Multi-trait convergent trends in the evolution of brains and cognition

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Abstract

Our target article proposed that vertebrates, cephalopod mollusks and euarthropods independently converged onto high levels of brain and cognitive complexity and that this macroevolutionary trend was coupled with and facilitated by the acquisition of a small set of pivotal traits, used in visuomotor control of three-dimensional and targeted movements. In response to commentaries that challenged our working premise and conclusions, we (1) use the concept of aggregate complexity to define brain and cognitive complexity and to dispel misconceptions about anthropocentric bias, (2) call attention to the explanatory value and power of convergence as an important evolutionary concept and approach, (3) highlight certain architectural and organizational features of the nervous system as neural scaffolds for the evolutionary expansion of behavioral and cognitive complexity, and (4) consider the phylogenetic distribution of phenomenal consciousness in relation to our findings. We also try to foster a greater appreciation for cognition as a process that involves whole animals as aggregate systems and that requires an extended repertoire of laws and principles to understand its evolution.

1. Introduction

First, many thanks to the authors of commentaries on our target article. We were delighted to hear from scholars with such diverse, interdisciplinary expertise. Indeed, we contributed to this diversity ourselves, with Trestman being a philosopher with long standing interests in the evolution of consciousness, and Coombs being a sensory biologist/ neuroethologist with a research career in the non-visual guidance of fish behaviors.

The commentaries prompted us to reexamine and reevaluate our basic assumptions and approach. They also gave us the opportunity to address some misconceptions about the multi-trait approach and to clarify our own thoughts on the principles and laws governing evolution and other concepts important to our findings, such as complexity, motor hierarchies, convergent evolution, and consciousness. Most of the time, we have a meeting of the ‘minds’ and respond to commentators with a single voice. On a few issues, however, we thought it best (and perhaps more interesting) to speak in our own individual voices (see sections 2.1 on aggregate complexity and 4.3 on consciousness).

In the final analysis, the evolution of complex brains and cognition involves concepts and principles that are themselves complex and evolving, even hotly debated. Furthermore, they involve a vast literature across multiple disciplines that is impossible to absorb in its entirety. Nevertheless, we found the commentary process to be a very thought-provoking and rewarding experience and hope that, in some small measure, it advances our overall understanding of how brains and cognition evolve.

2. Complexity and all its issues

Several contributors commented on the use of complexity as a defining characteristic of cognitively complex (CC) lineages and questioned our working premise that only vertebrates, cephalopod mollusks and euarthropods had this level of complexity. **Clark**, for example, argued that unicellular organisms exhibit complex cooperative behaviors, and that by implication, complex behaviors don't require a brain or nervous system. In a similar vein, **Agrillo and coauthors** argued that decentralized neural architectures can support complex forms of cognition in multicellular animals like jellyfish (Ctenophora) without a brain. **Finke and coauthors** thought that our working premise was based on anthropocentric criteria for cognitive complexity, setting us on a biased path. Similarly, **Markowitsch and Staniloiu** thought that our proposed evolutionary trajectories from simple to complex sounded like a throwback to *scala naturae,* in which lower (inferior) life forms like insects lead to higher (superior) life forms, with humans at the very top.

We can't help but think that some if not all of these concerns and misconceptions might have been allayed had we provided a more concrete, non-anthropocentric definition of complexity. Indeed, **Beasely** predicted this very problem, saying that it would be a "mistake to leave it (complexity) up to intuitive interpretation" especially since it might serve as a 'unifying concept' to replace terms like 'sophisticated', 'advanced' and 'higher'. For better or worse, we abandoned earlier attempts to define complexity, thinking that the phylogenetic distribution of behavioral and learning traits we selected as indicators of complex cognition would be more important than any definition we could devise. Here we merge the concepts of 'aggregate complexity' and 'systems-level' organismal biology as a way to think about brain and cognitive complexity in non-anthropocentric terms. Seen in this light, complexity has more to do with the number of integrated parts of the whole than it does with superlatives like 'superior' or 'advanced'.

2.1 Cognition and behavior as emergent properties of aggregate complexity (Coombs)

Although aggregate complexity means different things in different fields, we use it here to refer to the relationships between many different elements working together in an integrated fashion to create complex behavior. Manson (2001) describes aggregate complexity as having three defining characteristics, which are very similar to the 'systems' view of living organisms as integrated parts of the whole (e.g., Capra, 1996). These are that aggregate complexity is (1) self-organizing and autonomous and (2) flexible and dynamic, resulting in behaviors that can 'shape, react to or anticipate' changes in the environment. Aggregate complexity also (3) gives rise to emergent properties that cannot be traced directly back to attributes of individual elements but that arise from their synergistic interactions.

In terms of this view of aggregate complexity, animal behavior is thus an emergent property of synergistic interactions between the constituent elements of the organism's body, and the degree of complexity is a function of the number and type of interactions between elements. For unicellular organisms, elements are things like internal (e.g., nucleus, mitochondria and other organelles) and external (e.g., cell membrane, cilia, flagella) parts at the subcellular level of interactions, or different membrane ion channels or receptors at the molecular level. Multicellular organisms have these elements plus those associated with higher levels of organization, such as (1) different cell or tissue types – e.g., muscle, nerve, or connective tissue or (2) different body-wide systems consisting of different tissues and structures, such as musculoskeletal, nervous, circulatory, digestive and respiratory systems.

Cognitive processes underlying behavior (e.g., attention, learning and memory) in multicellular organisms can, in turn, be viewed as the emergent properties of interacting elements in the brain and/or nervous system, including different neuron types at the cellular level, different pathways and circuits at the network level, and different brain regions at the structural level (see Fig. 3 in target article and Appendix A). The dynamic and flexible nature of cognitive processes arise primarily from the inherent plasticity of neuronal connectivity, which changes during development and as a result of momentary or life-long experiences (von Benhardi et al, 2017; Sweatt, 2016).

Flexibility also depends on architectural and organizational features of the brain and nervous system, such as the laminar organization of first-order visual structures (section 2.3), the neural architecture of adaptive filters in the brain (see *Brain traits* in Appendix B of the target article) and motor hierarchies (Fig. 1). Motor hierarchies consist of a chain-of-command (process-oriented) organization in which there are several distinct brain (or nerve cord) regions that typically serve as high- mid- and low-level controllers of behavior with high levels playing more of a supervisory and decision-making role and low-level controllers, more of a semi-autonomous, final execution role (see also Fig. 2 in the target article and Tables 1 and 2 in Appendix A).

