The Fish Challenge to Vertebrate Cognitive Evolution

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Summary

There is tremendous taxonomic variation in the size, shape, and structure of vertebrate brains. While many studies aim at identifying the ecological factors (social and environmental) that explain brain size variation within taxa, a more fundamental divide exists between endotherm and ectotherm vertebrates. Ectotherms have ten times smaller brains than endotherms. The existing hypotheses cannot explain this divide, as some endotherm species with relatively simpler social organisation and diets still possess larger brains. Furthermore, research demonstrates that at least fishes possess a cognitive "toolkit" equivalent to that of many endotherms. This is the *fish challenge* to vertebrate cognitive evolution. We review hypothesised causes and consequences of brain size differences to propose two non-exclusive solutions. First, the fish brain achieves modularity at a lower cost, but it is less efficient in problem-solving than an endothermic brain with a more domain-general organisation. Second, brain size variation can be better explained by perception and motor skills rather than by cognitive processes. In that case, understanding brain size would require applying a broad definition of cognition. Specifically, it would be fitting to define animal cognition as how animals take in and process sensory information before deciding how to act on it with motor competencies.

Introduction

The size, shape, and structure of vertebrate brains show marked taxonomic variation. Brains are fascinating organs because they are energetically costly, yet they enable organisms to adapt their behaviour and physiology to ecological conditions [1–4]. The study of brain evolution has led to a vast body of literature from the early 20th century to the present day [5,6], exploring the costs and benefits of different brain traits. While there is substantial variation in these traits, such as neuron numbers and types, neuron size, glial cells, dendrites, and interconnections between areas within and across clades [7,8], the impact of this variation on costs and benefits remains unclear. As a result, brain size is one of the most widely used and relatively straightforward traits for studying a wide range of species, including existing and extinct species, and even fossils, with measurements such as volume, mass, or cranial capacity [9]. Consequently, the study of brain size has generated one of the most extensive datasets available across different species and taxonomic groups (e.g., [6,10]). In contrast, the physiological costs of brains are not well understood outside humans, where the brain consumes about 20% of the available energy in adults [11]. In this article, we use brain size as a proxy for physiological costs, recognising that this measure is likely to introduce an unknown amount of unexplained variation.

Using such datasets, researchers have conducted numerous phylogenetic comparative analyses, aiming to determine which ecological traits (such as social or environmental factors) offer the best explanation for variations in brain size and identify the most significant cognitive correlates of brain size. This led to the emergence of various hypotheses of brain and cognitive evolution. Although these hypotheses can explain a significant portion of the variation in brain size and cognitive capacities, they often only apply to specific groups of species and may be sensitive to the species included [2,4], potentially biasing the results in favour of one hypothesis over another. Currently, there is no consensus on which ecological traits and cognitive capabilities can explain variation in brain size across different groups of species. In addition, explicit analyses aiming to explain selective pressures underlying the brain size variation across major groups such as endotherms (mammals and birds) and ectotherms (fish, amphibians, and reptiles) have not been conducted.

The average endothermic vertebrate species typically possesses a brain about ten times larger than that of an average ectothermic vertebrate of the same body size [12,13]. This article therefore primarily focuses on this significant difference rather than on potential explanations for variations in relative brain size within major clades. One key ectotherm versus endotherm divide is thermoregulation, but this alone cannot explain the tenfold difference in relative brain size. In mammals, key areas for thermoregulation, such as the preoptic area and the dorsomedial hypothalamus [14], constitute only a tiny proportion of the brain. Additionally, based on current evidence, it seems that the tenfold difference cannot be attributed to endotherms having lower neuron densities in their brains. At least among amniotes, birds have the highest neuron densities, mammals somewhat lower ones and reptiles the lowest densities [15], although the densities of fishes may be different and more dependent on body size [16]. Endotherms have also larger forebrains relative to the rest of the brain compared to ectotherm vertebrates [17], suggesting a major role in cognition-related functions. Another crucial divide between endotherms and ectotherms is brain allometry. Linear regression of log-transformed brain size on log-transformed body size in adult mammals gives a slope value of about 0.27 within species [18], while the average slope in adult fishes is much steeper, about 0.45 [13,19]. These slopes are expected to reflect cognitive equivalence, i.e. how much brains must increase in volume to handle a larger body [19]. This marked difference is due to two main features of ectotherms: achieving continuous body size growth beyond the adult size due to indeterminate growth [20], accompanied by continued neurogenesis [21]. In general, while this is how ectotherms achieve neural plasticity, endotherms achieve this by changes in the connections among existing neurons [22]. Taken together, these systematic differences in brain size and organisation should lead to differences in brain capacities between endotherm and ectotherm vertebrates.

Larger brains relative to body size are thought to confer cognitive advantages, although the nature of these benefits is debated. With that in mind, what cognitive benefits might a mouse with a relatively large brain have compared to a bony fish like the goby, of similar body size but with a brain tenfold smaller than the mouse's? Here, in this opinion piece, we aim to reassess our current understanding of brain size evolution in general by including the often-overlooked ancestral group of vertebrates, the ectotherms. We question the idea that "bigger is better" for cognitive evolution as ectotherms, especially fish, can demonstrate impressive cognitive abilities often associated with primates. We then reevaluate the "bigger is better" concept, not specifically for cognition, but for other functions that may contribute to cognitive processing. These alternative perspectives lead us to consider updating the classic definition of animal cognition to account for the significant differences in sensory and motor systems across animal groups and the need to incorporate these capabilities into our understanding of cognition.

