

DISSERTATION

WHAT IN YOUR RIGHT MIND WOULD MAKE YOU DO THAT??
PROXIMATE AND ULTIMATE MECHANISMS OF PLASTICITY IN MATING STRATEGIES BY
THE TRINIDADIAN GUPPY (*POECILIA RETICULATA*)

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ABSTRACT

WHAT IN YOUR RIGHT MIND WOULD MAKE YOU DO THAT?? PROXIMATE AND ULTIMATE MECHANISMS OF PLASTICITY IN MATING STRATEGIES BY THE TRINIDADIAN GUPPY (*POECILIA RETICULATA*)

All animals must make decisions every day and often these decisions are directly linked to fitness outcomes, meaning better decisions are expected to be associated with higher fitness. Rapid decisions between alternative strategies allow animals to behave more appropriately for their environment. Thus, selection will shape not only how animals will respond to cues at different timescales, but also what cues they respond to at different timescales. Neural substrates of decisions are a vital component for our understanding of how experiences on different timescale influence decision-making strategies. The sensitivity of sensory systems to specific cues is tuned by genetics and then subsequently refined through developmental neural plasticity. The goal of this dissertation is to fill in gaps in understanding how experiences across multiple timescales influence neural mechanisms and behavioral strategies. I chose to address this question with the alternative mating strategies of male Trinidadian guppies (*Poecilia reticulata*), a sexually dimorphic tropical fish native to the island of Trinidad. In chapter two we compared how ancestral predation pressures influenced sensitivity to developmental exposure to predator cues and how those two timescales interacted to shape activity and reproductive behaviors when males were in different social contexts. Evolutionary history shaped how developmental contexts influence the resulting behavioral phenotypes across multiple acute contexts. However, the influence of experiences across timescales were not consistent between behaviors. We then

extended our study further in chapter three to investigate how developmental experiences with conspecifics influenced males' later abilities not only to respond to virgin and recently mated females, but also to refine mating strategies in response to the female behaviors over multiple exposures. Social experiences during developmental timescales also had distinct influences on the expression of the two reproductive strategies in chapter three. We showed that males modulated and refined mating strategies relatively independently of each other in relationship to their rearing experiences. We concluded with an investigatory probe into the cellular identities of neurons that are responding to a reproductive context in chapter four using a phosphoTRAP RNA-seq protocol. Chapter four provides evidence that several neuromodulatory pathways respond to cues in a reproductive context, which could point to constraints on evolution. In sum, this dissertation used an integrative approach to understand how experiences across multiple timescales influence decisions. We bridged several fields that can help provide insight into the evolution of decision-making processes and allow us to make future hypotheses about influences of multiple experiences with complex cues.

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I thank my advisor, Dr. Kim Hoke, who guided me through five years of ups and downs. She models what it means to strive for work-life balance, listening to goals of students (even when they are not towards a career in academia), and being an advocate for students. I also thank my committee who were so willing to be flexible with me as I progressed through the process of completing my PhD.

I doubt anyone will ever read this, so I am going to use the page as a promise to myself based on what I have learned over these last five years and particularly the last few months. This is the summer of 2020 and I am struggling through finishing my PhD during COVID-19 and black lives matter protests. This dissertation feels so inconsequential compared to how many people are suffering, but finishing this PhD will allow me to continue into my next career. As an instructor, I have a platform and obligation to educate myself in how to be and do better. I am promising myself to stay focused on the importance of keeping up with inclusive pedagogy, and to be open and honest with my future students.

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CHAPTER 1: INTRODUCTION

All animals must make decisions every day and often these decisions are directly linked to fitness outcomes, meaning better decisions are expected to be associated with higher fitness. Rapid decisions between alternative strategies allow animals to behave more appropriately for their environment. Theory proposes experiences on evolutionary, developmental, and acute timescales influence decisions (Stamps & Frankenhuis, 2016). Immediate or acute cues can help animals integrate information on potential aggressive intention of rivals, receptivity of potential mates, and risk of predation. Animals can also integrate experiences during development to better predict future environmental conditions (Groothuis & Taborsky, 2015). Moreover, how and where animals get cues in their environment and how they subsequently used that information may also be under selection (Schmidt, Dall, & van Gils, 2010). Thus, selection will shape not only how animals will respond to cues at different timescales, but also what cues they respond to at different timescales. An outstanding question is how experiences on historical or ancestral timescales interact with experiences on developmental and acute timescales to influence animal behaviors and decisions.

Effects of experience on developmental timescales pose a tradeoff: experiences during development may not be representative of later environmental conditions, but animals tend to possess greater plasticity during development than in adulthood (Snell-Rood, 2013; West-Eberhard, 2003). This tradeoff can result in diverse ways experiences on different timescales interact to influence later behavioral phenotypes. For example, some animals may weight experiences from development more heavily than acute experiences (e.g. Swanger & Zuk, 2015),

some may weight experiences equally across timescales (e.g. Stein, Bukhari, & Bell, 2018), while others may have flexible weightings, particularly when the information from experiences on risk or opportunity conflicts (reviewed in Hale, Piggott, & Swearer, 2016). Disentangling how complex experiences at different timescales influence decisions will help us understand constraints in flexible responses to heterogenous environments.

Animals differ not only in which cues trigger plasticity at different timescales, but also in the cognitive strategies they use to integrate and produce a decision from those cues. Environments that have predictable variation are expected to facilitate the evolution of learning when earlier experiences can reliably guide better decisions later in life (reviewed in Dunlap & Stephens, 2016). Bayesian updating has become a an influential model to predict how animals may integrate experiences to update their perception of the environment and influence their behavioral strategies (J. McNamara & Houston, 1980; Polverino, Palmas, Evans, & Gasparini, 2019; Stamps & Frankenhuis, 2016). Alternatively, animals may also use rules of thumb or heuristics to make decisions between behaviors. In environments that are heterogenous, evolution may select for the use of decision rules to direct behaviors, which result in decisions that on average do well enough despite not being optimal (Fawcett et al., 2014). Evolution is expected to select for the decision-making strategy that is the most ecologically rational, whether it is a fixed rule or a learning process (reviewed in Fawcett, Hamblin, & Giraldeau, 2013), but how decision strategies differ over the animal's lifetime has received less attention. Investigating the way animals weight specific cues across timescales may help us better understand what cognitive strategy they are using, and thus provide insight into the evolution and plasticity of decision-making processes.

A particularly complex environment animals must navigate is the social environment. Social experiences feature not only the focal individual, but also one or more conspecifics that dynamically respond to the decisions of the focal individual (Taborsky & Oliveira, 2012). Animals that use specific cues and behaviors of their social partners to guide accurate decision making during social experiences are termed socially competent (Taborsky & Oliveira, 2012). One approach to model social competency is the aforementioned Bayesian framework that predicts that animals use previous social experiences to refine their responses (J. McNamara & Houston, 1980; Polverino et al., 2019; Stamps & Frankenhuis, 2016). Such updating in courtship contexts can improve mating success (e.g. guppies (Guevara-Fiore & Endler, 2018); *Drosophila* (Saleem, Ruggles, Abbott, & Carney, 2014)), where as in aggressive encounters updating includes a winner and loser effects, in which animals tend to adopt submissive behaviors in future encounters after losing fights and increased aggression after winning fights (Hsu, Huang, & Wu, 2014; Lan & Hsu, 2011). Social competency depends on experiences during ontogeny. Social isolation or deprivation results in reduced performance in many social behaviors (e.g. Social learning (Lévy, Melo, Galef, Madden, & Fleming, 2003), decisions in aggressive behaviors (Arnold & Taborsky, 2010), social connectivity and neophobia (Bertin & Richard-Yris, 2005), and reviewed in Taborsky, 2016, 2017; Taborsky & Oliveira, 2012). Integration of social experiences during development could allow animals to better navigate the complexities of the social environment.

