Title: Executive functions and brain morphology of male and female dominant and subordinate cichlid fish

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Abstract

Living in a social dominance hierarchy presents different benefits and challenges for dominant and subordinate males and females, which might in turn affect their cognitive needs. Despite the extensive research on social dominance in group-living species, there is still a knowledge gap regarding how social status impacts brain development and cognitive abilities. Here, we tested male and female dominants and subordinates of *Neolamprologus pulcher*, a social cichlid fish species with size-based hierarchy. We ran three executive cognitive function tests for cognitive flexibility (reversal learning test), self-control (detour test), and working memory (object permanence test), followed by brain and brain region sizes measurements. Performance was not influenced by social status or sex. However, dominants displayed a more pronounced brain-body slope. Also, individual performance in reversal learning and detour tests correlated with brain morphology, with some trade-offs among major brain regions like telencephalon, cerebellum and mesencephalon. As individuals' brain growth strategies varied depending on social status without affecting executive functions, the different associated challenges might yield a potential effect on social cognition instead. Overall, the findings highlight the importance of studying the individual and not just species to understand better how the individual's ecology might shape its brain and cognition.

Keywords:
Cognitive flexibility, inhibitory control, object permanence, working memory, associative learning, social pressures, size-based hierarchy.

Introduction

Living in social groups poses various social challenges for individuals, such as sharing and defending territories and resources, finding mates, and bookkeeping (Lukas and Clutton-Brock 2018; De Dreu and Triki 2022). One of the important challenges that group-living animals face is adjusting behaviour to own position in a social dominance hierarchy (Strauss et al. 2022; Leimar and Bshary 2022). In most social species, dominant individuals are older and physically more capable of defending their status and hence enjoy more privileges than low-ranking younger subordinates. These privileges might include access to food, reproductive opportunities, and sometimes assistance from subordinates in caring for the offspring and defending the group against predators and intruders in cooperative breeding species (Bergmüller et al. 2005; Cant 2012; Fernald 2014). However, little is known about whether acquired privileges for the dominants would allow them to have fewer constraints on investing energy in neural tissue than subordinates and hence have improved cognitive abilities.

Despite the interest in social dominance hierarchy (Strauss et al. 2022; Leimar and Bshary 2022), to the best of our knowledge, only a few studies have looked either into the brain structure or into cognitive abilities of dominant and subordinate individuals but failed to examine the important relationship between brain structure and cognition simultaneously in order to understand individual differences. For instance, a study on paper wasps that looked at the connection between brain morphology and social hierarchy found that the mushroom body calyx, a crucial structure in insect brains that plays a significant role in memory and learning, is more developed in dominants than in subordinates (O′Donnell et al. 2007). In vertebrates, coupling MRI and fMRI scans, researchers were able to pinpoint throughout the whole brain the morphological neural correlates of social dominance and subordination in macaques, ruling out that all neural circuits are equally involved in social dominance hierarchy (Noonan et al. 2014). For the cognitive studies, dominant food caching chickadees display greater spatial learning and more efficient food caching than subordinates (Pravosudov et al. 2003). Similarly, dominant meadow voles and pheasants perform better in spatial learning tasks compared to the subordinates (Spritzer et al. 2004; Langley et al. 2018). Despite these valuable insights, there is still a gap in understanding how social dominance hierarchy affects brain morphology and cognitive performance across various domains in the same individual. To address this, we need to assess not only one cognitive ability but multiple key abilities of both dominant and subordinate individuals and examine the neural correlates of their performance. This will help us understand how the brain develops in response to social status and whether differences in brain structure can account for variation in cognitive performance between individuals.

Some key cognitive processes known as the main executive functions are pivotal to survival and reproduction and have important fitness consequences (Barkley 2012; Burkart et al. 2016). These complex executive function processes, cognitive flexibility, self-control, and working memory, control several other cognitive subprocesses (Miyake et al. 2000; Diamond 2013). For instance, cognitive flexibility helps to adjust behaviour when demands shift, which makes it easier to adapt and thrive in changing environments (Uddin 2021). Self-control requires resisting impulses in order to perform more goal-oriented behaviours (Köhler 1925; Kabadayi et al. 2018). Finally, working memory allows to hold temporarily information that is no longer perceptually present, guiding thus an optimal decision-making and behaviour

(Dudchenko et al. 2013; Read et al. 2022). Due to different status-dependent privileges, dominants and subordinates might have differing executive function capacities (Fernald 2014).

From previous research, we know that brain morphology can explain inter-individual variation in executive function abilities, where individuals with relatively larger brains or key brain areas can excel in various executive function tests for cognitive flexibility (mice, Elias 1970; guppies, Buechel et al. 2018; Triki et al. 2022b, 2023b, and a), self-control (guppies, Triki et al. 2022a, and 2023a) and object permanence (guppies, Triki et al. 2023a). This evidence stems mostly from fish research, because fishes possess more plastic brains than birds and mammals (La Rosa and Bonfanti 2018), making it more likely to link variation in performance to investment in relevant brain regions. Given the plastic brain development of fish, we used the highly social African cichlid, *Neolamprologus pulcher*, as a study model to address our question regarding the effect of social status and sex on brain morphology and executive function abilities.

