Equal performance but distinct behaviors: *Astatotilapia burtoni* sex differences in a novel object recognition task and spatial maze

Kelly J. Wallace[1] & Hans A. Hofmann[1]

[1]Department of Integrative Biology, University of Texas, Austin, TX, 78712, USA

Article Type: Research Article

Kelly J. Wallace ORCID: 0000-0002-2361-1213

Hans A. Hofmann ORCID: 0000-0002-3335-330X

Author for correspondence: Kelly J. Wallace

kwallace@utexas.edu

University of Texas at Austin, Department of Integrative Biology

1 University Station C0990

Austin, Texas 78712

Highlights

- To ask if sexual dimorphism in cognition is reduced in a species where both sexes navigate highly fluctuating social environments, we assessed performance and behavior of the cichlid fish *Astatotilapia burtoni* in a novel object recognition task and a spatial maze.
- Both sexes exhibited a preference for the familiar object during a novel object recognition task, with males exhibiting the preference early in the task, whereas females exhibiting the preference late in the task.
- In the spatial task, females reached the learning criterion more often than expected by chance, whereas males do not. Females exhibited significantly longer decision latencies and quicker error correction in the spatial task, suggesting a sex-specific speed-accuracy tradeoff.
- The sexes differ in behaviors related to neophobia and decision latencies.
- A model selection analysis to predict sex finds that novel object recognition task preference, approach, and interaction duration are the most important terms on average.

Abstract

Sex differences in behavior and cognition can be driven by differential selection pressures from the environment and in the underlying neuromolecular mechanisms of decision-making. The highly social cichlid fish *Astatotilapia burtoni* exhibits dynamic and complex social hierarchies, yet explicit cognitive testing (outside of social contexts) and investigations of sex differences in cognition have yet to be fully explored. Here we assessed male and female *A. burtoni* in two cognitive tasks: a novel object recognition task and a spatial task. We hypothesized that given both males and females navigate dynamic social environments, we would observe less pronounced sex differences in cognition relative to other species with more “static” sex differences. In the present study we find that both sexes prefer the familiar object in a novel object recognition task, but the time at which they exhibit this preference differs between the sexes. Females more frequently learned a spatial task, exhibiting longer decision latencies and quicker error correction, suggesting a potential speed-accuracy tradeoff. Furthermore, the sexes

differ in space use in both tasks and in a principal component analysis of the spatial task. A model selection analysis finds that preference, approach, and interaction duration in the novel object recognition task that reach a threshold of importance averaged across all models. This work highlights the need to explicitly test for sex differences in cognition to better understand how individuals navigate dynamic social environments.

Keywords

sex differences, spatial learning, novel object recognition, social behavior, *Astatotilapia burtoni*

Introduction

For humans and non-human animals alike, navigating dynamic social environments is a constant challenge (O'Connell & Hofmann 2011, Taborsky & Oliveira 2012). Individuals must attend to changing signals and cues, remember stimuli and their valence, assess risk, make inferences from often incomplete or ambiguous information, use and update prior associations, and display socially appropriate behaviors in varied contexts including mate choice (Phelps & Ophir 2009, White & Galef 1999, Hebets & Sullivan-Beckers 2010), territorial/dominance aggression (Reichert & Quinn 2017, Bshary & Brown 2014), social foraging (Rapaport & Brown 2008, Thornton & McAuliffe 2006), and nest building (Keagy et al. 2011). Individuals that vary in social phenotype can differ in decision-making even when in identical social environments. For example, an individual encountering a territorial male may fight or flee, but the decision depends on that individual's own status. If the individual is also a territorial male, fleeing could mean abandoning his own territory and potentially losing reproductive opportunities. Conversely, if the individual is a non-territorial subordinate there is no cost of losing a territory and furthermore there may be a higher chance of serious injury.

Males and females frequently make different decisions in the same social environment. Sex differences in cognition, "the mechanisms by which animals acquire, process, store, and act on information from the environment" (Shettleworth 2010) have been described

across taxa (rodents: Orsini & Setlow 2017, Dalla & Shors 2009, Rice et al. 2017, songbirds: Titulaer et al. 2012, lizards: Carazo et al. 2014, poeciliid fish: Lucon-Xiccato & Bisazza 2017, Wallace et al. 2020), although males and females do not always differ in this regard (Lucon-Xiccato & Bisazza 2014 and 2016; Healy 1999, Guillette et al. 2009, Etheredge et al. 2018). When present, sex differences in cognition likely arise from varying ecological demands and fitness benefits of cognitive abilities such as sexually divergent pressures related to dispersal, predation, and mate choice (Watson & Platt 2008). For example, males and females can differ in foraging patterns (mice: Maille & Schradin 2016, cormorants: Ishikawa & Watanuki 2002, sandperch Sano 1993) and response to predation (poeciliid fish: Magurran & Seghers 1994, Magurran & Nowak 1991). Cognition can additionally impact fitness via reproductive performance directly, such as sexual display quality (e.g. aspects of song quality in songbirds), (Smith et al 2015, Boogert et al. 2011, Farrell et al. 2011) mate preference, (Shohet & Watt 2009, Branch et al. 2019) or responses to sexual conflict (Cummings 2018, Buechel et al. 2016). Furthermore, behavior and decision-making can vary along many axes including time (seasonality: Clayton & Krebs 1995, Yaskin 2011), social status (Stowe et al. 2007, Layton & Fulton 2014), satiety (Caraco 1981)reproductive status (Lynch et al 2005), and social context (Rosati & Hare 2012).

Territoriality has been hypothesized to drive increased spatial cognitive performance (Heske & Ostfeld 1990), and several studies have indeed shown that the more territorial sex exhibits increased spatial cognition (Gaulin & Fitzgerald 1989, Carazo et al. 2014, Rice et al. 2017). Sex differences have been previously described in spatial learning in fish, and most studies have found greater male performance (Carazo et al. 2014, Lucon-Xiccato & Bisazza 2017, Fabre et al. 2014, Saucier et al. 2008, Jonasson 2005, but see Jones et al. 2003, Healy et al. 1999, Lucon-Xiccato & Bisazza 2017). Importantly, behavior exhibited during a task can vary by sex independently of cognitive performance (Burns & Rodd 2008, Mamuneas et al. 2015; Lucon-Xiccato & Bisazza 2016; Etheredge et al. 2018; Titulaer 2012, Dougherty & Guillette 2018), for instance due to where males are typically identified as the “bolder” or “more exploratory” sex (Lucon-Xiccato & Dadda 2016, Han et al. 2015, Harris et al. 2010, Overli et al. 2006,

Gagnon et al. 2016, but see Hughes 1968 & Swanson 1966). Regardless, if the ecological demands of the social environment are largely invariant over time for one or both sexes, one might expect robust sex differences in cognition. Conversely, if the social environment frequently fluctuates for both sexes, we may observe fewer sex differences.

Burton's mouthbrooder cichlid, *Astatotilapia burtoni,* is a highly social east African cichlid fish that provides a unique system in which to explore sex differences in cognition in a temporally dynamic social system (Hofmann & Fernald 2001, Maruska & Fernald 2018). In this species, *both* sexes navigate socio-ecological demands that fluctuate across time. Males exhibit either a dominant phenotype (colorful, aggressive, territorial) or a subordinate phenotype (drab coloration, submissive, non-territorial). The territories are contiguously distributed in space and their borders aggressively maintained and contested by dominant males, who also vigorously court females (Fernald & Hirata 1977). These male phenotypes are socially regulated: given a reproductive opportunity (e.g. the removal of a dominant male by a predator) a subordinate can ascend in status, within minutes changing behavior, coloration, and physiology (Burmeister et al 2005, Maruska & Fernald 2010, Huffman et al 2012). Although *A. burtoni* females usually shoal with other females and juveniles, when gravid they venture into the lek in search for mating opportunities (Fernald & Hirata 1977, Kidd et al. 2013a). They can also form complex social hierarchies and display remarkable behavioral plasticity (White et al. 1996, Renn et al. 2012), modulated by their reproductive cycle (Kidd et al. 2013 a,b).

Successfully navigating these complex and ever-changing social hierarchies requires cognitive abilities such as transitive inference and context-specific behavioral responses, (Fernald 2014, Alcazar et al. 2014, Grosenick et al. 2007, Desjardins. et al 2012, Weitekamp et al. 2017, Rodriguez-Santiago et al 2020). Furthermore, this species has emerged as a model system for understanding the neurobiological mechanisms of social behavior and decision-making (Hofmann 2003, O'Connell & Hofmann 2012, Maruska & Fernald 2018). While cognition has been examined in naturalistic

communities of *A. burtoni* (see Wood et al. 2011, Rodriguez-Santiago et al 2020), studies that assess cognitive performance independent of social context and across the sexes are lacking.

In the present study, we investigated whether *A. burtoni* males and females differed in cognition by assessing individuals in a novel object recognition task (NOR) and a spatial task (SPA). Both tasks require learning - a change in cognitive state or behavior resulting from prior experience (Shettleworth 2010, Staddon 1983)- and test abilities that are relevant to *A. burtoni*'s natural history, as males typically establish territories under specific objects (such as plant debris or rocks), to which they reliably return after extensive excursions in search for females, which in turn are found in the shoals in the periphery of the lek (Fernald & Hirata 1977). Females usually shoal, although when given the opportunity they can display a behavioral repertoire typical of males (Renn et al 2012). Thus, we hypothesized that *if* we were to find sex differences in cognition in this species it would manifest as greater male performance in the spatial task. We further hypothesized that across both tasks males would display stronger neophilic and exploratory behavior, either in terms of a stronger preference for the novel object and/or higher numbers of stimulus approaches and shorter latencies to approach. We also assessed whether behavior and cognition in the two tasks was correlated to the other via multidimensional analyses. We hypothesized that, since both memory and spatial learning are needed to successfully navigate the *A. burtoni* social environment, both sexes would successfully learn both tasks and additionally would exhibit correlated individual performance across tasks.

Materials and Methods

(a) Housing and Initial Community Formation

128 adult *A. burtoni* (64M/64F) were used from a lab population descended from wild-caught stock. Fish were maintained in naturalistic communities (114-liter aquaria) prior to testing. Both prior to and during testing, fish were kept in reverse osmosis water treated with Seachem® Lake Tanganyika salt and bicarbonate buffer. Lights were on a 12:12 light-dark cycle and fish were fed once daily with Omega One Natural Protein

Formula Cichlid Flakes. All individuals were tagged with colored plastic beads for individual identification. One week prior to testing, fish were placed as a community of 8M/8F (n= 8 replicate communities) in a circular pool (1m diameter, 25cm depth, lined with a PEVA curtain liner and Spectrastone White aquarium gravel) containing four halved terra-cotta pots to be used as territorial shelters (Supplemental Figure 1), and at this time fish were weighed and measured for standard length (average standard length: males = 4.78cm, females = 4.76cm).

(b) Novel Object Recognition Task (NOR)

To assess memory, we utilized a novel object recognition task (also referred to as the spontaneous object recognition task). The novel object recognition task, at its simplest, requires an individual to discriminate between a previously encountered object and a novel one. This paradigm is commonly used in the rodent literature to assess memory (Ennaceur & Delacour 1988, Broadbent et al. 2010), but additionally has the capacity to characterize recognition, neophobia, and exploration (Antunes & Biala 2012).

In the novel object recognition task conducted here, individuals were assessed for relative preference (physical proximity) to a familiarized object versus a novel object in a 114 liter acrylic aquarium filled to a depth of 20cm with a central alley way and two object regions (Figure 1A, B). Four objects were used as stimuli in the task: a pink centrifuge tube, a purple falcon tube cap, a blue weight boat (quartered), and a yellow table tennis ball filled with sand (Supplemental Figure 2). Object pairs and their roles (familiar vs novel) were counter-balanced across communities. Prior to testing, the entire community was familiarized at once (to maintain daily consistency in the timing of the experimental design) to two identical objects (coined the “familiar object”) for one hour (e.g. A + A). Approximately 24 hours later, each fish was individually presented with a familiar object and a novel object at the opposite ends of the aquarium (the side of the familiar object, left or right, was counter-balanced across communities) (e.g. A + B). Previous studies in zebrafish have shown that the delay between familiarization and testing can range between 2 and 24 hours without impacts on resulting performance (Lucon-Xiccato & Dadda 2014). During the trial, individuals were acclimated in an opaque PVC tube for one minute then allowed to swim freely in the apparatus for twelve

minutes. Following the trial, individuals were kept in a holding area until all community members were tested, then simultaneously returned to the community to prevent social hierarchy destabilization. Relative preference for the familiar object ("NOR familiar preference") was calculated as the relative proportion of time spent at the familiar object to time spent at the novel object, where a score of 1 means the entirety of time spent at an object was at the familiar object, a score of 0.5 means equal preference, and of 0 means the entirety of time spent at an object was at the novel object.