Neural substrates of decisions are a vital component for our understanding of how experiences on different timescale influence decision-making strategies. Circuits within the brain influencing decisions interact with physiological state of the individual (endogenous cues), and the information sensed in the external environment (exogenous cues) (e.g. Hau et al., 2017;

Kennedy et al., 2014). The sensitivity of sensory systems to specific cues is tuned by genetics and then subsequently refined through developmental neural plasticity. The brain cannot integrate all potential information from the environment so will tend to respond selectively to the cues that tend to be most relevant in an environment (e.g. in foraging with predators present (Dukas, 2004)). However, the relevance of specific cues may not be consistently weighted across ontogeny (Groothuis & Taborsky, 2015), so we may also expect shifts in neural sensitivity to cues across ontogeny. For example, honeybees experience age-specific division of labor, which require dramatic shifts in behaviors and cognitive abilities. There are shifts of neural sensitivities to specific stimuli, such as sucrose, that are associated with those changes between roles (reviewed in Arenas, Ramírez, Balbuena, & Farina, 2013). Moreover, experiences during sensitive periods of development can alter later patterns of neural circuit function due to neural plasticity processes, which leaves a permanent fingerprint from those previous experiences. In the honeybee, the exposure to specific scents during pre-foraging ages results in biases toward future foraging sites (reviewed in Arenas, Ramírez, Balbuena, & Farina, 2013). Age-specific shifts in sensitivity to sensory cues may be influenced by several different regulatory pathways. For example, serotonin (5-HT) is a prime example of a neuromodulator that has been linked to multiple sensory systems across a wide range of taxa (reviewed in Sizemore et al. 2020). Serotonin modifies the behavioral strategies of animals (e.g. swimming propensities in molluscs (Lillvis & Katz, 2013), aggression in lobsters (Kravitz, 2000), aversive social decision making (Crockett & Cools, 2015), male reproductive behaviors (Hull, Muschamp, & Sato, 2004)). When investigating how cues influence animals' behaviors, we must also incorporate these complex neural substrates and how they exhibit plasticity across multiple timescales.

Many neural pathways are implicated in social decision-making abilities and outcomes. In humans, serotonin has been shown to directly influence responses to social cues, and reduced serotonin signaling results in increased antisocial and aggressive behaviors (reviewed in Crockett & Cools, 2015). In fish, social interactions between competitors results in losers with chronically elevated serotonin levels and decreased aggressive behavior (reviewed in Oliveira, 2009). However, serotonin interacts with other pathways associated with behavioral plasticity such as gonadotropin releasing hormone (Sylvie Dufour et al., 2019; Groves & Batten, 1986) and dopamine (Adell et al., 2010; Sylvie Dufour et al., 2019; Monier, Nöbel, Danchin, & Isabel, 2019), resulting in complex control over social decisions by interacting pathways that are all sensitive to previous experiences. Different neuromodulatory pathways may be under different evolutionary constraints depending on their structures and functions (Katz & Lillvis, 2014), so the complex interactions between multiple pathways underlying decision-making processes may have important evolutionary impacts. Identifying the pathways influencing decisions, will help us better understand why decisions are made in specific contexts as well as the evolutionary trajectories of those systems.

The goal of this dissertation is to fill in gaps in understanding how experiences across multiple timescales influence neural mechanisms and behavioral strategies. I chose to address this question with the Trinidadian guppy (*Poecilia reticulata*), a sexually dimorphic tropical fish native to the island of Trinidad (Magurran, 2005). Guppies are well known for their ancestral high-predation and derived low-predation populations. Guppies in high-predation populations experience high levels of predator threat throughout their lifetime, while fish in low-predation populations have some predation risk as fry but as adults are largely removed from predator threat (reviewed in Magurran, 2005), creating an opportunity for shifts in attention to predator

cues over ontogeny in those populations. Male guppies employ either sigmoid courtship displays or forced copulatory behaviors to mate with females (Houde, 1997; Liley, 1966; Magurran, 2005). Sigmoid displays are higher energy, more conspicuous, and rely on female receptivity, but are also much more successful for mating than forced copulatory behaviors (Magurran, 2005). Both biotic and abiotic factors influence males' decisions between courtship displays and forced copulations across many timescales (e.g. Barbosa, Ojanguren, & Magurran, 2013; Cole & Endler, 2016; Endler, 1987; Guevara-Fiore, 2012; Houde, 1997; Magurran, 2005). Male guppies are highly motivated in mating contexts, and present acute differences in mating strategy depending on endogenous and exogenous cues (Houde, 1997; Liley, 1966; Magurran, 2005). These fish are also social and often shoal closely together, as well as having well defined behavioral responses to predators and alarm cues (Magurran, 2005). Males will modify their mating strategy depending not only on social context (e.g. Auld, Jeswiet, & Godin, 2015; Auld, Ramnarine, & Godin, 2017) and based on predator risk (e.g. Magurran & Seghers, 1990) independently, but predation risk also influences males' use of social information (foraging information from shoal (Kelly & Godin, 2001)). The Trinidadian guppy system allows us to manipulate all three timescales of interest: ancestral, developmental, and acute. However, few studies have looked across all three timescales while considering proximate mechanisms underlying plasticity in responses to different cues (except see Fischer, Ghalambor, & Hoke, 2016).

In chapter 2 we compared how ancestral predation pressures influenced sensitivity to developmental exposure to predator cues and how those two timescales interacted to shape activity and reproductive behaviors when males were in different social contexts. We then extended our study further in chapter 3 to investigate how developmental experiences with

conspecifics influenced males' later abilities not only to respond to virgin and recently mated females, but also to refine mating strategies in response to the female behaviors over multiple exposures. We concluded with an investigatory probe into the cellular identities of neurons that are responding to a reproductive context in chapter 4 using a phosphoTRAP RNA-seq protocol. We found complex interactions between timescales and environmental cues, as well as several exciting neural pathways that may influence decisions between alternative mating strategies in the male Trinidadian guppies. This work provides a framework for the extent of the plasticity demonstrated by these small fish, as well as novel insights into potential mechanisms driving that plasticity.

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CHAPTER 2: POPULATION OF ORIGIN INFLUENCES BEHAVIORAL AND NEURAL RESPONSES TO DEVELOPMENTAL AND ACUTE EXPERIENCES

Introduction

Plasticity allows animals to shift their behavioral phenotypes in response to environmental conditions, and selection shapes those shifts so phenotypes closely match the environment an animal is experiencing or may experience in the future (Pigliucci, 2005). Behavioral plasticity has been divided into developmental and acute (or activational) plasticity depending on the timeline of effects (Snell-Rood, 2013). Developmental plasticity molds phenotypes based on early life cues (reviewed in Kasumovic & Brooks, 2011; reviewed in West-Eberhard, 2003). Moreover, cues inducing developmental plasticity may be weighted based on their relevance and accuracy (Taborsky, 2017 Chapter 3). Reversible acute behavioral plasticity, or activational plasticity, is an animals first line of defense to acutely changing environments and can be rapidly modulated (Snell-Rood, 2013). Developmental plasticity is proposed to interact with acute plasticity by limiting the potential future repertoire of phenotypes possible as adults, or by creating phenotypes that are potentially maladaptive as adults (Kasumovic, 2013; Taborsky, 2017). Ancestral environments may play an important role in the interaction between developmental and acute plasticity by selecting for sensitivity to cues in different developmental windows (Fawcett & Frankenhuis, 2015) or by selecting for weighting of different cues (Taborsky, 2017 Chapter 3). However, a major outstanding question is how evolutionary shifts in sensitivity to cues during development influence acute plasticity later in life. We hypothesize that developmental plasticity may limit acute plasticity in adulthood, and that evolutionary history

shapes plasticity on multiple timescales. Tests of this hypothesis will provide better understanding of how ancestral pressures may constrain or potentiate future plastic responses on developmental and acute timescales.