N. pulcher is a cooperatively breeding fish species with a size-based social hierarchy (Heg et al. 2004; Hamilton et al. 2005). In this system, subordinates are smaller-bodied fish that forgo their own reproduction and help larger-bodied dominant breeders raise their offspring. In the wild, these fish form stable social groups composed of one larger dominant breeding pair and up to 20 smaller and younger subordinate helpers (Bergmüller et al. 2005; Wong and Balshine 2011; Taborsky 2017). In our study, we tested dominants and subordinates of captive-bred *N. pulcher* in three executive function tests. We used the reversal learning paradigm as the standard test for cognitive flexibility in animal cognition studies (Deaner et al. 2006; Izquierdo et al. 2017; Buechel et al. 2018; Ashton et al. 2018; Triki and Bshary 2021). In this test, we first trained fish to visually discriminate between two colours, where choosing the correct colour earned them a food reward. Only fish that successfully learned the initial cue-reward association passed to the next phase and had their reward contingency reversed, where the previously unrewarded colour became the new rewarding cue. The task, with its two phases, allows us to assess fish operant conditioning abilities during the initial learning phase, i.e. a non-executive function ability. Forming associations does not require a complex neural system, as it has been documented even in box jellyfish (Bielecki et al. 2023). The second test was an inhibitory control task (self-control). The test consists of having fish presented with a food reward inside a transparent cylinder open on either side. Individuals with low inhibitory self-control abilities tend to swim straight toward the visible food and hence get blocked by the barrier. In contrast, the ability to delay gratification by moving away from the visible goal and going around the see-through barrier without touching it to reach the food reward qualifies as a high inhibitory control ability (MacLean et al. 2014; Lucon-Xiccato et al. 2017; Triki and Bshary 2021; Triki et al. 2022a, 2023b, a). Finally, the third executive function test was an object permanence task (Goulet et al. 1994; Fiset et al. 2003; Lowe et al. 2009; Barkley 2012). Object permanence paradigms were initially developed to assess the cognitive development of human infants (Piaget 1952) and later adapted to test object permanence abilities in primates (Call 2001), dogs and cats (Triana and Pasnak 1981), marine mammals (Singer and Henderson 2015), birds (Hoffmann et al. 2011), and fish (Triki et al. 2023a). The task assesses if fish can memorise an object's location as it moves behind a screen and infer its continued existence when hidden.

Our experimental design aimed to investigate the executive function abilities and brain morphology of dominants and subordinates but also in males and females. Studies on various vertebrate species have shown that sex differences in specific cognitive performances and brain morphology can be attributed to selection based on different ecological needs (Choleris and Kavaliers 1999; Morand-Ferron et al. 2016; Cummings 2018). For instance, female parasitic cowbirds possess a relatively larger hippocampus, which underpins spatial navigation (Sherry et al. 1993), and perform better than males in spatial memory tests, using the information to successfully relocate potential hosts' nests. On the other hand, males do not need this skill (Guigueno et al. 2014). In some species, females perform better in cognitive flexibility tests, like in rats and guppies (Guillamón et al. 1986; Lucon-Xiccato and Bisazza 2014), while in other species, it is the males that perform better, like in great tits, zebra finches, and cleaner fish (Titulaer et al. 2012; Brust et al. 2013; Triki and Bshary 2021). The differences in brain development due to distinctive hormonal and neurohormonal pathways, which differ between sexes (Gemmell et al. 2019), might be the underlying mechanisms for both adaptive and non-adaptive differences between sexes (McEwen and Milner 2017).

Our study focused on social dominance hierarchy and its potential effects on brain development and resulting cognitive benefits in male and female cichlid fish. We would expect that social dominance privileges yield increased investment in brain development and hence improved performance in executive function. As for sex differences, our study is exploratory as the evidence is controversial in fish and can vary depending on the species being studied. According to an extensive review by Lucon-Xiccato on sex differences in executive functions across species and taxa, the inconsistency of evidence is apparent, and it varies significantly from one species to another (Lucon-Xiccato 2022).

Materials and methods

Study animals and experimental set-up

We ran our study between May and July 2023 at the Ethological Station of the University of Bern, Switzerland. We used captive-bred African cichlid, *Neolamprologus pulcher*, descendants of wild-caught populations from Lake Tanganyika. From nine stock tanks of 400 L, we transferred 24 males and 24 females to individual experimental aquaria of 50 L equipped with a water filter, shelter and 3 cm layer of sand as enrichment. Half of the collected males and females were the largest individuals (dominants) while the other half were the smallest (subordinates) (Lerena et al. 2021) but with a standard length larger than 3.5 cm, indicating sexual maturity (Antunes and Taborsky 2020). Water temperature was maintained at 27 ± 1 °C, and the light:dark cycle was set at 13:11h. The real identity of the tested fish was concealed with running numbers (#1, #2, etc.) to blind the experimenter and avoid potential subconscious observer bias in data collection.

In the stock tanks, fish received fish flakes five days a week and frozen zooplankton (that includes krill) once a week *ad libitum*. Once in the experimental tank, we fed fish on the first three days of acclimation with fish flakes. For the next three days, we habituated them to feed off 1 mL plastic pipettes delivering defrosted krill, which later served as food reward during the cognitive tests. Unfortunately, two fish did not eat from the pipette, so we returned them to their home stock tanks. Additionally, throughout the experiment, three fish were found dead, and some other fish did not systematically participate in all tests (see below), with one fish (#23) stopping completely to participate further after the associative learning. This led to sample size fluctuating from the original design across the tests (see Supplementary Table S1 for detailed sample size per dataset).