The same evolutionary hypotheses can be applied to both endotherm and ectotherm brain size

Multiple evolutionary ideas have emerged from the phylogenetic comparative approach, which has advanced our understanding of how ecological selective pressures, such as social and environmental challenges, requiring advanced cognition has led to brain expansion. These hypotheses are named after the ecological conditions they focus on. For instance, the Social Brain Hypothesis uses proxies for social complexity, like group size, coalition size, social and mating system, as predictors for brain size [23,24]. narrower version, the Cultural Brain Hypothesis, proposes that factors associated with cultural knowledge, such as social learning, best explain rapid brain expansion, especially in primates [3,25]. Alternatively, the Ecological Brain Hypothesis (or better termed ‘environmental brain hypothesis’ as ecology encompasses social interactions) proposes that factors related to the species' feeding ecology are linked to brain expansion to support the development of cognitive skills [4,26,27]. These hypotheses, while initially developed to explain variation in primate brain size, have been widely applied to other mammals, birds and also to fishes, typically using the comparative approach (birds: [28]; fishes [29]), but more recently also to identify variation in cognition and/or brain size within a species [30]. The application of the same hypotheses and parameters to both endotherm and ectotherm vertebrate clades shows that the concepts cannot be used to explain the endotherm-ectotherm divide: solitary mammals (like forest duikers) and mammalian grazers with simple diets (like wildebeests) still have far larger brains relative to body size than social fishes and fishes with more complex diets do. Thus, the hypotheses can be used to explain some of the variation in the elevation and slopes of brain- body relationships within well-defined clades but not across major clades.

Endotherms and ectotherms have comparable cognitive “toolkits”

The evolutionary hypotheses on brain size evolution use ecological variables like group size or diet complexity as surrogates or proxies for variation in cognitive demands purported to lead to species differences in ‘intelligence’. Therefore, more proximate versions of the evolutionary hypotheses, like the Machiavellian intelligence hypothesis [31], propose closely investigating the cognitive toolkit as a function of social life complexity. For example, living in stable complex social groups may select for the evolution of theory of mind and imitation learning, while extractive foraging may select for the evolution of a physical understanding of tool use. Based on this reasoning, species with larger brains are expected to have a more extensive cognitive toolkit and engage in energy-intensive cognitive processes that smaller-brained species lack. Therefore, an average endothermic vertebrate (a mouse) should overall outperform an average ectothermic vertebrate of the same body size (a goby fish). Any cognitive processes the mouse utilise that the goby lacks could be considered computationally demanding. However, there is currently little evidence confirming the assumption that the average mammal outperforms the average fish. In fact, fish, which are well-studied for their cognitive abilities among ectotherms [32–34], demonstrate impressive performances across various cognitive tests that were previously thought to be achieved only by endotherms, particularly primates [35].

Various fish species have been tested in numerous cognitive tasks, many of which were initially developed for primates, including humans. The list of skills documented to be present in fish encompasses many abilities [32,35,36]. It includes but is not limited to the following examples: social transmission and traditions [37,38], cognitive flexibility [39], inhibitory control [40], numerical capacities [41], spatial memory [42], transitive inference [43], object permanence [44], generalisation [45], cooperative hunting and gesturing [46], long-term memory [47], and self-recognition in the mirror test [48]. Thus, based on current evidence, the cognitive processes, or the cognitive toolkit, appear to be well-developed in both endothermic and ectothermic vertebrates. It, therefore, appears that many cognitive processes considered to require such large amounts of neuronal tissue that fishes and other ectotherms could not evolve them can actually be supported by modest-sized brains.

Potential explanations for the tenfold difference in brain size between endotherms and ectotherms

We consider four potential explanations for the observed absence of significant cognitive differences between endotherms and ectotherms, despite their tenfold difference in relative brain size. One idea is that fundamental cognitive differences do not exist as initially thought. This interpretation would imply that brain size variations merely reflect the requirements of regulating endothermic physiology, though as we've noted, this explanation is unlikely to account for most of the variation. Alternatively, it is possible that our current emphasis lies mainly on cognitive processes that minimally relate to brain size variation, and that considering other aspects of cognitive performance—requiring different experimental approaches—could produce more insightful results. Along these lines, we identify three promising, non-mutually exclusive hypotheses that merit further detailed investigation:

(i) the tenfold differences could be quantitative cognition (more vs. less) rather than qualitative (presence vs. absence).
(ii) ectotherms may lack certain cognitive abilities, best categorised as domain-general processes.
(iii) the differences might not stem from cognition itself but from the ‘support’ functions of sensory systems and motor control, which are also brain-regulated.

From here on, we focus our discussion on these last three points.

We first consider whether the tenfold brain difference results in differences in cognition quantitatively rather than qualitatively. This implies that ectotherms have a cognitive toolkit comparable to that of endotherms but on a smaller scale [49]. For example, fish perform below average in the Piaget’s object permanence test. The test increases in complexity and difficulty levels across stages, from stages 1 to 6. Success in complex stages of this test poses cognitive challenges that require substantial working memory and the ability to create a mental picture of an object out of sight [50]. So far, most Piaget’s object permanence test performed on fish used stage 4; a relatively easier stage compared to 5 and 6. Fish have to locate an object after being visually displaced behind a barrier (left or right side) and out of sight in order to receive a reward. There are no reports on fish being tested in stages 5 or 6. The performance in stage 4 yields scores between random 50% and 75 % in fish species tested so far, like cleaner fish, guppies and African cichlids [44,51,52] (Bonin, et al., unpublished). Meanwhile, primates, dolphins, and birds score up to 90% on this complexity level [50,53,54]. This evidence demonstrates that although fish have some skills of object permanence, they reach a lower level than most endothermic species. Another example involves testing various animal species on how many stimulus pairs can be remembered in an operant conditioning learning test [55]. In this framework, an animal must learn a series of colour-and-shape discrimination tasks, e.g., a red circle and a green square. Once the animal meets the learning criterion for pair A, they proceed to a new combination, pair B, until they achieve the learning criterion. Following this, they undergo a recall test to assess their memory for the earlier learned pair A. Ectotherm species such as trout, stickleback, and iguana retained memories of up to five pairs, whereas chicken, mice and rats managed to remember up to 8 pairs. The experiment also involved one elephant, which was concluded when the elephant showed no memory limitations after successfully recalling 22 pairs. Interestingly, this was also applied to bees, with the best performers scoring a memory recall of 4 pairs [55]. Future comparative research should involve applying similar tests to different animal groups, analysing error rates, and exploring the consistency of these error rates between endotherms and ectotherms.