(c) Spatial Task (SPA)

Spatial learning involves following a route composed of a sequence of stimuli that must occur in a specific order (Dodson 1988). There has been a long and extensive usage of spatial tasks ("mazes") to assess spatial learning in fish: see Salas et al. 1996 (goldfish), Lucon-Xiccato & Bisazza 2017 (guppy), Burns & Rodd 2008 (guppy), Jun et al. 2016 (electric fish) Wood et al. 2011 (cichlid). These tasks often rely on associative (Pavlovian) paradigms in which a location is associated with a reward (food or stimulus). Thus, in addition to spatial learning, these tasks require associative learning: learning that results from experiencing predictive relationships between stimuli and outcome (Shettleworth 2010). In the spatial task conducted here, individuals in a 57 liter acrylic aquarium filled to a depth of 20cm were required to detour around an opaque barrier in one of two directions (left or right) to reach a social reward consisting of a female in a clear plexiglass tube behind one side of the barrier (Figure 1C, D, average standard length of female conspecific reward = 4.49cm). Behind the other side of the barrier, an empty plexiglass tube was placed as a control stimulus. Transit between the rewarded and unrewarded area required an individual to navigate back out in front of the barrier, thus creating a penalty for errors. For all trials, individuals were initially placed in an opaque PVC tube for one minute to acclimate to the aquarium, then allowed to swim freely for twelve minutes. Each individual underwent an initial apparatus habituation trial (using two control stimuli) the day prior to the reward trials. Following this habituation trial, individuals were assayed over four rewarded trials over two days, with the reward stimulus present behind either the left or right barrier, counter-balanced across individuals. Across these trials the same reward female stimuli were used per individual

(excluding rare experimental limitations). As with the NOR task, following the trial, individuals were kept in a holding area until all community members were tested then simultaneously returned to the community. To assess performance, we established a learning criterion in which successful learners first approached the rewarded stimulus in all rewarded trials after the first trial (i.e. trials 2-4). Relative preference for the rewarded stimuli ("SPA reward preference") was calculated as the relative proportion of time spent at the rewarded stimulus to time spent at the unrewarded stimulus, where a score of 1 means the entirety of time spent near a stimulus was at the rewarded stimulus, a score of 0.5 means equal preference, and of 0 means the entirety of time spent at an object was at the unrewarded stimulus.

(d) Video Scoring

Videos were recorded overhead of the experimental apparat via the Alibi Security Camera system and scored by three human observers (who had not conducted the behavioral assays) in VLC media player using CowLog video scoring software version 3.0.2 (Hänninen & Pastell 2009), a software which has been validated to be highly consistent across multiple observers (Wallace et al. 2020). Focal fish location was recorded though the duration of the test trial of the novel object recognition task and the fourth (test) trial of the spatial task. Additionally, for trials one through three of the spatial task the first approach (rewarded or unrewarded) was recorded.

(e) Statistics

Data analysis and visualization were performed in R (R Core Team 2013) version 3.6.1 (2019). We conducted an unpaired t-test or unpaired two-sided Wilcoxon Rank Sum test with continuity correction for continuous data split into 2 categories, or a One-way ANOVA or Kruskal-Wallis test for continuous data split into >2 categories (determined by a Shapiro-Wilk normality test). For entirely categorical data we conducted Chi-squared tests. We conducted standard multiple linear regressions to determine correlations and effect sizes of relationships between continuous independent variables using the formula lm(x1 ~ x2) using the R function "lm()". To identify interaction effects of sex, we conducted linear models with interaction terms using the formula lm(x1 ~ x2 *

x3). Effect sizes were calculated as either Cohen's D using the R function "cohen.d()"in the R package "effsize" (Torchiano 2020) for categorical data or as the Pearson correlation coefficient using the R function "cor()" for continuous data. We conducted principal component analyses (PCA) on z-scored data via the R function "prcomp". Hierarchical clustering analyses were conducted using the R package "pvclust" (Suzuki et al 2019) with distance metric: "correlation", linkage metric: "average", and bootstrap values set to 100. Logistic regression models were constructed and selected using the R package "glmulti" (Calcagno 2020). Variables included in data analysis (including in the principal component analyses) were first assessed via a covariance matrix: any two variables with a Pearson's correlation coefficient above 0.8 were considered redundant, thus for subsequent analysis the authors used the variable more commonly used in previous literature. Raw data and analysis code can be found at https://github.com/kellyjwallace/Wallace_Hofmann_2020_sex_differences.

Results

(a) Novel Object Recognition Task (NOR)

Before quantifying performance on the NOR task, we first assessed if any objects were preferred independent of familiarity. No object was significantly preferred or avoided (average preferences: cap 55%, weigh boat 45%, ball 43%, tube 57%, Wilcoxon test on the two pairs: $W_{41,41}$= 389, p = 0.229 and $W_{55,55}$= 497, p = 0.054, respectively). However, because the ball/tube pair showed a near significant bias we additionally tested whether individuals' first choice (familiar or novel) differed by the pair of objects they received and found no significant difference (chi^2 test: p = 0.108, n = 97, X^2 = 2.577, df = 1).

We then asked whether males and females differed in task performance, even though both sexes face highly dynamic social environments. We quantified the proportion of individuals that first approached the familiar object in each sex and found that neither sex approached the familiar object more than would be expected by chance: 63 individuals (38M/25F) first approached the familiar object, and 47 individuals (20M/27F) first approached the novel object. Consistent with this result, we also found that a

continuous measure of performance across the length of the trial, the “NOR familiar preference,” did not differ by sex (average NOR familiar preference across both sexes = 0.52, Wilcoxon test: $p = 0.386$, $W_{64,64} = 1268$, Cohen’s D = 0.188) and did not diverge from a random 50% expectation in either sex. This preference score did not differ by round (rounds differed in the object pair presented) (Kruskal-Wallis df = 7, $\eta^2 = 0.038$).

Given that neither sex displayed a significant preference when averaged across the entire task (contrary to our hypothesis that both sexes would learn the task), we further asked whether a preference for either the familiar or novel object could be observed at any time during the task. Interestingly, we found that males exhibited a significant preference for the familiar object in the first minute of the task (Wilcoxon test: $p = 0.040$, $V = 742$, $n = 49$, Figure 2A), and preference was significantly correlated to time for both males (linear regression: $R^2 = 0.372$, $F_8 = 6.321$, $p = 0.036$,) and females (linear regression: $R^2 = 0.570$, $F_8 = 12.93$, $p = 0.007$), with a significant interaction effect of sex where male’s familiar object preference decreased across time whereas female’s increased (linear regression: $R^2 = 0.575$, $F_{16} = 9.55$, $p = 0.0009$) (Figure 2B).

To assess whether males were the more neophilic sex, we compared latencies to approach the objects and the proportion of time spent with objects: latency to approach either object did not differ by sex (Wilcoxon test: $p = 0.463$, $W_{64,64} = 1275$, Cohen’s D = 0.198), nor did the proportion of time spent interacting with either object (Wilcoxon test: $p = 0.180$, $W_{64,64} = 987$, Cohen’s D = 0.331) though a large proportion of time was spent in the corners near the objects (“association”), significantly more so in females with a small effect (average of females = 85%, average of males = 78%, Wilcoxon test: $p = 0.022$, $W_{64,64} = 1490$, Cohen’s D = 0.482) (Figure 2C). Visualizations of focal location across time in the NOR task are available in (Supplemental Figure 3).

We then conducted a multivariate analysis of variables measured in the NOR task (PCA) to further assess relationships between performance and other behaviors observed during the task. The analysis identified 9 PC axes, three of which explained >10% each (and together 74%) of the total variance in the dataset (Figure 3,

Supplemental Table 1). The variables that most strongly loaded onto first PC, comprising 31% of the variance, were variables associated with overall object association and interaction. Familiar preference variables most strongly loaded onto the second PC, comprising 24% of the variance. Neophobia metrics (non-engagement and latency to approach either object) most strongly loaded onto the third PC, comprising 19% of the variance. None of these PC's differed significantly between the sexes. To identify clusters of behaviors that shared similar loading patterns, we performed a hierarchical clustering analysis of behavior using the PCA eigenvalues. The analysis yielded one highly supported cluster (AU > = 95%, indicated by grey box in figure 3): NOR non-engagement (a neophobia metric) and NOR familiar preference.

(b) Spatial Task (SPA)

To first confirm that no cues (e.g. olfactory) from the reward fish could be detected by the focal fish, we compared the proportion of individuals who first chose the rewarded side during the first trial to a random expectation, and found that individuals first approached the rewarded and unrewarded sides randomly (chi^2 test: $p = 0.313$, $n = 111$, $X^2 = 1.0182$, $df = 1$). To test our hypothesis that the sexes would not differ in spatial learning or, alternatively, that males would outperform females due to territoriality-related cognitive demands, we assessed performance on the final trial of the task (trial 4) and surprisingly found that 31 of 51 females (61%) first chose the rewarded side, which was significantly more than the 25 of 59 males (42%) who first chose the rewarded side (chi^2 test: $p = 0.043$, $n = 111$, $X^2 = 4.064$, $df = 1$, Supplemental Figure 4). We then assessed performance based on a criterion of learning where we classified learners as those who first approached the rewarded stimulus in all rewarded trials after the first trial (trials 2-4). The probability for this to occur by random choice is 12.5%. Interestingly, 7 of 58 males (12.1%) reached this criterion (suggesting random choice), whereas 12 of 51 females (23.5%) reach this criterion, representing a significant cumulative binomial probability in which the females learn the task more than would be expected by chance ($p = 0.021$, Figure 4A). However, the proportion of males that reached the learning criterion did not differ from proportion of females that reached the learning criterion (chi^2 test: $p = 0.186$, $n = 109$, $X^2 = 1.744$, $df = 1$).

Next, we asked whether males were the more neophilic sex and whether behavior was related to performance in the task. To this end, we assessed several behavioral and performance metrics in the fourth trial of the assay. Interestingly, we detect a small effect where *males* spent significantly more time spent near the walls of the aquarium during the task (thigmotaxis), which is commonly considered an anxiety behavior (Maximino et al. 2010) (Wilcoxon test: $p = 0.045$, $W_{53,50} = 1023$, Cohen's D = 0.435). We found a small effect where females exhibited a significantly higher SPA reward preference across the duration of the task (female average = 0.6, male average = 0.4, Wilcoxon test: $p = 0.032$, $W_{64,64} = 1346$, Cohen's D = 0.447) (Figure 4B). Additionally, females tool significantly more time to decide than males with a moderate effect size (Wilcoxon test: $p = 0.0028$, $W_{64,64} = 1381$, Cohen's D = 0.538) (Figure 4C). Also, their latency to enter the rewarded area was highly correlated with this latency to decide, a relationship that was not present in males (linear regression: $R^2 = 0.851$, $F_{60} = 121.3$, $p = 1.296 \times 10^{-14}$) (Figure 3D), suggesting that the sexes might differ in error correction. To test this idea, we subsetted the results by individuals who first approached the unrewarded side and subsequently entered the rewarded side and measured the time between the first unrewarded entry and the subsequent rewarded entry. We found that, indeed, females correct these first approach "errors" significantly faster than males with a very large effect (female average = 101 seconds, male average = 309 seconds, Wilcoxon test: $p = 0.029$, $W_{7,8} = 9$, $n = 15$, Cohen's D = 1.193) (Figure 4E). Visualizations of focal location across time in the SPA task are available in (Supplemental Figure 5).

As with the NOR task, we conducted a principal component analysis of variables measured in the spatial task to understand the relationships between the behaviors observed during the task. Of the 10 PC axes identified, we explored further the four PCs that explained >10% each (and together 85%) of the total variance in the dataset (Figure 5A, Supplemental Table 2). Variables related to preference and engagement loaded primarily onto the first PC (which explained 36% of the variance). Interaction, association, decision latency, and interaction latency loaded most strongly onto PC2

(20% of the variance) and significantly differed by sex with a large effect (Wilcoxon test with FDR correction, p =0.008, $W_{26,24}$ = 481, Cohen's D = 0.884) (Figure 5B). None of the other PCs varied across sexes, and in a hierarchical clustering analysis of the eigenvalue patterns did not yield any well supported clusters (AU > = 95%) of behavior.