Cognitive tests

The experimental set-up and the cognitive test paradigms followed the protocols described by Triki et al. (Triki et al. 2023a). The experimental aquaria had housing and test compartments. To prevent isolation anxiety, the aquaria were placed next to each other so that the fish could see their neighbours in the housing compartment and not in the test compartment to avoid social learning during the tests. The experimenter used a see-through and an opaque Plexiglas barrier (length × width, 24 x 22 cm) to isolate the fish in their housing compartment before each test trial. Lifting the opaque barrier, followed by the transparent barrier, allowed the fish to see what was in the test compartment before accessing the test paradigm. This procedure was used throughout the different cognitive tests.

Colour discrimination test (associative learning test)

We used as cues yellow and red plastic chips of 1.5 cm diameter. Half of the fish had yellow as the initial rewarding cue, while the other half had red. During the first three days, we presented the fish once a day their corresponding rewarding coloured chip with a defrosted krill placed on the top. In the following three days, we presented the cue and fish received the food reward only if they swam very close to the chip (within half a body length). We then glued the yellow and red chips on a see-through Plexiglas support (length × width, 22 × 2.5 cm) allowing a fixed distance of 20 cm between the two cues. We offered the fish one acclimation trial with both cues presenting a food reward on the correct colour. Three trials were conducted where fish only received a food reward if they approached the rewarding cue, facing it within half a body length.

During the test (Supplementary Video S1), the experimenter rewarded the fish no matter whether they chose the correct colour first or second. However, a ‘success’ was only scored if the fish chose the correct colour on the first attempt. Otherwise, if the fish explored the other colour before approaching the correct one, we scored its performance as a ‘failure’. Some fish were relatively slow to perform, so we settled on a maximum of 15 min per trial. Fish received one test session per day (six trials), with the rewarding colour being presented on the left or right side 50% of the time in a random sequence, with no more than three successive presentations on the same side. We considered a fish has successfully learned the cue-reward association if they scored either six correct choices out of six consecutive trials in one session or five correct choices out of six trials in two consecutive sessions. These learning criteria fit a learning probability that is significantly higher than the 50 % chance level of scoring correct ($P < 0.05$, with a binomial test). We ended the test when all fish successfully learned the cue-reward association (11 sessions = 66 trials), except for one fish that even after 15 sessions (90 trials) did not learn (#23).

Reversal learning test

We reversed the cue-reward contingency for those that learned the initial association by making the previously unrewarding colour becoming the new rewarding cue. We delivered a food reward only if the fish scored correctly, providing thus positive reinforcement in case of success and negative reinforcement (no food) in failure. Individual performance was evaluated using the same learning criteria as in the associative learning test. The objective was to end the test when at least 70% of the population learn successfully the test (Triki et al. 2023a). However, after 144 trials, we had about 66% success, and we decided to end the test as the fish were not improving further.

Detour test

In the detour test, we used a transparent Plexiglas cylinder open on both sides (10 cm length and 8 cm diameter). We run two days of habituation, where we first habituated fish to feed off a green plastic chip (1.5 cm diameter), offering a defrosted krill in eight trials over two days. Afterwards, we exposed the fish to the transparent cylinder for four hours but with no food reward nor the green disc. During the test *per se,* we presented the fish with the cylinder with a food reward placed inside it. The food was placed on top of a green spot to eventually increase the salience of the food reward (Triki et al. 2023b, a). To reach the reward, the fish had to detour the cylinder and swim inside. We scored performance as 'success' if the fish detoured the cylinder without touching it (Supplementary Video S2). Otherwise, if the fish bumps to the cylinder walls before retrieving the food, we scored the performance as 'failure'. We allowed fish a maximum of 5 min to perform. We tested the fish over three days for a total of 16 trials: six trials on day 1 and 2 and four trials on day 3. Out of 43 tested fish, 33 participated in the detour test. The other 10 fish did not leave the home compartment in any of the 16 trials.

Object permanence test

As the object in this test, we used coloured (yellow or red) plastic chips (1.5 cm diameter) glued on a see-through Plexiglas handle (length × width, 22 × 2.5 cm). Fish had one trial acclimation with the object before the test, where they were given a food reward upon approaching or touching the object. For the test, we used an apparatus consisting of an opaque screen (22 × 6 cm) with see-through Plexiglas glued to its back (22 × 6 cm), forming a T shape that created left and right spaces where to hide the object. The opaque screen prevented the fish from seeing the object once completely hidden by the experimenter, while the see-through screen prevented access to the object if fish followed the wrong path (see Triki et al. 2023a). A test trial consisted of removing first the opaque divider, allowing fish to see but not access yet the test compartment. The experimenter then introduced the object in the middle of the test compartment and ensured the fish was facing the object before displacing and hiding it either on the left or right side. Within the first 10 seconds of having the object out of sight, we allowed the fish to enter the test compartment, and the experimenter recorded whether they followed the object's path successfully (Supplementary Video S3). Upon locating the object successfully on the first attempt, the experimenter rewarded the fish with a krill. We controlled for potential side biases by displacing the object 50% of the time on the left and 50% on the right in random sequences with no more than three successive displacements on the same side. Over three days, fish received 16 test trials: four trials on day 1 and six trials on day 2 and 3. Of the 43 fish tested, 31 participated in the object permanence test. The other 12 fish did not leave the home compartment in any of the 16 trials.