Our second potential explanation is that only endotherms show evidence for domain-general processes like *g* [51,56]. The latent *g*-factor represents the positive correlation of performance across various cognitive tasks and serves as a measure of general intelligence [56]. Notably, the overall score on the *g*-factor correlates positively with brain size in endotherms [57]. In ectotherms, by contrast, the various cognitive abilities are considered modular, because an individual's or a species' performance in one cognitive task does not necessarily correspond with their performance in another task [51,52,58,59]. This uncorrelated performance across tasks fits results on brain anatomy, given that the performance on specific tests is correlated with specific brain regions, in a pattern that is different for each task [52,60]. For example, African cichlids show a positive correlation between performance in the reversal learning task (a test for cognitive flexibility) and the relative (body-size corrected) cerebellum size and a negative correlation with the relative size of the optic tectum. On the other hand, performance in the detour task (an inhibitory control test) shows a positive correlation with relative optic tectum [52]. Although ideally, these results are replicated and also examined in many more species, they strongly suggest that the organisation of the fish brain is more modular, in contrast to that of the encephalised brain of endotherms, which generates system-level cognitive abilities that can be used across different tasks of various cognitive domains. In line with this view, there is currently little evidence that ectotherms possess important working memory capacities [51,52] (Bonin et al., unpublished), as working memory is a crucial executive function contributing to the ‘*g*’ factor [56]. Because working memory may be responsible for the poorer performance of ectotherms on higher levels of object permanence or serial-recall discrimination tasks, the two possible explanations may overlap or merge.

We anticipate that some of the differences in brain size between endothermic and ectothermic vertebrates can be attributed to endotherms having structures that support more integrated cognitive processes and enhanced memory capacities. However, we find it highly improbable that these factors alone account for the entire tenfold disparity in brain allometry. These variables can more effectively account for significant aspects of brain size variation among mammals, as average-brained species such as mice tend to underperform in general intelligence and memory assessments compared to a large-brained mammal like the chimpanzee [55]. Let us, therefore, pursue the remaing proposed explanation.

Understanding and interacting with the world relies not only on cognitive abilities but also on perception and action. Sensory and motor systems are functional systems that underlie adaptive behaviours, where perception is crucial for planning actions and guiding them toward optimal goals. Cognition combines the perceived information and translates it into action [61]. For example, object manipulation involves not only a motor process but also connects sensory information about object properties with the combined representation of motor and sensory properties of the action. This perspective suggests that measures of cognitive performance may often depend on the presence of specific sensory and motor mechanisms. We propose that these systems may hold the key to explaining most of the tenfold brain expansion of endothermic species.

Within the primate lineage, it has long been recognised that the sensory-motor integration of humans largely surpasses that of other species [62]. Homunculus drawings serve in scientific disciplines to depict a distorted scale representation of the human body, illustrating the relative space occupied by different body parts in the brain. They highlight how the motor cortex emphasises our coordination skills, particularly focusing on the hands for object manipulation and on the lips and tongue for language functions [63]. Developing these skills also involves the cerebellum, where a template is formed to assess if sensory information aligns with motor output. This close coordination allows humans to play musical instruments such as the violin and piano [64]. In humans, the brain regions involved are significantly larger compared to other primates [65]. However, primates, in general, have dedicated motor neurons that are directly controlled by the cortex to facilitate finger movements [66]. Only a few comparative studies have attempted to link sensory-motor integration to brain size. One major example concerns the expansion of the cerebellum and visual brain structures in primates, which seems to be the foundation for their precise visuomotor control and sophisticated manual dexterity [67,68]. The increased volume of these regions, which have distinct sensorimotor functions, is positively correlated with the overall brain size in this lineage [67,68]. More recently, Heldstab et al. [66] revealed a significant positive correlation within primates between manual dexterity and brain size.

A recent study on birds found that cognitive demands in response to social and environmental challenges do not directly correlate with relative brain size when other factors are considered in the statistical analysis. Specifically, eye size, as well as beak and limb morphology, are significant predictors of avian brain size [69]. Therefore, sensory-motor characteristics play a significant role in the evolution of brain size, similar to what is observed in primates. Additionally, in non-avian reptiles, limb reduction correlates with a lower relative brain size in Squamata (snakes and lizards) [70,71]. This is logical since limbs that are reduced or absent makes for less complex sensory-motor coordination for movement. Another compelling argument for the significance of 'non-cognitive' factors in brain evolution can be seen in fish. Mormyrids (elephant fishes) belong to a family whose species exhibit the largest brain-to-body ratios, comparable to average birds and mammals. These fish use complex electro-location techniques to find prey [72], i.e., they possess a neuron-hungry perception system that has caused an extreme enlargement of the cerebellum [73].

A working hypothesis framework for vertebrate brain evolution

From what we summarised above, a key conclusion is that many cognitive processes seem to require less neural tissue than commonly assumed. Consequently, ectotherm vertebrates, particularly fish, can exhibit cognitive abilities comparable to those of an average endotherm, provided current ecological conditions select on these skills. This is further supported by the increasing examples of invertebrates possessing relatively rich cognitive toolkits that extend well beyond basic classical and operant conditioning [74]. However, essential functions such as sensory systems, motor control systems, and sensory-motor integration may be fundamentally more complex in endotherms than in ectotherm vertebrates. We propose that these distinctions largely account for the tenfold difference in average relative brain size.