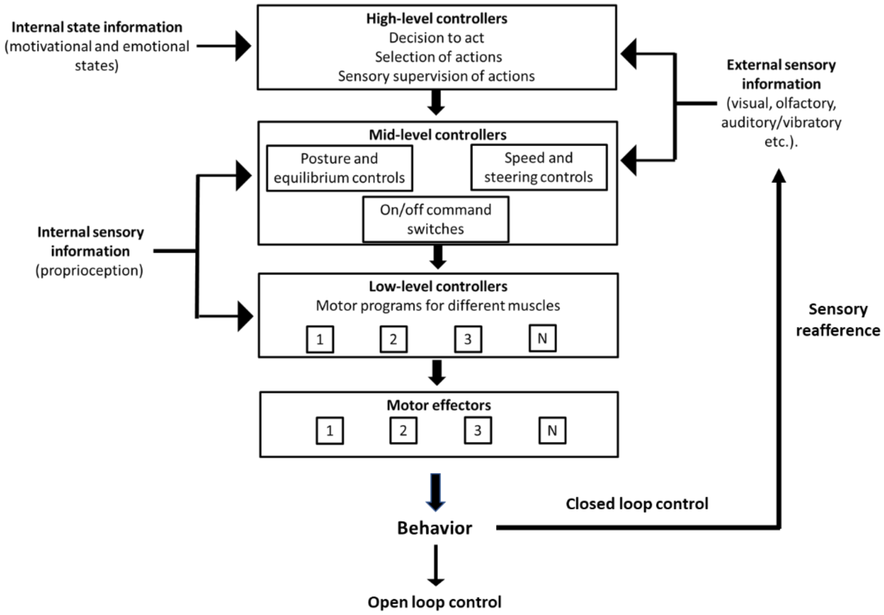

Figure 1 (from Appendix B in the target article). Hierarchically organized motor control system illustrating different levels and types (open vs closed loop) of motor control. Adapted from Orlovsky et al. (1999) and Merel et al. (2019). See *Motor hierarchy* in Appendix B for further information. Note that the flow chart does not depict the highly complex neural interconnections between brain structures that function as motor controllers.

In animals with complex brains and cognition, motor hierarchies are the organizational backbone of behavioral flexibility in that motor outputs (behavior) can be modulated by both internal and external sensory information, as well as internal state information on motivational (e.g., hunger, thirst, sexual drive) and emotional (e.g., positive and negative affects) states. Behavior is also modulated by learning and memory processes that take place in different controllers, each of which also function as multisensory and sensorimotor integration sites to support various behaviors and cognitive processes. As such, the motor hierarchy has all the components – "multimodal sensory integration, hierarchical sensorimotor loops and decentralized control structures" - that **Schilling and Risse** emphasize as being critical to a 'comprehensive perspective on cognitive evolution'. It also meets Barton and Bartlett's requirement that "cognition encompass all of the processes that guide and control behavior". Furthermore, high-level motor controllers in the motor hierarchy incorporate valenced signals related to bodily needs, pain, pleasure, emotions, and uncertainty (see section 4.2), which are critical for coherent control of behavior, as **Ainslie's** commentary illustrates. Finally, the motor hierarchy encompasses many, if not all of the stages of **Demetriou, Savva and Sanoudis's** model of evolving cognition. This is not to say that cognition in all living organisms requires a motor hierarchy, or even a brain or nervous system (Lyon et al., 2021), only that motor hierarchies involving distinct brain regions are characteristic of complex brains and cognition.

Coming full circle, we want to clarify that our working premise (that only vertebrates, cephalopod mollusks and euarthropods have complex brains and cognitive abilities) was based on more than just cognitive abilities like those listed in Table 1 of the target article. It was also based on the number of differentiated brain regions, as illustrated in Fig. 2 and Section 7.24 of the target article and in Tables 1 and 2 of Appendix A. In the final analysis, we view the multi-trait analysis as a work in progress. The distributions of operationalized (and non-anthropocentric) brain, behavior and cognitive traits will ultimately either support, modify or refute our initial working premise that animals in CC lineages have the most complex brains and cognitive abilities in the animal kingdom.

2.2 Complex cognition: How do we recognize it and how do we map cognitive traits?

From a computational perspective, cognition can be seen as a *process* that involves interactions between computational elements, such as neurons, and that enables animals to 'shape, react to or anticipate' changes in the environment – in other words, to solve problems and take actions that promote survival and reproductive success. Acquiring food, for example, can involve a relatively simple algorithm (solution) that enables animals to follow a chemical gradient to e.g., a specific odor source, or more complex solutions, such as the construction of a spatial map in the brain that enables animals to navigate to a food-enriched geographic area. Cognitive complexity can thus be seen as a rough measure of the difficulty and number of problems that can be solved and the degree to which knowledge from experiences can be acquired (learned), stored in memory, and applied to new problems.

The collection, storage and use of environmental information by an animal during its lifecycle, can be understood as a process of the animal statistically modeling or tuning internal *representations* to biologically relevant features of its environment, as **Schilling and Risse** emphasize. For example, *search images* encode biologically-relevant perceptual and spatial features that guide search behaviors for e.g., predators (Suzuki, 2018) or prey. As another example, the ability of honeybees to take a novel shortcut to an unseen destination after being displaced from their route (Menzel and Greggers, 2015) is taken as evidence that they have some sort of cognitive map of the terrain (Tolman,). From the perspective of our approach, forms of representation can only be thought of as traits when they can be directly observed as natural behaviors or determined from behavioral experiments.

Even with defining characteristics like these, cognitive traits are difficult to operationalize and apply to a wide range of animals, making them of limited use for wide phylogenetic comparison. Instead, we used two complex behavioral traits (central place foraging and construction behaviors) and one complex learning trait (unlimited associative learning, UAL) as indicators of complex cognition to see if they clustered in CC lineages, as hypothesized (see also section 4.3 for how these traits relate to consciousness). Thus, we did not "deploy UAL as a pivotal trait" to mark the emergence of complex cognition, as we think **Merker** perhaps misinterpreted. Traits that we regarded as pivotal consisted of body (flexible limbs), sensory (high resolution eyes, 3D rotational sense), brain (laminated visual structures) and motor (high speed locomotion and mobile eyes) traits only.

Nevertheless, we concede that UAL and two other learning traits (non-associative, NA and limited associative learning, LAL) are problematic, as pointed out by Merker and Markowitsch and Staniloiu, in that they are broad categories that encompass different forms of learning (e.g., habituation, sensitization, and classical and operant conditioning) and memory (e.g., short and long-term). It would have been better to map different forms of learning (and memory) separately rather than to bundle them into categories envisioned by Ginsburg and Jablonka (2021).

