically disparate as birds, primates, and arachnids. Cross & Jackson [34] detail an experimental test for numerical cognition that underwrite ‘intelligent’ behaviour in plants. He concludes that all organisms whose survival depends on coping with a complex environment must evolve ‘intelligence’, by which he means a set of sophisticated cognitive capacities that underwrite flexible responses to environmental contingencies. Cognition, on each of these ‘bottom-up’ accounts, can be expected to be biologically ubiquitous and modally robust (i.e. stable across alternative evolutionary histories).

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Moore [38] meanwhile, makes the case that animal communication bears a much stronger resemblance to human language-mediated communication by reinterpreting the demands of the prevailing theory of successful communication. According to Moore, the ability to direct a message to an intended audience ‘in pursuit of a communicative goal’ is found in many nonhuman animals and is likely to have evolved many times in the history of life. Finally, Clayton & Wilkins [39] draw simultaneously on Clayton’s extensive body of work on episodic-like memory in jays and on Wilkin’s literary exploration of the relation between memory and identity to make the case that the ability to remember past events to plan future events likely evolved to aid in prospection rather than recall. If they are correct, then evidence of episodic-like memory in jays may simultaneously constitute evidence of future-oriented cognitive abilities, such as planning. Moreover, they suggest that engaging science with narrative art may present a novel method for exploring questions about the unobservable phenomena that are the subject of study in comparative cognition.

A central research question in comparative cognition concerns the evolutionary and ecological circumstances that give rise to complex forms of cognition. Under what conditions does complex cognition tend to evolve and what is it used for? The prevailing theory is that cognitive evolution is an adaptive response to environmental complexity. Several contributors to this issue build on or test elements of this hypothesis in an effort to explore the ecological and evolutionary correlates of cognitive evolution. Dunlap et al. [40] investigate whether bumblebees modify their information-seeking behaviour in response to a changing and unstable foraging ecology. Holekamp & Benson-Amram [41] investigate the source of spotted hyaenas’ social intelligence by evaluating the ‘cognitive buffer hypothesis’. According to this hypothesis, domain-specific cognition such as social intelligence is a by-product of the selection for general intelligence, which is required to cope with a changing environment. The cognitive buffer hypothesis challenges the social intelligence hypothesis, according to which gregarious animals acquired their social intelligence (and correspondingly larger brains) in response to the demands of social living. If general intelligence has its casual-etiological roots in the demands of ecological complexity, then we should expect to find elements of intelligence in all organisms that face such demands, barring constraints or contingencies to the contrary.

Studies of cognitive convergence, though compelling, are fraught with conceptual and methodological difficulties that often make their findings difficult to interpret. For instance, how precisely should we delineate the cognitive traits that are putatively converged upon, and at what level of description are they convergent? Additionally, it is widely acknowledged that convergence judgements are relative to hierarchical level—a trait may be convergent at the level of macro-morphology but homologous at the level of tissues, proteins, or genes. Likewise, complex cognition can be convergent at the level of cognitive mechanisms, while arising from divergent neuroanatomical structures (e.g. the cortex in mammals and the telencephalon in birds) that are comprised of homologous neural substrates and formed by conserved patterning mechanisms. McShea [42] aims to pick apart the cognitive
traits that are convergent, making a Humean case for the conceptual decoupling of motivational and affective faculties (‘wants-preferences-cares’), on the one hand, and intellectual faculties (‘logic-calculation-problem-solving’), on the other. He argues that both are crucial yet distinct causal components of the behaviour typically associated with cognition, and he points out that the evolutionary histories of these two distinct faculties can be dissociated.

Establishing convergent cognitive mechanisms is an especially challenging task, because unlike other phenotypic traits such as morphological or even behavioural characters, cognition implicates unobservable processes and hence must be inferred from behavioural observations. Some convergent behavioural traits, such as the ‘agriculture’ phenotype in ants and humans, are unlikely to be underpinned by similar cognitive mechanisms, even if some prominent discussions of convergence have loosely described such outcomes as convergent minds (e.g. [5]). However, many observed animal behaviours can be explained equally well by simpler and more complex cognitive mechanisms, and thus the logical structure of the inference from observed behaviours to the presence of particular cognitive mechanisms remains underspecified. In some cases, a preference for simpler cognitive explanations may be justified by additional sources of evidence (e.g. neuroanatomy) conjoined with background theoretical assumptions (e.g. about the relation between neuroanatomy and cognition). For example, Cartmill [43] argues that behavioural convergence need not be evidence of cognitive convergence for animals whose neurophysiology is unlikely to sustain intentionality and consciousness—two features of mind that he takes to be of particular interest in the quest to discover cases of convergent cognition. Thus, the tiny brains (in terms of total number of neurons) of jumping spiders rule them out as plausible contenders of cognitive convergence even though, as Cartmill notes, their predatory behaviour, which involves alternating among attack strategies such as stalking, ambushing, and frontal attacks, is as flexible as those of large cats. For similar reasons, Cartmill urges scepticism in evaluations of cephalopod behaviour (e.g. puzzle-solving behaviours of octopuses) given the radically alien organization and developmental history of cephalopod brains.

Cognitive models, neuroanatomy and broader evolutionary—ecological considerations may therefore be drawn upon to strengthen or weaken inferences of cognitive complexity; but precisely how these respective lines of evidence should be weighted and integrated is unclear. Mikhailovich et al. [44] take up the question as to how sources of evidence beyond the behavioural experimental setting—in particular, evolutionary and ecological theory and data—can inform hypothesis choice and experimental design in comparative cognition. Rejecting a blanket preference for simple explanations, they propose an evolutionary—ecological model according to which the repeated emergence of trait-clusters including (i) flexible behaviours, (ii) complex neuroanatomy and (iii) heterogeneous selective environments can be used to infer complex cognitive abilities because they comprise a non-accidental convergent regularity. This convergent regularity, in turn, may be used to support the inference to one trait (e.g. complex cognition) whenever lineages exhibit two or more of the other traits in the cluster. On this view, while, for example, the jumping spider may possess just a few hundred thousand neurons, its behavioural flexibility, heterogeneous ecology and comparatively encephalized neuroanatomy collectively speak in favour of the convergent complexity of its cognitive toolkit. A direct prediction of this model is that complex cognitive capacities will begin to degrade under relaxed selection in less informationally demanding environments—which agrees with Cartmill’s reminder that convergences include convergent losses, such as decreased encephalization in response to relaxed predation pressures, and that these, too, deserve our theoretical and empirical attention.

In sum, the time is ripe for a conceptually rich, multidisciplinary investigation into the evolution of cognition in its multiplicity of forms. It is only by examining cognitive convergence—and the lack thereof—in clades as phylogenetically, developmentally, and ecologically disparate as corvids, whales, carnivores, primates, cephalopod molluscs, jumping spiders, insects, green plants, fungi, and unicellular organisms, that we can begin to map out the phylogenetic distribution of cognition as well as its evolutionary drivers, constraints and consequences. As this broad-based picture begins to resolve, it will illuminate the interplay of contingency and necessity in the evolution of cognitive worlds.

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