The key question is why mammals and birds have developed such advanced sensory-motor systems. A significant factor is the shift from aquatic to terrestrial and aerial life. This transition enables the perception of more complex environments. For instance, even in clear waters, such as coral reef seas, visibility is still limited to about 10-30 meters at best. In contrast, on land, good eyesight is essential for spotting conspecifics, predators, and prey from kilometres away. Additionally, while acoustic signals travel rapidly in water, making it challenging to extract directional information, olfactory communication flourishes on land. Thus, the evolution of more sophisticated sensory systems on land offers considerable fitness advantages than in water. Another critical aspect of terrestrial life is the challenge of gravity, which necessitated the evolution of limbs and significant motor control in the brain. Moreover, moving on land entails navigating diverse substrates, making sensory-motor integration crucial to prevent tripping or falling. Similarly, flying at high speeds in dense environments demands the ability to quickly adjust direction and speed, highlighting the importance of integration as movement speed increases. This speed is a vital factor differentiating mammals and birds from reptiles, which typically do not lift their bodies much above the ground, thus avoiding many potential hazards. Furthermore, it is evident that reptiles have not developed similarly complex sensory systems, a point that applies to amphibians as well (See review by MacIver and Finlay [75] for extended discussion and references).

How strong a demand might pure perception, motor control, and sensory-motor integration make on neuronal tissue? We view the evolution of complex sensory systems as a value in its own right. It may often pay to have detailed information about the world. For example, a gazelle relies on visual, auditory, and olfactory cues to detect predators while grazing, without immediately integrating this information into a motor response. In contrast, the same logic does not seem to hold for motor actions, which may appear less complex. In fact, even more complex motor tasks still depend on sensory feedback for accuracy, which means motor functions may be less advanced than sensory processes. This principle applies to activities such as running, flying, or using fingers and beaks for tool use, with specifics varying based on ecological niches [66,76].

Based on these considerations, we propose a working hypothesis regarding the relative contribution of various functions to brain size evolution (see Fig. 1). This working hypothesis seeks to outline the fundamental logic of our arguments. It begins with a somewhat arbitrary assumption: that approximately half of the average fish brain is dedicated to cognition in the classic sense, encompassing cognitive processes, learning, and memory. While this estimation may be inflated, it is important to highlight that studies connecting fish cognition with brain structure indicate that all significant brain regions, except for the brain stem, participate in these cognitive functions [77–79], where cognitive performance levels correlate (positively and negatively) with different brain regions in different species [52,60]. To illustrate this key point graphically, we chose a high value: if fish utilize roughly half of their brains for cognitive tasks, then the average mammal or bird would only be using about one-tenth for the same cognitive functions with the same level of complexity (Fig. 1). Attributing a relatively small brain mass to cognitive processes while reserving a larger portion for the sensory-motor system helps explain the surprising cognitive skills exhibited by fish in the classic cognitive tasks (e.g., mirror test). For instance, chimpanzees can recognise when they need a partner for a string-pulling task and are adept at selecting competent partners, which they then free from a cage [80]. Similarly, groupers (a fish) are aware they require a moray eel partner for cooperative hunting and can also identify proficient partners [81]. However, while groupers comprehend the ‘when’ and ‘with whom,’ they would struggle with the task of pulling a string and unlocking a door for their partner. Thus, although the cognitive processes may be relatively comparable, the sensory-motor integration required for achieving the objective is much simpler for groupers.

While we believe that variations in these features may significantly contribute to the differences in brain size among endotherms, we do not expect that the average gap between endotherms and ectotherms is primarily caused by these differences. Thus, we assign hypothetically 5% of the endotherm brain capacity to each integration, achieving quantitative superiority. In contrast, for ectotherms, we allocate minimal cognitive integration of about 1%, with any quantitative elements already included in the half mass allocated to the cognitive toolkit. Consequently, we hypothesise that most of the brain size disparity between endotherms and ectotherms can be linked to differences in sensory and motor control systems. We attribute the majority of neural tissue mass to sensory systems, a bit less to sensory-motor integration, and still less to 'pure' motor control. We hypothesise that the variation in brain size within endotherms (such as between a chimpanzee and a gazelle) is predominantly influenced by differences in sensory-motor integration abilities. Importantly, we acknowledge that these values are merely hypothetical and presented here to clarify our discussion. We understand that further empirical research is necessary to evaluate the relative importance of these various features in brain evolution, with the goal of creating a well-informed diagram to replace our current speculative model. Furthermore, we suggest a speculative pie chart for the average reptile. The size is the same as for fish. As reptiles have to cope with locomotion on land, we increased the share of neural tissue for motor control and, in turn, decreased the relevance of the cognitive toolkit for brain size.