Mapping specific learning traits was never our focus, however. Rather, we used NA and UAL as putative 'bookends' for simple and complex learning abilities in order to compare their distributions. We would welcome a refinement and extension of our analysis that did a more rigorous job of mapping different forms of learning and memory across lineages. We agree with **Figdor** that the ideal solution would be to discover "cognitive characters individuated at multiple grain sizes linked to phylogeny" and a "nested hierarchy of cognitive characters that can be mapped to clades in phylogeny". This could address Merker's concern that there is insufficient evidence to attribute UAL to all three CC lineages. The 'absence of evidence problem' still looms large for cognitive traits like these due to the lack of research, especially for non-CC lineages.

Given the difficulties of purely cognitive traits and "the incompleteness with which animal behavioral capacities have been mapped across phyla" (Merker's accurate assessment), we see the mapping of natural behaviors as a practical way forward. In fact, we are grateful to several commentators for suggesting good traits (section 4).

2.3 Neural scaffolds for bridging the gap between pivotal traits and complex cognition

Several commentators talked about the relationship between pivotal traits and complex cognition. Figdor thought that there were several challenges to bridging the gap between our 'pivotal traits' and complex cognition (see section 2.1). Similarly, **Wright and Clayton** noted that the "interplay between the sensorimotor system and complex cognition on a causal level remains elusive". **Marmolejo-Ramos and Ciria**, on the other hand, saw a direct link between laminated visual structures (one of our pivotal traits) and complex cognition in the form of predictive processing that occurs in the visual structure. Finally, Barton and Barrett argue that embodied traits, whether pivotal or not, "do not simply set the stage for cognitive evolution to occur", they are 'part and parcel' of it.

We certainly share Barton and Barrett's view of embodied traits as being part and parcel of cognition for any given species at any given point in evolutionary time. However, the addition of new elements over evolutionary time can expand cognitive abilities in ways that weren't possible before. For example, laminated visual structures, in combination with high resolution eyes, serve as new elements that significantly "open up downstream phenotypic space" (to quote Klein, Baron and Halina) for new behavioral and cognitive abilities (see column 5, Fig. 5 in target article).

In this case, new cognitive abilities are made possible by the computational architecture of laminated structures and the retinotopic mapping of light from different directions. Each layer in the laminated structure consists of a two-dimensional matrix of neurons arranged in rows and columns, which when stacked together form the equivalent of a three-dimensional spreadsheet. This organization plus the pixelation of light by high resolution eyes greatly expands the computational ability of the visual system to extract spatiotemporal features of the visual world, such as well-defined (dark/light) edges of discrete objects and their direction of movement (as detailed in section 3.3 of the target article). Each feature represents the computational output of a local circuit or *neural motif* (see Fig. 4 in target article).

One of the best and perhaps oldest known examples of a neural motif is lateral inhibition, first discovered in the retina and optic lobe of the phylogenetically ancient horseshoe crab (*Limulus limulus*)(~ 445 mya) by Hartline (1969). It is most widely recognized for its edge enhancing features at light/dark boundaries, but it also has multipurpose applications, thus capturing the idea of *neural reuse,* as mentioned by **Radomski and colleagues** as an important mechanism for the expansion of cognitive abilities. That is, lateral inhibitory circuits have a predictive function that "suppresses predictable features, while enhancing novel and unexpected features" (Srinivasan et al., 1982, Hosoya et al., 2005;

Johnston et al., 2019). Marmolejo-Ramos and Ciria describe this function in a slightly different way as “enhancing contrast by filtering expected correlations”.

Inspired by magicians who excel at manipulating visual expectations, Wright and Clayton see feature extraction by laminated visual structures as an efficient way to form generalizations about different objects and thus, to create visual expectations. Drawing from Tuefel and Fletcher’s (2020) neurocomputational predictive framework, Marmolejo-Ramos and Ciria further propose that these structures represent a “context-independent, bottom-up predictive mechanism that anticipates environmental regularities”, and that this goes hand-in-hand with “context-dependent, top-down predictions (expectations)” that rely on learning and memory processes in higher brain centers (see also section 4.3). The bottom line is that these laminated, first-order processing areas support a front-end, expandable filter with multiple feature detectors to shape what the rest of the brain ‘sees’ .

2.4 What is so special about vision when it comes to the evolution of complex brains and cognition?

Several commentators questioned whether visual abilities, in the form of three pivotal traits (high resolution eyes, laminated brain structures and mobile eyes), were truly as pivotal to the evolution of complex brains and cognition as our findings suggest. Finke et al, for example, thought that it was “unclear why senses like echolocation would be less cognitively demanding” than vision and that our emphasis on vision reflects an anthropocentric (or at the very least, vertebrate-centric) bias. Radomski and colleague**s** felt that we overemphasized the importance of active visual sensing, while neglecting the importance of other forms of active sensing. Similarly, **Schilling and Risse** worried that an “overemphasis on a single modality as vision would miss out on the complexity arising from multimodal sensory integration as a form of representation building ”.

First, we did not arbitrarily focus on vision because of some preconceived notion of its importance. Rather, we let the distribution of many traits, which included several non-visual senses as well as multisensory integration sites in the brain, reveal the importance of visual (and other pivotal traits) to CC, but not non-CC lineages. Second, it is important to remember that diverse and complex body forms (including complex eyes and brain regions) first arose during the Cambrian explosion, somewhere between 520 and 515 mya (Fig. 7 in target article). The fossil evidence indicates that euarthropods were the first to evolve complex eyes, leading to their dominance in early Cambrian communities (Zhao et al, 2013), and, as many hypothesize, the subsequent predator/prey arms race and diversification of body forms that followed (Parker, 2004; Marshall 2006; Smith and Harper, 2013). Image vision may or may not be more computationally demanding than something like echolocation, but the circumstances that enabled its evolution occurred hundreds of millions of years ago, long before vertebrates transitioned to land and subsequently took to the air as echolocating bats or reinvaded the oceans as echolocating cetaceans (Cabrera et al., 2021). For whatever reasons, vision arose much earlier and is far more widespread than echolocation, which evolved only after vertebrate brains were adapted for vision.

2.4.1 Active photo-sensing vs active visual sensing

Radomski and colleagues make a valid point about the importance of active sensing to a wide spectrum of organisms, irrespective of whether the sensing is done by mechanosensory (auditory/vibratory/tactile), chemosensory (olfactory) or photosensory cells, and irrespective of whether sensors are embedded in the cellular membrane of a single-cell eukaryote or in a dedicated sense organ in a multicellular animal.