Developmental plasticity may elicit a range of acute behavioral patterns, and through selection the developmental trajectories may be refined (Snell-Rood 2013). However, few studies compare how populations have diverged in their use of developmental and acute cues to influence behavioral strategies. Animals have been shown to have heritable variation in population-specific responses to experiences on developmental timescales (e.g. cane toads (Hudson et al. 2017), guppies (Brown et al. 2015)), but studies that compare population-specific effects of developmental plasticity in multiple acute contexts are lacking. Effects of developmental experience pose a unique tradeoff: experiences during development may not be representative of later environmental conditions, but animals tend to possess greater plasticity during development than in adulthood (Snell-Rood, 2013; West-Eberhard, 2003). This tradeoff can result in diverse ways in which experiences on different timescales interact to influence later behavioral phenotypes. For example, some animals may weight experiences from development more heavily than acute experiences (e.g. Swanger & Zuk, 2015), some may weight experiences equally across timescales (e.g. Stein, Bukhari, & Bell, 2018), while others may have flexible weightings, particularly when the information from experiences on risk or opportunity conflicts (reviewed in Hale, Piggott, & Swearer, 2016). Studies on acute plasticity that integrate evolutionary history with developmental experiences will better inform our understanding of how evolution may refine developmental trajectories to shape behavioral diversity.

We investigated how ancestry influences the impact of developmental predator exposure on context dependent courtship behaviors by comparing two populations of Trinidadian guppies

Poecilia reticulata). One population represents a high-predation population and the other a derived low-predation population. Guppies in high-predation populations experience high levels of predator threat throughout their lifetime, while low-predation populations have some predation as fry but as adults are largely removed from predator threat (reviewed in Magurran, 2005). Male guppies use two condition-dependent mating strategies, either a conspicuous courtship display called a sigmoid or a forced copulatory strategy (reviewed in Magurran, 2005). Ancestral pressures, developmental experiences, and acute contexts including social and predator presence all influence the use of these two mating strategies (reviewed in Houde, 1997; Kolluru, 2014; Magurran, 2005). The reduced predator threat for adults in low-predation populations has been linked to greater sexual selection for bright coloration and more sigmoid behaviors in males (reviewed in Magurran, 2005). We tested male guppies from a high-predation population and a paired low-predation population that were either reared in the presence or absence of predator chemical cues in five social contexts. We predicted that fish from both populations would maintain sensitivity to predator cues during development, but that predator exposure to during development may limit behavioral flexibility in acute social contexts later in life. Because sexual selection is typically stronger in low-predation populations (reviewed in Magurran, 2005), we predicted that low-predation population fish will be more sensitive to social contexts on acute timescales than high-predation fish, consistent with a low-predation fish having selection for greater sensitivity to social cues. Previous research indicates that low-predation guppies are more likely to use acute social information than high-predation fish (Kolluru, 2014; Rodd & Sokolowski, 1995), but how this use of social information varies with development and acute experiences has not been tested. Alternatively, high-predation males may be more flexible in adjusting behavioral strategies if their historical selection for tuning strategies to the acute

predation threat makes them more sensitive to acute risks and opportunities (e.g. Burns & Rodd, 2008).

Furthermore, behavioral phenotypes result from neural mechanisms that are responding to endogenous and exogenous cues. We measured neural activity in guppies as they experienced these acute social contexts. We measured activity throughout the social decision-making network (SDMN), a group of brain regions implicated in rapid decisions between alternative behaviors across vertebrates (O'Connell & Hofmann, 2011). We predict that regions within this network will reflect behavioral patterns of mating strategies in male guppies. Our study demonstrates the population differences in the sensitivity to developmental and acute cues and the complex interaction between ancestral, developmental, and acute timescales.

Methods

Husbandry

Fish collected in Trinidad (2016) from the high-predation Quare population and the low-predation Campo population were bred in the lab for two generations before being used in the assays. All fish were maintained on a recirculating system in 0.5 gallon acrylic tanks. At birth, second generation fish were split and reared either on a recirculating system that contained predator chemical cues or fresh water. To provide ongoing predator exposure in the predator cue treatment, recirculating systems had a pike cichlid (*Crenicichla frenata*) living in a sump tank that was fed live guppies daily to provide alarm cue (Brown and Godin 1999) as well as the chemical cues of the predator (as in Fischer et al. 2014 and Torress-Dowdall et al. 2012).

Fish were fed once per day on a diet of measured Tetramin™ tropical fish flake paste or measured hatched brine shrimp on alternating days. Food quantities were dependent on the age

of the fish. The room had a 12:12 light:dark cycle and average room temperature of 25 degrees Celsius. Fish were kept in family tanks until they were 6-weeks old when we determined sex under a dissecting scope after anesthetizing them in MS-222. We then placed fish in single-sex tanks with densities between three to four fish. We began behavioral assays when fish were approximately 1 year old. Due to single-sex housing, experimental males had no previous sexual experience with females when the experiment started.

Social treatments

Sets of five brothers were split into five acute social treatments, with each brother assigned to one context. The contexts were “courtship” with two females, “predation” with two females and predator cue, “competition” with a female and a male, “aggression” with two males, and “solo” where the focal male was alone in the experimental tank (Fig 2.1). We chose these densities to keep the total number of fish (three, except “solo”) consistent in all contexts.

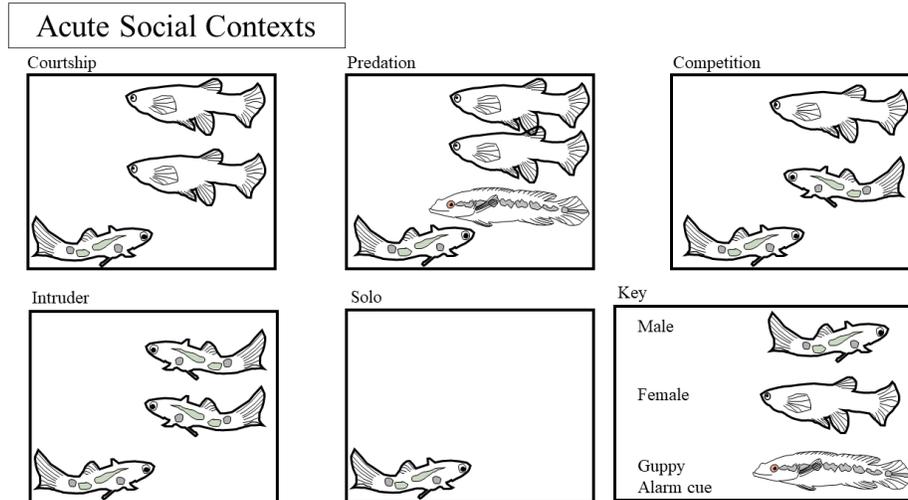
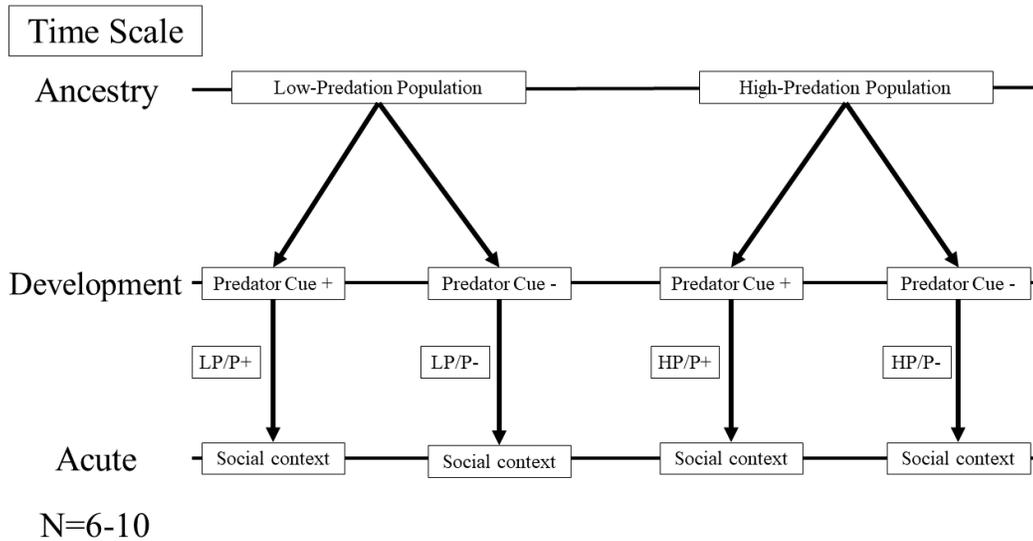


Figure 2.1: Experimental design of rearing treatment acute social contexts. Fish from low-predation (LP) and high-predation (HP) populations were reared either in the presence (P+) or absence (P-) of chemical predator cue. As adults, focal males were put in one of five acute social contexts. “Courtship” was a focal male with two females, “Predation” was a focal male with two females and the addition of guppy alarm cue (Brown et al. 1999), “Competition” was a focal male with a female and another male, “Intruder” was a focal male with two other males, and “solo” was a focal male isolated in the tank”.