(d) Relationships across the tasks

Completing the NOR task requires learning and memory, and both abilities are likely important for successfully navigating the cognitive demands of *A. burtoni* social life. We therefore asked whether performance across the two tasks was correlated. When first simply using the categorical metric of "first choice" (rewarded or unrewarded in SPA, familiar or novel in NOR) the two tasks are not correlated. However, performance in the two tasks can be compared appropriately only for those individuals who entered both the familiar and novel object recognition task areas *and* the rewarded and unrewarded areas of the spatial task. 13 males and 7 females met this criterion. When we then correlated the continuous preference metrics across the tasks (relative preference for the familiar object in the novel object recognition task and relative preference for the rewarded stimuli in the spatial task), we found that they were indeed significantly correlated in a sex-invariant manner (linear regression: R^2 = 0.229, F_{18} = 5.359, p = 0.032) (Figure 6A). Because we had previously discovered that decision latencies differed by sex in the SPA tasks, we next asked whether decision latencies related to choices across tasks (Figure 4C), and observed a modest effect where individuals who first approached the novel object in NOR task showed longer decision latencies in SPA (Wilcoxon test: p = 0.033, $W_{58,39}$= 427, Cohen's D = 0.333), and conversely, individuals who first approach the rewarded stimulus in SPA exhibit longer decision latencies in NOR (Wilcoxon test: p = 0.010, $W_{53,50}$ = 1062, Cohen's D = 0.029) (Figure 6B,C).

To better understand the relationships between variables across both tasks, we conducted a principal component analysis that included the variables from both the SPA and NOR tasks (Figure 7, Supplemental Table 3), and identified four principal components (of ten total) that explained at least 10% each (and together 61%) of the total variance. The first two principal components were largely defined by task: PC1

(accounting for 24% of the variance) loaded most strongly with measures of activity and reward preference in the spatial task, whereas PC2 (accounting for 16% of the variance) loaded primarily by object preference and approaches, though it also included latency variables across both tasks. PC3 (11%) loaded most strongly by variables associated with stimulus interaction across both tasks, and PC4 (10%) loaded primarily by a single variable: SPA reward latency. No PC axes in this combined analysis differed significantly by sex. When clustering behaviors by their eigenvalue patterns in this PCA, we identified five highly supported clusters (AU > = 95%), some of which were with a task and some which spanned across tasks (Figure 7, highlighted in grey boxes).

Finally, to identify which variables across both tasks were best able to distinguish males and females, we conducted three logistic regression model selection analyses to predict sex via an exhaustive screening of all possible models and selecting based on AICc: one with variables from the NOR task, one with variables from the SPA task, and a combined model. Using variables from the NOR task, the selected model (of 511 possible models, McFadden's Pseudo-R^2 value of 0.032) included only NOR novel object interaction bout duration (Supplemental Table 4). Using variables from the SPA task, the selected model (of 1023 possible models, McFadden's Pseudo-R^2 value of 0.213) included the SPA preference measure and % association (Supplemental Table 5). For each of analysis we additionally conducted a model-averaged importance of terms analysis. In a model-averaged importance of terms analysis, the importance of a term is determined by the number of models the term appears in and their weights (a metric of the model's likelihood to be the "best" model). Neither of these task-specific models identified a term that reached the importance threshold of 0.8 (Supplemental Tables 4,5). Using variables from both tasks, the selected model (of 524,287 possible models, McFadden's Pseudo-R^2 value of 1.00) included the following variables from both tasks: NOR novel object interaction bout duration, NOR familiar preference, NOR novel object approaches, NOR association, NOR interaction, NOR object approach latency, SPA decision latency, SPA % association, SPA reward latency, NOR non-engagement, SPA reward preference, SPA reward preference following solution, and SPA thigmotaxis (Table 1, bolded). The terms in a model-averaged importance of

terms analysis that reached the importance threshold were three NOR variables: NOR novel object interaction bout duration (0.994), NOR familiar preference (0.938), and NOR novel object approaches (0.927). (Table 1, highlighted with an asterisk)

Discussion

The central question motivating the present study asked whether a species in which both sexes navigate temporally dynamic socio-ecological pressures would show less sex differences in cognition. To assess this question, we used Burton's mouthbrooder cichlid, *Astatotilapia burtoni,* a species well-characterized for its fast-paced and complex social system (Hofmann & Fernald 2001). We assessed male and female *A. burtoni* in two cognitive tasks: a novel object recognition task and a spatial task. In the novel object recognition task, both sexes exhibited a preference for the familiar object but at different times of the task, and males spent less time associating with the objects than females. In the spatial task, females reached a learning criterion above chance levels and exhibited stronger preferences for the reward stimulus. Females exhibited longer decision latencies and quicker error correction speeds. These differences were also captured in a principal component analysis of the spatial task, which identified a PC axis that significantly varied by sex and loaded most strongly by stimulus interaction and latency. Broadening our analysis to look at relationships across both tasks, we found that in a sex-invariant manner preference scores across the two tasks significantly correlated to each other (preference for the familiar object in the novel object recognition task, and preference for the rewarded stimulus in the spatial task), and decision latencies predicted first choice behaviors across tasks. The first axis of a principal component analysis using variables from both tasks was primarily loaded by SPA preference and activity. A hierarchical clustering analysis of eigenvalue patterns validated behavioral relationships both within and across tasks and identified a potential neophobia relationship across the tasks. Finally, using a logistic regression model selection approach, we found that the behavioral variables that best predicted sex spanned both tasks. However, when assessing the importance of variables across all models, only NOR measures (novel object interaction bout duration, familiar preference, and number of novel object approaches) reached an importance threshold.

(a) Sex differences in the Novel Object Recognition Task

In the novel object recognition task, both sexes exhibited a significant preference for the familiar object, confirming our hypothesis that both sexes would learn the task. While rodents (of both sexes) typically prefer the *novel* object, studies in fish have yielded conflicting results (May et al. 2016, guppies: Miletto Petrazzini et al. 2012, Lucon-Xiccato & Dadda 2016). Miletto Petrazzini et al. 2012 hypothesized that this difference in familiar preference across taxa may be due to the size of the objects relative to the focal individual and thus a reflection of neophobia or anti-predator responses.

Where we did identify sex differences was in the timing of the NOR preference for the familiar object: males exhibited the familiar preference early on in the task, whereas females exhibited the familiar preference later in the task. Studies in fish have found cases where preferences are only exhibited during for the first few minutes of the task (Lucon-Xiccato & Dadda 2016, Miletto Petrazzini et al. 2012). Similarly, a sex-specific relationship between thigmotaxis (wall hugging, a proxy of anxiety behavior, Maximino et al 2010) and associative learning has been documented in mosquitofish (Cummings 2018). This is also reflected in our study: in the combined principal component analysis the NOR relative preference behaviors cluster with SPA thigmotaxis (and total activity, suggesting NOR preference is related to neophobia/anxiety/anti-exploratory behavior in another context. Thus, we suggest that this sex difference in the timing of the preference is likely related to neophobia. This is reflected in the hierarchical clustering of eigenvalues based on the NOR PCA: familiar preference significantly clusters with NOR non-engagement, a metric likely reflecting anxiety/neophobia. But neophobia is likely not the only factor explaining the difference in timing of familiar object preference in the NOR task, as *males* exhibited lower overall levels of object association during the task, and furthermore the sexes did not differ in other measures of neophobia (object approach latency or proportion of time interacting with the objects).

One additional consideration that may explain the sex difference in NOR familiar preference is that, in our experimental design, the animals were familiarized to the task

(all individuals from a given community were familiarized together). A study in juvenile guppies also conducted object familiarization trials in a social setting and found during test a preference for the familiar object (Miletto Petrazzini et al. 2012). In ravens, dominance status influenced approach latencies in a novel object task, and this relationship between dominance status and approach varied by social context (e.g. same-sex vs mixed-sex pair) (Stowe et al. 2006). Dominance status has been shown to relate to exploratory behavior (Dingemanse & de Goede 2004, Stapley & Keogh 2004, Carazo et al. 2014) and cognitive performance across multiple tasks and taxa (pheasants, Madden et al. 2018, starlings, Boogert et al. 2006, dogs, Pongracz et al. 2008). In *A. burtoni*, males vary in dominance status, with dominant males aggressively establishing and defending territories (Fernald & Hirata 1977). Because the familiarization phase of the NOR task was conducted in a social setting, the preferences exhibited during the test may be the result of social associations (e.g. males more readily seeking the familiar object as a territory). This within-sex variation in male dominance status (as well as in female reproductive status) may also explain the relatively moderate effect sizes seen in our significant results from the NOR task, in that these within-sex phenotypes may better capture the observed variation. Further experiments assessing within-sex variation in *A. burtoni* and a possible role of dominance and reproductive status are needed to identify potential social factors driving NOR preferences.

(b) Sex differences in the Spatial Task

Across both sexes only a small proportion of individuals successfully reached the learning criterion in the spatial task. This is not unexpected, given that our experimental paradigm has few trials and a strict learning criterion ("learners" had to learn after only one training trial and not make a mistake in the following three trials). A similar design has been used in another cichlid species, the Nile tilapia *Oreochromis niloticus* (Lombardi Brandão et al. 2015). This study also used a T-shaped barrier in which a focal individual had to navigate around by making either a left turn or right turn to reach a reward and after 30 trials (2x/day) with a criterion of 9/10 correct trials in a row 50% of their focal individual successfully learned the task.

Contrary to our expectations, we found that in the spatial task it was *females* who reached the learning criterion more than would be expected by chance and thus successfully learned the task, whereas males did not. Based on prior studies in other species and more pronounced territoriality behavior in males of this species, we had hypothesized that, if we were to identify a sex difference in performance, males would show higher performance in the spatial task (Carazo et al. 2014, Lucon-Xiccato & Bisazza 2017, Fabre et al. 2014, Saucier et al. 2008, Jonasson 2005, but see Jones et al. 2003, Healy et al. 1999, Lucon-Xiccato & Bisazza 2017). Despite females reaching the learning criterion more than expected by chance, the sexes did not differ in performance when compared to each other, supporting our hypothesis that sexual dimorphism in cognition is reduced in *A. burtoni* compared to other species. Female *A burtoni* must also attend to spatial locales for spawning in male territories, and furthermore females are capable of exhibiting male-typical behavior (including territory defense) in the absence of males (Renn et al. 2012), suggesting that despite rarely exhibiting territory defense under normal conditions the cognitive abilities needed for territory defense are present in both sexes (White et al. 1996). Further research in *A. burtoni* females on foraging, predation, risk assessment, and shoaling is necessary to validate these explanations.

In the PCA of the spatial task, PC2 (explaining 20% of the variance) significantly differed by sex. This PC2 loaded most strongly by variables of stimuli interaction, association, and latencies. Additionally, females exhibited longer latencies to decide in the spatial task with medium effect and more frequently reached the learning criterion. Taken together these results suggest a possible speed-accuracy tradeoff, such that females are the slower but more accurate sex in this task. Speed accuracy tradeoffs have been previously identified in the literature (chickadees: Guillette et al. 2011, voles: Mazza et al. 2018, see Chittka et al. 2009 for review). This interpretation is further supported by the finding that females exhibit their NOR familiar preference later in the task, suggesting that females may be the “slower” sex in the NOR as well. Additionally, females corrected errors much faster than males, suggesting higher accuracy as well as

increased cognitive flexibility. Cognitive flexibility is the ability to modify behavior in response to variations in consequences or context of the environment (Bond et al. 2007; Easton 2005). While we did not specifically assess cognitive flexibility in this task, our observations of quicker female error correction (a term used to assess cognitive flexibility in other tasks, see Mazza et al. 2018) complements previous findings that female guppies have been shown to outperform males in tests of cognitive flexibility (Miletto Petrazzini et al. 2017, Lucon-Xiccato & Bisazza 2017). Given the large effect size of the sex difference in error correction found in this study, further experiments in this species quantifying sex differences in cognitive flexibility are likely to yield fruitful insights.