In our paper, active visual sensing refers to multi-pixel light sensing or *image* (low- or high-resolution) vision (Nilsson, 2022), which requires additional elements besides photoreceptors (e.g., lenses and brain structures for processing multi-pixel inputs) to parse ambient light levels. These are not available to single-celled organisms and, in so far as we know, animals below complexity level 3 in the multi-trait framework (Table 2 in target article). Without image-forming eyes, there is no optic flow for closed-loop guidance of behavior (Fig 1) and no way for animals to gauge either relative speed or position with respect to the surrounding (stationary) environment through photo-sensing alone. Non-imaging forms of active *photo-sensing,* which include things like phototaxis (e.g., moving up a light gradient) or photokinesis (e.g., increasing motor activity or speed when moving from a light to dark area or vice versa), do not provide this kind of guidance. Nevertheless, non-visual forms of active sensing by mechanosensory flow sensors could have provided information about speed and position with respect to the surrounding environment, but only at very close distances (<~ 1 body length away) (Hassan, 1989; Windsor, 2014). These are all important distinctions to make, and we thank the commentators for drawing them to our attention.

2.4.2 Multisensory and sensorimotor integration in the evolution of brains, behavior and cognition.

We certainly agree with Schilling and Risse on the importance of multisensory integration to the evolution of cognition. This is why we mapped a range of traits related to multisensory processing, including multimodal sensing abilities (>= 2 senses present) and multisensory integration sites in the brain (as best we could determine them based on criteria in Appendix B). Also included were several non-visual senses (auditory/vibratory, olfactory, gravistatic, flow and body motion senses). None of these sensory traits were remotely unique to CC lineages (Fig. 3A in target article). So, if, by hypothesis, CC lineages are unique in having the most complex brains, then multimodal sensing and integration abilities cannot, by themselves, explain how or why CC but not non-CC lineages reached the highest levels of brain complexity. Non-visual senses and multimodal sensing/integration are nevertheless critical to the evolution of brains and cognition (see Appendix C of target article). Based on the distribution of traits, however, we think it more likely that multisensory integration areas in the brain were *already* in place as foundational or intermediate building blocks before the emergence of high-resolution eyes and other pivotal traits.

From a sensory-ecology perspective, multisensory integration is a way for animals to increase information content and reduce uncertainty about e.g., the identity or whereabouts of a predator or prey. Most importantly, it did not evolve to produce perceptions of the external world that are ‘accurate’ in the abstract, but to control behaviors important to an animal’s survival. As a prime example, retinotopically mapped, mid-level structures in the motor hierarchy (e.g., the optic tectum of vertebrates and lobula plate of euarthropod optic lobes) control egocentric (self-centered) orienting behaviors, which direct animals towards a potential prey, mate or item of interest, or away from e.g., an obstacle or predator (see Appendix C of the target article and Coombs and Montgomery, 2014 for multisensory control of orienting behaviors). In vertebrates, a retinotopic visual map resides in the superficial (dorsal) layer of the optic tectum, whereas the deepest (ventral) part contains a dynamic motor ‘error’ map that determines the degree to which an animal must turn in order to close the gap between its current heading and the desired direction (Sparks, 1988;King, 2004). Sandwiched in between are non-visual maps (e.g., somatosensory maps of body space and auditory maps of sound source locations computed from binaural cues). Most importantly, the different sensory maps in this structure are mutually aligned (in spatial register with each other) for the sole purpose of enabling animals to orient their eyes, limbs, head, or entire body in a particular direction with respect to 'something else'(King, 2004). As such, egocentric orientation can be viewed as an observable indicator of phenomenal consciousness as it relates to a sense of bodily and spatial self (see section 4.3).

2.5. The progression from less to more complex biological forms is a real phenomenon, not a backwards glance at 'scala naturae'

A few contributors took issue with the notion of an evolutionary progression from simple to complex. Markowitsch and Staniloiu saw our approach and transitional framework as being little more than a regurgitation of Aristotle's *scala naturae*, an ordering of the natural world from lowly and inferior creatures like worms and insects to the highest of life forms, humans (Fig. 1a). And Barton and Barrett, who were generally supportive of our approach, were "wary of the potentially distorting effects of terminology such as "advanced" or "apical" vs "basal" (Fig. 5) and the notion of progression through evolutionary stages (Fig. 6)". We understand and appreciate these misgivings, as a healthy skepticism of progressive trends is well-founded (Hodos and Campbell, 1969; McShea, 1996; Gregory 2008).

Despite superficial similarities, however, the trend we reported is very different from that depicted by *scala naturae.* Aristotle's approach was similar to ours in two ways. One, he used multiple traits - different body, sensory and motor traits - that could be easily observed in a wide variety of vertebrates and invertebrates. Two, he started with a working premise, albeit very different from ours, that humans represented the 'highest' form of life. He then used these traits to gauge the degree to which different life forms had characteristics similar to those in humans. Aristotle's 'ordering' of life forms on the stepladder was thus very much an anthropocentric endeavor.

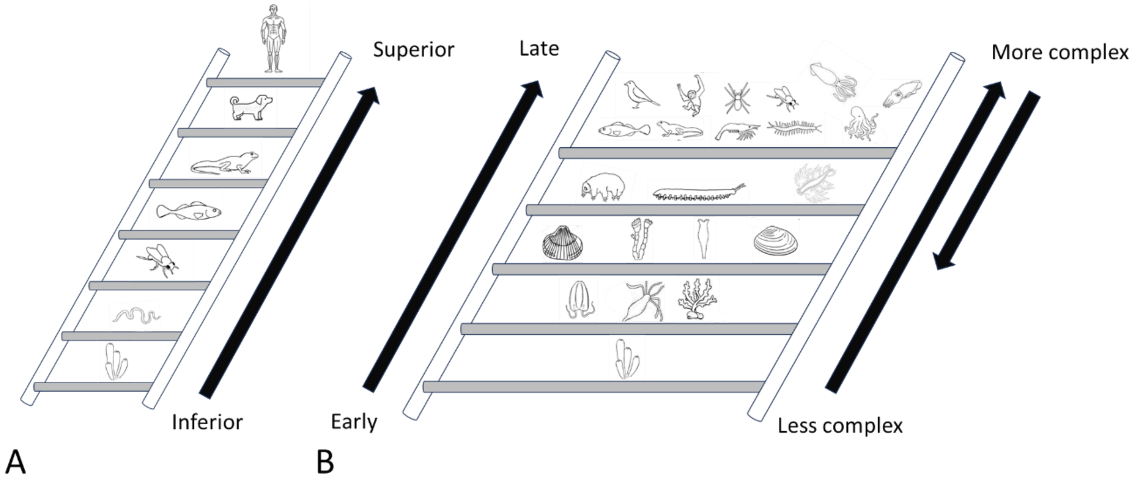

Fig. 1 Comparing *scala naturae* (A) and multi-trait (B) stepladders. *Scala naturae* depicts a hierarchically organized, one-way progression of life forms from inferior to superior without respect to evolutionary histories or time, whereas the multi-trait stepladder depicts a non-hierarchical, two-way progression of life forms from early and less complex to later and more complex.