Dissection and brain morphology measurements

We euthanised the fish with an overdose of MS222. We then measured their standard length (SL) and weight before fixing the whole bodies in 4% paraformaldehyde (PFA) at 4 °C for seven days. We collected and placed the brains in 2 % PFA at 4 °C for another three days. We used Nikon SMZ1000 Microscope to take pictures of the dorsal, ventral, right lateral and left lateral panels of the brain. With the open-access Fiji software (Schindelin et al. 2012), we estimated the length (L), width (W), and height (H) of the telencephalon, mesencephalon, hypothalamus, cerebellum, and brain stem. We calculated the volume of each brain region by fitting their corresponding measurements in an ellipsoid function using the formula: Volume = $(L \times W \times H) \pi / 6$ (Triki et al. 2022b).

During dissection, we examined the internal reproductive organs to verify the accuracy of our visual inspection of the external genitalia and to avoid potential experimenter errors. Four fish were found to have such errors. After correcting the sex, we had 19 females (11 dominants, 8 subordinates) and 24 males (10 dominants and 14 subordinates).

Data analysis

We run all the statistical analyses and generated the figures using the open-access software R, version 4.2.1 (R Core Team 2022).

Cognitive performance data, social status and sex

To test learning performance in the associative and reversal learning tests, we run two survival analyses with the Cox proportional hazards mixed models (*coxme*). We fitted as a response variable the success and failure and time, as the number of sessions to reach learning. The models had social status (dominant vs subordinate) and sex (male vs female) as categorical predictors, while the stock tank identity was the random factor. For the detour and object permanence performances, we run two Bayesian Generalized Linear Mixed Models (BGLMM) with binomial error distribution. We fitted performance with a *cbind* function for number of successes and number of failures across the 16 test trials as a response variable. Social status and sex were the categorical variables, while stock tank identity was the random variable.

Brain morphology data, social status and sex

We fitted a set of Bayesian Linear Mixed Models (BLMM) to test for brain morphology. The response variable was one of the six brain measurements (in mm^3) log-transformed, i.e., total brain, telencephalon, hypothalamus, mesencephalon, cerebellum, and brain stem. The predictors were social status, sex and body size (log-transformed and standardized SL in cm with the *scale* function) (Nakagawa et al. 2017), while stock tank identity was the random variable.

Individual cognitive performance and brain morphology data

To test whether the brain measurements explained the individual variation in the cognitive performance, we run a set of statistical mixed effects models where cognitive performance was the response variable while brain measurements were the continuous predictors. Similar to the logic above, we run survival analyses (coxme) on learning data and BGLMMs on detour and object permanence data. First set of the models had log-transformed and standardized total brain and body sizes as continuous predictors. The other set of tests had the five brain region sizes also log-transformed and standardized as well as body size as continuous predictors. All models accounted for stock tank identity as a random variable

For further details, we provide a step-by-step R code and the corresponding data used to generate the findings (see the Data and Code accessibility statement).

Results

Our statistical analyses showed no significant effect of social status nor sex on fish performance in the cognitive tests (Fig. 1, detailed statistics are in Supplementary Table S2). For the brain morphology, we found an effect of social status on brain allometry (BLMER: N = 43, estimate = 0.157, $p = 0.02$). With post hoc analyses, the brain-body slope for subordinates (n = 22) had a value of (estimate [low, high 95% Confidence Interval], 0.08 [-0.03, 0.19]) while the dominants (n = 21) had a slope of 0.24 [0.16, 0.32] with a partial R^2 of 0.17. It appeared that brain region sizes were driving these slope differences. Particularly, we found that the regions mesencephalon and cerebellum also had significantly steeper slopes in dominants than subordinates (mesencephalon: subordinates (0.03 [-0.08, 0.14]), dominants (0.20 [0.11, 0.28]), partial $R^2 = 0.18$); cerebellum: subordinates (0.07 [-0.10, 0.25]), dominants (0.32 [0.19, 0.45]), partial $R^2 = 0.16$) (Fig. 2, detailed statistics are in Supplementary Table S3). The other brain regions (telencephalon, hypothalamus and brain stem) did not show significant differences for dominants vs subordinates. Additionally, we did not detect sexual dimorphism in the brain morphology of the tested fish.

In the analyses looking into whether brain morphology correlate with individual performance in the cognitive tests, we found significant effects in reversal learning and detour performances, but not for associative learning or object permanence performances. Total brain size relative to body size correlated positively with reversal learning performance (coxme: 0.417 [0.06, 0.77], $p = 0.02$). Different brain regions appeared to be driving this outcome. On the one hand, reversal learning performance correlated positively with cerebellum size relative to body size (coxme: 0.417 [0.68, 4.10], $p = 0.02$), and with absolute hypothalamus size (coxme: 0.417 [0.68, 4.10], $p = 0.02$). On the other hand, the performance in this task correlated negatively with mesencephalon and brain stem relative sizes to body size (coxme: mesencephalon: -1.850 [-3.47, -0.23], $p = 0.025$; brain stem: -1.554 [-2.71, -0.39], $p = 0.009$) (Fig. 3, detailed statistics are in Supplementary Table S4).

In the detour task, telencephalon and mesencephalon had opposite relationships with performance. While the performance correlated positively with mesencephalon relative size to body size (BGLMER: 1.803 [0.33, 3.28], *p* = 0.017), it had a negative correlation with telencephalon relative size (BGLMER: -1.442 [-2.71, -0.17], *p* = 0.026) (marginal R^2 = 0.42, conditional R^2 = 0.67) (Fig. 3, detailed statistics are in Supplementary Table S4).