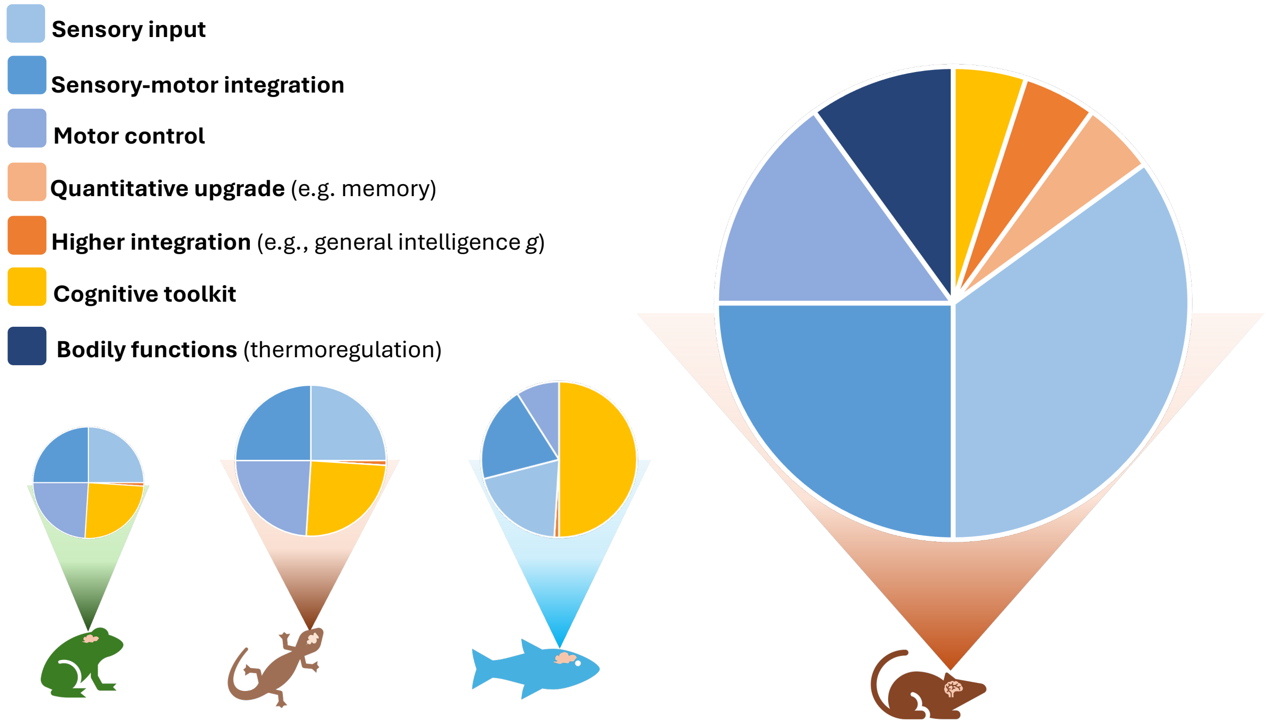

Figure 1. A hypothetical illustration of brain organisation in major ectotherm clades compared to an average endotherm. Using pie charts, we illustrate graphically the ideas proposed within the text. Based on the literature, we assume that the average fish and the average endotherm possess comparable cognitive toolkits, as indicated by the yellow part being of identical size. In contrast, reptiles and amphibians are suggested to have relatively smaller cognitive toolkits. Endotherms may outperform ectotherms if cognitive tasks are more quantitative in nature (like memory capacities) or focus on the integration of information (indicated by the presence of a general intelligence factor *g*). Otherwise, the largest share of the endotherm brain is used for sensory and motor systems and sensory-motor integration. Note that reptiles and amphibians have a larger share of these systems than fish, which are suggested based on the challenges posed by life on land vs life in water. Endotherms, in addition, allocate an additional portion of their brain to bodily functions such as thermoregulation.

Implication for brain evolution hypotheses

Hypotheses on brain evolution, such as the social and ecological brain hypotheses, have primarily concentrated on 'intelligence,' operating under the assumption that the main selective forces influencing brain size are related to cognitive processes, such as learning and cognitive flexibility. Our emphasis on the sensory-motor systems invites a re-evaluation of the brain functions that demand the most neural tissue. Did complex sensory systems, advanced motor systems, and sensory-motor integration evolve mainly to help individuals cope with social or environmental challenges? To illustrate, we witness that juvenile primates engage in extensive social play, which eventually helps them to navigate their social challenges. Meanwhile, repeated engagement with object manipulations in their environment allows them to cope with environmental challenges. Also, primates use advanced motor skills during foraging and grooming. Furthermore, visual acuity is crucial for recognising individuals and their emotions but also for differentiating between ripe and unripe fruits. Thus, one needs to investigate whether one domain is more complex than the other or whether sensory-motor control evolved indeed as a holistic tool. In this context, the classification of interspecific interactions as either social or non-social is important within our framework of brain evolution, since key sensory-motor skills play a vital role in evading predation and locating or capturing prey.

Independently of the sensory – motor system, there is still the question in which context the cognitive tool kit of species and clades evolved. Although certain cognitive processes, like theory of mind, imitation, and transitive inference, are closely associated with the social domain, and environmental skills, such as understanding the physics of tool use, sensory and motor skills can apply to both areas seamlessly. Similarly, executive functions—such as working memory, flexibility, and self-control—are easily applicable to both social and environmental challenges when the brain is organized in an integrative way, which appears to be characteristic of endotherms. Hypotheses linking brain size to the evolution of intelligence face challenges due to significant noise in data sets, largely from the critical role of sensory-motor systems. Therefore, we must explore new ways to test the social and ecological brain hypotheses related to the evolution of intelligence.

Conclusions

In this opinion piece, we highlight specific clades as promising models for exploring vertebrate brain evolution. For instance, amphibians tend to have smaller brains on average than fish and reptiles [13]. What implications does this have for their cognitive abilities and sensory-motor skills [82]? Reptiles are a significant clade as they share a comparable average brain size with fish despite their terrestrial lifestyle, which offers different sensory opportunities and movements. According to our hypothesis, their sensory-motor systems should require more brain mass than what fishes need. Accordingly, we would predict that their cognitive abilities are lower than what has been described in fish. Current evidence does not indicate that reptiles have large cognitive toolkits, but this could, at least in part, be due to relatively little research in this direction [33,83]. Furthermore, we need to study two clades that have relatively large brains despite living in water: First, cetaceans moved back to water and yet possess large brains, even for a mammal [75]. Second, elasmobranchs (sharks and rays) have larger brains than other ectotherm vertebrates [13]. According to our hypothesis, these clades will mostly yield insights into costly (i.e., energy-hungry neural tissue) sensory-motor systems rather than insights into major differences regarding cognitive processes.

In summary, building on our earlier discussion, we wish to present a revised definition of animal cognition that makes Shettleworth's classic definition more explicit regarding what we hypothesise concerns the majority of the brain functions. Our proposal defines animal cognition as the array of skills animals utilise to gather information via their sensory systems, process that information through cognitive processes, store it, and make decisions, executing them through sensory-motor integration and motor skills. This definition fits the quest to understand brain evolution in a holistic way. In contrast, for scientists interested in the evolution of the mind and cognitive toolkits, the challenge will be to design experiments that remove sensory-motor constraints to allow the subject to show its cognitive abilities.