Behavioral trials

All fish experienced the same schedule in timing of experiences leading up to their behavioral trial. We ran sets of brothers from the same population and rearing treatment each day (trial) that each experienced different acute context. Population and rearing condition groups

were haphazardly distributed in order across the experiment timeline. We accounted for the day/block in our model during analysis by including the trial as a random variable.

We removed brothers from the recirculating system and photographed then using MS-222 for light anesthetization. Following recovery, the males were placed in individual 0.5-gallon acrylic tanks with a female for reproductive experience. Mating experience has been shown to increase mating success in many animals (e.g. (Milonas, Farrell, & Andow, 2011; Pérez-Staples, Martínez-Hernández, & Aluja, 2010; Saleem, Ruggles, Abbott, & Carney, 2014b) and to shift behavioral strategies in male guppies (Guevara-Fiore, Svensson, & Endler, 2012), so to standardize experience we chose to give our experimental males one 24-hour exposure with a female before running experiments. After 24 hours' experience, we transferred males to individual 2.5-gallon glass tanks in our observation room to acclimate to the experimental set up for another 24 hours.

The following morning, we added the assigned acute stimulus one hour after lights on. Males remained in their social context for a total for 1 hour (n per group =6-10, table 1), before euthanasia using ice and rapid decapitation (IACUC protocol # 16-651AA). We chose 1 hour based on previous findings of staining intensity with our measure of neural activation, pS6 (Fischer et al. 2018). We recorded behaviors using a video camera to minimize observer effects. We scored male mating behaviors, sigmoids and forced copulations (Liley, 1966), using Jwatcher (Blumstein, Evans, & Daniel, 2006).

Tissue collection

After euthanasia we fixed whole heads in 4% paraformaldehyde for 4-6 hours prior to storage in 30% sucrose with sodium azide until sectioning. Prior to cryosectioning, we embedded heads in mounting media (Tissue-Tek® O.C.T. Compound, Electron Microscopy Sciences,

Hatfield, PA, USA) and flash froze them in an isopentane bath on dry ice. We stored the embedded heads in -80C for at least 24 hours before cryosectioning. We sectioned the heads in the coronal plane at 14 micrometers and thaw-mounted sections on charged slides (Superfrost Plus, VWR, Randor, PA, USA) in two replicate series.

Immunohistochemistry

We used an anti-phospho-S6 (pS6) antibody as a marker for neural activation. When a neuron is activated, the electrical signal leads to the phosphorylation of the S6 ribosomal subunit, so pS6 acts as a label of recent neural activity, similar to immediate-early genes (Knight et al. 2012). We closely followed the immunohistochemistry procedure uses in Fischer et al. (2018) to visualize phospho-S6 immunoreactive neurons.

Quantification of phospho-S6 immunoreactive neurons

We used the guppy brain atlas (Fischer et al. 2018) to identify brain regions. We used a light microscope (Zeiss AxioZoom, Zeiss, Oberkochen, Germany) attached to a camera (ORCA-ER, Hamamatsu, San Jose, CA, USA) to photograph brain regions and we counted cells present in each region by hand. We counted the left hemisphere of the brain and the most rostral sections of each atlas identified section, except we used the right hemisphere when the left was damaged.

Statistical analysis

Most analyses were done in SAS Enterprise 7.11 (SAS Institute, Cary, NC, USA) using procedure GLIMMIX. We used a negative binomial distribution for the analysis of the male behaviors, female behaviors, and the neural count data. We made this decision based on qq-plots and metrics of model fit compared to Poisson and normal distribution models.

For the behavior data we ran the model with a three-way interaction between ancestral population, developmental rearing condition, and acute social context as independent variables, and the male behavior as the dependent variable. Data from the solo acute treatment was excluded in all behavioral analyses. Trial and family were accounted for as random variables. With all models we began analysis with the largest interaction of all variables and then removed higher level interactions if their F-tests yielded p-values below 0.05. We acknowledge that there are mixed opinions about the validity of this process, but this allowed us to test hypotheses of the interactions of each timescale that may be missed with inclusion of higher-level interactions due to smaller sample sizes. We looked at slices as a post-hoc analysis and considered alpha 0.10 as marginally significant due to small sample sizes.

We ran a similar model for the neural activation data, but with ancestral population, developmental rearing condition, acute social context, and brain region as independent variables predicting the counts of activated cells. For brain regions that extended across multiple sections, we averaged counts in all sections to get a single region count for each individual. We then rounded to the nearest whole number so the averaged cell counts would still be integers and meet with assumptions of the negative binomial distribution. We also included individual nested within family as a random effect to account for multiple measures within each individual and relatedness among brothers. Stain group was another random effect in the model to account for differences across staining batches. As with analysis of the behaviors, when four-way interactions were not significant, we re-ran our models omitting the four-way interaction terms. For post-hoc analyses, we looked at effect slices to investigate the differences within regions between ancestral population, developmental rearing condition, and acute social context as

independent variables. Sample sizes range between 4 and 6 for unique population +rearing +treatment +brain region groups.

We performed correlation tests between sigmoids and forced copulations using cor.test in R (R Core Team, 2019) with the Kendall Tau specification for each of the population of origin and rearing treatment groups (four groups).

Results

Behavior

Table 2.1: Sample sizes of the groups for the behavioral analyses

	Courtship	Predation	Competition	Intruder
CMNP	10	10	10	9
CMP	8	8	7	8
QHNP	7	7	7	7
QHP	8	7	6	7

Sigmoids

After removing the non-significant three way interaction (population*rearing*treatment $F[3,81]=0.58$, $p=0.6308$), we found that population differed in how rearing environment influenced the number of sigmoids performed (rearing*population $F[1,84]=5.28$, $p=0.0241$) (Fig. 2.2), and rearing condition influenced how fish altered sigmoids depending on acute context (rearing*treatment $F[3,84]=2.97$, $p=0.0364$) (Fig.2.2). In addition, population of origin had a marginal influence on sigmoid usage across acute treatments (treatment*population $F[3,84]=2.18$, $p=0.096$). Post-hoc slices did not provide unequivocal evidence for significant effect of rearing in either population (HP ($F[1,84]=2.74$, $p=0.1018$) or LP ($F[1,84]=2.50$, $p=0.1177$)) (Fig. 2.2). Fish reared without predator cue (P-) varied in their sigmoid displays

depending on acute contexts acute treatment (treatment slice, $F[3,84]=5.36$, $p=0.0020$), but fish reared with predator cue (P+) produced a similar number of sigmoids in all acute contexts (treatment slice, $F[3,84]=1.18$, $p=0.3212$). Post-hoc slices provided evidence that the low-predation population responded to acute context (treatment slice, $F[3,84]=3.74$, $p=0.0141$) but the evidence was equivocal in the high-predation population (treatment slice, $F[3,84]=5.36$, $p=0.0647$).

