Attentional control and vertebrate cognitive evolution

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Abstract

How might brain functioning differ between endotherm and ectotherm vertebrates? Recent results suggest that ectotherms lack proper working memory, which could reflect a lack of attentional control. Ectotherms may nevertheless excel in cognitive tasks if their ecological needs and learning opportunities compensate for their lower computing power.

Keywords

working memory, comparative cognition, cognitive evolution, attentional control, LAC hypothesis, CON framework

Introduction

The average 10-fold difference in relative brain size of endotherms compared to ectotherm vertebrates [1] raises the question about a potential cognitive gap between these two groups. This question is surprisingly challenging, as research on fish cognition reveals that their cognitive tool kit matches the ones reported for most endotherms (e.g. [2]). In particular, the cleaner wrasse *Labroides dimidiatus* has emerged as a model system to study fish cognition, and led to the discovery of a wide set of cognitive tools that go beyond basic reinforcement learning [3].

Recent research on cleaner wrasse focused on three executive functions: flexibility, inhibitory control, and working memory (WM). Cleaner wrasse perform well in tasks measuring flexibility and self-control, i.e. the attentional control-free component of inhibitory control [4], while they consistently fail in WM paradigms (Box 1).

Despite this, cleaner wrasse are clearly able to modulate their behavior in the present thanks to past knowledge as they do, for example, remember with whom they have recently interacted or not in a sequence of interactions [5]. This suggests their WM failure may result from a lack of attentional control rather than an inherent limitation in memory capacity. Consequently, their cognitive abilities may only become apparent in tasks that do not rely on attentional control.

At this stage, the lack of WM in cleaner wrasse cannot be taken as representative for ectotherm vertebrates. Instead, the results should be verified in other ectotherms before any conclusion can be drawn regarding systematic differences between ectotherms and endotherms regarding WM. Nevertheless, the emerging picture on both cognitive capacities and limitations in cleaner wrasse inspired us to propose here two complementary hypotheses that may explain the existing empirical evidence. First, to explain observed limitations, we develop the "lack of attentional control" hypothesis (LAC hypothesis). Second, to explain the strategic sophistication and large cognitive tool kit in cleaner wrasse we introduce the 'Cognition-Opportunity-Need' (CON) framework, a conceptual guide for the evolution of cognitive abilities within vertebrates.

Box 1: Working Memory

In Bonin et al. [6], we followed Manrique et al. [7] who defined WM as a "brain system that provides us with temporary short-term storage and management of perceptual or other information (...), which we need for efficiently (...) carrying out, and updating, such complex cognitive tasks as mental reading, reasoning, forecasting, manipulation, (...)". Among all existing models of WM, this definition follows Cowan's Embedded-Processes model of WM, that relies on attentional control [8]. Given that past methodological inconsistencies have led to mixed results and conclusions across various species, we designed spatial and visual experiments that incorporate the critical components of WM as defined by Manrique et al. [7]. The results on cleaner wrasse were consistently negative across these paradigms, which call into question previous studies that used other experiments and reported supposedly positive WM findings in other fish species (see [6] for detailed explanations). The experimental designs can be used on other species, facilitating cross-species comparisons.

The Lack of Attentional Control (LAC) Hypothesis

In the Embedded-Processes model of Cowan, the process of WM entirely relies on attention, the center of information manipulation being the "focus of attention" (Fig. 1 in [8]). In this model, both the conscious control of attention and environmental cues can activate and regulate the process of WM [8]. Van Ede and Nobre [9] distinguish between two types of (selective) attention: outside-in attention, which processes external perceptual information, and inside-out attention, which focuses on relevant content within WM to guide behavior. For instance, a sudden movement of an object in our environment will automatically attract the focus of our outside-in attention. Our control ability allows us to decide to direct this focus toward another object instead. The control over the inside-out attention is used, for instance, when we loose our keys. While the WM process allows us to trace back potential locations in memory, we can direct the focus of the inside-out attention on one or the other component of the information held in WM. Without control over these attention mechanisms, only environmental cues can direct their focus and hence, be the basis for the behavioral response. We hypothesize that both attention mechanisms are present to some degree in endotherms but largely absent in cleaner wrasse and hence, potentially, in other ectotherms. Note that research on the inside-out attention is generally almost non-existent in non-human animals, thus, there is a large unexplored field of research that could shed light on potentially fundamental differences between endotherm and ectotherm vertebrates brain functioning.

