Cognitive evolution in major vertebrate clades: the Lack of Attentional Control hypothesis and the Cognition-Opportunities-Needs framework

Léonore Bonin[1]*, Randall W. Engle[2], & Redouan Bshary[1]

[1]: University of Neuchâtel, Institute of Biology, Eco-Ethology Lab, Emile-Argand 11, 2000 Neuchâtel, Switzerland
[2]: Georgia Institute of Technology, School of Psychology, Attention and Working Memory Lab, 654 Cherry Street, Atlanta, USA
*: corresponding author

ORCID & emails:
Leonore Bonin: 0000-0001-9349-0616 | leonorebonin@gmail.com
Randall W. Engle: 0000-0003-0816-7406 | randall.engle@gatech.edu
Redouan Bshary: 0000-0001-7198-8472 | redouan.bshary@unine.ch

Abstract

The observed difference in relative brain size between endotherms and ectotherms raises questions about potential resulting disparities in brain function between these two groups. Until recently, no clear cognitive advantage was found in endotherms, with ectotherms occasionally even outperforming them in seemingly complex tasks. However, recent research on working memory—a core executive function—in a teleost fish species suggests that cognitive differences may lie in more fundamental processes. Here, we develop two working hypotheses that arose from this finding. First, the apparent absence of working memory in a fish, and possibly other ectotherms, may stem from their inability to voluntarily control their attentional focus. Instead, only the environment would be causing changes in that focus. In the dichotomic vision of Kahneman's (2011) consisting of automatic System 1 and voluntary System 2, fish could only rely on System 1. We call this the Lack of Attentional Control (LAC) hypothesis. Second, to explain why smaller-brained species may nevertheless outperform larger-brained species in some cognitive tasks, we propose the Cognition – Opportunities – Needs (CON) framework, which posits that cognitive abilities and learning opportunities provide non-mutually exclusive mechanisms for meeting ecological demands. While these hypotheses require further empirical validation, they offer a comprehensive theoretical perspective on cognitive diversity and evolution across species and major vertebrate clades.

Keywords

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

Introduction

There is an amazing amount of variation in both absolute and relative brain weight across vertebrates. Within endotherms and within ectotherm vertebrates, species of the same body weight may differ in brain weight by a factor ten (Jerison, 1969; Tsuboi et al., 2018), and there is an on average tenfold difference in the brain to body weight ratio between ectotherm and endotherm vertebrates (Jerison, 1969; Tsuboi et al., 2018). So far, there are two main hypotheses to explain the latter difference. The first one is related to environmental temperature, with the logic that bigger brains are found in colder environments (Atkinson, 1994; Blackburn et al., 1999; James, 1970). The second possible explanation, which we are more interested in, is that it might reflect a gap in cognitive abilities, following the idea that a bigger brain should provide cognitive advantages. This is coherent as brains consist of energetically costly tissue (e.g. Aiello et al., 2001; Heldstab et al., 2022; Martin, 1981), therefore the cost should be compensated for. This is stated by the "Expensive Brain hypothesis" (Isler & van Schaik, 2009). In other words, what can a typical endotherm species do with its relatively larger brain that a typical ectotherm species cannot do, or can only do to a lesser extent? A major research effort has focused on identifying systematic differences in the cognitive tool-kit. Initially, such comparative research focused on variation within primates, and also on variation within endotherms (e.g. Conway & Christiansen, 2001; Fernandes et al., 2014; Watzek et al., 2019). Only fairly recently, ectotherms have been added, with most of such research being conducted on fishes. Typical projects tested for cognitive processes that had previously been described in endotherms, often only in large-brained species such as primates within the mammals, and corvids and parrots within the birds. The results largely challenged the idea that some cognitive processes are exclusive to endotherms (Brown, 2015; Bshary et al., 2014; Bshary & Triki, 2022; Salena et al., 2021; Triki et al., 2025). The many positive results mean that we currently lack strong candidate cognitive processes that would require substantial amounts of brain tissue, i.e. exceeding what an ectotherm could plausibly allocate due to their smaller brain.

The cleaner wrasse case

Importantly, while evidence for cognitive processes in fishes is spread out over diverse fish taxa, a large number of fish social cognition capacities have been accumulated in a single species, the cleaner wrasse *Labroides dimidiatus* (Triki et al., 2025). This reef-dwelling fish removes ectoparasites from other species, the so-called "clients" (Côté, 2000). While the relationship between the cleaner wrasse and its clients is unambiguously mutualistic (Bshary, 2003; Clague et al., 2011; Grutter, 1999; Grutter et al., 2003; Ros et al., 2011; Waldie et al., 2011), there is still a major conflict of interest as cleaner wrasse prefer to eat protective client mucus over ectoparasites, a behavior that is termed 'cheating' (Grutter & Bshary, 2003). This conflict has selected for sophisticated social strategies in cleaner wrasse, including audience effects (Pinto et al., 2011), social tool use (Bshary et al., 2002), manipulation of client decisions (Soares et al., 2011), and within-species third-party punishment (Raihani et al., 2010). Furthermore, cleaner wrasse must distinguish between client species that, thanks to their larger territories, can also visit other cleaner wrasse, and client species that can only visit the local cleaner within their smaller territory. In the second case, the cleaner wrasse has exclusive access and so, can prioritize the former type of client over the latter (Triki et al., 2019). In this 'biological market task' or 'ephemeral reward task', cleaner wrasse outperform a number of mammals and birds, including orangutans and chimpanzees (Salwiczek et al., 2012; Zentall et al., 2016). A number of these abilities apparently relate to the ecological needs of cleaner wrasse (Barbu et al. 2011; Gingins & Bshary, 2016; Prétôt et al. 2016). Follow-up research on the cleaner wrasse cognitive tool-kit revealed many cognitive processes beyond simple Pavlovian or operant conditioning (Pavlov, 2010; Skinner, 1937; Thorndike, 1927). According to available evidence, cleaner wrasse exhibit payoff-based social learning (Truskanov et al., 2020), generalized rule learning (Wismer et al., 2016), mirror self-recognition based on a mental representation of the fish's own face (Kohda et al., 2019, 2022, 2023), monkey-like levels of self-control in the ability to delay gratification (Aellen et al., 2021), concept learning (Aellen, Siebeck, et al., 2022), behavioral flexibility (Triki & Bshary, 2021), perspective-taking (McAuliffe et al., 2021), as well as configurational learning and chaining (Prat et al., 2022; Quiñones et al., 2020).

While *L. dimidiatus* shows an impressive range of cognitive processes, recent research has finally yielded some negative results in cognitive experiments that had not been conducted in other ectotherms previously. First, there is no evidence for a general intelligence factor 'g' in cleaner wrasse, based on their performances in three experiments commonly used in endotherm 'g' studies to evaluate individual performances in different cognitive domains: reversal learning assessing flexibility, a detour task testing for self-control and a number discrimination task measuring counting abilities (Aellen, Burkart, et al., 2022). The lack of a 'g' factor means that individual performance in one cognitive task does not predict the performance in any of the other cognitive tasks. All bivariate correlations were close to zero and partly negative, and a principal component analysis (PCA) yielded one vector for each experiment (Aellen, Burkart, et al., 2022). Furthermore, there was a negative correlation for individual performance in two tasks that supposedly tested the same cognitive domain, i.e. self-control (detour task and feeding against preference task; Aellen, Burkart, et al., 2022). While the value of the 'g' factor varies and may become pretty small when bivariate analyses are conducted in instead of a PCA (Poirier et al., 2020), a significant 'g' factor has so far been found in all mammals tested, including average-brained mammals such as mice and rats (Burkart et al., 2017). Furthermore, the 'g' factor value correlates positively with brain size within mammals (Deaner et al., 2007). Thus, variation in the strength of 'g' may potentially explain, in part, the factor 10 variation in brain-body ratios documented within mammals (Tsuboi et al., 2018).