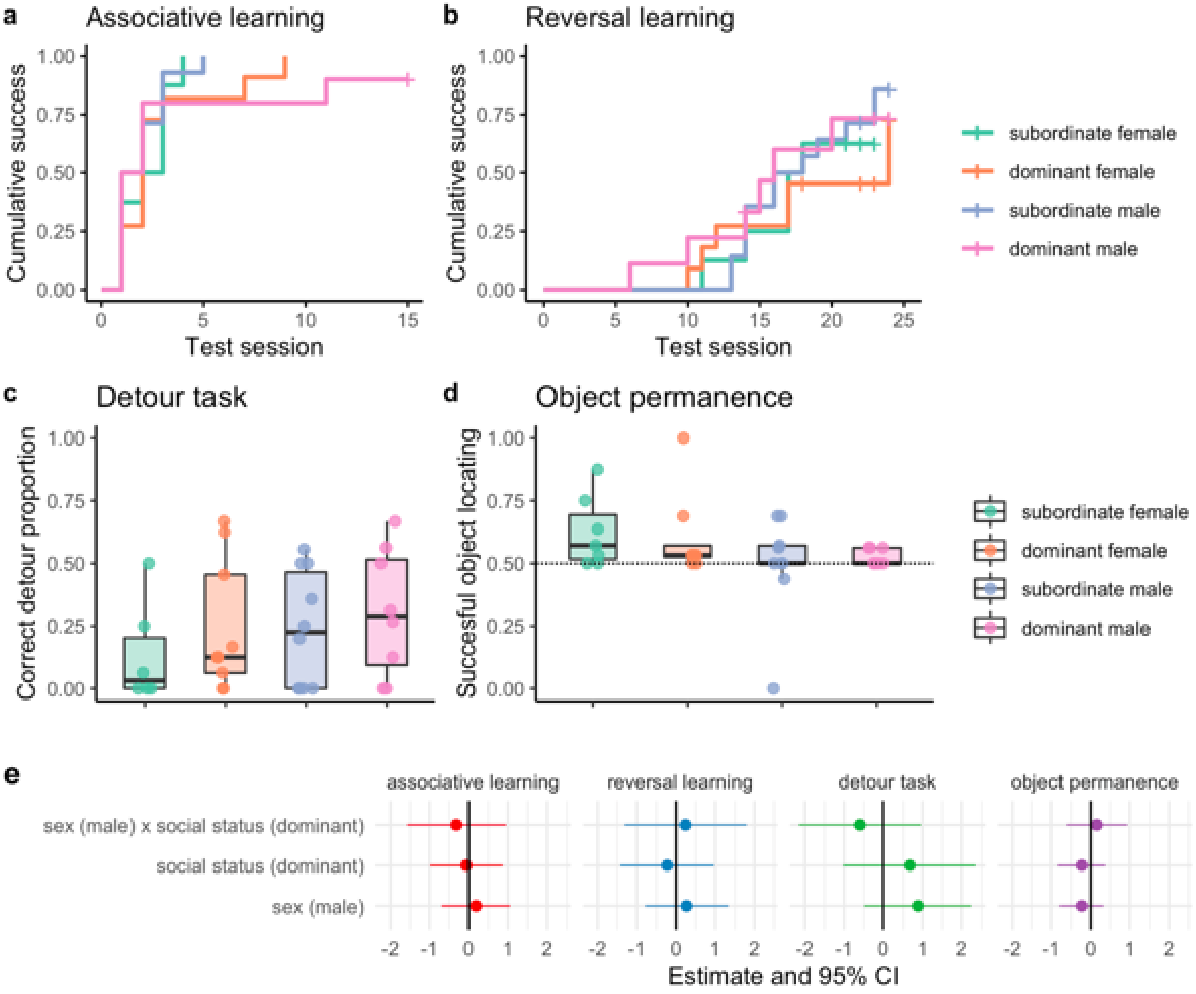

Figure 1. Performance in the cognitive tests. Cumulative success in (a) associative (N = 43) and (b) reversal learning (N = 42) tests. Boxplots of median, interquartile and ranges of proportion of (c) correct detours (N = 33) and (d) successful object locating in object permanence (N = 31) tests. Dashed line in (d) indicates the 50% chance level of performing correctly. (e) Estimate and 95% Confidence Interval extracted from the statistical models for each cognitive performance as a function of social status and sex.