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References

1. Aiello LC. 1997 Brains and guts in human evolution: The Expensive Tissue Hypothesis. *Braz. J. Genet.* **20**, 141–148. (doi:10.1590/S0100-84551997000100023)

2. Dunbar RIM. 1998 The social brain hypothesis. *Evol. Anthropol. Issues News Rev.* **6**, 178–190. (doi:10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)

3. van Schaik CP, Burkart JM. 2011 Social learning and evolution: the cultural intelligence hypothesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 1008–1016. (doi:10.1098/rstb.2010.0304)

4. DeCasien AR, Williams SA, Higham JP. 2017 Primate brain size is predicted by diet but not sociality. *Nat. Ecol. Evol.* **1**. (doi:10.1038/s41559-017-0112)

5. Hughes CH. 1903 HISTORY OF THE EVOLUTION OF THE BRAIN. *Alienist Neurol. 1880-1920* **24**, 153.

6. Venditti C, Baker J, Barton RA. 2024 Co-evolutionary dynamics of mammalian brain and body size. *Nature Ecology and Evolution*

7. Herculano-Houzel S. 2011 Not All Brains Are Made the Same: New Views on Brain Scaling in Evolution. *Brain. Behav. Evol.* **78**, 22–36. (doi:10.1159/000327318)

8. Liu H, Zeng Q, Zhou J, Bartlett A, Wang B-A, Berube P, Tian W, Kenworthy M, Altshul J, Nery JR. 2023 Single-cell DNA methylome and 3D multi-omic atlas of the adult mouse brain. *Nature* **624**, 366–377.

9. Rowe TB, Macrini TE, Luo Z-X. 2011 Fossil Evidence on Origin of the Mammalian Brain. *Science* **332**, 955–957. (doi:10.1126/science.1203117)

10. Herberstein ME, McLean DJ, Lowe E, Wolff JO, Khan MK, Smith K, Allen AP, Bulbert M, Buzatto BA, Eldridge MDB, Falster D, Fernandez Winzer L, Griffith SC, Madin JS, Narendra A, Westoby M, Whiting MJ, Wright IJ, Carthey AJR. 2022 AnimalTraits - a curated animal trait database for body mass, metabolic rate and brain size. *Sci. Data* **9**, 265. (doi:10.1038/s41597-022-01364-9)

11. Shulman RG, Hyder F, Rothman DL. 2009 Baseline brain energy supports the state of consciousness. *Proc. Natl. Acad. Sci.* **106**, 11096–11101.

12. Jerison H. 1973 Evolution of the Brain and Intelligence. New York: Academic Press. *N. Y. Acad. Press*

13. Tsuboi M, Bijl W van der, Kopperud BT, Erritzøe J, Voje KL, Kotrschal A, Yopak KE, Collin SP, Iwaniuk AN, Kolm N. 2018 Breakdown of brain–body allometry and the encephalization of birds and mammals. *Nat. Ecol. Evol.* **2**, 1492–1500. (doi:10.1038/s41559-018-0632-1)

14. DiMicco JA, Zaretsky DV. 2007 The dorsomedial hypothalamus: a new player in thermoregulation. *Am. J. Physiol.-Regul. Integr. Comp. Physiol.* **292**, R47–R63.

15. Kverková K, Marhounová L, Polonyiová A, Kocourek M, Zhang Y, Olkowicz S, Straková B, Pavelková Z, Vodička R, Frynta D. 2022 The evolution of brain neuron numbers in amniotes. *Proc. Natl. Acad. Sci.* **119**, e2121624119.

16. Olkowicz S, Kocourek M, Lučan RK, Porteš M, Fitch WT, Herculano-Houzel S, Němec P. 2016 Birds have primate-like numbers of neurons in the forebrain. *Proc. Natl. Acad. Sci.* **113**, 7255–7260. (doi:10.1073/pnas.1517131113)

17. Striedter GF, Northcutt RG. 2019 *Brains Through Time: A Natural History of Vertebrates*. Oxford University Press.

18. van Schaik CP, Triki Z, Bshary R, Heldstab SA. 2021 A Farewell to the Encephalization Quotient: A New Brain Size Measure for Comparative Primate Cognition. *Brain. Behav. Evol.* , 1–12. (doi:10.1159/000517013)

19. Triki Z, Aellen M, van Schaik CP, Bshary R. 2022 Relative Brain Size and Cognitive Equivalence in Fishes. *Brain. Behav. Evol.* **96**, 124–136. (doi:10.1159/000520741)

20. Sebens KP. 1987 The Ecology of Indeterminate Growth in Animals. *Annu. Rev. Ecol. Syst.* **18**, 371–407.

21. Zupanc GKH. 2008 Adult neurogenesis and neuronal regeneration in the brain of teleost fish. *J. Physiol.-Paris* **102**, 357–373. (doi:10.1016/j.jphysparis.2008.10.007)

22. Diamond M. 1988 Enriching heredity: The impact of the environment on the anatomy of the brain.

23. Humphrey NK. 1979 The social function of intellect. *Grow. Points Ethol.* , 303–317.

24. Dunbar RIM. 1992 Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **22**, 469–493. (doi:10.1016/0047-2484(92)90081-J)

25. Reader SM, Hager Y, Laland KN. 2011 The evolution of primate general and cultural intelligence. *Philos. Trans. R. Soc. B Biol. Sci.* **366**, 1017–1027. (doi:10.1098/rstb.2010.0342)

26. Clutton-Brock TH, Harvey PH. 1977 Primate ecology and social organization. *J. Zool.* **183**, 1–39. (doi:10.1111/j.1469-7998.1977.tb04171.x)

27. Hutcheon JM, Kirsch JAW, Garland Jr T. 2002 A Comparative Analysis of Brain Size in Relation to Foraging Ecology and Phylogeny in the Chiroptera. *Brain. Behav. Evol.* **60**, 165–180. (doi:10.1159/000065938)

28. Shultz S, Dunbar RIM. 2010 Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biol. J. Linn. Soc.* **100**, 111–123. (doi:10.1111/j.1095-8312.2010.01427.x)

29. Huber R, Staaden MJ van, Kaufman LS, Liem KF. 1997 Microhabitat Use, Trophic Patterns, and the Evolution of Brain Structure in African Cichlids. *Brain. Behav. Evol.* **50**, 167–182. (doi:10.1159/000113330)

30. Speechley EM, Ashton BJ, Foo YZ, Simmons LW, Ridley AR. 2024 Meta-analyses reveal support for the Social Intelligence Hypothesis. *Biol. Rev.*

31. Byrne R, Whiten A. 1989 *Machiavellian Intelligence : Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans (Oxford Science Publications)*. {Oxford University Press, USA}. See http://www.amazon.ca/exec/obidos/redirect?tag=citeulike09-20&path=ASIN/0198521758.