Working memory and cleaner wrasse

In humans, the 'g' factor is calculated from IQ tests, where performance correlates with individual variation in working memory abilities (discussed in Conway et al., 2003). Also in mice, individual working memory (WM) performance is a predictor of performance in various cognitive tasks (Kolata et al., 2005). WM is one of the three core executive functions (EFs), and underlies reasoning, planning, decision-making, and problem-solving abilities (also called higher-level EFs; Diamond, 2013). WM is a capacity-limited manipulative type of short-lived storage one uses for goal-directed behavior (e.g., Baddeley & Hitch, 1974, 1974; Cowan, 1988, 1995). According to the Embedded-Processes model of Cowan (1988, 1995, 2019), both the control of attention and environmental cues can activate relevant and specific content in memory, which content can then be used in the present situation for goal-directed behavior (Figure 1, from Cowan et al., 2024). Due to this link with attention, WM abilities are also sensitive to distraction (e.g. Engle, 2002). Given the tight link between WM and general intelligence, a fitting recent result on cleaner wrasse was that there was no evidence for WM in four different tasks that were specifically designed to test for that capacity in this species (Bonin et al., 2025; summary in Box 1). The importance of short-term manipulation of information became most apparent in an experiment in which we simultaneously presented two plates with different

Box 1: Extract of the methods and results from Bonin et al. (2025)		
Methods	Windows experiment: Spatial paradigm	Comparison of the foraging efficiency of cleaners on plates with four fully visible food items compared to plates with reduced visual information (the food items were placed inside Plexiglas windows that made them invisible depending on how cleaner wrasse approached the location).
	Movable arena: Spatial paradigm	The cleaner had to navigate in an arena where it could make successive choices as to inspect a compartmentalized plate. The plate was made of four compartments, each with a single food item. A perfect sequence of choices would lead the cleaner to inspect all compartments only once.
	Two plates experiment: Visual paradigm	The cleaner was given a plate to inspect during a first inspection. After he got the food reward from it, the plate was removed, the experimenter waited 5 to 10sec then presented two plates to the cleaner wrasse for a second inspection. One of the plate was the same as the one from the first inspection and hence, was not rewarded. The cleaner had to choose the unfamiliar plate to get the reward.
	Dynamic two plates: Visual paradigm	The principle was the same as in the two plates experiment, but the paradigm was adjusted so that both plates were always visible.
Results	Windows experiment:	Cleaners forage less efficiently on a plate with windows.
	Movable arena:	Cleaners visited compartments randomly.
	Two plates experiment:	Weak inconsistent success in choosing the unfamiliar plate.
	Dynamic two plates:	Cleaners failed to choose the unfamiliar plate.

features (color and pattern) to a subject, then we made one accessible so that the cleaner wrasse could eat a food item placed on the plate's backside. After a 5 - 10s delay, the subject had access to both plates and had to choose the second plate (that is, the one with a different color and pattern than the one it ate from) in order to obtain a second food item on the back. Cleaner wrasse performed at chance levels at this task, whereas they had performed very well in an earlier study where they had to remember both plates, when the last interaction with each had taken place in a 2.5 - 15 min time interval (Salwiczek & Bshary, 2011). Thus, while cleaner wrasse may use various types of memory (Bonin et al., 2025; Manrique & Walker, 2017; Pause et al., 2013; Tulving, 1972, 2002) to remember with whom they have recently interacted or not in a sequence of interactions, they cannot use immediate updates of information, suggesting a lack of WM. Cleaner wrasse failed in four paradigms, based on visual or spatial information, partly in ecologically relevant contexts using a gradual methodology, i.e., the complexity was designed to increase throughout the experimentation. Because cleaner wrasse failed at the earliest stages of all paradigms, we did not test further on some key points of the WM definition, such as sensitivity to disturbance (Bonin et al., 2025). A critical assessment of other studies that claimed to measure WM in fish species (and other ectotherms) revealed that the methods do not allow to exclude alternative mechanisms, leading to the conclusion that there is currently no evidence for WM in bony fish or other ectotherm vertebrates (Bonin et al., 2025). For example, while fish may perform above chance level in an object permanence task involving the ability to retrieve an object that is fully hidden in one of two possible places (Piagetian stage 4; Piaget, 1954; Piaget & Cook, 1952; (Bonin et al., 2024; Triki et al., 2023), this task does not require the manipulation of information. In contrast, as the only fish species tested so far, cleaner wrasse failed in a stage 5 task from Hoffmann et al. (2011), a design that requires the information to be updated to avoid making the A-not-B error (Bonin et al., 2024), thus more clearly targeting WM.

While we currently have coherent data on the apparent lack of WM and general intelligence factor in cleaner wrasse and hence, in the species that arguably contributed most to the accumulating evidence that fishes have a large cognitive tool-kit, the hypothesis that ectotherms lack any notable WM capacity will still require multiple studies on various ectotherm species to be validated. Nevertheless, the negative results on cleaner wrasse inspired us to develop a framework about how species without WM may achieve highly sophisticated decision-making. In this manuscript, we develop two aspects that we consider crucial to understand cleaner wrasse (and other small-brain species) learning and decision-making. We first consider what kind of attention control they might have, and then we develop the hypothesis that cleaner wrasse perform so well in various tasks because of the many opportunities to learn from interactions with clients, then further generalize this concept to other species.

Working memory and attention

According to conceptual thinking based on human research, WM and attention are tightly linked together (e.g; Cowan's Focus of Attention, Fig. 1). According to D'esposito and Postle (2015), "information is encoded into working memory by allocating attention to internal representations"; and Van Ede and Nobre (2023) noted "the importance of selective attention in selecting and prioritizing the relevant contents within working memory" (p.139). Conway et al. (2003) argued that "the basic processes that contribute to WM span tasks suggest that they critically tap an executive attention-control process […]" (p.550) while Kane et al. (2001) highlighted that "it is the individual differences in the controlled-attention component of WM that are responsible for the correlations among WM span and complex cognition measures" (p.170). Although the terminology differs between these quotations, the substance remains unchanged—these all highlight how WM and the ability to control attention are linked together. As a result of this constatation, we hypothesize that the failure of cleaner wrasse in the WM paradigms might stem from a lack of attentional control. This would deprive them from voluntarily modulate the content of their attentional focus, an ability also called executive attention (e.g. Engle & Kane, 2003; Shipstead et al., 2016). We want to refer to this as the "Lack of Attentional Control" hypothesis, which reflects the inability to voluntarily control the content of one's focus of attention. Under such conditions, an individual would fail in usual WM paradigms as we found in cleaner wrasse (Bonin et al., 2025) for instance.

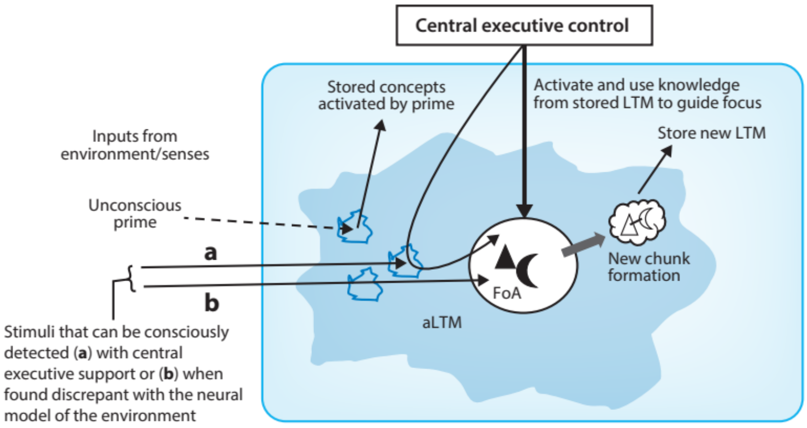

Figure 1: Recent representation of the Embedded-Processes model, taken with authorization from Cowan et al. (2024, Fig. 1)
FoA: Focus of Attention
aLTM: Activated portion of the long-term memory (*LTM*)
Unconscious prime: Environmental inputs priming without "explicit awareness" (Fig. 1; Cowan et al., 2024, p.5).
A stimulus can be consciously detected when supported by the central executive or when it arises from a relevant change in the environment; otherwise, it remains unconscious. The central executive also plays a key role in determining which stimuli to focus on: it can bring a stimulus into the FoA, which is influenced not only by executive control but also by environmental cues. Once within the FoA, information is organized into meaningful units called "chunks," which can then be transferred back into LTM for storage.