Through the formulation of the LAC hypothesis, what we think could be a key difference between large and small brains is the capacity to consciously act on knowledge by directing the focus of attention towards the chosen information instead of relying only on environmental cues.

The Cognition-Opportunity-Need (CON) framework

Since the ability to control attention seems crucial for everyday life, it is essential to develop a theoretical evolutionary model where its absence does not impede cognitive performance, hence explaining the great diversity of cognitive abilities found in fishes so far. Combining the ecological approach to cognition [10] with an anthropocentric approach that emphasizes the advantages of high brain complexity, we propose that cognitive performance arises from three factors: i) the cognitive component 'C' that largely reflects the brain's computing capacities; ii) the learning opportunities 'O' that depend on how often an individual faces a certain problem in nature; and iii) the ecological need 'N' that causes selection on individuals to solve the problem at hand.

While a lack of need strongly increases the probability of failure, the CON framework offers two options for solving a relevant task: having strong computing powers or frequent exposure to the problem (Fig. 1). Cleaner wrasse exemplify the latter, with up to 3000 daily interactions with 'client' reef fish reported [11]. During each interaction, random shifts in the focus of their attention could occur and lead to different behaviors. Successful behaviors, tied to relevant environmental stimuli and reinforced through associative learning, are retained and can further be repeated. This simple strategy of behavioral pattern repetition, based on positive-outcome random attentional shifts could underly cleaner wrasse's impressive natural strategies, like reputation management, prioritizing some clients over others, responding to client aggression with reconciliation, etc. [3]. Based on the CON framework, we can predict that ectotherm vertebrates will only excel at complex tasks if they have plenty of learning opportunities. Conversely, the cognitive power of endotherms would allow them to succeed even with few learning opportunities.

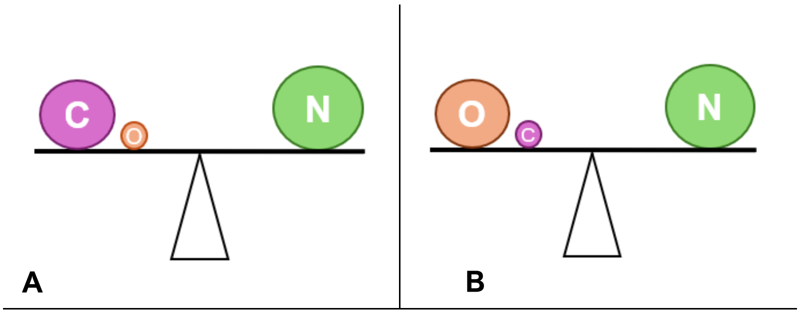

Figure 1: The CON framework
Schematic illustration of the hypothesized relationship between the cognitive component 'C', the number of learning opportunities 'O', and the ecological needs 'N'. In this simplified model, 'N' is represented equally in both scenarios to simplify the logic. In scenario A, a species can meet its ecological needs despite limited learning opportunities due to high computational power (i.e., a strong cognitive component). In scenario B, a species with lower computational power can still meet its ecological needs by having abundant learning opportunities.

Conclusion

As represented by multiple findings in cleaner wrasse, the cognitive abilities of ectotherm vertebrates challenge assumptions about the cognitive gap between endotherms and ectotherms. While ectotherms might lack attentional control abilities, as formulated by the LAC hypothesis, their cognitive performance can potentially be explained by the CON framework, which emphasizes the interplay between computing capacities, learning opportunities, and ecological needs. This framework highlights how repeated problem-solving scenarios can compensate for limited brain computational power, offering a nuanced perspective on the evolution of cognitive abilities across vertebrates. Future research should explore these mechanisms in other ectotherms vertebrates to draw evolutionary conclusions across vertebrates.

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