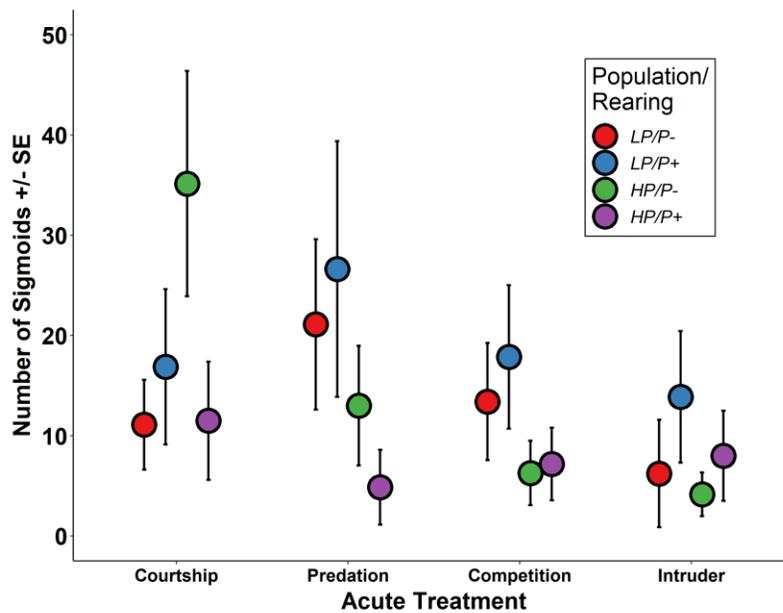


Figure 2.2: Population of origin, rearing environment, and acute social context jointly influence sigmoid display propensity. Points represent the average number of sigmoids with error bars showing the standard error. Red and blue points are low-predation fish (LP) that were reared without (P-) or with (P+) predator chemical cues respectively. Green and purple points are high-predation fish (HP) that were reared without (P-) or with (P+) predator chemical cues respectively. Fish from LP and HP populations differed in their responses to developmental experiences with predator cue, although post-hoc tests were not significant. Rearing treatment with predator cues influenced males' responses to acute social context. Fish reared without predator cues varied consistently in sigmoid numbers across social contexts while fish reared with predator cue did not differ in sigmoids across acute contexts.

Forced copulations

After removing the non-significant three way interaction (population*rearing * acute treatment $F[3,81]=1.06$, $p=0.3721$), we found that population of origin influenced how fish adjusted forced copulation attempts to acute contexts (Fig2.3: population * acute treatment $F[3,84]=4.32$, $p=0.007$). Fish from the low-predation population produced consistently different numbers of forced copulations attempts in the four acute contexts (treatment slice, $F[3,84]=8.96$, $p<0.0001$), where as fish from the high-predation population did not adjust forced copulation based on acute contexts (treatment slice, $F[3,84]=1.40$, $p=0.2492$).

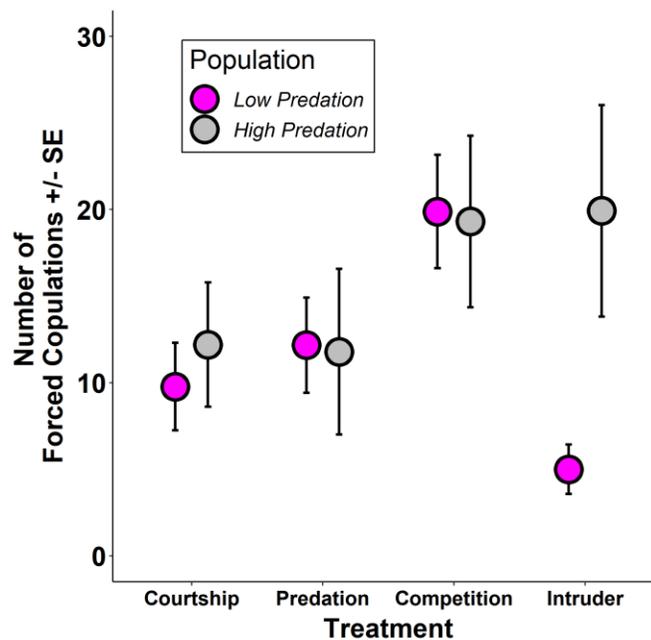


Figure 2.3: Fish from the high- and low-predation populations differed in how acute context affected forced copulation numbers, with low-predation fish more sensitive to context. Points represent the average number of forced copulation attempts and the color of the points represent the population of origin of those fish. Grey indicates high-predation population fish (HP) and pink is low-predation population fish (LP). Error bars are standard error.

Sigmoid and forced copulation tradeoff

We compared if there was a correlation between forced copulations and sigmoids (Fig. 2.4) within the four population by rearing groups and found that only HP fish reared without predator chemical cues (HP/P-) showed a negative correlation between mating behaviors (Table 2.2).

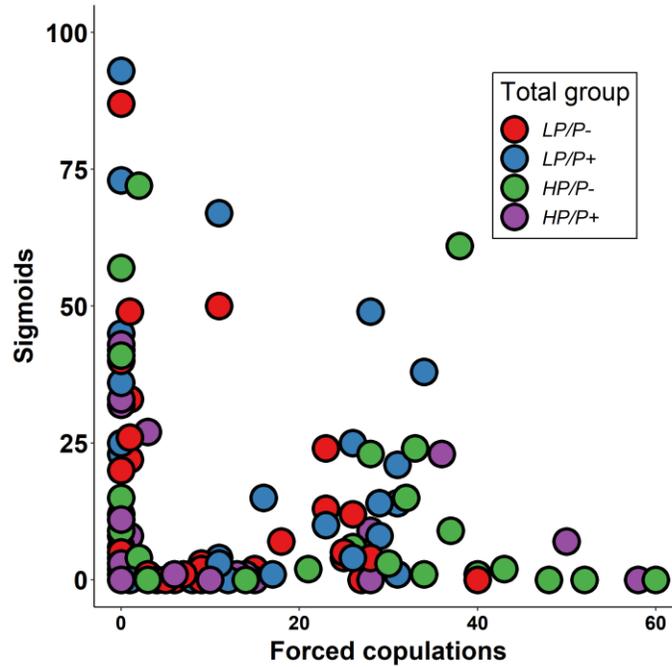


Figure 2.4: Associations between forced copulation attempts and the number of sigmoid behaviors are weak. Each point represents one individual and colors demonstrate the population of origin and rearing condition. Only HP/P- had a negative correlation between forced copulations and sigmoid behaviors.

Table 2.2: Correlation between sigmoids and forced copulation statistics for each population of origin (LP or HP) and rearing treatment (P- or P+) group.

Group	Z statistic	P-value	Tau
LP/P-	-1.000	0.319	-0.120
LP/P+	0.087	0.931	0.012
HP/P-	-2.258	0.024	-0.319
HP/P+	-1.451	0.147	-0.217

Neural Activity

Brain regions differed in how population, rearing, and acute treatment altered phospho-S6 immunoreactive cells (population*rearing*treatment*region, $F[43,553]=1.40$, $p=0.049$) (Fig. 2.5). Post-hoc slices by region and population of origin demonstrated that Vc, Vd, and Vs brain region cell counts depended on rearing-acute context interactions in both populations (Table 2.4). Further, Div and OB had significant rearing-context interactions in the high-predation but not low-predation population, while Tpp, vTn, and aTn had significant rearing-context interactions in the low-predation fish (Table 2.4).