The LAC Hypothesis

The social science literature on attentional control is vast and there are important disagreements, both in the concepts themselves as well as the use of terminology (e.g. Awh et al., 2012; Gaspelin & Luck, 2018; Oberauer, 2019; Pinto et al., 2013). Among all visions, we prioritized the two-systems divisions of Kahneman (2011) according to which there is an automatic, fast, intuitive system 1 and a slow, effortful, voluntary system 2. We established a visual representation of our vision of the two systems and the relation to both internal content and perceptual information in Fig. 2. Other dichotomic visions presented *top-down* and *bottom-up* processes (Macaluso et al., 2016; Sobel et al., 2007), control (Buschman & Miller, 2007; Oberauer, 2019), or attention (Katsuki & Constantinidis, 2014; Y. Pinto et al., 2013), but the notion of voluntary process is not always clear (Gaspelin & Luck, 2018; Luck et al., 2021). This aspect was decisive in our decision to follow Kahneman's vision as we consider that the ability to control (reflecting a voluntary aspect) the focus of attention—also called executive attention, executive control, cognitive control, or attentional control (e.g. Engle, 2002; Vandierendonck, 2014)—might represent a major achievement in mental abilities. Indeed, by having voluntary control over thoughts and perceptions, one is capable of conscious and voluntary decision-making. Opposingly, relying solely on System 1 means an individual's behavior is driven entirely by environmental stimuli. In the *stimulus-driven* capture of attention framework (Theeuwes et al., 2010), a feature in the environment will automatically capture an individual's attention. The likelihood that an environmental stimulus will capture one's attention depends on its salience, here both in term of relevance and physical properties (i.e. value-driven and salience-based attentional capture; Anderson et al., 2011a, 2011b). The salience can change through associative learning (discussed in Hall & Rodríguez, 2017). It can increase with reinforcement (Treviño, 2016), i.e., acquired salience (Esber & Haselgrove, 2011), or decrease through repeated exposure, i.e., habituation (Rankin et al., 2009). Consequently, the focus of attention can be affected by purely automatic processes (such as associative learning) as well and lead to different behavioral outcomes. In simpler terms, it means that the chances that an environmental stimulus will capture one's attention will depend on how important the stimulus is to the subject (e.g. your name being called is highly relevant to you, hearing it will capture your attention), and how powerful are its characteristics (such as a very loud noise, or a bright red object in a very green forest). This importance can be modulated with learning: it can both increase (you strengthen the importance of the stimulus) or decrease (this is called habituation, less attention is given to it). Due to this link between learning and importance given to a stimulus, the focus of one's attention can be modulated automatically.

Here, we propose the "Lack of Attentional Control" hypothesis (LAC hypothesis) that predicts that cleaner wrasse and other ectotherm species might not be capable of voluntary control over the content of the focus of their attention, i.e., a lack of attentional control. Lacking this deliberate control means that an individual could not have the ability to voluntarily retrieve the relevant information from stored knowledge that could be manipulated to solve a specific problem, nor could they voluntarily decide which perceptual information to focus on. Under such circumstances, the individual depends on the environment to supply cues that automatically direct relevant information (both from internal or external sources) into the focus of attention. In other words, ectotherms would possess Kahneman's System 1 only (Kahneman, 2011; Fig. 2) whereas endotherms would possess both automatic System 1 and voluntary System 2. To give an example, attentional control is crucial in a situation where one is approached by a lion on the African savannah, a highly salient external stimulus. To respond effectively, one must override the instinct to focus on the threat and instead shift attention toward information that is necessary to protect oneself, such as the internal knowledge used to load and fire a gun in the air to scare the lion away. These voluntary shifts in the focus of attention are what characterize attentional control ability.

Independently of whether voluntary or automatic processes are at work, efficient decisions depend on individuals directing their attention to the relevant information. Given that there are many stimuli in the outside world and various information in the memory, individuals need a filter. This filter is called ‘selective attention’. Following Vandierendonck (2014) and Van Ede & Nobre (2023), we view attentional control (that they call executive attention) as the conscious, deliberate control over selective attention (Fig. 2). According to Van Ede et Nobre (2023), we can distinguish between two types of selective attention. One type that acts on the perceptual (i.e., external) information for internal processing, called the outside-in selective attention, is an equivalent to Baddeley’s (1986) concept of perceptual selective attention. The second type, referred to as the inside-out selective attention, also called internal selective attention (e.g., Ester & Nouri, 2023), selects the relevant content of the WM to create a goal-directed behavior. We would like to expand this definition to the selection of relevant information from internal content or knowledge more generally (Fig. 2). This, because an information can be used as is from another type of short-term storage, without being manipulated and processed in WM (Bonin et al., 2025; Manrique et al., 2024).

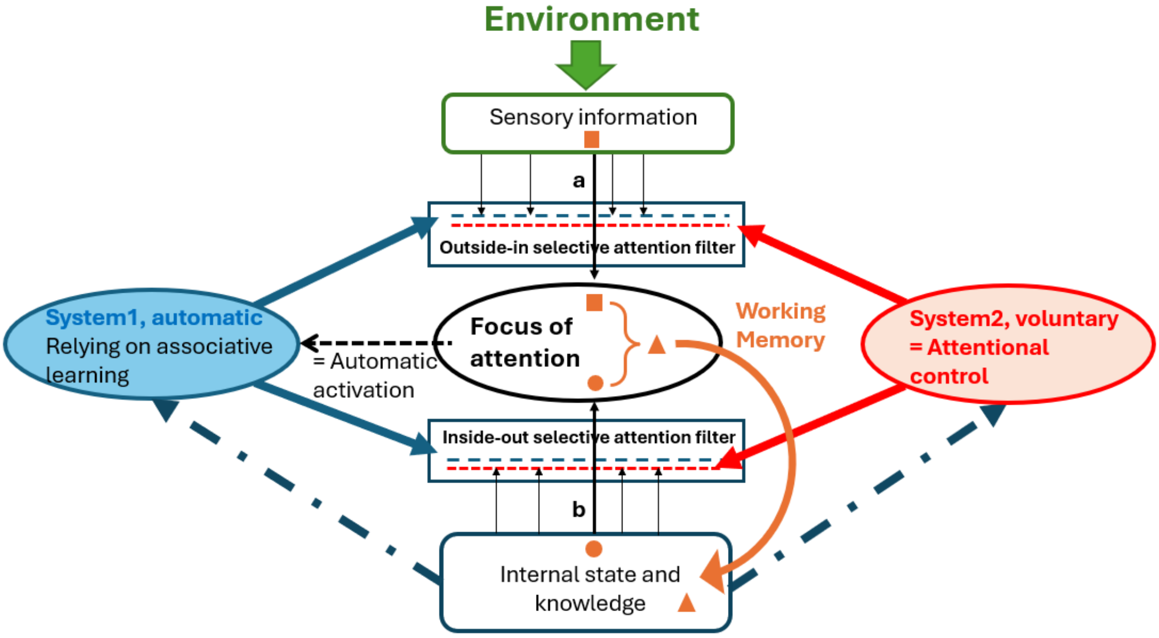

Figure 2: Schematic representation of the two systems that modulate the content of the focus of attention via their actions on outside-in and inside-out selective attention filters. “a pretty good imperfect figure”
The environment is at the origin of constant sensory information. The outside-in selective attention filter filters the relevant sensory information (Van Ede & Nobre, 2023). This filter can be modulated by two systems: the automatic system 1 and the voluntary System 2 (Kahneman, 2011), also called attentional control. Via acting on the “mesh size” of the filter, whether positively or negatively, these two systems can vary the type of, or how many, sensory information can be transferred into the focus of attention (arrow a). Similarly, the systems can act on the inside-out selective attention filter that selects which information from our knowledge (Van Ede & Nobre, 2023) or internal state can be transferred into the focus of attention (arrow b).
When an information is within the focus of attention, it can act on the systems, influencing those that will then act on the selective attention filters so that associated relevant information can be perceived from the environment or brought from our knowledge (dashed arrows from the focus of attention to each system).
In addition, knowledge and internal state have a direct impact on both systems. The automatic system 1 mainly relies on associative learning (Kahneman, 2011); newly learned information can further impact how the system modulates the selective attention filters. Similarly, the voluntary choices operated by system 2 will also vary with learning.
Lastly, we represented the process of working memory. When facing a problem in the present, individuals are provided with sensory information (brown square). In order to solve the problem, relevant information from the knowledge must be brought in the focus of attention (brow circle). Together, these information are manipulated, combined, and processed to create a new information (brown triangle) that can, in turn, be transferred to our storage unit and become part of the knowledge. It is currently unclear whether the voluntary system 2 is required for WM or whether the automatic system 1 would be enough.
We acknowledge that this figure is a rather simplified representation, highlighting only the aspects most relevant to our argument rather than capturing the full complexity of attentional control and its mechanisms. It does not explicitly link attention to behavior, as this would require distinguishing between conscious and unconscious processes (e.g. instinct), which would further complicate the figure. It also omits an intermediate state of information activation that allows individuals to *be aware of* stimuli without fully focusing on them (a notion similar to Cowan’s activated portion of long-term memory (Fig. 1) that we also did not include, but for sensory information). Finally, the figure’s layout might suggest that we reject certain attentional models, such as the spotlight model (Posner et al., 1980), whereas this is not the case. We chose to show information moving into the focus of attention, rather than the focus itself shifting, as a simpler way to illustrate our point.