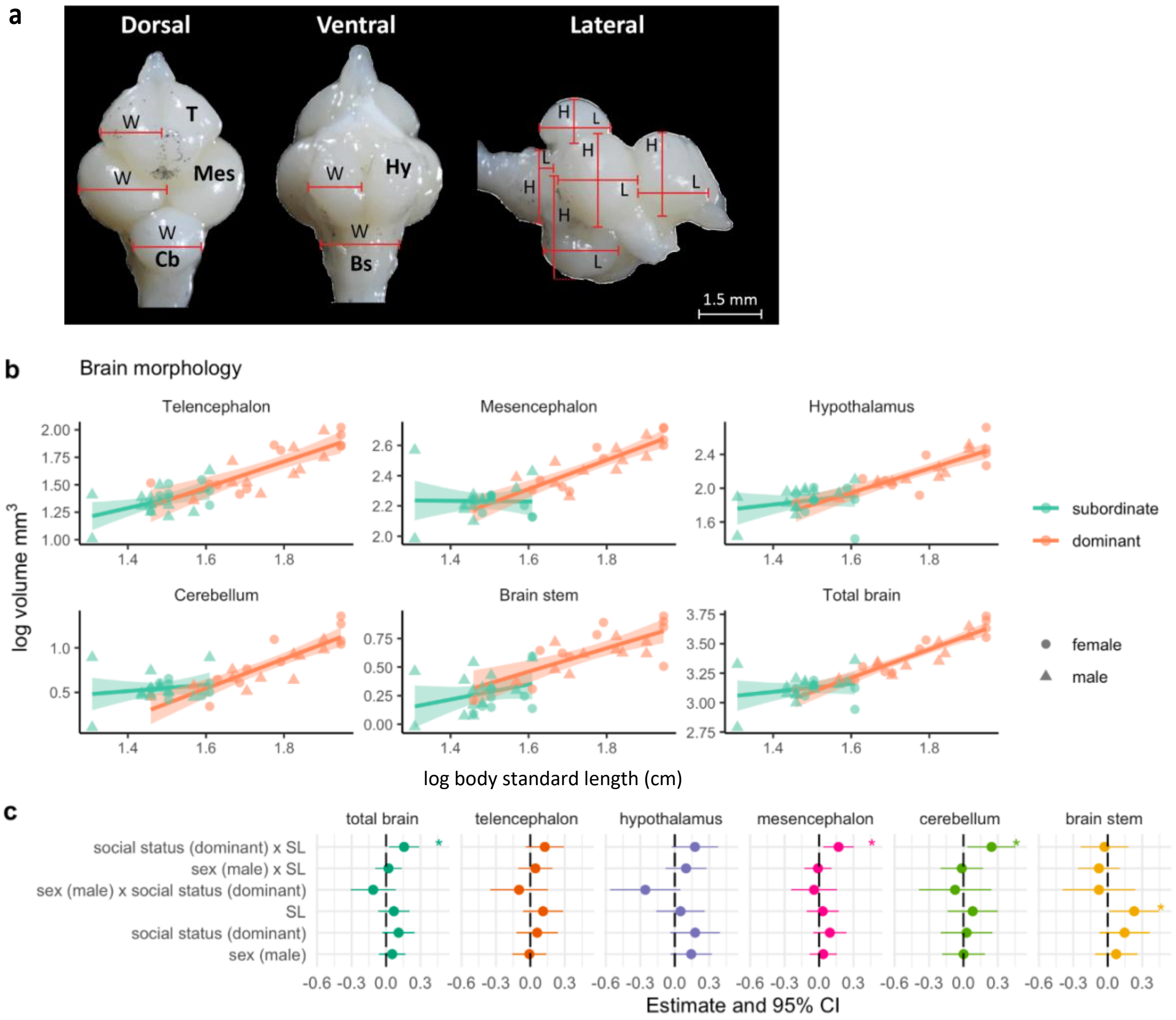

Figure 2. Brain morphology. (a) Brain images prepared for ellipsoid calculations for brain region volumes: T, telencephalon; Mes: mesencephalon; Cb: cerebellum; Hy, hypothalamus; Bs, brain stem; W, width; H, height; L, length. (b) Regression line and 95% CI of log-transformed brain measurements on log-transformed and standardized body size (SL) (N = 43). (c) Estimate and 95% CI extracted from the statistical models for each brain measurement as a function of social status and sex, and corrected for body size (SL). *$p < 0.05$.

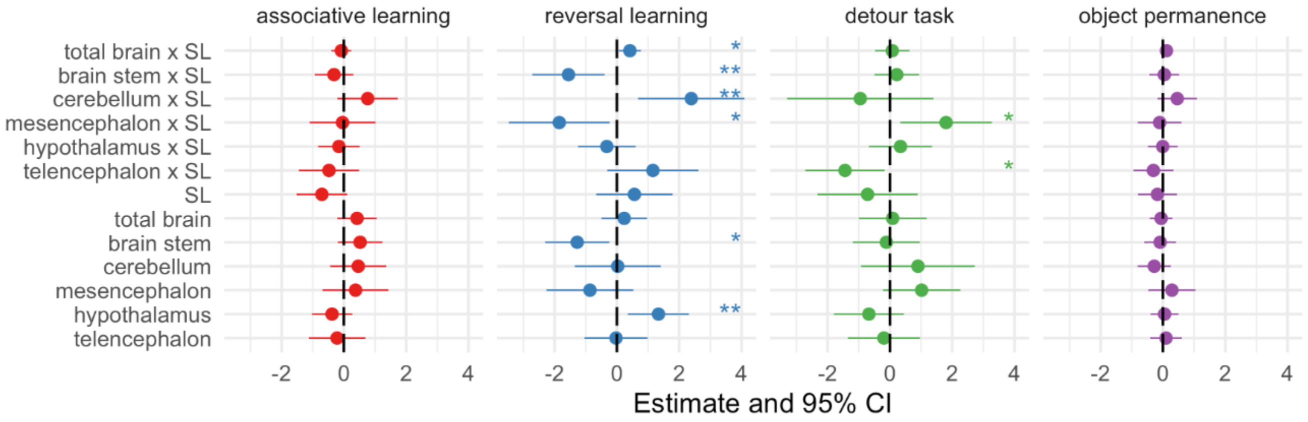

Figure 3. Estimates and 95% Confidence from statical models testing the relationship between brain morphology and cognitive performance. **p < 0.05; **p < 0.01.*

Discussion

Across three tests of executive functions, reversal learning, detour, and object permanence tasks, dominants and subordinates of *N. pulcher* performed similarly, with no sex differences in their performance. Yet, social dominance hierarchy had notably an effect on brain allometry, where dominants had steeper brain-body regression slope than subordinates, mostly driven by the mesencephalon and cerebellum brain regions. Moreover, brain morphology explained individual variation in reversal learning and detour performance.