(c) Relationships across tasks

A growing body of literature has demonstrated a high correlation in performance across cognitive tasks (Chiappe & McDonald 2005, Kolata et al. 2008, Banerjee et al. 2009). At this current state of research on sex differences in (animal) cognition, relatively few studies have specifically investigated sex differences across multiple cognitive tasks. Those that do often find sex differences in specific tasks rather than general greater performance by one sex across all tasks (e.g. Dalla & Shors 2009, Lucon-Xiccato & Bisazza 2017, Wallace et al. 2020, Miletto Petrazzini et al. 2017; Lucon-Xiccato & Bisazza 2014; Brust et al. 2013; Carazo et al. 2014; Laland & Reader 1999). Because both memory and spatial learning are likely needed by *A. burtoni* males and females to successfully navigate the dynamic and fast-paced social environment typical for this species, we predicted performance would be correlated across tasks for both sexes. In a PCA of both tasks, SPA variables largely load on PC1 (explaining 24% of variance) and NOR variables load on PC2, suggesting that these tasks are not strongly correlated. However, preference for the familiar object in the NOR task correlates significantly preference for the reward stimulus in the SPA task at an individual level. Furthermore, when clustering variables by their eigenvalue patterns in this PCA, a majority of clusters contain variables from both tasks. NOR novel object approaches clusters with SPA interaction, both potential measures reflecting boldness/neophilia. SPA thigmotaxis (wall-hugging) clusters with SPA activity (number of entries during the

task), which is unsurprising given both these behaviors reflect anxiety-like behaviors. NOR familiar preference clusters with the number of familiar object approaches, consistent with what we would expect. The two SPA latencies (decision and interaction) cluster with NOR non-engagement, reflecting another possible boldness/anxiety/neophobia cluster. Lastly, NOR novel object interaction bout duration, SPA decision (time spent in both the association and interaction areas), and SPA preference (both over and preference following solution) cluster together. It is important to note that these hierarchical clusters of eigenvalues not only help identify potential dimensions where the sexes might differ; more generally, they can validate the interpretation of our behavioral measurements. For example, the clustering of SPA thigmotaxis and activity confirm our expectation that both these behaviors relate to anxiety (Maximino et al 2010). Additionally, these clusters elucidate some behavioral patterns that may not be as expected: the clustering of NOR novel object approaches and SPA interaction suggests that close contact with the conspecific reward in the SPA should perhaps not be considered a measure of “social affiliation,” rather it may additionally relate to boldness.

Finally, we hypothesized that the spatial task would capture greater sexual dimorphism in cognition than the novel object recognition task, and indeed a PCA of variables in the SPA task identified an axis (PC2) that significantly differs by sex, whereas no axis in the NOR PCA differed significantly. Furthermore, the only sex differences with large effect sizes resulted from the SPA task, suggesting that the sexes diverge in this task more than the NOR task. But counter to this hypothesis, only variables in the NOR task (novel object bout duration, familiar preference, and number of novel object approaches) reached an average importance threshold across all models. These three variables are all related to exploration of a novel object, indicating that variation in neophobia may be at the root of the observed sex differences in *A. burtoni*. Additional experiments that directly quantify exploratory behavior, stress response, and neophobia in this species will help disentangle these behavioral factors from cognitive performance and will facilitate improved cognitive assay design in the future.

(d) Conclusion

In the present study, we asked to which extent sexes differ in cognition in a species that lives in a highly dynamic social environment. This question reflects a larger theoretical framework on the reduction or exaggeration of sex differences depending on the social environment. This framework has been successfully applied as it relates to mating system. In voles, monogamous species show a lower degree of sexual dimorphism in morphology, behavior, and cognition relative to their non-monogamous congeners (Kleiman 1977, Jacobs 1995, Heske & Ostfeld 1990, Jacobs et al. 1990, Gaulin & Fitzgerald 1989). And in two species of polygynandrous fish (the shanny and the Azorean rock-pool blenny), females have larger home ranges and a larger dorsolateral telencephalon (hippocampus) than males, though this has yet to be correlated to their learning and memory abilities (Costa et al. 2011). In the present study we hypothesized that in more dynamic or fluctuating social environments we would find fewer sex differences in cognition performance, and indeed found no significant differences in *performance* in either task. We did, however, identify several behavioral differences between the sexes primarily related to neophobia and action latencies. Without a rigorous, phylogenetically controlled species comparison and without a more detailed understanding of the variation in ecologically relevant behaviors (e.g. shoaling, foraging, anti-predation behavior) between the sexes in *A. burtoni,* we cannot definitively know whether the sex differences we have observed here are greater or less than “expected”, but we contribute to this question by uncovering previously undescribed differences in cognition and behavior across the sexes. Our findings were facilitated by an experimental design employing two distinct cognitive tasks followed by multivariate analyses to describe the complex relationships observed in the data. We argue that pairing a more “reductionist” design of discrete suites of cognitive tasks with a strong foundation of more “naturalistic” observations of behavior is a powerful approach to understanding the relationship between the social environment and cognition. Future research across suites of cognitive tasks specifically designed to test variation within each sex and between other social phenotypes (e.g. mating systems, reproductive status, dominance status) will allow us to further relate cognitive performance to ecologically-relevant behaviors. Ultimately, these research endeavors will allow us to

better understand the evolution of cognition and decision-making in a dynamic social world.

Data Accessibility

Raw data (Microsoft excel) as well as analysis and visualization R code can be found at https://github.com/kellyjwallace/Wallace_Hofmann_2020_sex_differences or via request to the corresponding author.

Acknowledgements

The authors would like to thank Kavyaa Choudhary, Layla Kutty, Don Le, Matthew Lee, and Karleen Wu for assistance in data collection, and to Mike Ryan, Tessa Solomon-Lane, and all members of the Hofmann Lab for discussion and assistance.

Funding

This work was supported by the National Science Foundation (NSF) Bio/computational Evolution in Action Consortium (BEACON) Center for the Study of Evolution in Action and an NSF Grant IOS1354942 (to HAH), a Ford Foundation Predoctoral Fellowship (National Academies of Sciences, Engineering, & Medicine), a UT Austin Graduate School Continuing Fellowship, The Zoology Scholarship Endowment for Excellence (Graduate School at the University of Texas at UT Austin), and a Department of Integrative Biology Doctoral Dissertation Improvement grant (to KJW).

Competing interests

The authors have no competing interests.

Ethical approval

The authors certify that this work followed ethical treatment of animals outlined in their IACUC protocol (AUP-2018-00236).

Author's Contributions

HAH and KJW conceived of the study. KJW designed and constructed the experimental apparatus and data collection procedures, collected behavioral data, and performed statistical analyses. HAH and KJW interpreted the results. KJW wrote the initial draft of the manuscript, and HAH provided feedback and comments during manuscript writing. All authors give final approval for publication.

Figure Legends

Figure 1. Experimental Designs. The novel object recognition task (A,B) consisted of a 1-hour familiarization (community) (A) then a 12-minute test (individual) ~ 24 hours later (B). The spatial task (C,D) consisted of a 1 trial unrewarded habituation (C) then 4 rewarded trials over two days (D).

Figure 2. Sex Differences in the Novel Object Recognition Task. Males, but not females, exhibited a significant preference for the familiar object during the first minute of the task (A), and when assessing preference across time male preference decreased over the length of the task whereas female preference increased, with a significant interaction effect of sex (B). Females spent proportionally more time in the object association zone (C).

Figure 3. Principal Component Analysis of the Novel Object Recognition Task. A PCA of variables assessed in the NOR task identified three axes that explain >10% of the variance. Shown here are the proportion of variance for each PC axis (top) and a heatmap of the eigenvalues of each behavioral variable for each PC axis (bottom). The first PC axis (31%) can be described by variables of overall object association and interaction. The second PC axis (24%) can be described by familiar object preference. The third PC axis (19%) can be described by measures related to neophobia. A hierarchical clustering of variables by loading patterns (dendrogram) identified a highly supported cluster (AU > = 95%) of NOR familiar preference with NOR non-engagement (highlighted in grey box).

Figure 4. Sex differences in the Spatial Task. More females reached the spatial task learning criterion than would be expected by chance, whereas males did not (A). Females exhibited a greater preference for the reward stimuli during the task (B). Females also demonstrated longer decision latencies (C) and their decision latencies significantly predicted their latency to solve the task (enter the reward area) whereas this relationship was not seen in males (D). When subsetting individuals who first

entered the unrewarded side and then corrected and entered the rewarded side, females' error correction speed was faster than males' (E).

Figure 5. Principal Component Analysis of the Spatial Task. A PCA of variables assessed in the SPA task identifies four axes that explain >10% of the variance. Shown here are the proportion of variance for each PC axis (top) and a heatmap of the eigenvalues of each behavioral variable for each PC axis (bottom) (A). The first PC axis (36%) can be described by variables of preference and engagement. The second PC axis (20%) load most strongly by decision and interaction latencies. The third PC axis (18%) loads primarily with stimuli association. The fourth PC axis (11%) can be described by variables related to the reward stimulus (latency and preference). A hierarchical clustering of variables by loading patterns (dendrogram) identified a highly supported cluster (AU > = 95%) of NOR familiar preference with NOR non-engagement (outlined in black). PC2 significantly differs by sex (B).

Figure 6. Individual Variables are Related Across Tasks. When subsetting by individuals who had an intermediate level of preference, relative preference scores are correlated across tasks (A). Decision latency in the NOR task correlates to the first choice made in the SPA task (rewarded or unrewarded) (B), and decision latency in the SPA task correlates to the first choice made in the NOR task (familiar or novel) (C).

Figure 7. Principal Component Analysis of Variables from Both Tasks. A PCA of variables assessed in both tasks identifies four axes that explain >10% of the variance. Shown here are the proportion of variance for each PC axis (top) and a heatmap of the eigenvalues of each behavioral variable for each PC axis (bottom) (A). The first PC axis (24%) can be described by measurements of activity and preference in the spatial task. The second PC axis (16%) load most strongly by preference in the novel object recognition task as well as measurements of latency across both tasks. The third PC axis (11%) loads most strongly with interaction variables across both tasks. The fourth PC axis (10%) loads very strongly by a single variables: SPA latency to solve the task. A hierarchical clustering of variables by loading patterns (dendrogram) identified five

highly supported clusters (AU > = 95%, grey boxes), three of which contain variables form both tasks.

Table 1. Model Selection and Model-Averaged Importance of Terms Analysis. Through an exhaustive “all-possible models” selection analysis, we identified the model with the lowest AICc value, which included 13 variables spanning both tasks (variables in the resulting model in bold). In a model-averaged importance of terms analysis (in which each term’s importance score is related to the number of models it appears in and the weight of those models), three NOR variables reach the importance threshold (highlighted with asterisks).

References

Alcazar RM, Hilliard AT, Becker L, Bernaba M, Fernald RD (2014) Brains over brawn: Experience overcomes a size disadvantage in fish social hierarchies. J. Exp. Biol. 217: 1462–1466. https://doi.org/10.1242/jeb.097527

Antunes M, Biala G (2012) The novel object recognition memory: Neurobiology, test procedure, and its modifications. Cogn Process 13: 93–110. https://doi.org/10.1007/s10339-011-0430-z

Banerjee K, Chabris CF, Johnson VE, Lee JJ, Tsao F, Hauser MD (2009) General intelligence in another primate: Individual differences across cognitive task performance in a new world monkey (Saguinus oedipus). PLoS One 4(6): e5883. https://doi.org/10.1371/journal.pone.0005883

Bond AB, Kamil AC, Balda RP (2007) Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica). J Comp Psychol 121: 372-379. https://doi.org/10.1037/0735-7036.121.4.372

Boogert NJ, Reader SM, Laland KN (2006) The relation between social rank, neophobia and individual learning in starlings. Anim Behav 72(6):1229-39. https://doi.org/10.1016/j.anbehav.2006.02.021

Boogert NJ, Giraldeau LA, Lefebvre L (2008) Song complexity correlates with learning ability in zebra finch males. Anim Behav 76: 1735–1741. https://doi.org/10.1016/j.anbehav.2008.08.009

Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Pravosudov VV (2019) Smart is the new sexy: female mountain chickadees increase reproductive investment when mated to males with better spatial cognition. Ecol Lett 22: 897–903. https://doi.org/10.1111/ele.13249

Broadbent NJ, Gaskin S, Squire LR, Clark RE (2004) Object recognition memory and the rodent hippocampus. Learn Memory 17:5-11. https://doi.org/10.1101/lm.1650110

Brust V, Wuerz Y, Krüger O (2013) Behavioural Flexibility and Personality in Zebra Finches. Ethology 119: 559–569. https://doi.org/10.1111/eth.12095

Bshary R, Brown C (2014) Fish cognition. Curr Biol 24(19): R947–R950. https://doi.org/10.1016/j.cub.2014.08.043

Buechel SD, Booksmythe I, Kotrschal A, Jennions MD, Kolm N (2016) Artificial selection on male genitalia length alters female brain size. Proc R Soc B Biol Sci 283: 20161796. https://doi.org/10.1098/rspb.2016.1796

Burmeister SS, Jarvis ED, Fernald RD (2005) Rapid behavioral and genomic responses to social opportunity. PLoS Biol 3:e363. https://doi.org/10.1371/journal.pbio.0030363

Burns JG, Rodd FH (2008) Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. Anim Behav 76: 911–922. https://doi.org/10.1016/j.anbehav.2008.02.017

Calcagno V (2020) glmulti: Model Selection and Multimodel Inference Made Easy. R package version 1.0.8. https://CRAN.R-project.org/package=glmulti