1. Outside-in selective attention

It is intuitive to think that individuals must pay attention to the problem they face in order to solve it. It is no different with cleaner wrasse. In general, when working with cleaner wrasse, we are able to manipulate the focus of their outside-in attention so that they participate in experiments. We hypothesize that cleaner wrasse might be able to maintain their attention on an object using behavioral adjustments (such as body orientation), but that, if the focus breaks due to internal factors (such as a time delay) or external factors (such as a distraction, e.g. sudden appearance of a predator), they are not able to *decide* to focus again on the object. Support for this idea can be found in Aellen et al. (2021). They found that adding objects to enable subjects to use self-distraction did not increase the success of cleaner wrasse in a delayed-gratification paradigm. This may occur as self-distraction is a distractor, hence breaking the focus of cleaner wrasse’s attention without them being able to voluntarily re-focus (i.e., top-down processes) on the relevant information. This would contrast with what studies on human infants and primates revealed, with self-distraction having a positive impact on the success (Evans & Beran, 2007; Raghunathan et al., 2023), highlighting that individuals were able to re-focus (again, via top-down processes) to complete the task.

More broadly, the outside-in selective attention was found in multiple ectotherm vertebrate species (review in Krauzlis et al., 2018). One example Krauzlis et al. (2018) highlight involves *Anolis* lizards, which face the challenge of detecting prey movement amid dynamic environmental backgrounds, such as swaying leaves. To overcome this, *Anolis* lizards exhibit an automatic visual preference, i.e. an involuntary attraction of gaze, toward specific types of motion patterns. This demonstrates the existence of selective attention directed toward ecologically relevant features of their environment. However, no study to date has tested the voluntary control over it. Hence, this could only reflect the action of the automatic System 1 (as supposed by the terms “automatic visual preference” or “involuntary attraction”) instead of the voluntary System 2 (Fig. 2; Kahneman, 2011)

In other words, outside-in selective attention might differ between ectotherms and endotherms in its unique reliance on automatic processes or the possibility of controlling it through voluntary processes. Therefore, attentional control over outside-in selective attention should be broadly investigated across multiple vertebrate species to verify this possibility.

2. Inside-out selective attention

We know that the attentional control over internal information (i.e., the content of memory) is essential for solving complex problems in humans (i.e., Kane et al., 2001; Van Ede & Nobre, 2023). The research on inside-out selective attention is almost non-existent in non-human animals and is completely non-existent in ectotherm species. However, we can still think about it. Because cleaner wrasse were able to use past knowledge to adapt in a foraging task (Salwiczek & Bshary, 2011) without showing WM abilities in more specific experimental designs (Bonin et al., 2025), we hypothesize that they can use past knowledge according to the present situation as long as the present environmental context provides the information that will result in the transfer into the focus of their attention of the relevant stored information (i.e. that will allow to solve the problem), without them having voluntary control over it. Following the representation of Figure 2, the sensory information would arrive into the focus of attention, whether because it is relevant (importance was learned in the past, hence affecting the outside-in selective attention filter through the automatic system) or because it acts as a disturbance. Then it can, in turn, impact the automatic system via the automatic activation (for instance, if you are told the word “mother”, you will automatically think of a range of other words associated with it) that will act on the inside-out selective attention filter to let stored information related to that information enter the focus of attention. This would explain how cleaner wrasse are able to engage in seemingly complex problem-solving by adapting their cleaning behaviors depending on multiple factors in the present (e.g., Bshary & Grutter, 2002, 2005; Pinto et al., 2011; Raihani et al., 2012) without having a voluntary control over their inside-out selective attention.

3. Potentially challenging previous findings

If ectotherms lack attentional control, one may ask how cleaner wrasse and guppies have performed well in tasks commonly used to assess inhibitory control (i.e., another executive function; Diamond, 2013). These include detour tasks, where individuals must go around a transparent obstacle (e.g., a cylinder or barrier) to reach a reward (Aellen, Burkart, et al., 2022; Guadagno & Triki, 2024; Lucon-Xiccato et al., 2017; Triki & Bshary, 2021), and delayed gratification tasks that require waiting to obtain a better outcome (Aellen et al., 2021).Indeed, at first glance, such results might seem inconsistent with the LAC hypothesis. However, these tasks primarily assess self-control—also called behavioral inhibition, which does not seem to involve voluntary attentional shifts as opposed to interference control (Diamond, 2013). In detour tasks, the goal and obstacle are both directly perceptible and the testing environment typically lacks competing distractions (for a review and discussion, see Kabadayi et al., 2018), which reduces the need for attentional control. Moreover, encountering physical obstacles is common in the wild for most species, meaning that prior experience and learning may contribute to successful performance (Van Horik et al., 2020; Kabadayi et al., 2018), allowing the automatic System 1 to be at play. Similarly, in delayed gratification paradigms, success can rely on passive waiting or the inhibition of motor impulses without requiring voluntary attentional shifts. Even if self-control and interference control are correlated, those are still separate mechanisms (Diamond, 2013; Wolff et al., 2016), which means that cleaner wrasse (and other species) could possess self-control without interference control. In this light, the cognitive abilities demonstrated in these tasks do not contradict the LAC hypothesis. Rather, they raise an additional question related to executive functions in general: could all EFs possess two subcomponents, one requiring attentional control and one not? Meaning, one version relying only on Kahneman's automatic System 1? This question will not be addressed here, but it is a possibility for further thinking.

How do cleaner wrasse, and other species, face ecological challenges? The CON framework

The LAC hypothesis proposes that the capacity to voluntarily decide which stored information (i.e. knowledge, Fig. 2) or sensory information from the environment can be in the focus of attention, instead of exclusively relying on environmental changes, could separate endotherms from ectotherm vertebrates. This ability seems crucial for everyday life as it allows voluntary decision-making when facing a precise situation in the present, so it is essential to develop a theoretical evolutionary model where the lack of such attentional control does not impede cognitive performance, especially in ecologically relevant tasks.

1. Repeated exposure and associative learning in cleaner wrasse

One possible solution for ectotherms (and to a lesser degree for small-brained endotherms) is to rely on more automatic mechanisms. We already cited Daniel Kahneman's work previously, but here are more details. On the basis of considerable previous literature in cognitive psychology and years of investigations, he defines two reasoning processes (Kahneman, 2011). The first, System 1, is automatic, intuitive, effortless, and fast and could be the base for ectotherms cognition following our framework. An example of an automatic process is familiarity. It is a process defined as the ability to react to a previously encountered stimulus without explicit recollection of the information associated with it (see Yonelinas, 2002, for the distinction between familiarity and recollection). In other words, it is an automatic reaction to a known stimulus, it does not require voluntary control (e.g., such as the automatic retrieval of the name of someone you know well). In addition to such an automatic process, numerous learning opportunities may be at play. For instance, cleaner wrasse have up to 3000 cleaning interactions per day (Triki et al., 2018), providing them with these numerous opportunities. During each one of these interactions, the focus of cleaner wrasse's attention could change through the *stimulus-driven* capture of attention (Theeuwes et al., 2010). This means that across the many interactions, cleaner wrasse may eventually have the relevant information in the focus of their attention for solving the problem, and the resulting reward will initiate reinforcement learning processes. Repeated exposure will increase the salience of the information (see previous section for details), and the new behavior may eventually become familiar enough to be executed automatically. Hence, the emergence of a new successful behavior could occur without the intervention of voluntary control, but via a 'simple' behavioral pattern repetition strategy based on positive-outcome random shifts in focus of attention. This could be the basis for cleaner wrasse impressive diversity of natural strategies (e.g., Binning et al., 2017; Bshary & Noë, 2003; Gingins & Bshary, 2016; Kohda et al., 2023; Soares et al., 2008). This view is coherent with Kahneman's statement that associative learning is the primary process supporting the functioning of the automatic System 1 (Kahneman, 2011).