32. Salena MG, Turko AJ, Singh A, Pathak A, Hughes E, Brown C, Balshine S. 2021 Understanding fish cognition: a review and appraisal of current practices. *Anim. Cogn.* **24**, 395–406. (doi:10.1007/s10071-021-01488-2)

33. Szabo B, Noble DWA, Whiting MJ. 2021 Learning in non-avian reptiles 40 years on: advances and promising new directions. *Biol. Rev.* **96**, 331–356. (doi:10.1111/brv.12658)

34. Bshary R, Triki Z. 2022 Fish ecology and cognition: insights from studies on wild and wild-caught teleost fishes. *Curr. Opin. Behav. Sci.* **46**, 101174. (doi:10.1016/j.cobeha.2022.101174)

35. Bshary R, Wickler W, Fricke H. 2002 Fish cognition: a primate's eye view. *Anim. Cogn.* **5**, 1–13. (doi:10.1007/s10071-001-0116-5)

36. Bshary R, Brown C. 2014 Fish cognition. *Curr. Biol.* **24**, R947–R950. (doi:10.1016/j.cub.2014.08.043)

37. Helfman GS, Schultz ET. 1984 Social transmission of behavioural traditions in a coral reef fish. *Anim. Behav.* **32**, 379–384.

38. Warner RR. 1988 Traditionality of mating-site preferences in a coral reef fish. *Nature* **335**, 719–721. (doi:10.1038/335719a0)

39. Warren JM. 1960 Reversal learning by paradise fish (Macropodus opercularis). *J. Comp. Physiol. Psychol.* **53**, 376–378. (doi:10.1037/h0044187)

40. Lucon-Xiccato T, Gatto E, Bisazza A. 2017 Fish perform like mammals and birds in inhibitory motor control tasks. *Sci. Rep.* **7**, 13144. (doi:10.1038/s41598-017-13447-4)

41. Agrillo C, Dadda M, Serena G, Bisazza A. 2008 Do fish count? Spontaneous discrimination of quantity in female mosquitofish. *Anim. Cogn.* **11**, 495–503. (doi:10.1007/s10071-008-0140-9)

42. White GE, Brown C. 2014 A comparison of spatial learning and memory capabilities in intertidal gobies. *Behav. Ecol. Sociobiol.* **68**, 1393–1401. (doi:10.1007/s00265-014-1747-2)

43. Hotta T, Ueno K, Hataji Y, Kuroshima H, Fujita K, Kohda M. 2020 Transitive inference in cleaner wrasses (Labroides dimidiatus). *PloS One* **15**, e0237817.

44. Triki Z, Fong S, Amcoff M, Vàsquez-Nilsson S, Kolm N. 2023 Experimental expansion of relative telencephalon size improves the main executive function abilities in guppy. *PNAS Nexus* **2**, pgad129. (doi:10.1093/pnasnexus/pgad129)

45. Wismer S, Grutter A, Bshary R. 2016 Generalized rule application in bluestreak cleaner wrasse (Labroides dimidiatus): using predator species as social tools to reduce punishment. *Anim. Cogn.* **19**, 769–778. (doi:10.1007/s10071-016-0975-4)

46. Bshary R, Hohner A, Ait-el-Djoudi K, Fricke H. 2006 Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. *PLoS Biol.* (doi:10.1371/journal.pbio.0040431)

47. Triki Z, Bshary R. 2019 Long-term memory retention in a wild fish species *Labroides dimidiatus* eleven months after an aversive event. *Ethology* (doi:10.1111/eth.12978)

48. Kohda M, Takashi H, Takeyama T, Awata S, Tanaka H, Asai J, Jordan A. 2018 Cleaner wrasse pass the mark test. What are the implications for consciousness and self-awareness testing in animals? *bioRxiv* , 397067. (doi:10.1101/397067)

49. Bshary R. 2011 Machiavellian intelligence in fishes. *Fish Cogn. Behav.* , 277–297.

50. Call J. 2001 Object permanence in orangutans (Pongo pygmaeus), chimpanzees (Pan troglodytes), and children (Homo sapiens). *J. Comp. Psychol.* **115**, 159–171. (doi:10.1037/0735-7036.115.2.159)

51. Aellen M, Burkart JM, Bshary R. 2022 No evidence for general intelligence in a fish. *Ethology* **128**, 424–436. (doi:10.1111/eth.13275)

52. Guadagno A, Triki Z. 2024 Executive functions and brain morphology of male and female dominant and subordinate cichlid fish. *Brain Behav.* **14**, e3484. (doi:10.1002/brb3.3484)

53. Jaakkola K, Guarino E, Rodriguez M, Erb L, Trone M. 2010 What do dolphins (Tursiops truncatus) understand about hidden objects? *Anim. Cogn.* **13**, 103–120. (doi:10.1007/s10071-009-0250-z)

54. Hoffmann A, Rüttler V, Nieder A. 2011 Ontogeny of object permanence and object tracking in the carrion crow, Corvus corone. *Anim. Behav.* **82**, 359–367. (doi:10.1016/j.anbehav.2011.05.012)