Caraco T (1981) Energy budgets, risk and foraging preferences in dark-eyed juncos (Junco hyemalis). Behav Ecol Sociobiol 8: 213–217. https://doi.org/10.1007/BF00299833

Carazo P, Noble DWA, Chandrasoma D, Whiting MJ (2014) Sex and boldness explain individual differences in spatial learning in a lizard. Proc R Soc B Biol Sci 281: 20133275. https://doi.org/10.1098/rspb.2013.3275

Chiappe D, MacDonald K (2005) The evolution of domain-general mechanisms in intelligence and learning. J Gen Psychol 132: 5–40. https://doi.org/10.3200/GENP.132.1.5-40

Chittka L, Skorupski P, Raine NE (2009) Speed-accuracy tradeoffs in animal decision making. Trends Ecol Evol 24: 400–407. https://doi.org/10.1016/j.tree.2009.02.010

Clayton NS, Krebs JR (1995) Memory in food-storing birds: from behaviour to brain. Curr Opin Neurobiol 5: 149–154. https://doi.org/10.1016/0959-4388(95)80020-4

Costa SS, Carneiro LA, Gonçalves J (2011) Sex Differences in the Dorsolateral Telencephalon Correlate with Home Range Size in Blenniid Fish. Brain Behav Evolut 77(1): 55–64. https://doi.org/10.1159/000323668

Cummings M (2018) Sexual conflict and sexually dimorphic cognition — reviewing their relationship in poeciliid fishes Behavioral Ecology and Sociobiology. Behav Ecol Sociobiol 72: 73. https://doi.org/10.1007/s00265-018-2483-9

Dalla C, Shors TJ (2009) Sex differences in learning processes of classical and operant conditioning. Physiol Behav 97: 229–238. https://doi.org/10.1016/j.physbeh.2009.02.035

Desjardins JK, Hofmann HA, Fernald RD (2012) Social context influences aggressive and courtship behavior in a cichlid fish. PLoS One 7:e32781. https://doi.org/10.1371/journal.pone.0032781

Dingemanse NJ, De Goede P (2004) The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behav Ecol 15:1023–1030. https://doi.org/10.1093/beheco/arh115

Dodson JJ (1988) The nature and role of learning in the orientation and migratory behavior of fishes. Environ Biol Fishes 23:161-182.

Dougherty LR, Guillette LM (2018) Linking personality and cognition: a meta-analysis. Philos Trans R Soc B Biol Sci 373: 20170282. https://doi.org/10.1098/rstb.2017.0282

Easton A (2004) Behavioural flexibility, social learning, and the frontal cortex. The cognitive neuroscience of social behaviour. Psychology Press, Routledge, pp 71–92

Ennaceur A, Delacour J (1988) A new one-trial test for neurobiological studies of memory in rats. 1: Behavioral data. Behav Brain Res 31: 47–59. https://doi.org/10.1016/0166-4328(88)90157-X

Etheredge RI, Avenas C, Armstrong MJ, Cummings ME (2018) Sex-specific cognitive–behavioural profiles emerging from individual variation in numerosity discrimination in Gambusia affinis. Anim Cogn 21: 37–53. https://doi.org/10.1007/s10071-017-1134-2

Fabre N, García-Galea E, Vinyoles D (2014) Spatial learning based on visual landmarks in the freshwater blenny Salaria fluviatilis (Asso, 1801). Learn Motiv 48:47–54. https://doi.org/10.1016/j.lmot.2014.10.002

Farrell TM, Weaver K, An YS, MacDougall-Shackleton SA (2011) Song bout length is indicative of spatial learning in European starlings. Behav Ecol 23: 101–111. https://doi.org/10.1093/beheco/arr162

Fernald RD (2014) Cognitive skills needed for social hierarchies. Cold Spring Harb Symp Quant Biol 79: 229–236. https://doi.org/10.1101/sqb.2014.79.024752

Fernald RD, Hirata NR (1977) Field study of Haplochromis burtoni: quantitative behavioural observations. Anim Behav 25(4):964-975. https://doi.org/10.1016/0003-3472(77)90048-3

Gagnon KT, Cashdan EA, Stefanucci JK, Creem-regehr SH (2016) Sex Differences in Exploration Behavior and the Relationship to Harm Avoidance. Hum Nat 27:82–97. https://doi.org/10.1007/s12110-015-9248-1

Gaulin SJC, Fitzgerald RW (1989) Sexual selection for spatial learning ability. Anim Behav 37: 322–331. https://doi.org/10.1016/0003-3472(89)90121-8

Grosenick L, Clement TS, Fernald RD (2007) Fish can infer social rank by observation alone. Nature 445:429–432. https://doi.org/10.1038/nature05511

Guillette LM, Reddon AR, Hurd PL, Sturdy CB (2009) Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, Poecile atricapillus. Behav Processes 82:265–270. https://doi.org/10.1016/j.beproc.2009.07.005

Guillette LM, Reddon AR, Hoeschele M, Sturdy CB (2011) Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proc R Soc B Biol Sci 278:767–773. https://doi.org/10.1098/rspb.2010.1669

Han CS, Jablonski PG, Brooks RC (2015) Intimidating courtship and sex differences in predation risk lead to sex-specific behavioural syndromes. Anim Behav 109:177–185. https://doi.org/10.1016/j.anbehav.2015.08.017

Hänninen L, Pastell M (2009) CowLog: open-source software for coding behaviors from digital video. Behav Res Methods 41(2):472-476. doi:10.3758/BRM.41.2.472

Harris S, Ramnarine IW, Smith HG, Pettersson LB (2010) Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy Poecilia reticulata. Okios 119(11):1711–1718. https://doi.org/10.1111/j.1600-0706.2010.18028.x

Healy SD, Braham SR, Braithwaite VA (1999) Spatial working memory in rats: No differences between the sexes. Proc R Soc B Biol Sci 266: 2303–2308. https://doi.org/10.1098/rspb.1999.0923

Hebets E, Sullivan-Beckers L (2010) Mate Choice and Learning. *Encyclopedia of Animal Behavior*. Elsevier pp 389-393

Heske EJ, Ostfeld RS (1990) Sexual Dimorphism in Size, Relative Size of Testes, and Mating Systems in North American Voles. J Mammal 71: 510–519. https://doi.org/10.2307/1381789

Hofmann HA (2003) Functional genomics of neural and behavioral plasticity. J Neurobiol 54:272–282. https://doi.org/10.1002/neu.10172

Hofmann HA, Fernald RD (2001) What cichlids tell us about the social regulation of brain and behaviour. Journal of Aquaculture & Aquatic Sciences 9:17-31.

Huffman LS, Mitchell MM, O'Connell LA, Hofmann HA (2012) Rising StARs: Behavioral, hormonal, and molecular responses to social challenge and opportunity. Horm Behav 61:631-641. https://doi.org/10.1016/j.yhbeh.2012.02.016

Hughes RN (1968) Behaviour of male and female rats with free choice of two environments differing in novelty. Anim Behav 16:92–96. https://doi.org/10.1016/0003-3472(68)90116-4

Ishikawa K, Watanuki Y (2002) Sex and individual differences in foraging behavior of Japanese cormorants in years of different prey availability. J Ethol 20:49–54. https://doi.org/10.1007/s10164-002-0053-z

Jacobs LF, Gaulin SJC, Sherry DF, Hoffman GE (1990) Evolution of spatial cognition: Sex-specific patterns of spatial behavior predict hippocampal size. PNAS 87:6349–6352. https://doi.org/10.1073/pnas.87.16.6349

Jacobs LF (1995) The Ecology of Spatial Cognition. Adaptive Patterns of Space Use and Hippocampal Size in Wild Rodents. Behavioural Brain Research in Naturalistic and Semi-Naturalistic Settings. Nato Science Series D 82:301–322.Springer

Jonasson Z (2005) Meta-analysis of sex differences in rodent models of learning and memory: A review of behavioral and biological data. Neurosci Biobehav Rev 28:811–825. https://doi.org/10.1016/j.neubiorev.2004.10.006

Jones CM, Braithwaite VA, Healy SD (2003) The evolution of sex differences in spatial ability. Behav Neurosci 117:403–411. https://doi.org/10.1037/0735-7044.117.3.403

Jun JJ, Longtin A, Maler L (2016) Active sensing associated with spatial learning reveals memory-based attention in an electric fish. J Neurophysiol 115:2577–2592. https://doi.org/10.1152/jn.00979.2015

Kidd MR, Dijkstra PD, Alcott C, Lavee D, Ma J, O'Connell LA, Hofmann HA (2013a) Prostaglandin F2alpha facilitates female mating behavior based on male performance. Behavioral Ecology and Sociobiology 67:1307 - 1315. https://doi.org/10.1007/s00265-013-1559-9

Kidd MR, O'Connell LA, Kidd CE, Chen CW, Fontenot MR, Williams SJ, Hofmann HA (2013b) Female preference for males depends on reproductive physiology in the African cichlid fish Astatotilapia burtoni. General and Comparative Endocrinology 180:56 - 63. https://doi.org/10.1016/j.ygcen.2012.10.014

Kleiman DG (1977) Monogamy in Mammals. Q Rev Biol 52(1):39-69

Kolata S, Light K, Matzel LD (2008) Domain-specific and domain-general learning factors are expressed in genetically heterogeneous CD-1 mice. Intelligence 36:619–629. https://doi.org/10.1016/j.intell.2007.12.001

Laland KN, Reader SM (1999) Foraging innovation in the guppy. Anim Behav 57:331–340. https://doi.org/10.1006/anbe.1998.0967

Layton C, Fulton CJ (2014) Status-dependent foraging behaviour in coral reef wrasses. Coral Reefs 33:345–349. https://doi.org/10.1007/s00338-014-1138-1

Lombardi Brandão M, Braithwaite VA, Gonçalves-de-Freitas E (2015) Isolation impairs cognition in a social fish. Appl Anim Behav Sci 171:204–210. https://doi.org/10.1016/j.applanim.2015.08.026

Lucon-Xiccato T, Bisazza A (2014) Discrimination reversal learning reveals greater female behavioural flexibility in guppies. Biol Lett 10:20140206. https://doi.org/10.1098/rsbl.2014.0206

Lucon-Xiccato T, Dadda M, Bisazza A (2016) Sex Differences in Discrimination of Shoal Size in the Guppy (Poecilia reticulata). Ethology 122:481–491. https://doi.org/10.1111/eth.12498

Lucon-Xiccato T, Bisazza A (2017) Sex differences in spatial abilities and cognitive flexibility in the guppy. Anim Behav 123:53–60. https://doi.org/10.1016/j.anbehav.2016.10.026

Lynch KS, Rand AS, Ryan MJ, Wilczynski W (2005) Plasticity in female mate choice associated with changing reproductive states. Anim Behav 69:689–699. https://doi.org/10.1016/j.anbehav.2004.05.016

Madden JR, Langley EJG, Whiteside MA, Beardsworth CE, Van Horik JO (2018) The quick are the dead: Pheasants that are slow to reverse a learned association survive for longer in the wild. Philos Trans R Soc B Biol Sci 373: 20170297. https://doi.org/10.1098/rstb.2017.0297

Magurran AE, Nowak MA (1991) Another battle of the sexes: The consequences of sexual assymmetry in mating costs and predation risk in the guppy, Poecilia reticulata. Proc R Soc B Biol Sci 246: 31–38. https://doi.org/10.1098/rspb.1991.0121

Magurran AE, Seghers BH (1994) A Cost of Sexual Harassment in the Guppy, Poecilia reticulata. Proc R Soc B Biol Sci 258:52–89. https://doi.org/10.1098/rspb.1994.0147

Maille A, Schradin C (2016) Survival is linked with reaction time and spatial memory in African striped mice. Biol Lett 12: 20160346. https://doi.org/10.1098/rsbl.2016.0346

Mamuneas D, Spence AJ, Manica A, King AJ (2015) Bolder stickleback fish make faster decisions, but they are not less accurate. Behav Ecol 26: 91–96. https://doi.org/10.1093/beheco/aru160

Maruska KP, Fernald RD (2010) Behavioral and physiological plasticity: rapid changes during social ascent in an African cichlid fish. Horm Behav 58:230–240. https://doi.org/10.1016/j.yhbeh.2010.03.011

Maruska KP, Fernald RD (2018) Astatotilapia burtoni: A Model System for Analyzing the Neurobiology of Behavior. ACS Chem Neurosci 9:1951–1962. https://doi.org/10.1021/acschemneuro.7b00496