The above-presented framework may also explain why cleaner wrasse outperform primates in the basic and complex biological market / ephemeral reward task when the relevant information is in the two plates (Salwiczek et al., 2012). The plates represent the client fish, which for cleaner wrasse represent the most relevant indicators of food rewards (Grutter, 1995; Roche et al., 2021). It is thus likely that they can easily associate plate features with consequences (using chaining and configurational learning; Prat et al., 2022; Quiñones et al., 2020), while primates never focus their attention on the plates. If the relevant information is in the color of the food items or an icon on a screen, capuchin monkeys focus their attention correctly and hence also solve the task (Prétôt et al., 2016).

2. Generalization: The CON framework

To generalize the results from the biological market / ephemeral reward test to other species, we propose that cognitive performance largely arises from three factors: i) the cognitive component 'C' that 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, such that cognition and opportunities combined will allow individuals to fulfil their ecological needs: $C + O \rightarrow N$ (Fig. 3). While a lack of need strongly increases the probability of failure in a task (i.e. if a task does not reflect an ecological need, in laboratory setup for example), the CON framework offers two options for solving a relevant problem: evolving strong computing powers (Fig. 3a) or having frequent exposure to the problem (Fig. 3b). Based on the CON framework, we can predict that ectotherm vertebrates will only excel at complex tasks if they have plenty of learning opportunities or an innate/already developed automatic attention for the relevant stimuli (Fig. 3b). This is important to consider when testing wild-caught individuals (Bshary & Triki, 2022). For example, in cleaner wrasse, performance in the biological market / ephemeral reward task depends on their previous exposure to visitor clients leaving if being made to wait for inspection (Triki et al., 2019, 2020). More generally, cleaner wrasse fail in tasks in which the correct solution mismatches with what they face in nature, such as giving priority to the smaller of two look-alike plates (Wismer et al., 2016) or learning that one laminated fish picture provides a safe haven against being chased while a simultaneously present other one does not when both species are functionally equivalent in nature (i.e. both are predators or visitors). Conversely, the cognitive power of endotherms could allow them to succeed even with few (or no) learning

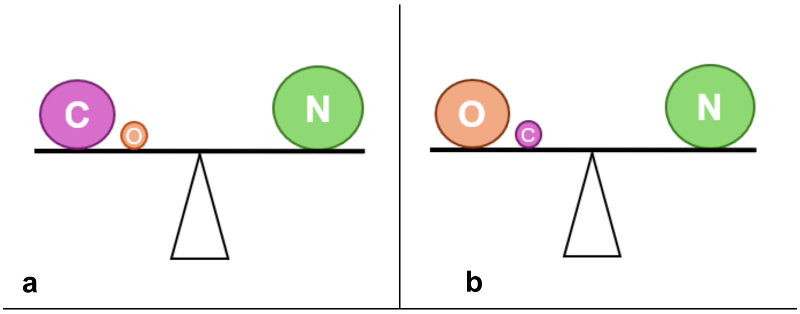

Figure 3: The CON framework
Schematic illustration of the hypothesized relationship between the cognitive component 'C', the number of learning opportunities 'O', and the ecological needs 'N'. In this simplified model, 'N' is represented equally in both scenarios to simplify the logic. In scenario (a), 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 numerous learning opportunities.

opportunities and in tasks of little (or no) ecological relevance. Within endotherms, such abilities should correlate with relative brain size. Lastly, it is important to note that the N component would be mostly defined by the variability of an environment. For instance, even if a species faces numerous problems in its daily life, if those are always the same, then simple learning mechanisms could be sufficient. However, a changing environment, even with fewer problems, would require adaptability, potentially in a shorter time period than what learning based on a bottom-up process would allow. Such conditions would require voluntary control over the focus of attention to enable quick and appropriate responses.

Conclusion

Research in the past 20 years on the cognitive abilities of ectotherm vertebrates, in particular fishes, has challenged assumptions about a cognitive gap between endotherms and ectotherms. Here, we propose that such a gap may exist for the attentional control ability, that is, the voluntary control over the content of the focus of attention, which we formulated in the LAC hypothesis. While ectotherms might lack attentional control abilities, their cognitive performance can potentially be explained by the CON framework which emphasizes the interplay between computing capacities, learning opportunities, and ecological needs. In other words, the evolution of computing power leads to less reliance on frequent learning opportunities for survival. This framework highlights how repeated problem-solving scenarios can compensate for limited brain computational power, offering a new perspective on why cleaner wrasse, in particular, show so much evidence for sophisticated interspecific social strategies. Future research should explore attentional control abilities in both endo- and ectotherm vertebrates to draw evolutionary conclusions across vertebrates. A crucial prediction from our framework is that we need to complement neatly designed laboratory experiments, usually performed with minimal distraction, with experimental setups that include distractors in order to potentially find clear patterns of endotherms outperforming ectotherms, and to explain performance variation within endotherms.

References

Aellen, M., Burkart, J. M., & Bshary, R. (2022). No evidence for general intelligence in a fish. *Ethology*, *128*(5), 424–436. https://doi.org/10.1111/eth.13275

Aellen, M., Dufour, V., & Bshary, R. (2021). Cleaner fish and other wrasse match primates in their ability to delay gratification. *Animal Behaviour*, *176*, 125–143. https://doi.org/10.1016/j.anbehav.2021.04.002

Aellen, M., Siebeck, U. E., & Bshary, R. (2022). Cleaner wrasse *Labroides dimidiatus* perform above chance in a “matching-to-sample” experiment. *PLOS One*, *17*(1), e0262351. https://doi.org/10.1371/journal.pone.0262351

Aiello, L. C., Bates, N., & Joffe, T. (2001). In defense of the Expensive Tissue Hypothesis. In D. Falk & K. R. Gibson (Eds.), *Evolutionary Anatomy of the Primate Cerebral Cortex* (pp. 57–78). Cambridge University Press. https://doi.org/10.1017/CBO9780511897085.006

Anderson, B. A., Laurent, P. A., & Yantis, S. (2011a). Learned Value Magnifies Salience-Based Attentional Capture. *PLOS One*, *6*(11), e27926. https://doi.org/10.1371/journal.pone.0027926

Anderson, B. A., Laurent, P. A., & Yantis, S. (2011b). Value-driven attentional capture. *Proceedings of the National Academy of Sciences*, *108*(25), 10367–10371. https://doi.org/10.1073/pnas.1104047108

Atkinson, D. (1994). Temperature and Organism Size—A Biological Law for Ectotherms? *Advances in Ecological Research*, *25*, 1–58. https://doi.org/10.1016/S0065-2504(08)60212-3

Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences*, *16*(8), 437–443. https://doi.org/10.1016/j.tics.2012.06.010

Baddeley, A. (1986). *Working memory* (pp. xi, 289). Clarendon Press/Oxford University Press.