In contrast, we did not 'order' life forms according to their similarity or dissimilarity to humans or any other animal in our CC groupings (vertebrates, euarthropods and cephalopod mollusks). Our working premise was not that one species (*Homo sapiens*) was more superior to others, but that three entire lineages had converged upon the highest levels of brain and cognitive complexity. Life forms were thus ordered according to levels of combined body, sensory, brain and motor complexities, as illustrated in Fig. 5 and Table 3 of the target article. According to modern phylogenetic trees (Fig. 1 in the target article), they are also ordered somewhat chronologically, with phylogenetically older (basal), non-bilateral life forms in the phyla Porifera, Ctenophora and Cnidaria at the bottom of the stepladder, and more recently derived (apical), bilateral forms, such as vertebrates, euarthropods and cephalopod mollusks (CC lineages) at the top (Fig. 1B).

Finally, unlike *scala naturae*, the multi-trait stepladder captures an increase in body complexity over evolutionary time that is a two-way street, with the potential for some lineages to reach their current-day life forms by climbing all the way to the top of the stairs and then taking one or two steps backwards (see Fig. 6 and section 4.2 in the target article). The notion of backward steps (regressive loss of traits) is entirely consistent with the evidence for gene loss in some phyla (e.g, annelids and tardigrades, see section 4.3 in target article). Moreover, some lineages, like echinoderms and cnidarians (see section 6 in target article), veer off the ladder entirely to land on a different combination of traits than those prescribed by the stepladder. So, in this sense, the stepladder does not depict an inexorable march towards complexity, but a major 'freeway' that many, if not most lineages take, but from which there are several off ramps and alternate routes.

Last, but certainly not least, there is independent evidence, apart from our multi-trait analysis, for patterns of increasing biological complexity over evolutionary time scales (McShea, 2021). In addition, theoretical models of this phenomenon predict that the complexity of life forms will increase, even in the absence of natural selection (McShea, 2021). Thus, there may be other 'laws' besides Darwinian laws of natural selection that govern patterns of increasing biological complexity.

2.6. Complexity and species diversity

There are many roads to evolutionary success and many different types of complexity. Nematodes and Platyhelminthes, for example, exceed vertebrates, mollusks, and even arthropods in their 'lifecycle complexity' (number and diversity of metamorphic stages and pathways), and also their 'parasitic complexity' (number and diversity of parasitic ecological niches) (Benesh 2016). Vertebrates, arthropods, and cephalopod mollusks, on the other hand, appear to exceed other phyla in terms of their body, brain, and behavioral/cognitive complexity. This level of complexity allowed these three lineages to rapidly explore the space of morphological and ecological possibilities, using new types of limbs, perceptual abilities, and behavior to conquer and create new niches and transform ecosystems (Trestman, 2013). In this regard, it is indeed noteworthy, as Markowitsh and Staniloui point out, that CC lineages have very high levels of species diversity. Fig. 1B gives a feel for the nature of this diversity.

Using the Catalog of Life web site (www.catologueoflife.org) to determine the number of species per phylum, we examined the relationship between species diversity and the number of foundational, intermediate and pivotal traits. Species diversity showed a weak, but positive correlation with the number of traits in all three categories, with pivotal traits (our highest level of complexity) producing the strongest correlation (Fig. 2). Correlations do not prove causation, of course, and the phylum unit of measurement is somewhat problematic. Moreover, several non-CC phyla (Bryozoa, Platyhelminthes and Nematoda) have high levels of species diversity (~20000 species) despite having zero pivotal traits and low levels of brain complexity. Nevertheless, the trend is in the right direction, suggesting that pivotal traits are one among many factors that contribute to species diversity.

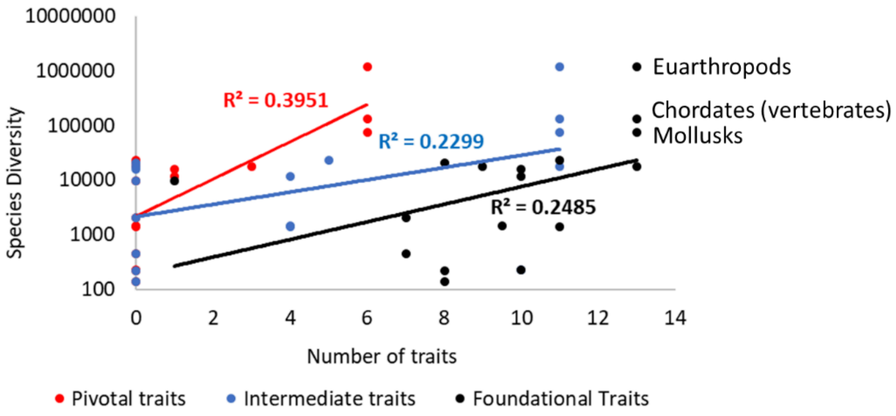

Fig. 2. Relationship between species diversity and total number of body, sensory, brain and motor traits in each of three categories (foundational, intermediate and pivotal) for each phylum.

3. Keeping evolutionary principles in 'mind'

Fink and coauthors argued that "cognitive complexity cannot be meaningfully compared across taxa without considering their various niches and environments". Similarly, Markowitsch and Staniloiu couldn't see value in such comparisons since "their members differ immensely with respect to cognition and the nervous system - both within and between the three lineages".

It is certainly true that there is tremendous diversity within and between each of the three CC lineages (Fig. 2), but it is also true that the traits that bind each lineage may be just as or even more important than those that divide them. With the exception of hagfish, vertebrate brains consist of five highly conserved brain structures (Northcutt, 2002) (see Fig. 2 and Appendix A in target article). Similarly, euarthropods share the same brain organization and constituent regions (Fig 2 and Appendix A). Even more astonishing, in our opinion, is that the brains of all three CC lineages appear to have converged onto very similar organizational themes and complexities (Fig. 2 and Appendix A of the target article).

3.1. The explanatory value and power of convergence: What does it tell us?

Convergent evolution is a ubiquitous phenomenon in animal evolution and a central concept in evolutionary biology that has both explanatory value and power (Stayton, 2015). The explanatory value of convergent trends is in terms of associations that are revealed, such as the association between flying abilities and non-homologous wing structures in birds, flying insects and some mammals (bats). In our case, the association is between combined pivotal traits and complex brains and cognition in three distantly related CC lineages. The power of the association (in a statistical sense) thus lies in the number of times (n = 3 lineages) the association can be replicated. In our study, we were also able to show the converse – i.e., the lack of this association in non-CC lineages (n = 14).

Identifying convergent trends that reveal associations between two variables like pivotal traits and complex brains is one thing, but explaining their evolutionary genesis in independent lineages is quite another. Turner and colleagues thus rightly ask: what are the selection factors that led to the evolution of pivotal traits and complex brains? Do we need a plethora of different factors to explain their evolution in millions of species and ecological niches, or can we apply a more general principle?