Maximino C, Marques de Brito T, de Mattos Dias CAG, Gouveia Jr A, Morato S (2010) Scototaxis as anxiety-like behavior in fish. Nat Protoc 5(2): 221-228. https://doi.org/10.1038/nprot.2009.225

May Z, Morrill A, Holcombe A, Johnston T, Gallup J, Fouad K, Schalomon M, Hamilton TJ (2016) Object recognition memory in zebrafish. Behav Brain Res 296:199–210. https://doi.org/10.1016/j.bbr.2015.09.016

Mazza V, Eccard JA, Zaccaroni M, Jacob J, Dammhahn M (2018) The fast and the flexible: cognitive style drives individual variation in cognition in a small mammal. Anim Behav 137: 119–132. https://doi.org/10.1016/j.anbehav.2018.01.011

Miletto Petrazzini ME, Agrillo C, Piffer L, Dadda M, Bisazza A (2012) Development and application of a new method to investigate cognition in newborn guppies. Behav Brain Res 233:443–449. https://doi.org/10.1016/j.bbr.2012.05.044

Miletto Petrazzini ME, Bisazza A, Agrillo C, Lucon-Xiccato T (2017) Sex differences in discrimination reversal learning in the guppy. Anim Cogn 20:1081–1091. https://doi.org/10.1007/s10071-017-1124-4

O'Connell LA, Hofmann HA (2011) Genes, hormones, and circuits: an integrative approach to study the evolution of social behavior. Front Neuroendocrinol 32:320-35. https://doi.org/10.1016/j.yfrne.2010.12.004

O'Connell LA, Hofmann HA (2012) Evolution of a Vertebrate Social Decision-Making Network. Science 336:1154–1157. https://doi.org/10.1126/science.1218889

Orsini CA, Setlow B (2017) Sex differences in animal models of decision making. J Neurosci Res 95:260–269. https://doi.org/10.1002/jnr.23810

Øverli Ø, Sørensen C (2006) Behavioral indicators of stress-coping style in rainbow trout: Do males and females react differently to novelty? Physiol Behav 87:506–512. https://doi.org/10.1016/j.physbeh.2005.11.012

Phelps SM, Ophir AG (2009) Monogamous Brains and Alternative Tactics: Neuronal V1aR, Space Use, and Sexual Infidelity among Male Prairie Voles. Cognitive Ecology II. University of Chicago Press. pp 156-176.

Pongrácz P, Vida V, Bánhegyi P, Miklósi Á (2008) How does dominance rank status affect individual and social learning performance in the dog (Canis familiaris)? Anim Cogn 11:75–82. https://doi.org/10.1007/s10071-007-0090-7

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rapaport LG, Brown GR (2008) Social Influences on Foraging Behavior in Young Nonhuman Primates: Learning What, Where, and How to Eat. Evol Anthropol 17:189–201. https://doi.org/10.1002/evan.20180

Reichert MS, Quinn JL (2017) Cognition in Contests: Mechanisms, Ecology, and Evolution. Trends Ecol Evol 32:773–785. https://doi.org/10.1016/j.tree.2017.07.003

Rice MA, Hobbs LE, Wallace KJ, Ophir AG (2017) Hormones and Behavior Cryptic sexual dimorphism in spatial memory and hippocampal oxytocin receptors in prairie voles (Microtus ochrogaster). Horm Behav 95: 94–102. https://doi.org/10.1016/j.yhbeh.2017.08.003

Renn SCP, Fraser EJ, Aubin-Horth N, Trainor BC, Hofmann HA (2012) Females of an African cichlid fish display male-typical social dominance behavior and elevated androgens in the absence of males. Horm Behav 61:496–503. https://doi.org/10.1016/j.yhbeh.2012.01.006

Rodriguez-Santiago M*, Nührenberg P*, Derry J, Deussen O, Francisco FA, Garrison LK, Garza SF, Hofmann HA, Jordan A (2020) Behavioral traits that define social dominance are the same that reduce social influence in a consensus task. PNAS. https://doi.org/10.1073/pnas.2000158117

Rosati AG, Hare B (2012) Decision making across social contexts: Competition increases preferences for risk in chimpanzees and bonobos. Anim Behav 84:869–879. https://doi.org/10.1016/j.anbehav.2012.07.010

Salas C, Rodríguez F, Vargas JP, Durán E, Torres B (1996) Spatial learning and memory deficits after telencephalic ablation in goldfish trained in place and turn maze procedures. Behav Neurosci 110(5):965–980. https://doi.org/10.1037/0735-7044.110.5.965

Sano M (1993) Foraging activities and diets of males and females in a haremic sandperch (Pisces: Pinguipedidae). Mar Ecol Prog Ser 98: 55–59. https://doi.org/10.3354/meps098055

Saucier DM, Shultz SR, Keller AJ, Cook CM, Binsted G (2008) Sex differences in object location memory and spatial navigation in Long-Evans rats. Anim Cogn 11:129–137. https://doi.org/10.1007/s10071-007-0096-1

Shettleworth SJ (2010) Cognition, evolution, and behaviour, 2nd edn. Oxford University Press, Oxford

Shohet AJ, Watt PJ (2009) Female guppies Poecilia reticulata prefer males that can learn fast. J Fish Biol 75:1323–1330. https://doi.org/10.1111/j.1095-8649.2009.02366.x

Smith C, Phillips A, Reichard M (2015) Cognitive ability is heritable and predicts the success of an alternative mating tactic. Proc R Soc B Biol Sci 282: 20151046. http://dx.doi.org/10.1098/rspb.2015.1046

Staddon, JER (1983) Adaptive behavior and learning. Second Edition. New York: Cambridge University Press

Stapley J, Keogh JS (2004) Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. Anim Behav 68:841–846. https://doi.org/10.1016/j.anbehav.2004.02.008

Stowe M, Kotrschal K (2007) Behavioural phenotypes may determine whether social context facilitates or delays novel object exploration in ravens (Corvus corax). J Ornithol 148(Supple 2): 179–184. https://doi.org/10.1007/s10336-007-0145-1

Suzuki R, Terada Y, Shimodaira H (2019) pvclust: Hierarchical Clustering with P-Values via Multiscale Bootstrap Resampling. R package version 2.2-0. https://CRAN.R-project.org/package=pvclust

Swasnson HH (1966) Sex differences in behaviour of hamsters in open field and emergence tests: effects of pre- and post-pubertal gonadectomy. Anim Behav 14(4): 522-529 https://doi.org/10.1016/S0003-3472(66)80054-4

Taborsky B, Oliveira RF (2012) Social competence: an evolutionary approach. TREE 27:679-688. https://doi.org/10.1016/j.tree.2012.09.003

Thornton A, McAuliffe K (2006) Teaching in Wild Meerkats. Science 313:227–229. https://doi.org/10.1126/science.1128727

Titulaer M, van Oers K, Naguib M (2012) Personality affects learning performance in difficult tasks in a sex-dependent way. Anim Behav 83:723–730. https://doi.org/10.1016/j.anbehav.2011.12.020

Torchiano M (2020) effsize: Efficient Effect Size Computation. doi: 10.5281/zenodo.1480624 (https://doi.org/10.5281/zenodo.1480624), R package version 0.8.0. https://CRAN.R-project.org/package=effsize

Wallace KJ, Rausch RT, Ramsey ME, Cummings ME (2020) Sex differences in cognitive performance and style across domains in mosquitofish (Gambusia affinis). Anim Cogn 23:655-669. https://doi.org/10.1007/s10071-020-01367-2

Watson KK, Platt ML (2008) Neuroethology of reward and decision making. Philos Trans R Soc B Biol Sci 363:3825–3835. https://doi.org/10.1098/rstb.2008.0159

Weitekamp CA, Hofmann HA (2017) Neuromolecular correlates of cooperation and conflict during territory defense in a cichlid fish. Horm Behav 89: 145–156. https://doi.org/10.1016/j.yhbeh.2017.01.001

Galef Jr BG, White DJ (1998) Mate choice copying and conspecific cueing in Japanese quail, Coturnix coturnix japonica. Anim Behav 55: 545-552. https://doi.org/10.1006/anbe.1997.0616

White SA, Nguyen T, Fernald RD (2002) Social regulation of gonadotropin-releasing hormone. J Exp Biol 205:2567–2581.

Wood LS, Desjardins JK, Fernald RD (2011) Effects of stress and motivation on performing a spatial task. Neurobiol Learn Mem 95: 277–285. https://doi.org/10.1016/j.nlm.2010.12.002

Yaskin VA (2011) Seasonal changes in hippocampus size and spatial behavior in mammals and birds. Biol Bull Rev 1: 279. https://doi.org//10.1134/S2079086411030108

Figure 1

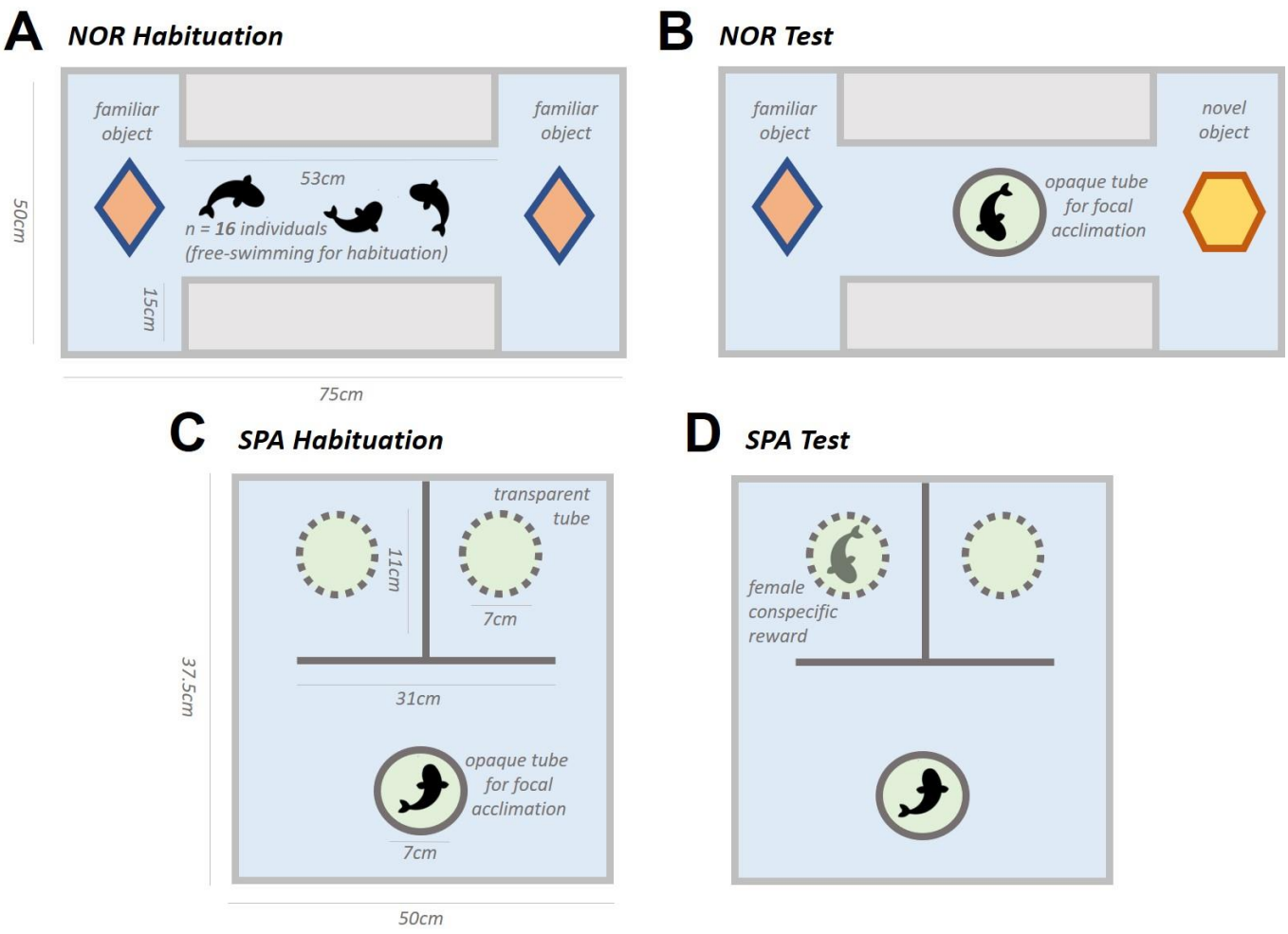
A
NOR Habituation
familiar object
familiar object
53cm
50cm
n = 16 individuals
(free-swimming for habituation)
15cm
75cm
B
NOR Test
familiar object
novel object
opaque tube for focal acclimation
C
SPA Habituation
transparent tube
11cm
7cm
37.5cm
31cm
opaque tube for focal acclimation
7cm
50cm
D
SPA Test
female conspecific reward