Baddeley, A. D., & Hitch, G. (1974). Working Memory. In G. H. Bower (Ed.), *Psychology of Learning and Motivation* (Vol. 8, pp. 47–89). Academic Press. https://doi.org/10.1016/S0079-7421(08)60452-1

Binning, S. A., Rey, O., Wismer, S., Triki, Z., Glauser, G., Soares, M. C., & Bshary, R. (2017). Reputation management promotes strategic adjustment of service quality in cleaner wrasse. *Scientific Reports*, *7*(1), 8425. https://doi.org/10.1038/s41598-017-07128-5

Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distributions*, *5*(4), 165–174. https://doi.org/10.1046/j.1472-4642.1999.00046.x

Bonin, L., Duc, S., & Bshary, R. (2024). *Cleaner wrasse can reach Piagetian stage 4 of object permanence when primarily exposed to stage 3*. Research Square. https://doi.org/10.21203/rs.3.rs-5117879/v1

Bonin, L., Manrique, H. M., & Bshary, R. (2025). Cleaner wrasse failed in early testing stages of both visual and spatial Working Memory paradigms. *Animal Cognition*, *28*(43). https://doi.org/10.1007/s10071-025-01959-w

Brown, C. (2015). Fish intelligence, sentience and ethics. *Animal Cognition*, *18*(1), 1–17. https://doi.org/10.1007/s10071-014-0761-0

Bshary, R. (2003). The cleaner wrasse, *Labroides dimidiatus*, is a key organism for reef fish diversity at Ras Mohammed National Park, Egypt. *Journal of Animal Ecology*, *72*(1), 169–176. https://doi.org/10.1046/j.1365-2656.2003.00683.x

Bshary, R., Gingins, S., & Vail, A. L. (2014). Social cognition in fishes. *Trends in Cognitive Sciences*, *18*(9), 465–471. https://doi.org/10.1016/j.tics.2014.04.005

Bshary, R., & Grutter, A. S. (2002). Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: The cleaner fish case. *Ecology Letters*, *5*(1), 130–136. https://doi.org/10.1046/j.1461-0248.2002.00295.x

Bshary, R., & Grutter, A. S. (2005). Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters*, *1*(4), 396–399. https://doi.org/10.1098/rsbl.2005.0344

Bshary, R., & Noë, R. (2003). Biological markets: The ubiquitous influence of partner choice on the dynamics of cleaner fish–client reef fish interactions. In *Genetic and Cultural Evolution of Cooperation*.

Bshary, R., & Triki, Z. (2022). Fish ecology and cognition: Insights from studies on wild and wild-caught teleost fishes. *Current Opinion in Behavioral Sciences*, *46*, 101174. https://doi.org/10.1016/j.cobeha.2022.101174

Bshary, R., Wickler, W., & Fricke, H. (2002). Fish cognition: A primate's eye view. *Animal Cognition*, *5*(1), 1–13. https://doi.org/10.1007/s10071-001-0116-5

Burkart, J. M., Schubiger, M. N., & Van Schaik, C. P. (2017). The evolution of general intelligence. *Behavioral and Brain Sciences*, *40*, e195. https://doi.org/10.1017/S0140525X16000959

Buschman, T. J., & Miller, E. K. (2007). Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices. *Science*, *315*(5820), 1860–1862. https://doi.org/10.1126/science.1138071

Clague, G. E., Cheney, K. L., Goldizen, A. W., McCormick, M. I., Waldie, P. A., & Grutter, A. S. (2011). Long-term cleaner fish presence affects growth of a coral reef fish. *Biology Letters*, *7*(6), 863–865. https://doi.org/10.1098/rsbl.2011.0458

Conway, A. R. A., Kane, M. J., & Engle, R. W. (2003). Working memory capacity and its relation to general intelligence. *Trends in Cognitive Sciences*, *7*(12), 547–552. https://doi.org/10.1016/j.tics.2003.10.005

Conway, C. M., & Christiansen, M. H. (2001). Sequential learning in non-human primates. *Trends in Cognitive Sciences*, *5*(12), 539–546. https://doi.org/10.1016/S1364-6613(00)01800-3

Côté, I. (2000). Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology Annual Review*, *38*, 311–355.

Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information-processing system. *Psychological Bulletin*, *104*(2), 163–191. https://doi.org/10.1037/0033-2909.104.2.163

Cowan, N. (1995). *Attention and memory: An integrated framework* (pp. xv, 321). Oxford University Press.

Cowan, N. (2019). Short-term memory based on activated long-term memory: A review in response to Norris (2017). *Psychological Bulletin*, *145*(8), 822–847. https://doi.org/10.1037/bul0000199

Cowan, N., Bao, C., Bishop-Chrzanowski, B. M., Costa, A. N., Greene, N. R., Guitard, D., Li, C., Musich, M. L., & Ünal, Z. E. (2024). The Relation Between Attention and Memory. *Annual Review of Psychology*, *75*(1), 183–214. https://doi.org/10.1146/annurev-psych-040723-012736

Deaner, R. O., Isler, K., Burkart, J., & Van Schaik, C. (2007). Overall Brain Size, and Not Encephalization Quotient, Best Predicts Cognitive Ability across Non-Human Primates. *Brain, Behavior and Evolution*, *70*(2), 115–124. https://doi.org/10.1159/000102973

D'Esposito, M., & Postle, B. R. (2015). The Cognitive Neuroscience of Working Memory. *Annual Review of Psychology*, *66*(1), 115–142. https://doi.org/10.1146/annurev-psych-010814-015031

Diamond, A. (2013). Executive Functions. *Annual Review of Psychology*, *64*(1), 135–168. https://doi.org/10.1146/annurev-psych-113011-143750

Engle, R. W. (2002). Working Memory Capacity as Executive Attention. *Current Directions in Psychological Science*, *11*(1), 19–23. https://doi.org/10.1111/1467-8721.00160

Engle, R. W., & Kane, M. J. (2003). Executive Attention, Working Memory Capacity, and a Two-Factor Theory of Cognitive Control. In *Psychology of Learning and Motivation* (Vol. 44, pp. 145–199). Elsevier. https://doi.org/10.1016/S0079-7421(03)44005-X

Esber, G. R., & Haselgrove, M. (2011). Reconciling the influence of predictiveness and uncertainty on stimulus salience: A model of attention in associative learning. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1718), 2553–2561. https://doi.org/10.1098/rspb.2011.0836

Ester, E. F., & Nouri, A. (2023). Internal selective attention is delayed by competition between endogenous and exogenous factors. *iScience*, *26*(7). https://doi.org/10.1016/j.isci.2023.107259

Evans, T. A., & Beran, M. J. (2007). Chimpanzees use self-distraction to cope with impulsivity. *Biology Letters*, *3*(6), 599–602. https://doi.org/10.1098/rsbl.2007.0399

Fernandes, H. B. F., Woodley, M. A., & Te Nijenhuis, J. (2014). Differences in cognitive abilities among primates are concentrated on G: Phenotypic and phylogenetic comparisons with two meta-analytical databases. *Intelligence*, *46*, 311–322. https://doi.org/10.1016/j.intell.2014.07.007

Gaspelin, N., & Luck, S. J. (2018). “Top-down” Does Not Mean “Voluntary.” *Journal of Cognition*, *1*(1), 25. https://doi.org/10.5334/joc.28

Gingins, S., & Bshary, R. (2016). The cleaner wrasse outperforms other labrids in ecologically relevant contexts, but not in spatial discrimination. *Animal Behaviour*, *115*, 145–155. https://doi.org/10.1016/j.anbehav.2016.02.022

Grutter, A. S. (1995). Relationship between cleaning rates and ectoparasite loads in coral reef fishes. *Marine Ecology Progress Series*, *118*, 51–58. https://doi.org/10.3354/meps118051

Grutter, A. S. (1999). Cleaner fish really do clean. *Nature*, *398*(6729), 672–673. https://doi.org/10.1038/19443

Grutter, A. S., & Bshary, R. (2003). Cleaner wrasse prefer client mucus: Support for partner control mechanisms in cleaning interactions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(suppl_2). https://doi.org/10.1098/rsbl.2003.0077

Grutter, A. S., Murphy, J. M., & Choat, J. H. (2003). Cleaner Fish Drives Local Fish Diversity on Coral Reefs. *Current Biology*, *13*(1), 64–67. https://doi.org/10.1016/S0960-9822(02)01393-3

Guadagno, A., & Triki, Z. (2024). Executive functions and brain morphology of male and female dominant and subordinate cichlid fish. *Brain and Behavior*, *14*(5), e3484. https://doi.org/10.1002/brb3.3484

Hall, G., & Rodríguez, G. (2017). Habituation and conditioning: Salience change in associative learning. *Journal of Experimental Psychology: Animal Learning and Cognition*, *43*(1), 48–61. https://doi.org/10.1037/xan0000129