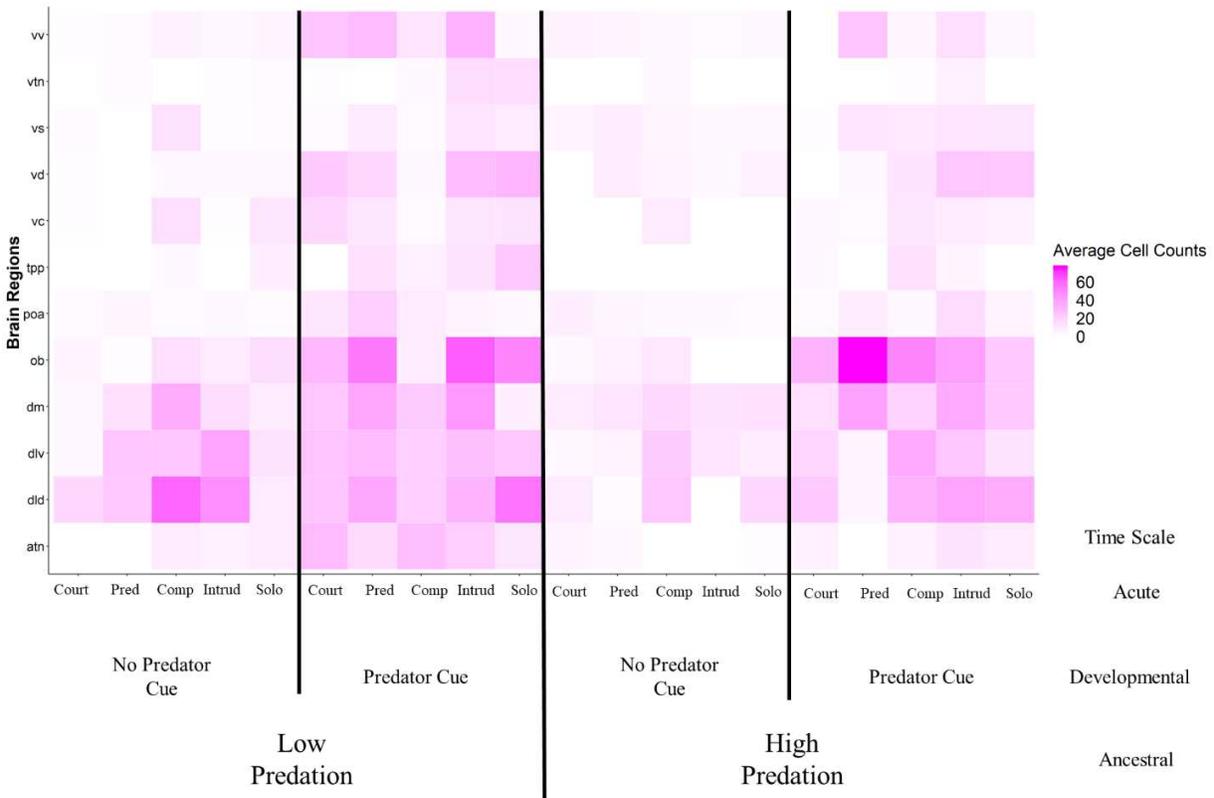


Figure 2.5: Heatmap of average cell counts with brain regions along the Y-axis and the treatment groups along the X-axis. Darker pink represents high average cell counts. Brain regions differed in how population, rearing, and acute treatment altered phospho-S6 immunoreactive cells.

Table 2.3: Key for brain region abbreviations used in Figure 2.5 and Table 2.4.

Regions directly associated with the SDMN		
Brain region	Mammalian Homolog (O'Connell and Hoffman, 2011)	Putative function (O'Connell and Hoffman, 2011)
anterior tuberal nucleus (aTn)	Ventromedial hypothalamus (VMH)	Potentially reproductive behaviors
Dorsal part of the dorsal telencephalon (Dld)	Hippocampus (HIP)	memory representations of the environment and/ or experiences
Ventral part of the dorsal telencephalon (Dlv)	Hippocampus (HIP)	memory representations of the environment and/ or experiences
medial part of the dorsal telencephalon (Dm)	Basolateral amygdala (blAMY)	Integration of multiple sensory inputs
Preoptic area (POA)	Preoptic area (POA)	regulation of sexual behavior, aggression, and parental care,
posterior tuberculum (TPp)	Ventral tegmental area (VTA)	High levels of dopaminergic cells, potentially reward system
Central part of the ventral telencephalon (Vc)	Striatum (STR)	Reinforcement learning and action selection *potentially in conjunction with Vd
Dorsal part of the ventral telencephalon (Vd)	Nucleus accumbens (NAcc)	Sensorimotor information integrator for behavioral response *potentially in conjunction with Vc
supracommissural part of the ventral pallium (Vs)	Bed nucleus of the stria terminalis (BNST)/medial amygdala (meAMY)	Regulation of aggression and reproduction
ventral tuberal region (vTn)	Anterior hypothalamus (AH)	Potentially reproductive behaviors
Ventral part of the ventral telencephalon (Vv)	Lateral septum (LS)	Goal directed social behaviors and stimulus novelty

Table 2.4: Test effects of rearing and acute treatments sliced by population and region, significance at 0.05 is highlighted.

Four-way interaction (population*rearing*treatment*region) effects					
Sliced By pop*region					
Population	Brain region	Num DF	Den DF	F Value	Pr > F
LP	atn	9	553	2.79	0.0033
HP	atn	9	553	1.21	0.2843
LP	dld	9	553	1.11	0.3518
HP	dld	9	553	1.78	0.0688
LP	dlv	9	553	1.3	0.2319
HP	dlv	9	553	2.01	0.0361
LP	dm	9	553	1.25	0.2632
HP	dm	9	553	1.44	0.1656
LP	ob	9	553	1.33	0.2201
HP	ob	9	553	4.08	<.0001
LP	poa	9	553	1.25	0.2594
HP	poa	9	553	0.66	0.7456
LP	tpp	9	553	1.96	0.0419
HP	tpp	9	553	0.87	0.5524
LP	vc	9	553	2.9	0.0023
HP	vc	9	553	2.43	0.0104
LP	vd	9	553	2.12	0.0261
HP	vd	9	553	3.37	0.0005
LP	vs	9	553	2.05	0.0319
HP	vs	9	553	2.27	0.017
LP	vtn	9	553	2.64	0.0053
HP	vtn	9	553	1.41	0.1808
LP	vv	9	553	1.73	0.0801
HP	vv	8	553	1.7	0.0965

Discussion

Our results demonstrate that ancestral selection pressures can shift developmental and acute plasticity, but these patterns are not consistent across populations or even behaviors. We compared effects of developmental experiences with predator cues on behaviors in acute social

contexts in both a high-predation and low-predation population. Previous work has shown differences in sensitivity to predation cue between low and high-predation populations (Fischer, Ghalambor, & Hoke, 2016; reviewed in Kolluru, 2014; Magurran, 2005; Magurran & Seghers, 1990). We hypothesized that developmental plasticity may limit acute plasticity in adulthood, and that evolutionary history shapes plasticity on multiple timescales. In line with our hypothesis, population of origin influenced how rearing condition altered the decision to perform sigmoid behaviors (Fig. 2.2), and low-predation fish tended to be more sensitive to acute social cues in their decisions to perform forced copulations than high-predation fish were (Fig. 2.3). However, counter to our hypothesis, developmental experience with predator cue reduced sensitivity of sigmoid behaviors to acute cues for both populations (Fig.2.2). Moreover, we demonstrated that ancestry, developmental exposure to predator cues, and acute social context also alter neural activation in parts of the Social Decision-Making Network (SDMN) in complex ways (Fig. 2.5). Below we discuss differences between the two main mating strategies we measured in developmental and acute plasticity, and the extent to which patterns of these effects in brain and behavior match predicted population differences in sensitivity to predator and social cues.

Ancestry, rearing environment, and acute context influenced the two main mating behaviors of guppies differently, supporting the independent regulation of these strategies. Male guppies are extremely motivated to mate, and the expectation is often males will adjust the ratio of forced copulations to sigmoids depending on the presence of predators rather than stopping mating attempts (Godin, 1995), leading to the prediction that these behaviors are inversely correlated to maintain mating effort while managing tradeoffs. We did not find strong evidence for negative correlations between sigmoid and forced copulation behaviors (Fig.2.4, Table 2.2)

as would have been predicted by a tradeoff hypothesis. Moreover, we found that fish reared without predator cue differed across acute contexts in sigmoids (Fig. 2.2) but not in forced copulations. Our results further support growing evidence that these two strategies are relatively independent and may be adjusted differently depending on the cue experienced and the selection pressures within the population (e.g. Dill et al., 1999; Head, Wong, & Brooks, 2010; Magurran & Seghers, 1990; Ojanguren & Magurran, 2004). Tight correlations between behaviors have been predicted to inhibit evolution of strategies (Endler, 1995; Schluter, 1996), so the independent responses of sigmoids and forced copulation behaviors to predator and social cues may be key to understanding how plasticity influences evolutionary trajectories. An outstanding question in evolutionary research is how plasticity shapes evolutionary trajectories (e.g. Fischer et al. 2016), and considering behavior specific levels of responses to cues across timescales may directly inform when, why and how plasticity can influence evolution of novel behaviors and strategies.