Figure 2

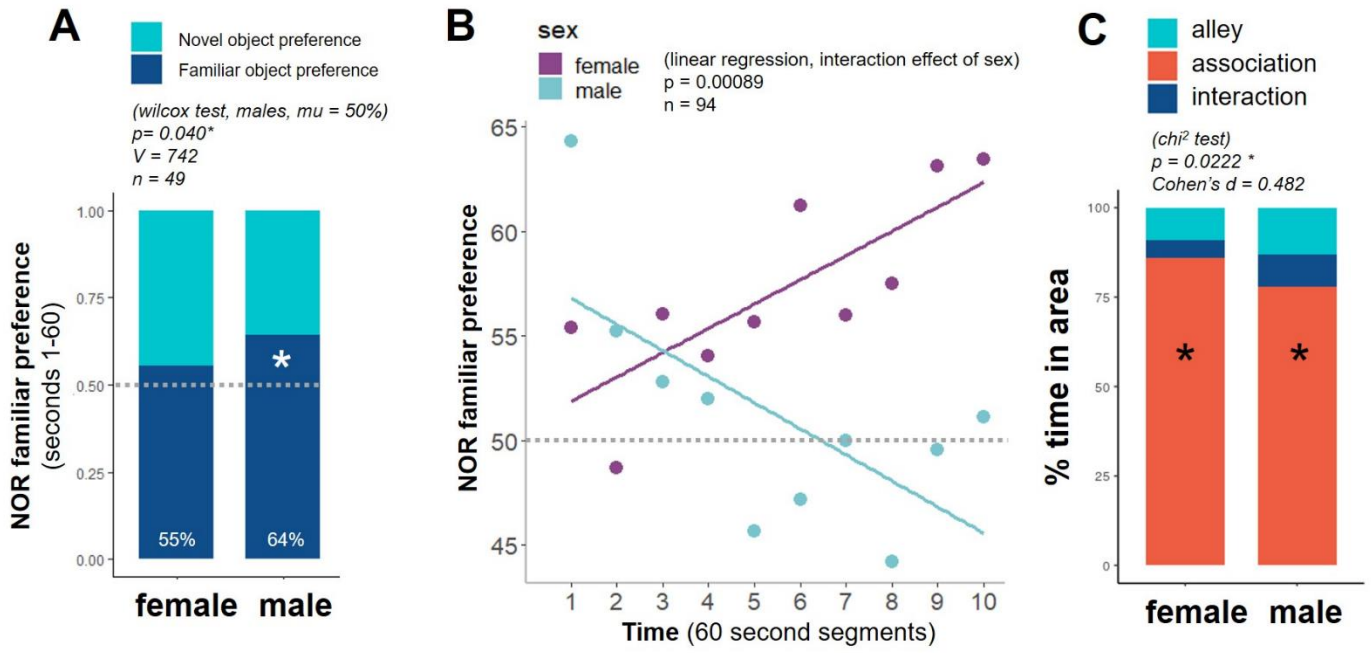
A
Novel object preference
Familiar object preference
(wilcox test, males, mu = 50%)
p= 0.040*
V = 742
n = 49
NOR familiar preference
(seconds 1-60)
1.00
0.75
0.50
0.25
0.00
*
55%
64%
female
male
B
sex
female
male
(linear regression, interaction effect of sex)
p = 0.00089
n = 94
NOR familiar preference
65
60
55
50
45
1
2
3
4
5
6
7
8
9
10
Time (60 second segments)
C
alley
association
interaction
(chi² test)
p = 0.0222 *
Cohen's d = 0.482
% time in area
100
75
50
25
0
*
*
female
male

Figure 3

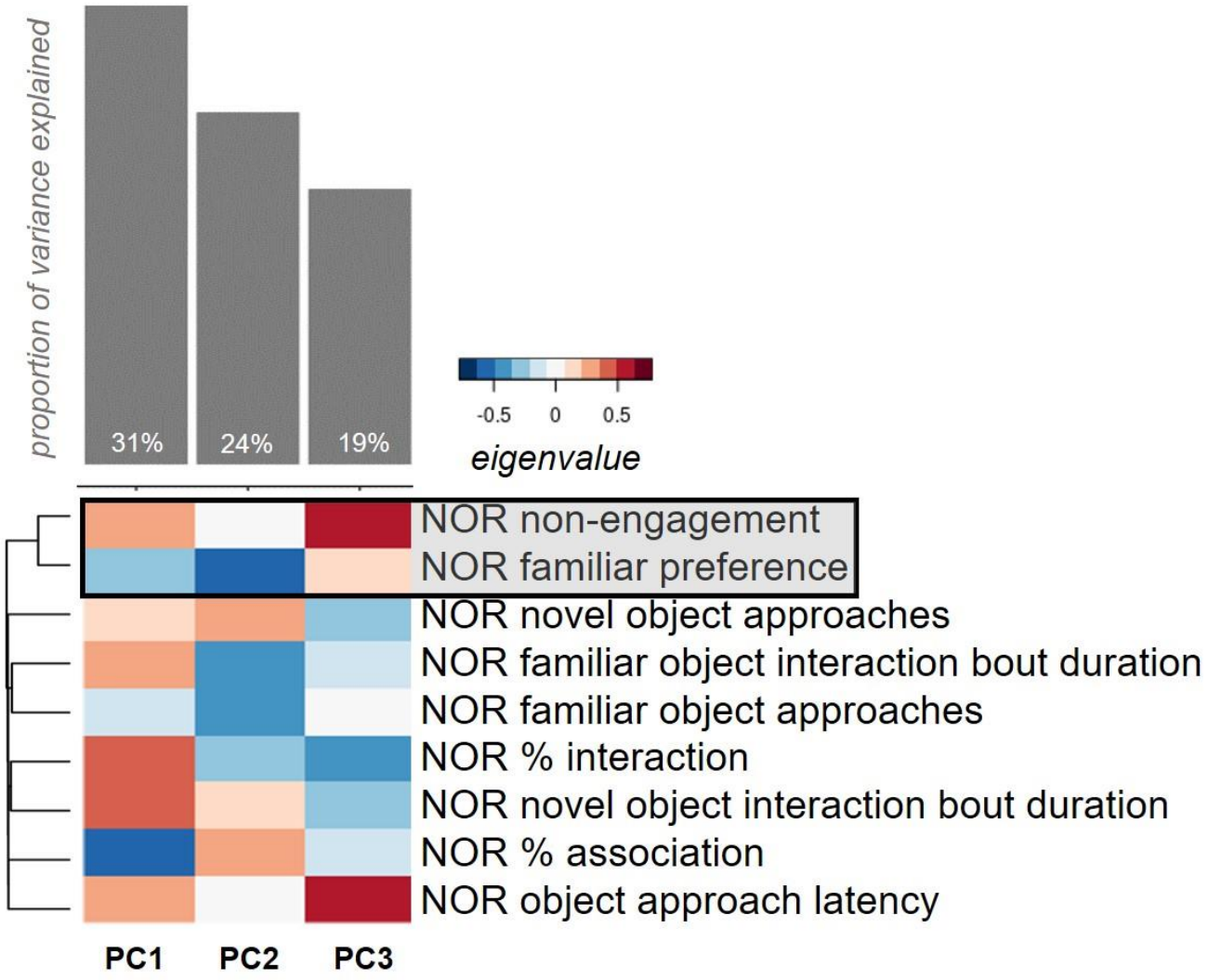
proportion of variance explained
31%
24%
19%
-0.5
0
0.5
eigenvalue
NOR non-engagement
NOR familiar preference
NOR novel object approaches
NOR familiar object interaction bout duration
NOR familiar object approaches
NOR % interaction
NOR novel object interaction bout duration
NOR % association
NOR object approach latency
PC1
PC2
PC3

Figure 4

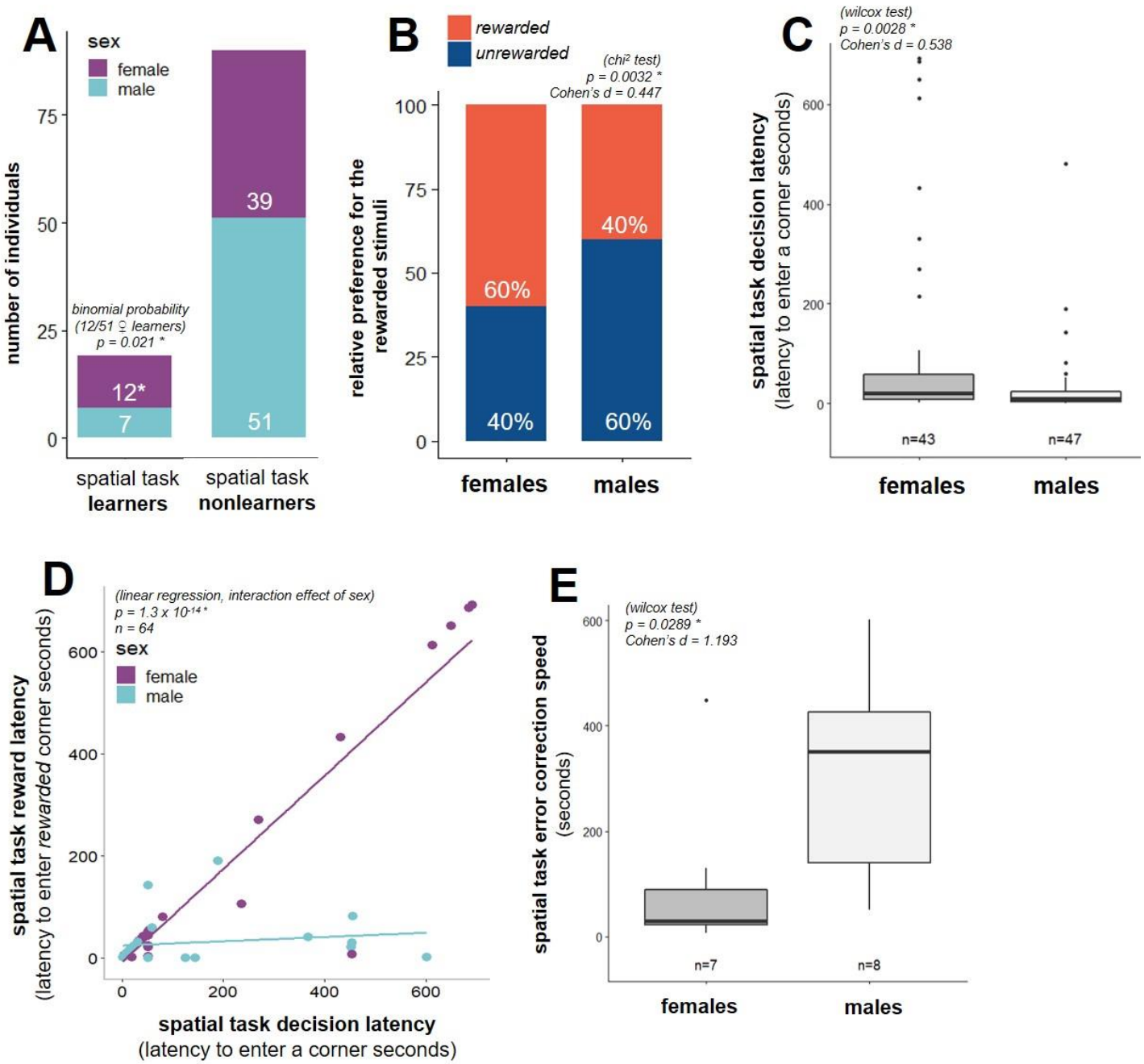
A
sex
female
male
number of individuals
75
50
25
0
39
51
12*
7
binomial probability
(12/51 ♀ learners)
p = 0.021 *
spatial task learners
spatial task nonlearners
B
rewarded
unrewarded
(chi² test)
p = 0.0032 *
Cohen's d = 0.447
relative preference for the rewarded stimuli
100
75
50
25
0
60%
40%
40%
60%
females
males
C
(wilcox test)
p = 0.0028 *
Cohen's d = 0.538
spatial task decision latency
(latency to enter a corner seconds)
600
400
200
0
n=43
n=47
females
males
D
(linear regression, interaction effect of sex)
p = 1.3 x 10-14 *
n = 64
sex
female
male
spatial task reward latency
(latency to enter rewarded corner seconds)
600
400
200
0
0
200
400
600
spatial task decision latency
(latency to enter a corner seconds)
E
(wilcox test)
p = 0.0289 *
Cohen's d = 1.193
spatial task error correction speed
(seconds)
600
400
200
0
n=7
n=8
females
males