Heldstab, S. A., Isler, K., Graber, S. M., Schuppli, C., & van Schaik, C. P. (2022). The economics of brain size evolution in vertebrates. *Current Biology*, *32*(12), R697–R708. https://doi.org/10.1016/j.cub.2022.04.096

Helfman, G. S., & Schultz, E. T. (1984). Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour*, *32*(2), 379–384. https://doi.org/10.1016/S0003-3472(84)80272-9

Hoffmann, A., Rüttler, V., & Nieder, A. (2011). Ontogeny of object permanence and object tracking in the carrion crow, *Corvus corone*. *Animal Behaviour*, *82*(2), 359–367. https://doi.org/10.1016/j.anbehav.2011.05.012

Isler, K., & van Schaik, C. P. (2009). The Expensive Brain: A framework for explaining evolutionary changes in brain size. *Journal of Human Evolution*, *57*(4), 392–400. https://doi.org/10.1016/j.jhevol.2009.04.009

James, F. C. (1970). Geographic Size Variation in Birds and Its Relationship to Climate. *Ecology*, *51*(3), 365–390. https://doi.org/10.2307/1935374

Jerison, H. J. (1969). Brain Evolution and Dinosaur Brains. *The American Naturalist*, *103*(934), 575–588. https://doi.org/10.1086/282627

Kabadayi, C., Bobrowicz, K., & Osvath, M. (2018). The detour paradigm in animal cognition. *Animal Cognition*, *21*(1), 21–35. https://doi.org/10.1007/s10071-017-1152-0

Kahneman, D. (2011). *Thinking, Fast And Slow* (Farrar, Straus and Giroux).

Kane, M. J., Bleckley, M. K., Conway, A. R., & Engle, R. W. (2001). A controlled-attention view of working-memory capacity. *Journal of Experimental Psychology: General*, *130*(2), 169. https://doi.org/10.1037/0096-3445.130.2.169

Katsuki, F., & Constantinidis, C. (2014). Bottom-Up and Top-Down Attention: Different Processes and Overlapping Neural Systems. *The Neuroscientist*, *20*(5), 509–521. https://doi.org/10.1177/1073858413514136

Kohda, M., Bshary, R., Kubo, N., Awata, S., Sowersby, W., Kawasaka, K., Kobayashi, T., & Sogawa, S. (2023). Cleaner fish recognize self in a mirror via self-face recognition like humans. *Proceedings of the National Academy of Sciences*, *120*(7), e2208420120. https://doi.org/10.1073/pnas.2208420120

Kohda, M., Hotta, T., Takeyama, T., Awata, S., Tanaka, H., Asai, J., & Jordan, A. L. (2019). If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals? *PLoS Biology*, *17*(2), e3000021.

Kohda, M., Sogawa, S., Jordan, A. L., Kubo, N., Awata, S., Satoh, S., Kobayashi, T., Fujita, A., & Bshary, R. (2022). Further evidence for the capacity of mirror self-recognition in cleaner fish and the significance of ecologically relevant marks. *PLOS Biology*, *20*(2), e3001529. https://doi.org/10.1371/journal.pbio.3001529

Kolata, S., Light, K., Townsend, D. A., Hale, G., Grossman, H. C., & Matzel, L. D. (2005). Variations in working memory capacity predict individual differences in general learning abilities among genetically diverse mice. *Neurobiology of Learning and Memory*, *84*(3), 241–246. https://doi.org/10.1016/j.nlm.2005.07.006

Krauzlis, R. J., Bogadhi, A. R., Herman, J. P., & Bollimunta, A. (2018). Selective attention without a neocortex. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *102*, 161–175. https://doi.org/10.1016/j.cortex.2017.08.026

Luck, S. J., Gaspelin, N., Folk, C. L., Remington, R. W., & Theeuwes, J. (2021). Progress toward resolving the attentional capture debate. *Visual Cognition*, *29*(1), 1–21. https://doi.org/10.1080/13506285.2020.1848949

Lucon-Xiccato, T., Gatto, E., & Bisazza, A. (2017). Fish perform like mammals and birds in inhibitory motor control tasks. *Scientific Reports*, *7*(1), 13144. https://doi.org/10.1038/s41598-017-13447-4

Macaluso, E., Noppeney, U., Talsma, D., Vercillo, T., Hartcher-O'Brien, J., & Adam, R. (2016). The Curious Incident of Attention in Multisensory Integration: Bottom-up vs. Top-down. *Multisensory Research*, *29*(6–7), 557–583. https://doi.org/10.1163/22134808-00002528

Manrique, H. M., Read, D. W., & Walker, M. J. (2024). On some statistical and cerebral aspects of the limits of working memory capacity in anthropoid primates, with particular reference to *Pan* and *Homo,* and their significance for human evolution. *Neuroscience & Biobehavioral Reviews*, *158*, 105543. https://doi.org/10.1016/j.neubiorev.2024.105543

Manrique, H. M., & Walker, M. J. (2017). *Early Evolution of Human Memory: Great Apes, Tool-making, and Cognition*. Springer International Publishing. https://doi.org/10.1007/978-3-319-64447-9

Martin, R. D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature*, *293*, 57–60. https://doi.org/10.1038/293057a0

McAuliffe, K., Drayton, L. A., Royka, A., Aellen, M., Santos, L. R., & Bshary, R. (2021). Cleaner fish are sensitive to what their partners can and cannot see. *Communications Biology*, *4*, 1127. https://doi.org/10.1038/s42003-021-02584-2

Oberauer, K. (2019). Working memory and attention–A conceptual analysis and review. *Journal of Cognition*, *2*(1), 36. https://doi.org/10.5334/joc.58

Pause, B. M., Zlomuzica, A., Kinugawa, K., Mariani, J., Pietrowsky, R., & Dere, E. (2013). Perspectives on Episodic-Like and Episodic Memory. *Frontiers in Behavioral Neuroscience*, *7*. https://doi.org/10.3389/fnbeh.2013.00033

Pavlov, P. I. (2010). Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex. *Annals of Neurosciences*, *17*(3), 136–141. https://doi.org/10.5214/ans.0972-7531.1017309

Piaget, J. (1954). *The Construction of Reality in the Child* (Routledge).

Piaget, J., & Cook, M. (1952). *The origins of intelligence in children* (Vol. 8). International Universities Press New York.

Pinto, A., Oates, J., Grutter, A. S., & Bshary, R. (2011). Cleaner Wrasses *Labroides dimidiatus* Are More Cooperative in the Presence of an Audience. *Current Biology*, *21*(13), 1140–1144. https://doi.org/10.1016/j.cub.2011.05.021

Pinto, Y., van der Leij, A. R., Sligte, I. G., Lamme, V. A., & Scholte, H. S. (2013). Bottom-up and top-down attention are independent. *Journal of Vision*, *13*(3), 16–16.

Poirier, M.-A., Kozlovsky, D. Y., Morand-Ferron, J., & Careau, V. (2020). How general is cognitive ability in non-human animals? A meta-analytical and multi-level reanalysis approach. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20201853. https://doi.org/10.1098/rspb.2020.1853

Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, *109*(2), 160. https://doi.org/10.1037/0096-3445.109.2.160

Prat, Y., Bshary, R., & Lotem, A. (2022). Modelling how cleaner fish approach an ephemeral reward task demonstrates a role for ecologically tuned chunking in the evolution of advanced cognition. *PLOS Biology*, *20*(1), e3001519. https://doi.org/10.1371/journal.pbio.3001519

Prétôt, L., Bshary, R., & Brosnan, S. F. (2016). Factors influencing the different performance of fish and primates on a dichotomous choice task. *Animal Behaviour*, *119*, 189–199. https://doi.org/10.1016/j.anbehav.2016.06.023

Quiñones, A. E., Leimar, O., Lotem, A., & Bshary, R. (2020). Reinforcement Learning Theory Reveals the Cognitive Requirements for Solving the Cleaner Fish Market Task. *The American Naturalist*, *195*(4), 664–677. https://doi.org/10.1086/707519

Raghunathan, R. S., Musci, R. J., Knudsen, N., & Johnson, S. B. (2023). What children do while they wait: The role of self-control strategies in delaying gratification. *Journal of Experimental Child Psychology*, *226*, 105576. https://doi.org/10.1016/j.jecp.2022.105576