To our knowledge, no other studies have explored the performance of dominants and subordinates in the three main executive functions: cognitive flexibility, inhibitory control and working memory. The existing studies on potential links between social dominance hierarchy and cognition have primarily focused on testing for spatial abilities. Most of the evidence points towards dominants having improved spatial skills than subordinates, like in pheasants, meadow voles and chickadees (Pravosudov et al. 2003; Spritzer et al. 2004; Langley et al. 2018). Yet, in another African cichlid fish, *Astatotilapia burtoni*, with dynamic social hierarchy, dominance does not improve this spatial faculty. However, it seems that social status has a strong influence on social competence in this species. Fish that ascend in social status are more socially competent, which means they are better at using social information to perform optimal behaviours (Wallace et al. 2022). Based on the results of our study, it appears that the dominance hierarchy does not have an impact on the three executive functions we tested. This is in line with the findings of Wallace et al. (2022) and suggests that social hierarchy might only affect performance related to social cognition. It is worth noting that the executive function tests we conducted did not involve any social interaction, as animals were only exposed to non-social cues. Combining social and non-social tests in future research can help to get a better understanding of this issue.

Although social status might not have a significant impact on executive functions, it does affect brain allometry in *N. pulcher*. This is evidenced by the fact that subordinates had an almost flat slope of brain-body size regression, with a value of approximately 0.08, while dominants had a slope of 0.24. In other words, as subordinates grew, their brains did not grow proportionally, whereas dominants' brains did, to some extent. We speculate two possible alternative explanations for such observations. The first explanation is based on *N. pulcher*'s strategic growth pattern that is dependent on its status. Subordinates remain smaller than dominants to avoid aggression and eviction from the group (Hamilton et al. 2005; Jungwirth et al. 2023). This suggests that they might also be strategic in their energy expenditure on expensive tissues such as the brain, and would only start investing in the brain once they become dominants. The second alternative explanation suggests that subordinates might not be strategic in their energy investment, but rather constrained by the presence of dominants. Moreover, it seems that the difference in brain allometry between dominants and subordinates is mainly due to two regions of the brain: the mesencephalon, which is typically the largest brain region in teleost, and the cerebellum, which is the most densely packed with cells compared to other brain parts (Van Essen et al. 2018). While there is no concrete evidence, it is possible that either these two areas require more energy to grow or that the other regions, like telencephalon and hypothalamus, are given a higher priority for energy investment under constraints.

Currently, there is limited research on the brain structure of individuals in dominant and subordinate positions. Nevertheless, there is an abundance of evidence that shows how social dominance hierarchy can affect the activity of different neural circuits in the brain. For instance, dominant *N. pulcher* have lower brain levels of the neuropeptide vasotocin (Reddon Adam R. et al. 2015), and in *Haplochromis burtoni*, another cichlid fish, monoamines levels can vary across brain regions depending on social status (Winberg et al. 2008). Moreover, in *A. burtoni*, social ascent can significantly increase the activation of all nuclei within the social decision-making network, which is a collection of brain nuclei responsible for regulating social behaviours in vertebrates (Maruska et al. 2013). Despite the advances regarding social status impact on brain activity, there is still a need for further studies to address the connection between morphology and functionality. Ultimately, this will help us understand how the interplay between morphology and functionality affects cognitive abilities and social behaviour.

Our study yielded an interesting finding that brain morphology was correlated with individual performance in two tasks: reversal learning and detour. Regarding the different parts of teleost brain, each region has a specific function. The classic understanding of these functions is that the telencephalon is responsible for cognition and decision-making, while the mesencephalon receives visual sensory input and sends it to the telencephalon. The hypothalamus regulates basic functions, as well as motivation and certain aspects of social behaviour. Lastly, The cerebellum controls motor coordination abilities and some aspects of cognition, while the brain stem controls autonomic functions (Kotrschal et al. 1998; Butler and Hodos 2005; Rodriguez et al. 2005; Striedter 2005; Braithwaite 2006; O′Connell and Hofmann 2011; Calvo and Schluessel 2021). Here, once we statistically corrected for fish body size, which is crucial because dominants are bigger than subordinates, total brain size and cerebellum correlated positively with reversal learning performance. In contrast, mesencephalon and brain stem were negatively associated with this task performance. Thus, fish with improved cognitive flexibility had a relatively larger brain with a larger cerebellum and, eventually, a smaller mesencephalon and brain stem. Although evidence suggests that enlarged brains facilitate cognitive flexibility across different species (Deaner et al. 2007; Buechel et al. 2018), little is known about how specific brain region sizes are associated with performance. Based on the limited research available from guppies, large telencephalons often facilitate individual performance in this task (Triki et al. 2022b, 2023b, a). Our study suggests that brain regions other than the telencephalon might also play a significant role in cognitive flexibility. Specifically, the cerebellum seems to be important (Butler and Hodos 2005) in *N. pulcher*. These findings suggest that having more neural tissue in the cerebellum might enhance the potential for acquiring and processing information about updating an existing decision rule. This is supported by lesion experiments in mice, which have shown that impairment in the acquisition of flexible learning is associated with lesions in the cerebellum (De Bartolo et al. 2009).