Following Godfrey-Smith's 1998 Environmental Complexity Hypothesis, Turner and colleagues propose that complex environments may be the unifying (external) selection pressure that drives the evolution of complex brains and cognition within and between these independent lineages. As we understand it, complex environments can include complex spatial distributions of resources in the physical environment, complex interactions between conspecifics as part of an animal's social environment, or complex predator and prey interactions as part of the overall ecological environment. As such, this hypothesis provides a very broad but unifying construct for explaining convergent trends in the face of all the "diverse ecological, social and cultural factors" that Finke and coauthors faulted us for ignoring. The precise details and nature of the complex environment (e.g., social vs ecological factors) will vary for different species both within and between lineages, but the overall adaptive advantage – the behavioral (and cognitive) flexibility to "cope with a heterogeneous and changing environment" (Turner and colleagues) - remains the same.

If complex environments represent a unifying selection pressure that drove the evolution of combined pivotal traits and complex brains (and cognition) in three, distantly related CC lineages, then what explains the convergence of non-CC lineages on different multi-trait combinations at lower levels of complexity (Fig 1B and Table 2 in the target article)? Did non-CC lineages with lower levels of complexity live in correspondingly less complex environments? Were traits linked because they (a) contributed to the same 'adaptive syndrome', (b) were subject to the same developmental constraints involving gene regulatory networks, or (c) a little of both? Did any other factors play a role, like the laws of physics or those that give rise to overall patterns of increasing biological complexity (McShea, 2021)?

We certainly don't have all the answers, but it is important to point out that evolution involves both external (e.g., selection pressures and the laws of physics) and internal (e.g., developmental processes governed by gene regulatory networks) factors. This is similar, in principle, to what Turner and colleagues refer to as *externalist* vs *internalist* modes of explanation. The bottom line is that "natural selection has to work with raw materials that are subject to a variety of other principles or laws, including what we generally call developmental and/or physical constraints" (Streidter, 2020). In our opinion, the convergence of CC lineages onto pivotal traits and complex brains/cognition involved both external and internal factors, with perhaps gene regulatory networks favoring the development of certain trait combinations over others.

3.2 Convergence and macro evolution

The convergence of CC lineages onto pivotal traits, complex brains and cognition represents a major macro evolutionary trend in the history of animal life, one that first emerged during the Cambrian explosion and amazingly, has been maintained (and even expanded upon) ever since – even through several mass extinctions. Big picture questions about the macro evolution of brains and cognition challenge us to consider evolutionary processes spanning hundreds of millions of years and leading to millions of current-day species. Causation at this level is qualitatively different from micro evolutionary processes like natural selection, where differences between individuals within a population influence the later makeup of the population. Macro evolution does not occur at a steady pace, but is punctuated by singular events in history during which the diversity of life suddenly increases (e.g., the Cambrian explosion) or crashes (e.g., the Permian extinction). We must look to the complicated circumstances (abiotic + biotic factors) of the Cambrian explosion to explain the beginning of the convergent trend identified in our study. But once pivotal traits were in place, we propose that the many and varied adaptive advantages of the resultant embodied 'toolkit' for cognition, in the face of 'heterogenous and changing environments" (to quote Turner and colleagues), were responsible for maintaining it for hundreds of millions of years.

3.3. Evolutionary transitions

Klein, Barron, and Halina challenge us to think about how our proposed transitions truly identify "breaks with the past that open up downstream phenotypic space" (sensu Maynard Smith and Szathmáry, 1995). They also argue that changes in brain architecture have unidirectionally driven changes in behavioral and cognitive abilities, and that changes in brain architecture are best accounted for by "resource-usage grounds alone". We certainly agree that the conservation of energy and resources plays an important role in the evolution of brains. Laminated visual structures (one of our pivotal traits) is an excellent example of an architectural strategy for reducing the distance between adjacent cells in local circuits (Striedter, 2005), and also the energy and time required to make connections between adjacent cells during development (Nikolaou and Meyer, 2014).

As discussed in section 3.1, however, there are many factors besides resource usage governing the evolution of complex brains and cognition. Moreover, it is difficult to understand how resource usage alone can explain the evolution of laminar visual structures without the accompanying inputs from high resolution eyes. Without the multi-pixel parsing of ambient light levels by the sensory apparatus, there would be no need (advantage) for small numbers of clustered neurons to expand into multiple layers of many more neurons.

In terms of 'phenotypic space openings', these are not just those for expanded cognitive abilities, but also those for new motor and behavioral capacities (columns 4 and 5 in Fig 5 of the target article), which depend on multiple combined traits, not just the brain. That is what our analysis appears to show, not that complex brains precede or drive complex bodies or cognition, but that a certain set of body, sensory, and brain traits serve as a collective key to unlock a new level of complexity for all traits,

In this regard, it is also important to point out that individual body parts like the brain do not develop or evolve in isolation from other body parts and furthermore, that natural selection operates on whole individuals and their behavioral interactions with the environment, not on isolated body parts. The fact that we made no a priori assumptions about what constitutes a major transition means that we let the data (trait distributions) lead us to the transitions. In this regard, it is reassuring to know that most if not all of our multi-trait transitions coincide with those identified by Klein and coauthor, as they themselves note.

3.4 Widening the phylogenetic spectrum to unicellular organisms

Both Radomski et al. and Clark called for a widening of the phylogenetic spectrum of our analysis to include unicellular organisms. Radomski et al felt that it would "add a complementary *past-to-present* perspective to our *present-to-past* perspective", given that our multi-trait framework was based on traits observed in current-day (extant) living forms. Clark, on the other hand, was more interested in the collective behaviors observed among single cell organisms, arguing that even single celled organisms have complex behaviors and cognitive abilities. Regardless of the reason, we think it is an excellent idea to include single-celled organisms in the mix.

Per Radomski et al., the metazoan lineage evolved from a unicellular ancestor much like the living choanoflagellates (see Ros-Rocher and Burnet, 2023; Fairclough, 2015; Carr et al, 2023; Koehl, 2021 for recent reviews on this topic). Choanoflagellates and metazoans share cellular mechanisms for basic chemo-, mechano- and photo-sensing abilities (Ros-Rochet and Brunet, 2023). Thus, if we were to revise our pyramid of traits, these general sensing abilities would be broadly shared with CC and non-CC lineages alike. Tellingly, metazoans and choanoflagellates also share signaling and adhesion genes (as part of gene regulatory networks) involved in cell division and the development of metazoan tissues (Fairclough, 2015).