Raihani, N. J., Grutter, A. S., & Bshary, R. (2010). Punishers Benefit From Third-Party Punishment in Fish. *Science*, *327*(5962), 171–171. https://doi.org/10.1126/science.1183068

Raihani, N. J., Pinto, A. I., Grutter, A. S., Wismer, S., & Bshary, R. (2012). Male cleaner wrasses adjust punishment of female partners according to the stakes. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1727), 365–370. https://doi.org/10.1098/rspb.2011.0690

Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., Coppola, G., Geyer, M. A., Glanzman, D. L., Marsland, S., McSweeney, F. K., Wilson, D. A., Wu, C.-F., & Thompson, R. F. (2009). Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, *92*(2), 135–138. https://doi.org/10.1016/j.nlm.2008.09.012

Roche, D. G., Jornod, M., Douet, V., Grutter, A. S., & Bshary, R. (2021). Client fish traits underlying variation in service quality in a marine cleaning mutualism. *Animal Behaviour*, *175*(6), 137–151. https://doi.org/10.1016/j.anbehav.2021.03.005

Ros, A. F. H., Lusa, J., Meyer, M., Soares, M., Oliveira, R. F., Brossard, M., & Bshary, R. (2011). Does access to the bluestreak cleaner wrasse Labroides dimidiatus affect indicators of stress and health in resident reef fishes in the Red Sea? *Hormones and Behavior*, *59*(1), 151–158. https://doi.org/10.1016/j.yhbeh.2010.11.006

Salena, M. G., Turko, A. J., Singh, A., Pathak, A., Hughes, E., Brown, C., & Balshine, S. (2021). Understanding fish cognition: A review and appraisal of current practices. *Animal Cognition*, *24*(3), 395–406. https://doi.org/10.1007/s10071-021-01488-2

Salwiczek, L. H., & Bshary, R. (2011). Cleaner Wrasses Keep Track of the “When” and “What” in a Foraging Task. *Ethology*, *117*(11), 939–948. https://doi.org/10.1111/j.1439-0310.2011.01959.x

Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., Wismer, S., Stoinski, T., Brosnan, S. F., & Bshary, R. (2012). Adult Cleaner Wrasse Outperform Capuchin Monkeys, Chimpanzees and Orang-utans in a Complex Foraging Task Derived from Cleaner – Client Reef Fish Cooperation. *PLOS One*, *7*(11), e49068. https://doi.org/10.1371/journal.pone.0049068

Shipstead, Z., Harrison, T. L., & Engle, R. W. (2016). Working Memory Capacity and Fluid Intelligence: Maintenance and Disengagement. *Perspectives on Psychological Science*, *11*(6), 771–799. https://doi.org/10.1177/1745691616650647

Skinner, B. F. (1937). Two Types of Conditioned Reflex: A Reply to Konorski and Miller. *The Journal of General Psychology*, *16*(1), 272–279. https://doi.org/10.1080/00221309.1937.9917951

Soares, M. C., Bshary, R., & Côté, I. M. (2008). Does cleanerfish service quality depend on client value or choice options? *Animal Behaviour*, *76*(1), 123–130. https://doi.org/10.1016/j.anbehav.2008.01.015

Soares, M. C., Oliveira, R. F., Ros, A. F. H., Grutter, A. S., & Bshary, R. (2011). Tactile stimulation lowers stress in fish. *Nature Communications*, *2*(1), 534. https://doi.org/10.1038/ncomms1547

Sobel, K. V., Gerrie, M. P., Poole, B. J., & Kane, M. J. (2007). Individual differences in working memory capacity and visual search: The roles of top-down and bottom-up processing. *Psychonomic Bulletin & Review*, *14*(5), 840–845. https://doi.org/10.3758/bf03194109

Theeuwes, J., Olivers, C. N. L., & Belopolsky, A. (2010). Stimulus-driven capture and contingent capture. *WIREs Cognitive Science*, *1*(6), 872–881. https://doi.org/10.1002/wcs.83

Thorndike, E. L. (1927). The law of effect. *The American Journal of Psychology*, *39*(1/4), 212–222.

Treviño, M. (2016). Associative learning through acquired salience. *Frontiers in Behavioral Neuroscience*, *9*, 353. https://doi.org/10.3389/fnbeh.2015.00353

Triki, Z., & Bshary, R. (2021). Sex differences in the cognitive abilities of a sex-changing fish species *Labroides dimidiatus*. *Royal Society Open Science*, *8*(7), 210239. https://doi.org/10.1098/rsos.210239

Triki, Z., Emery, Y., Teles, M. C., Oliveira, R. F., & Bshary, R. (2020). Brain morphology predicts social intelligence in wild cleaner fish. *Nature Communications*, *11*(1), 6423. https://doi.org/10.1038/s41467-020-20130-2

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*(6), pgad129. https://doi.org/10.1093/pnasnexus/pgad129

Triki, Z., van Schaik, C., & Bshary, R. (2025). The fish challenge to vertebrate cognitive evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *380*(1929), 20240124. https://doi.org/10.1098/rstb.2024.0124

Triki, Z., Wismer, S., Levorato, E., & Bshary, R. (2018). A decrease in the abundance and strategic sophistication of cleaner fish after environmental perturbations. *Global Change Biology*, *24*(1), 481–489. https://doi.org/10.1111/gcb.13943

Triki, Z., Wismer, S., Rey, O., Ann Binning, S., Levorato, E., & Bshary, R. (2019). Biological market effects predict cleaner fish strategic sophistication. *Behavioral Ecology*, *30*(6), 1548–1557. https://doi.org/10.1093/beheco/arz111

Truskanov, N., Emery, Y., & Bshary, R. (2020). Juvenile cleaner fish can socially learn the consequences of cheating. *Nature Communications*, *11*(1), 1159. https://doi.org/10.1038/s41467-020-14712-3

Tsuboi, M., van der Bijl, W., Kopperud, B. T., Erritzøe, J., Voje, K. L., Kotrschal, A., Yopak, K. E., Collin, S. P., Iwaniuk, A. N., & Kolm, N. (2018). Breakdown of brain–body allometry and the encephalization of birds and mammals. *Nature Ecology & Evolution*, *2*(9), 1492–1500. https://doi.org/10.1038/s41559-018-0632-1

Tulving, E. (1972). Episodic and semantic memory. In *Organization of memory* (pp. xiii, 423–xiii, 423). Academic Press.

Tulving, E. (2002). Episodic Memory: From Mind to Brain. *Annual Review of Psychology*, *53*(1), 1–25. https://doi.org/10.1146/annurev.psych.53.100901.135114

Van Ede, F., & Nobre, A. C. (2023). Turning Attention Inside Out: How Working Memory Serves Behavior. *Annual Review of Psychology*, *74*(1), 137–165. https://doi.org/10.1146/annurev-psych-021422-041757

Vandierendonck, A. (2014). Symbiosis of executive and selective attention in working memory. *Frontiers in Human Neuroscience*, *8*, 588. https://doi.org/10.3389/fnhum.2014.00588

Waldie, P. A., Blomberg, S. P., Cheney, K. L., Goldizen, A. W., & Grutter, A. S. (2011). Long-Term Effects of the Cleaner Fish *Labroides dimidiatus* on Coral Reef Fish Communities. *PLOS One*, *6*(6), e21201. https://doi.org/10.1371/journal.pone.0021201

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

Watzek, J., Pope, S. M., & Brosnan, S. F. (2019). Capuchin and rhesus monkeys but not humans show cognitive flexibility in an optional-switch task. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-49658-0

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

Wolff, M., Krönke, K.-M., & Goschke, T. (2016). Trait self-control is predicted by how reward associations modulate Stroop interference. *Psychological Research*, *80*(6), 944–951. https://doi.org/10.1007/s00426-015-0707-4

Yonelinas, A. P. (2002). The Nature of Recollection and Familiarity: A Review of 30 Years of Research. *Journal of Memory and Language*, *46*(3), 441–517. https://doi.org/10.1006/jmla.2002.2864

Zentall, T. R., Case, J. P., & Luong, J. (2016). Pigeon's (*Columba livia*) paradoxical preference for the suboptimal alternative in a complex foraging task. *Journal of Comparative Psychology*, *130*(2), 138–144. https://doi.org/10.1037/com0000026