In the detour task, the fish with larger mesencephalons and smaller telencephalons showed better inhibitory control performance. As the mesencephalon is responsible for the visual sensory perception (Northmore 2011), it can be inferred that those with better visual processing abilities detoured more correctly without touching the cylinder. However, it was unexpected to find a negative correlation between the telencephalon size and performance in this task, given that guppies that have been artificially selected for larger telencephalons show improved performance in detour tests (Triki et al. 2022a, 2023a). Different species with different ecologies might have varying relationships between brain morphology and cognitive performance. Additionally, different brain regions with distinct functionalities might contribute varying levels of cognitive performance. Animal cognition can be broadly defined as the ability to take information through the senses, process, retain and act on it (Shettleworth 2001). Hence, each of the main teleost brain regions, including the sensory and motor centres, play a cognitive role. Our data showed that the variable roles of these regions can be attributed to the cognitive tests. For example, the detour test might have required enhanced perception, such as seeing a transparent cylinder with a food reward inside, and hence those with relatively larger mesencephalons performed better. On the other hand, reversal learning had a flexibility component, where individuals had to update a learned decision rule with new information. In this case, total brain size, mainly driven by the cerebellum, facilitated the process in those with improved flexibility performance. Together, the findings suggest a size trade-off among these brain regions and its subsequent relationship with cognitive flexibility and inhibitory control.

It is not uncommon to observe that variation in performance is associated with trade-offs in teleost brains. Cleaner fish residing in coral reefs with varying population densities also exhibit marked trade-offs in terms of the size of the forebrain (telencephalon and diencephalon) against the other brain regions and this was associated with their performance in a social competence test (Triki et al. 2019, 2020). Here, we observed that performance in two executive function tests was correlated positively with one brain region and at the same time negatively associated with the size of another region. We consider it likely that the enlarged region improved cognitive performance, while the reduced part is more likely due to an allocation trade-off but without contributing directly to performance. Two aspects drive such trade-offs: limited energy and needs (Striedter 2005). Individuals with limited energy would thus invest in expanding brain regions depending on their ecological needs that stem from environmental and social challenges. In animals raised in captivity, factors such as *ad libitum* food and the suppression of key variables that play a vital role in shaping brain and cognitive development such as predation pressure and feeding ecology (Huber et al. 1997; Brown and Braithwaite 2005), can potentially impact these trade-offs. Indeed, captive animals tend to have smaller brains (Marchetti and Nevitt 2003). Despite these limitations, we still observed brain region size trade-offs in our captive fish. Living in social groups, such as our fish in large tanks of 400L, still poses to some extent ecological challenges like aggression, competition over shelters, and the cohabitation of males and females with various social dominance status. Although we did not find any group-level effects of status or sex on cognitive performance, individual-level variation in the expression of executive functions were captured by the individual brain morphology.

There was no difference in fish performance in the associative learning test across social status or sex, and brain morphology did not explain individual performance. A plausible explanation is that forming simple associations does not necessarily require complex processing, as even box jellyfish can perform well in such tests (Bielecki et al. 2023). In contrast, an important result was that fish did not perform above chance in the object permanence test. Our study is the third to test fish object permanence abilities, and it seems that fish tend to perform at chance level with 50% success in this task (Aellen et al. 2022; Triki et al. 2023a). Only guppies artificially selected to have larger telencephalons performed relatively better with 60% success (Triki et al. 2023a). It is unclear whether the test itself is generally challenging for fish, or if we need to run all object permanence test stages in sequence to better understand individual performance and compare it to the performance of other taxa (Triana and Pasnak 1981; Call 2001; Hoffmann et al. 2011; Singer and Henderson 2015). For instance, in the first stages of the test applied to children, mammals and birds, the object is typically not fully hidden from the test subject. This does not rule out the possibility of learning and sequence effects on individual performance, but by following similar test steps, we can generalize our findings and confirm whether fish lack this capacity.

N. pulcher does not appear to have sex-specific selective pressures that cause differences in brain structure and executive functions between males and females. This is indicated by our data, which reveals no sex differences in cognitive performance or brain morphology. In another study by La Loggia et al. (2022) that examined *N. pulcher*'s transitive inference abilities, no sex differences were observed either. It is possible that our captive conditions have relaxed sex-specific selection on the brain and cognitive abilities. To confirm or reject this hypothesis, we need to conduct studies of cognition and brains in both wild and captive-bred fish (Bshary and Triki 2022).

In conclusion, our study highlights that *N. pulcher* performance in executive function tasks may not be linked to group-level characteristics like social status and sex, but it can be explained by individual brain morphology. Thus, what was previously considered as mere noise around the population mean can now be attributed to individual neural traits. Furthermore, depending on species, executive functions in fishes are associated with the size of different brain regions, like telencephalon, mesencephalon and cerebellum. Exploring species and individual-level cognitive performance as a function of brain morphology is a crucial step towards advancing the field of cognitive sciences.

Ethics

This work was approved by the ethics committee of the Veterinary Office of the canton of Bern in Switzerland [Licence number: BE133/2022].

Data availability

Source data from this study will be made available upon peer-reviewed publication.

Author contribution

ZT conceived the idea and designed the study. AG collected the data. ZT and AG analysed the data, generated the figures, and wrote the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgement

We express our gratitude to Barbara Taborsky for generously providing us with the fish and laboratory space, as well as her constant support and invaluable insights about African cichlids. We also extend our thanks to Redouan Bshary, Carel van Schaik, and Michael Taborsky for their thoughtful discussions on the study findings. This work was supported by the Swiss National Science Foundation [grant number PZ00P3_209020 to ZT].

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