Choanoflagellates also form tight-knit colonies with outwardly directed flagella that improve the flux of prey-bearing currents to these filter feeding creatures (Koehl, 2021). However, these colonies are not formed by individuals sensing each other and coming together for social reasons, but rather by cell division of a single individual to produce multiple, genetically identical clones that fail to break apart (Koehl, 2021). Collaboration between different individuals thus turns out to be the result of cell division and adhesion, rather than behavioral choices driven by perception, memory, and predictive cognition, as in CC animals. This example illustrates how different organisms can have deceptively similar behaviors (collective feeding) for similar adaptive advantages (maximizing food acquisition) but involving entirely different mechanisms. This is why Turner and colleagues wisely advise that all of Tinbergen's (1963, 2005) four questions on mechanisms, phylogeny, ontogeny, and adaptive significance be considered when thinking about the evolution of behavior (see also Liu and Konopka, 2020).

4. Other traits

Several commentators suggested the following additional traits for consideration.

4.1. REM sleep as a pivotal brain/motor trait

Becchetti presents us with the intriguing possibility that rapid eye movement (REM) sleep may be another pivotal motor and/or brain trait in CC lineages. As Becchetti suggests, the activation of both sensory and motor pathways during REM sleep would serve as a useful mechanism for consolidating visuomotor integration circuits used during awake behaviors. The idea that REM sleep is exclusive to CC lineages is entirely consistent with our findings that mobile eyes are likewise exclusive, and that mobile eyes, along with other pivotal traits, are important for active visual sensing. We agree with Becchetti that further research in this area would help elucidate the evolutionary function of REM sleep and its potential relationship to more complex forms of cognition.

4.2 Social behaviors as indicators of complex cognition

Bhattacharya and Gosh felt that we neglected social cognition as a prominent "aspect of cognition, especially in non-human animals". Similarly, Clark thought that "specific capabilities for presumed higher-order social interactions had been curiously omitted", and that we ignored the possibility that collective behaviors in uni-cellular organisms might also be complex.

The overwhelming task of researching 35 traits in 17 lineages made it impossible for us to do justice to all the behavioral traits that might prove useful. Instead, we focused on a few behavioral and cognitive traits as 'token' indicators of complex cognition to provide a preliminary test of our working hypothesis. Thus, we welcome a more comprehensive look at the distribution of complex social and other types of complex behaviors as an obvious direction for future research.

With respect to collective behaviors in unicellular organisms, we contend that they are not anywhere near as complex as those found in multicellular organisms for two compelling reasons. First, the mechanisms underlying uni- and multi-cellular group behaviors may be entirely different, especially when examined in a phylogenetically relevant context (see section 3.4). Second, in terms of aggregate complexity, unicellular organisms are much less complex than multicellular organisms. Unicellular organisms have interactive elements at subcellular and molecular levels of organization, but only one cell. Multicellular organisms in CC lineages have millions to trillions of cells, each containing interactive elements at subcellular and molecular levels, but also a multitude of other elements at higher levels of organization (see section 2.1).

4.3 Consciousness, self-hood, and valence (Trestman)

Baron, Minert and Devor ask "When did consciousness, the “me inside”, arise in Darwinian evolution?". We chose not to include consciousness and related mental phenomena explicitly in our original analysis, as cognitive complexity was tricky to operationalize (see section 1.2), and we did not want to introduce another heavy layer of theory between our findings and interpretation. However, though we avoided loading theoretical assumptions about consciousness into the analysis, our results are highly relevant to resolving questions about its evolutionary origins and phylogenetic distribution.

Consciousness is notoriously tricky to define. Setting aside the usage of the term to simply mean awake or responsive, we follow Block’s (1995) notion of ‘phenomenal’ consciousness, denoting the subjective dimension of life: *‘what it is like to be*’ a bat (Nagel 1974), a bee (Chittka 2019), a human, or any of the *beings* that that seem to have such an individual *perspective* of their own. Consciousness is *subjectivity* itself, the possibility of, or ‘container for’, the domain of lived experience (sensations, thoughts, feelings). But “what it is like to be” a *particular* creature, human or otherwise, includes a cluster of subtly distinct aspects of mental life.

Baron et al.’s 'me-inside’, has *layers*. The ***bodily self*** (the perception of one's body, its needs, and its capabilities) can be distinguished from the ***social self*** (awareness of one’s relationships to and perception by others), although the two domains are intimately related (E.g. James 1892). The bodily self can also be thought of as the ***spatial self***, since space and the body emerge in relation to each other. For example, Merker (2005, 2013) and Rudrauf et al. (2023) highlight the sense of self implicit in visual perspective and target orientation – the self as the ‘pivot point’ about which lines of sight intersect, as an important scaffold for egoentric behavior and experience (see section 2.4.2 for multisensory brain sites dedicated to egocentric orientation). Jekely, Godfrey-Smith and Keijzar (2021) highlight *reafferance,* as critical for the body-self, consistent with our emphasis on active sensing.

The most fundamental layer of self-hood in consciousness is *temporal*. ***Temporal self-hood*** is the self-awareness of the *stream* of experience itself, the fusion of perspectives across moments in time that holds together that stream. The fusion of perspectives across experiences makes possible the experience of *change*, and is required for the distinctions between *object* and *appearance* (an object *could* appear different ways, and a given appearance *could* disclose different objects), and *self* and *world* (self/body being the part of the world that responds to direct control, that feels and senses, etc.). The fusion of temporal perspectives is fundamental to consciousness in the sense that other layers of the self, such as the spatial/bodily and social, are constructed upon it as a developmental and computational scaffold, and could not exist without it (Trestman 2013, 2017). It is held to be the basis of subjectivity itself in Husserl’s phenomenological system (Zahavi 1999; Husserl 1919/1964).

Temporal selfhood is logically essential to both a) ***agency*** (the ability to *choose,* intend outcomes, and act purposefully), and b) ***valenced intentionality*** (the ability to judge any *thing (physical object, social other, location, state, configuration, etc)* as *good* or *bad.* When any subject *anticipates* an experience (for example, how a food item *will* taste, as they prepare to bite into it), the *anticipating* 'self' must be identified (fused into a single logical object) with the subject of the *anticipated* experience. The subsequent experience of tasting the food, must be experienced *with* the remembered anticipation of and the sensorimotor sequence leading to and composing the bite–the ‘self’ who anticipated and acted is fused with the ‘self’ who now tastes and remembers.

To make a choice is to anticipate a plurality of possible futures as contingent on one’s possible actions. The conscious self fuses together the present *possible actor* with the *anticipated observer of the various* *possible effects of possible actions*. Therefore, each moment of conscious experience must include a) a recursive chain of *retained* previous moments that constitute the short-term subjective past, and b) a recursively branching tree of *predicted* possible moments that constitute the short-term subjective future. This logical schema, called 'BITRIP' for 'branched, iterated, retention-impression-protention' (Trestman 2013b), is hypothesized to account for a number of properties of consciousness, including the distinctive *streaming* or *flow* property of subjective time, the contrast of expectation and observation implicit in surprise, and the counterfactual logical structure of causal relationships (Trestman 2013b, 2017, 2023, Husserl 1919/1964; Zahavi 1999; Yoshimi 2016). Without it, there can be no continuity of subjectivity integrated over time, and there can be no bodily self – i.e., no sense of the body's needs, sensitivities and capacities.