We proposed two alternative scenarios based on selection pressures in the guppy system: (A) low-predation fish shift from reliance on predator cues during development to reliance on social context in adulthood when predator cues are no longer relevant, whereas high-predation fish are less sensitive to social context; or (B) high-predation fish are more sensitive to acute contexts in general due to their need to balance predation risk and mating opportunity on fine timescales. Similar to previous studies, we found that both populations were sensitive to predator cues during development, but the populations diverged in behavioral plasticity responses to social cues as adults (e.g. Fischer et al. 2016). We found that only low-predation fish demonstrated plasticity in response to acute cues in their forced copulations (Fig. 2.3), but both populations were sensitive to predator cues during rearing in their adjustments of sigmoid

numbers across social cues (Fig. 2.2). We interpret these results as evidence that both populations are sensitive to developmental predator cues, but low-predation population fish demonstrate greater reliance on social cues as adults in acute contexts. Rodd and Sokolowski (1995) demonstrated that males from a low-predation population demonstrated greater behavioral plasticity in response to social contexts than high-predation fish, but their social exposures were developmental rather than acute (Rodd & Sokolowski, 1995). Low-predation fish also tend to more readily adopt social strategies like shoaling from conspecific cues than high-predation fish (Kolluru, 2014; Song, Boenke, & Rodd, 2011). High-predation fish are not blind to social cues and may also tailor responses to indirect information about predators that we did not account for in this study. For example, males shift their mating strategies in response to female behaviors when the female has been exposed to a predator stimulus (Dill et al. 1999). Unlike Dill et al. 1999, we did not account for female behaviors and we did not provide visual cues of a predator, so we cannot distinguish whether alarm cue in our “predation” context was not substantial enough to elicit a behavioral response in the high-predation males on an acute scale or whether males were subtly cueing into female behaviors. One caveat to generalizing our results is that we only tested one population pair, so this shift should be further investigated in other drainages to test if social cues are generally more influential across other low-predation populations and if females are selecting for greater social information use and learning (e.g. Shohet & Watt, 2009).

Behavioral phenotypes result from neural mechanisms that are responding to endogenous and exogenous cues; however, our neural activity results did not align with our overall behavioral sensitivities to developmental and acute treatments. We found region specific interactions between population of origin, developmental condition, and acute treatments (Fig.

2.5), and populations differed in which brain regions demonstrated an effect from developmental experiences on acute neural responses to social contexts (table 4). Both populations overlapped in developmental influences on neural responses in acute contexts for the supracommissural part of the ventral pallium (Vs), dorsal part of the ventral telencephalon (Vd), and the central part of the ventral telencephalon (Vc) (Table 2.4). These regions are putatively important for reproduction, sensory integration, and decision-making respectively (table 2.3, reviewed in O'Connell and Hoffman, 2011), so may represent a conserved mechanism between populations to integrate information and decide between alternative mating strategies. However, due to small sample sizes we are not able to compare the directionality of these responses between populations. Low-predation population fish had developmental effects across acute social contexts in the neural activity of the anterior tuberal nucleus (aTn), posterior tuberculum (TPp), and the ventral tuberal region (vTn), but high-predation fish did not show this sensitivity to both timescales in these regions. The aTn and vTn are both associated with reproductive behaviors and the TPp is largely populated by dopaminergic cells, which are associated with motivated behaviors (table 3, reviewed in O'Connell and Hoffman, 2011) and thus may present an interesting opportunity to investigate their role in defining social-context specific behaviors in each population. In high-predation fish, developmental environment influenced neural responses to acute social contexts in the ventral part of the dorsal telencephalon (Dlv) and the olfactory bulb (OB), but low-predation fish did not have a similar interaction in these regions. The Dlv is putatively associated with memory-based behaviors (table 2.3, reviewed in O'Connell and Hoffman, 2011) and the OB is a primary component of the olfactory sensory system and directly connected to several regions within the SDMN (reviewed in Kermen, Franco, Wyatt, & Yaksi, 2013). The predator cues we used in this study were chemical so these results are particularly

interesting candidate contributors to behavioral plasticity of high-predation fish in response to the predator cues. These connections are largely speculative, but complex interactions within neural responses to cues across timescales may help explain the population differences in response to developmental and acute cues on sigmoid and forced copulation behaviors and deserve further investigation.

Plasticity allows animals to modify their behaviors in response to cues from the environment, and plasticity evolves under natural selection (Pigliucci, 2005). Animals use information from experiences to inform decisions between behavioral strategies (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Dore et al., 2018; Schmidt et al., 2010). Differences in how animals handle information and manage uncertainty in their environment will directly influence behaviors and thus fitness consequences (Mathot, Wright, Kempenaers, & Dingemanse, 2012). Both ancestral and developmental timescales can influence acute responses to environmental contexts, but the mechanisms underlying those influences are often treated as a black box (Taborsky, 2017). Our results demonstrate divergence in timescale-specific responses to cues, where fish in low-predation populations are more sensitive to social context in adulthood than fish from high-predation populations, and exposure to predator cues during development shapes responsiveness to context. Furthermore, we have shown differences between populations in the neural responses to acute contexts and the interaction with developmental experiences. Future work is needed to investigate how selection pressures and genetic drift have shifted animals' sensitivity to experiences on different time scales. In sum, our results provide novel insights into how ancestral pressures influence acute responses to different social contexts and change responses to developmental conditions that influence later acute plasticity.

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CHAPTER 3: PREVIOUS EXPERIENCES INFLUENCE LATER ASSOCIATIONS BETWEEN MALE AND FEMALE MATING BEHAVIORS

Introduction

Among the most complex environments animals navigate is the social environment. Social interactions feature not only the focal individual, but also one or more conspecifics that dynamically respond to the decisions of the focal individual (Taborsky & Oliveira, 2012). Animals that use specific cues and behaviors of their social partners to guide accurate decision making are termed socially competent (Taborsky & Oliveira, 2012). One approach to model social competency is a Bayesian framework that predicts that animals use previous social experiences to refine their responses (J. McNamara & Houston, 1980; Polverino et al., 2019; Stamps & Frankenhuis, 2016). Such updating in courtship contexts can improve mating success (e.g. guppies (Guevara-Fiore & Endler, 2018); *Drosophila* (Saleem, Ruggles, Abbott, & Carney, 2014)). In aggressive encounters, updating includes winner and loser effects, where animals tend to increase aggression after winning fights and adopt submissive behaviors in future encounters after losing fights (Hsu et al., 2014; Lan & Hsu, 2011). Social competency depends on experiences during ontogeny. Social isolation or deprivation results in reduced performance in many social behaviors (e.g. social learning (Lévy et al., 2003), decisions in aggressive behaviors (Arnold & Taborsky, 2010), social connectivity and neophobia (Bertin & Richard-Yris, 2005), and reviewed in Taborsky, 2016, 2017; Taborsky & Oliveira, 2012). Integration of social experiences during development could allow animals to better navigate the complexities of the social environment. However, we lack information about how developmental social experiences shape an animal's ability to refine behavioral strategies in adulthood.

We studied mating strategies because they may impact males' mating success, can depend on social competency, and vary between individuals, populations, and species (reviewed in Sih, Sinn, & Patricelli, 2019). Both developmental social experiences and earlier mating opportunities greatly influence later mating strategies (reviewed in Kasumovic & Brooks, 2011; reviewed in Taborsky, 2016; Taborsky, Arnold, Junker, & Tschopp, 2012). Developmental social environments allow animals to anticipate their adult social environment based on densities of potential rivals and mates during development (reviewed in Bretman, Gage, & Chapman, 2011; Kasumovic & Brooks, 2011). Males are also sensitive to recent mating experiences with females, and rapidly change strategies based on recent mate densities and the variation in size of mates (e.g. Jordan & Brooks, 2011; Saleem et al., 2014). Because developmental social environment influences social competency, we asked whether developmental social environment influences an animal's ability to refine mating strategies across repeated mating opportunities later in life.