55. Rensch B. 1973 *Gedächtnis, Begriffsbildung und Planhandlungen bei Tieren*. Parey.

56. Burkart JM, Schubiger MN, Schaik CP van. 2017 The evolution of general intelligence. *Behav. Brain Sci.* **40**. (doi:10.1017/S0140525X16000959)

57. Deaner RO, Isler K, Burkart J, van Schaik C. 2007 Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain. Behav. Evol.* **70**, 115–124. (doi:10.1159/000102973)

58. Triki Z, Bshary R. 2021 Sex differences in the cognitive abilities of a sex-changing fish species *Labroides dimidiatus*. *R. Soc. Open Sci.* **8**, 210239. (doi:10.1098/rsos.210239)

59. Triki Z, Zhou T, Argyriou E, Sousa de Novais E, Servant O, Kolm N. 2024 Social complexity affects cognitive abilities but not brain structure in a Poeciliid fish. *Behav. Ecol.* **35**, arae026. (doi:10.1093/beheco/arae026)

60. Triki Z, Granell-Ruiz M, Fong S, Amcoff M, Kolm N. 2022 Brain morphology correlates of learning and cognitive flexibility in a fish species (Poecilia reticulata). *Proc. R. Soc. B Biol. Sci.* **289**, 20220844. (doi:10.1098/rspb.2022.0844)

61. Shettleworth SJ. 1998 *Cognition, evolution, and behavior*. New York: Oxford University Press.

62. Vauclair J. 1982 Sensorimotor intelligence in human and non-human primates. *J. Hum. Evol.* **11**, 257–264.

63. Navarro-Guerrero N, Toprak S, Josifovski J, Jamone L. 2023 Visuo-haptic object perception for robots: an overview. *Auton. Robots* **47**, 377–403.

64. Zatorre RJ, Chen JL, Penhune VB. 2007 When the brain plays music: auditory–motor interactions in music perception and production. *Nat. Rev. Neurosci.* **8**, 547–558.

65. Kaas JH. 2008 The evolution of the complex sensory and motor systems of the human brain. *Brain Res. Bull.* **75**, 384–390. (doi:10.1016/j.brainresbull.2007.10.009)

66. Heldstab SA, Kosonen ZK, Koski SE, Burkart JM, van Schaik CP, Isler K. 2016 Manipulation complexity in primates coevolved with brain size and terrestriality. *Sci. Rep.* **6**, 24528. (doi:10.1038/srep24528)

67. Barton RA. 2004 Binocularity and brain evolution in primates. *Proc. Natl. Acad. Sci.* **101**, 10113–10115. (doi:10.1073/pnas.0401955101)

68. Barton RA. 2012 Embodied cognitive evolution and the cerebellum. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2097–2107. (doi:10.1098/rstb.2012.0112)

69. Song Z, Drobniak SM, Liu Y, van Schaik CP, Griesser M. 2024 Bird brains fit the bill: morphological diversification and the evolution of avian brain size. *bioRxiv* , 2024–07.

70. Heesy CP, Hall MI, Ruiz SA, Wells N. 2017 Decreases in relative cerebellum volume are correlated with digit reduction and limb loss in squamates. *FASEB J.* **31**, 748–8.

71. De Meester G, Huyghe K, Van Damme R. 2019 Brain size, ecology and sociality: a reptilian perspective. *Biol. J. Linn. Soc.* **126**, 381–391.

72. Sukhum KV. 2018 *The costs of a big brain: How region scaling and energetic costs influence brain size evolution in weakly electric african fishes (Mormyridae)*. Washington University in St. Louis.

73. Amey-Özel M, von der Emde G, Engelmann J, Grant K. 2015 More a finger than a nose: The trigeminal motor and sensory innervation of the Schnauzenorgan in the elephant-nose Fish Gnathonemus petersii. *J. Comp. Neurol.* **523**, 769–789. (doi:10.1002/cne.23710)

74. Chittka L, Niven J. 2009 Are Bigger Brains Better? *Curr. Biol.* **19**, R995–R1008. (doi:10.1016/j.cub.2009.08.023)

75. MacIver MA, Finlay BL. 2021 The neuroecology of the water-to-land transition and the evolution of the vertebrate brain. *Philos. Trans. R. Soc. B Biol. Sci.* **377**, 20200523. (doi:10.1098/rstb.2020.0523)

76. Navalón G, Bright JA, Marugán-Lobón J, Rayfield EJ. 2019 The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution* **73**, 422–435.

77. López JC, Broglio C, Rodríguez F, Thinus-Blanc C, Salas C. 2000 Reversal learning deficit in a spatial task but not in a cued one after telencephalic ablation in goldfish. *Behav. Brain Res.* **109**, 91–98. (doi:10.1016/s0166-4328(99)00167-9)

78. Broglio C, Rodríguez F, Salas C. 2003 Spatial cognition and its neural basis in teleost fishes. *Fish Fish.* **4**, 247–255. (doi:10.1046/j.1467-2979.2003.00128.x)

79. Ebbesson LOE, Braithwaite V. 2012 Environmental effects on fish neural plasticity and cognition. *J. Fish Biol.* **81**, 2151–2174. (doi:10.1111/j.1095-8649.2012.03486.x)

80. Melis AP, Hare B, Tomasello M. 2006 Chimpanzees Recruit the Best Collaborators. *Science* **311**, 1297–1300. (doi:10.1126/science.1123007)

81. Vail AL, Manica A, Bshary R. 2013 Referential gestures in fish collaborative hunting. *Nat. Commun.* **4**, 1765. (doi:10.1038/ncomms2781)

82. Burmeister SS. 2022 Chapter Three - Brain-behavior relationships of cognition in vertebrates: Lessons from amphibians. In *Advances in the Study of Behavior* (eds S Healy, J Podos), pp. 109–127. Academic Press. (doi:10.1016/bs.asb.2022.01.004)

83. Matsubara S, Deeming DC, Wilkinson A. 2017 Cold-blooded cognition: new directions in reptile cognition. *Curr. Opin. Behav. Sci.* **16**, 126–130.