The schema (BITRIP) closely matches the requirements of Karl Friston's theory of ***active inference*** by prediction-error minimization, an important aspect of the 'predictive paradigm' in the brain and behavioral sciences, as discussed Demetriou et al**.**, **Friedrich and Fischer**, and Marmolejo-Ramos and Ciria. Active inference theory identifies *minimization of expected, weighted, prediction-error* as an overarching normative epistemic principle driving the brain's function in perception, cognition, and behavior. While prediction-error minimization (PEM) is a general heuristic that occurs at many levels of organization in the brain, active inference theory (AIT) postulates that PEM operates in the high-level controllers of the brain's motor hierarchy (Fig. 1), integrating perception, memory, motivation, learning, energy-budgeting, planning, and action-selection. AIT equates this integrative process with consciousness and attempts to model a variety of neuro-psychological phenomena (Solms and Friston 2018).

Active inference requires an agent to possess a generative model of action-contingent future outcomes. This model not only supports the *contrast* between prior expectations and subsequent outcomes (once they are actually observed), but also *predictions* about how *predicted expectations* will match *outcomes*. This theory provides a mathematical framework for combining an agent's preferences and attachments (valence) with *belief* (hypotheses in what Friedrich and Frische call an agent's *world model*), in relation to incoming sensory evidence and the need for sequential action-selection. In AIT, preferences are represented as *weighted* predictions (what Marmolejo-Ramos and Ciria call *constraints*), in contrast with un-weighted predictions representing neutral expectations. Valence, on this theory, is understood in terms of free energy (aggregate expected, weighted, prediction error), with higher free energy corresponding to more strongly negative (i.e. *aversive*, *bad, unpleasant, dysphoric*) experience, and low free energy corresponding to more strongly positive (i.e. *rewarding, good, pleasant, euphoric*) experience (Solms 2019; Joffily and Coricelli 2013).

It is encouraging that the structural requirements for active inference closely match the structure of BITRIP, a model of consciousness grounded in pure phenomenology. It suggests the possibility of a unified theory that can explain how agents build knowledge of their world while surviving danger and uncertainty, while also accurately describing how value, uncertainty, choice, and agency factor into conscious experience for humans and other animals (Solms and Friston 2018). We agree wholeheartedly with Ainslie that valenced cognition is ancient and fundamental to complex animal behavior, and that mapping more fine-grained behaviors related to valenced cognition will prove fruitful.

Temporal selfhood is also fundamental to *intentionality*, the ability to cognize *objects* in the general sense of any *thing* that has *properties* and *identity*, and can be tracked across situations. A subject must be able to compare observations to conceptualize whether an object, pattern, property, or signal, is present in both. Observing *self*, observed *object*, and observation *event* all depend on synthesis across observations. The distinctions between object and appearance and between self and world are logically entangled and emerge together with the origins of subjective time, as the fundamental building blocks of more complex forms of object-oriented cognition and experience (Trestman 2013b).

This line of thinking inspired the insight that a ***macroevolutionary signature of consciousness*** could be formulated in terms of traits that depend on ***object-oriented*** and ***place-oriented spatial cognition*** for their function (Trestman 2017). Consciousness grants morphological and sensorimotor evolvability to a lineage by allowing and motivating individuals to discover spatiotemporal relationships between action and outcome. This evolvability opened phenotypic space for novel forms of body, sensorimotor function, cognition, behavior, and ecological space for novel niches. This inspired our choice of *construction* and *central place foraging* as indicator traits, since both classes of behavior involve manipulating the spatial arrangement of an animal's environment in relation to its bodily/spatial 'self'. Control of orientation is a good proxy for consciousness in the brain because it "requires access to situational, motivational, and context information determining behavioral priorities" Merker (2013), which involve top-down inputs at the highest levels of the motor hierarchy (Fig. 1, section 2.1).

Our current findings support the hypothesis that consciousness is present in each of the CC lineages: vertebrates, arthropods, and cephalopod mollusks (as per Trestman 2017). Each of these lineages is distinctively characterized by a proliferation of various modes of object-oriented and place-oriented behaviors, and related morphological, sensorimotor, and neuroarchitectural traits. This corroborates claims for consciousness in these taxa based on other evidence (Jablonka and Ginsburg 2019; Feinberg and Mallat 2016,2020; Barron and Klein 2016; reviewed in Trestman and Birch, forthcoming/2025) .

It remains uncertain whether consciousness arose independently in each lineage, or only once much earlier in Bilateria. Other non-CC animals, such as tardigrades, velvet worms, jellyfish or nematodes, may have cryptic forms of conscious 'me inside' that have not yet been revealed. Alternatively, it may be that the energy and information flowing through their bodies is never integrated into the structure of subjectivity; perhaps there is life but no fusion of moments into an ongoing lived experience, no awareness of a 'me' that survives moment to moment.

5. Concluding remarks

Only time will tell if the convergent trends and pivotal traits identified in the target article hold up and how or whether they relate to the evolution of brains and cognition. We certainly acknowledge that there is still much to be learned about the evolution of cognition in all its forms by examining different species in terms of their own ecological niches and the selection pressures that shaped them. But if we dive into every nook and cranny of life's diversity, we risk losing the ability to see the forest through the trees and miss the opportunity for discovering major trends and unifying principles.

Moving forward, we argue for painting with a wider brush, not only in terms of a wider phylogenetic spectrum, but also in terms of a wider spectrum of integrated traits. Animals are aggregate systems with many different parts, levels of organization and emergent properties like cognition. But we cannot understand the evolution of cognition by investigating only one part (e.g., the brain) without respect to other parts (e.g., senses and limbs). Similarly, we cannot understand cognition in the absence of behavior.

We must also consider a wider spectrum of laws and principles to explain both micro- and macro-evolutionary trends and associations that we observe, recognizing that Darwin's law of natural selection is not the only game in town; other laws and principles are at play when it comes to the evolution of brains and cognition (Finlay et al., 2001; Streidter, 2005; Striedter and Northcutt, 2020) and even biological complexity in and of itself (McShea, 2020, see section 1.3). In terms of vertebrate brain evolution, Streidter (2005) makes a particularly compelling case for this point of view, stating that "most complex systems, including those studied by physicists, tend to be governed by a variety of laws, forces and factors that interact. Therefore, evolutionary biologists ought not to whittle down their set of laws but seek a unitary theory that accommodates and unifies a lot of different laws."

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