Figure 5

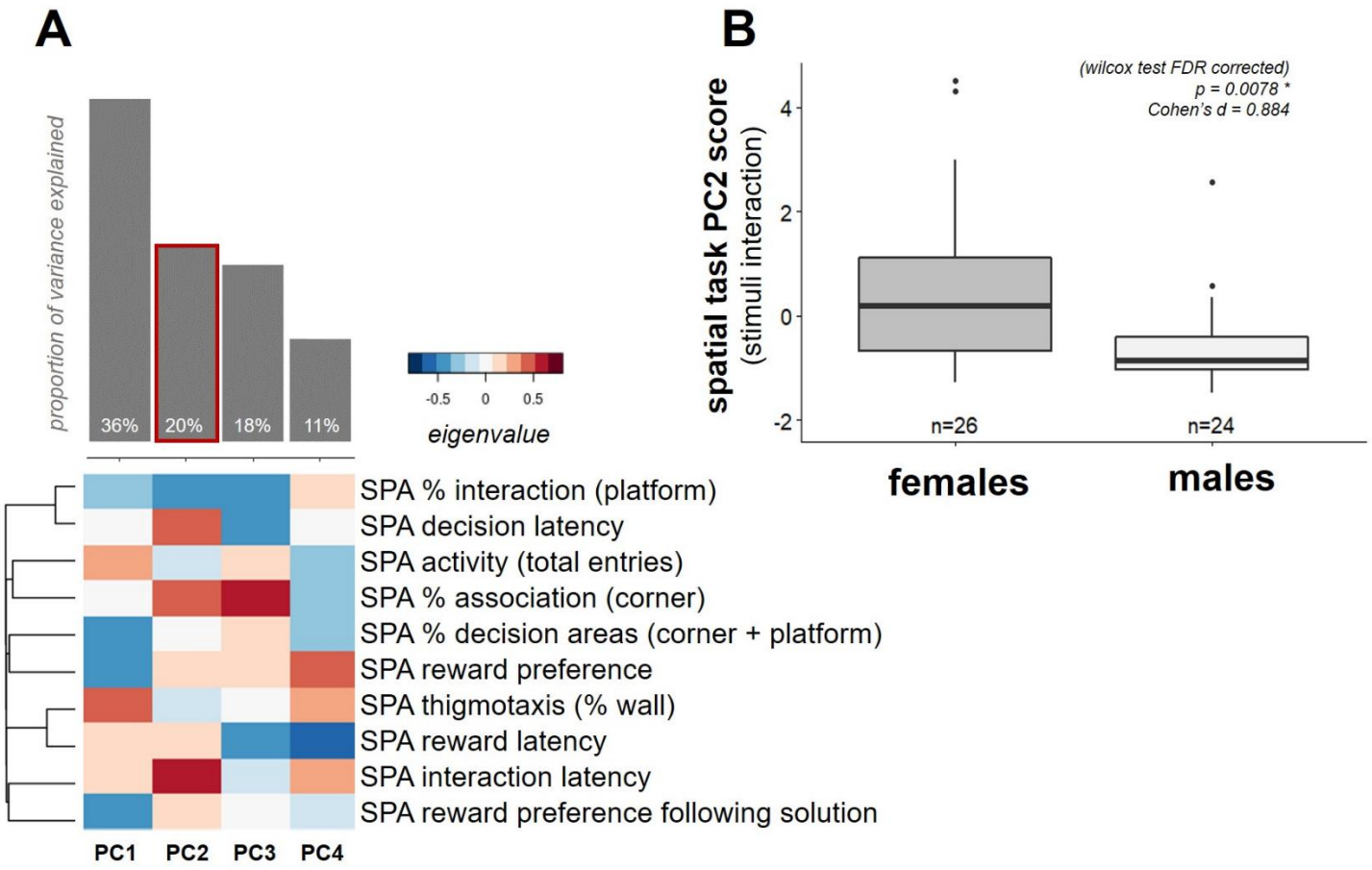
A
proportion of variance explained
36%
20%
18%
11%
-0.5
0
0.5
eigenvalue
SPA % interaction (platform)
SPA decision latency
SPA activity (total entries)
SPA % association (corner)
SPA % decision areas (corner + platform)
SPA reward preference
SPA thigmotaxis (% wall)
SPA reward latency
SPA interaction latency
SPA reward preference following solution
PC1
PC2
PC3
PC4
B
spatial task PC2 score
(stimuli interaction)
(wilcox test FDR corrected)
p = 0.0078 *
Cohen's d = 0.884
4
2
0
-2
n=26
n=24
females
males

Figure 6

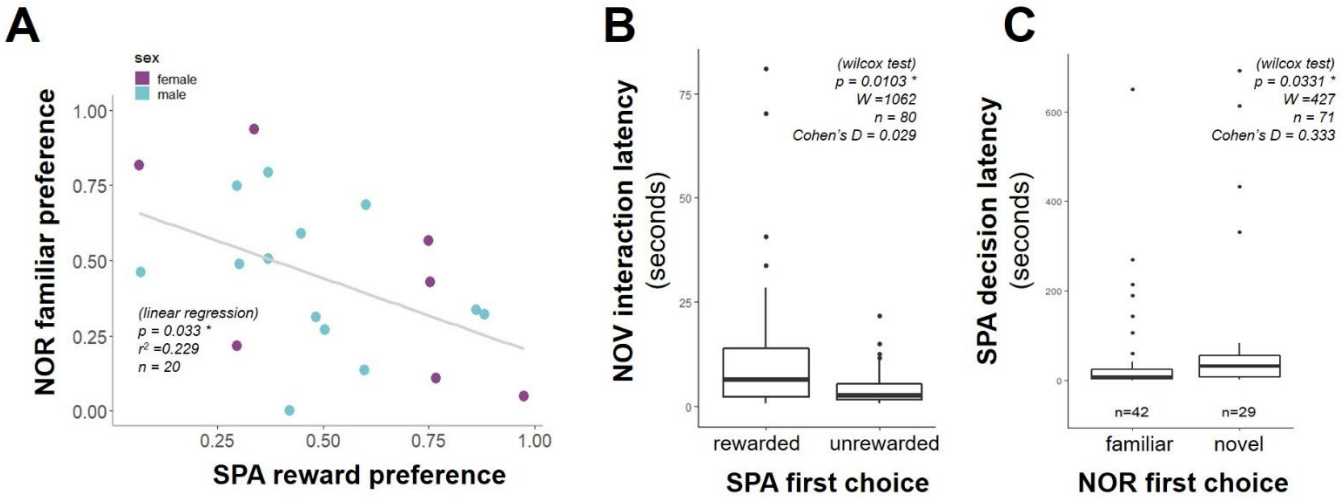
A
sex
female
male
NOR familiar preference
1.00
0.75
0.50
0.25
0.00
(linear regression)
p = 0.033 *
r² =0.229
n = 20
0.25
0.50
0.75
1.00
SPA reward preference
B
NOV interaction latency
(seconds)
(wilcox test)
p = 0.0103 *
W =1062
n = 80
Cohen's D = 0.029
75
50
25
0
rewarded
unrewarded
SPA first choice
C
SPA decision latency
(seconds)
(wilcox test)
p = 0.0331 *
W =427
n = 71
Cohen's D = 0.333
600
400
200
0
n=42
n=29
familiar
novel
NOR first choice

Figure 7

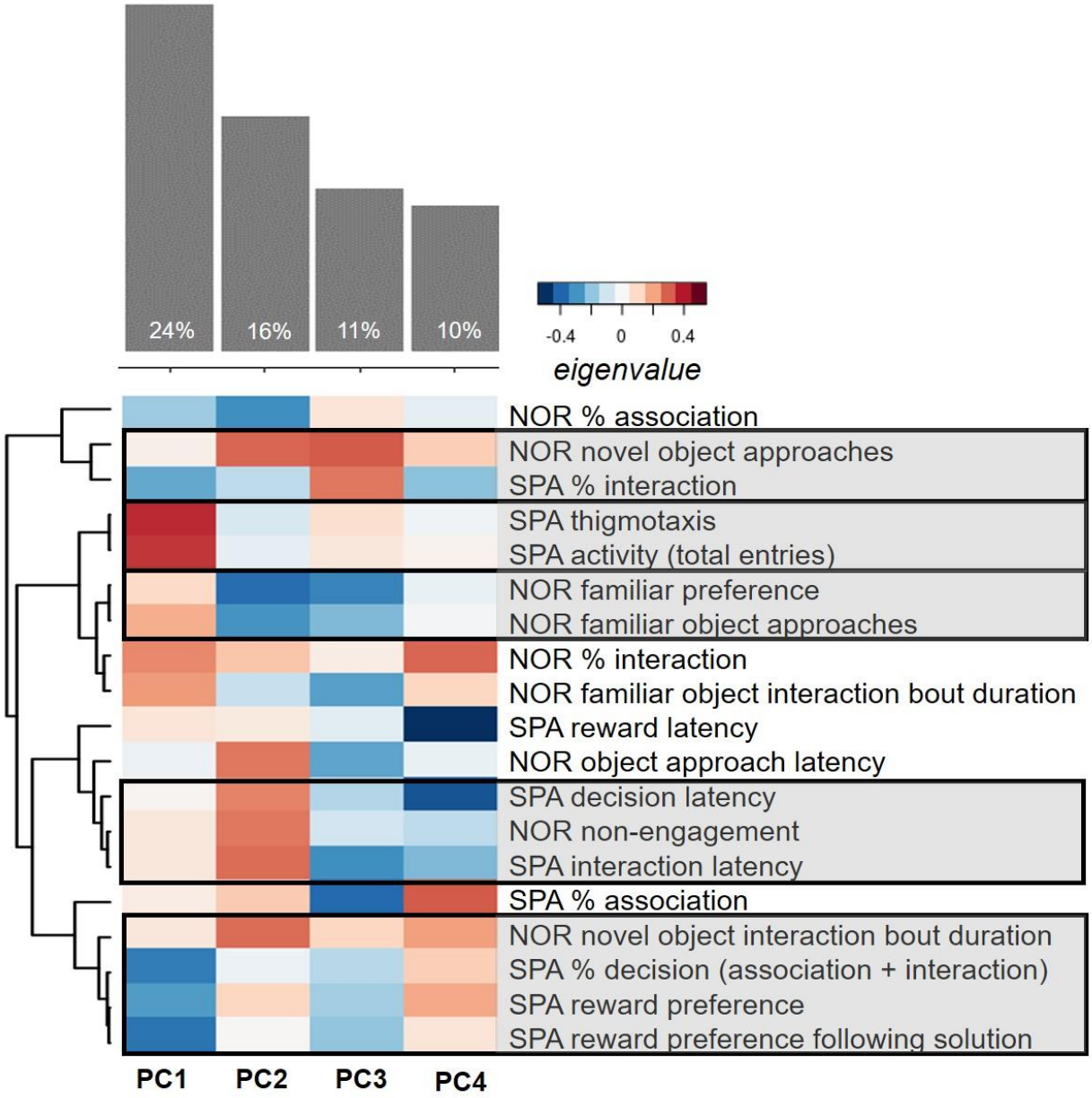
24%
16%
11%
10%
-0.4
0
0.4
eigenvalue
NOR % association
NOR novel object approaches
SPA % interaction
SPA thigmotaxis
SPA activity (total entries)
NOR familiar preference
NOR familiar object approaches
NOR % interaction
NOR familiar object interaction bout duration
SPA reward latency
NOR object approach latency
SPA decision latency
NOR non-engagement
SPA interaction latency
SPA % association
NOR novel object interaction bout duration
SPA % decision (association + interaction)
SPA reward preference
SPA reward preference following solution
PC1
PC2
PC3
PC4

Table 1

Table 1. Model Selection and Model-Averaged Importance of Terms Analysis

Term Name	Importance Score
NOR novel object interaction bout duration	0.994 *
NOR familiar preference	0.938 *
NOR novel object approaches	0.927 *
SPA decision latency	0.800
SPA % association	0.769
NOR % interaction	0.758
SPA reward latency	0.622
NOR non-engagement	0.548
NOR % association	0.520
SPA reward preference	0.394
SPA % decision (association + interaction)	0.365
SPA reward preference following solution	0.358
SPA % interaction	0.352
NOR familiar object interaction bout duration	0.281
SPA thigmotaxis	0.239
NOR object approach latency	0.183
SPA interaction latency	0.161
SPA activity	0.096
NOR familiar object approaches	0.033

Note: Terms in bold are those present in the selected model (all possible models assessed, selected via AICc, McFadden's Pseudo R^2 = 1.00). Importance scores (shown rounded) >0.8 are denoted with an asterisk (*).