We chose to address this question in the Trinidadian guppy (*Poecilia reticulata*), a sexually dimorphic tropical fish native to the island of Trinidad (Magurran, 2005). Males employ two approaches to mate with females: sigmoid courtship displays and forced copulatory behaviors (Houde, 1997; Liley, 1966; Magurran, 2005). Sigmoid displays are higher energy, more conspicuous, and rely on female receptivity, but are also much more successful for mating than forced copulatory behaviors (Magurran, 2005). Both biotic and abiotic factors influence males' decisions to engage in courtship displays and forced copulations across many timescales (e.g. Barbosa, Ojanguren, & Magurran, 2013; Cole & Endler, 2016; Endler, 1987; Guevara-Fiore, 2012; Houde, 1997; Magurran, 2005). Barbosa et al. (2013) showed complex interactions between developmental social experiences (including isolation) and acute sex-biased social

densities in regulating males' use of sigmoids and forced copulations. Moreover, rearing with adult males or mixed sex groups increased the length of sigmoid displays and decreased the number of forced copulation behaviors compared to males reared with only females (Guevara-Fiore, 2012). Male mating strategy also depends previous mating experiences with receptive or unreceptive females (Guevara-Fiore & Endler, 2018). We build on these previous studies to ask how developmental social experiences influences males' refinement of mating strategies toward receptive and unreceptive females. Specifically, do experiences with conspecific males during development alter how males adjust mating strategy across multiple reproductive experiences?

We hypothesized that developmental social experience facilitates rapid refinement of mating strategy due to higher social competency (Fig.3.1, Developmental Priming Refinement Hypothesis). Under this hypothesis, we predict males reared with conspecifics will more rapidly allocate sigmoid behaviors toward receptive females than males who are reared in isolation. If isolation during development impairs social competency, we expect that isolation-reared males may not direct sigmoids toward more receptive females even after multiple courtship experiences. Alternatively, if males refine strategies based on female responses independently of developmental experiences (Fig.3.1, Experience Refinement Hypothesis)., we predict that both conspecific-reared and isolation-reared males will alter sigmoid and forced copulation use over the course of their early courtship experiences.

We compared how males reared in different social groups of conspecific males modified their mating strategy over three days when interacting with a virgin and recently mated non-virgin female. We reared males after 6 weeks with either older experienced "tutor" males, an equally naïve brother, or in isolation. We exposed males to a virgin and a recently mated female for 1 hour each day for three consecutive days. We used virgin females as our proxy for

receptive females because they tend to be more willing to mate during initial encounters with males compared to recently mated females that lose responsiveness towards males after a few days (reviewed in Houde, 1997; A. N. R. Liley & Wishlow, 1974; N. R. Liley, 1966). In addition to comparing how males directed behavior to virgin and recently mated females, we assessed the associations between behaviors of individual male and female pairs. Our results highlight the importance of accounting for reciprocal behaviors of all players during social experiences, as this reciprocity influences behavioral decisions and plasticity.

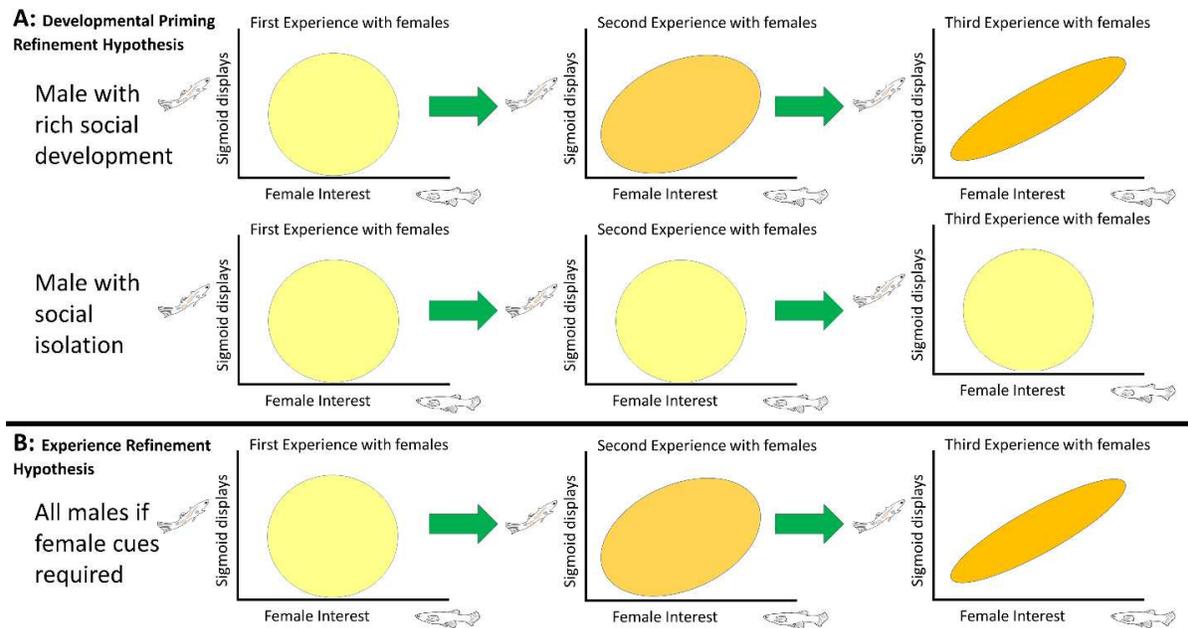


Figure 3.1: Schematic representing two possible hypotheses for how developmental experience might shape later refinement of mating behaviors during early mating opportunities **(A) Developmental priming refinement hypothesis:** We hypothesize that developmental social experiences with male conspecifics primes male guppies for greater social competency in later experiences with females. We predict that males reared in richer environments will be better able to refine their mating strategy to allocate expensive sigmoid displays based on receptivity of females. **(B) Experience refinement hypothesis:** Alternatively, if previous experiences with males during development are not critical to social competency, we predict that all males will refine their strategies with females equally over time.

Methods

Husbandry

Fish were first generation offspring from fish collected from the Garden Grove population in Trinidad in May 2016. This source population is considered a high-predation site in the low lands of Trinidad (Lat: 10.5893, Long:-61.3552). All fish were maintained on a fresh water recirculating system in 0.5-gallon acrylic tanks. Fish were fed once per day on a diet of Tetramin™ fish flakes alternating with brine shrimp. Fish were maintained on a 12:12 light:dark cycle at an average of 25 C° room temperature. We kept the fish in tanks with their siblings until they were 6-weeks old when we determined the sex of each fish by examining them under a dissecting scope for dark coloration around the cloaca while anesthetized in MS-222. We then placed the males in their rearing treatment (see below, Fig. 3.2) and females with their sisters back on the circulating system.

Rearing conditions

At 6 weeks of age, we randomly assigned males to one of the three treatments by dice roll (Figure 2) and raised them in that condition until they were adults at 12- weeks. All treatments had a plastic mesh barrier in the middle of the tank to prevent males from directly interacting with each other, because previous work demonstrated that visual cues alone altered future behaviors (Guevara-Fiore, 2012). Black plastic bags were attached to the sides of the tanks to prevent visual cues from neighboring tanks.

In the *Tutor* rearing treatment, focal males were raised with experienced tutor males from different populations that had been housed with females for the previous few months. These males were placed on one side of the barrier and the naïve focal male was placed on the other side.

The side of the tank was selected using a coin flip to randomize any confounding variables such as light and food availability.

In the *Brother* treatment, focal males were placed similarly in their respective tanks, but with an individual from their same brood on the other side of the barrier. Both these males were measured for behaviors. Focal males assigned the *Solo* treatment also had the barrier in their tank and were randomly assigned to one side of the tank.

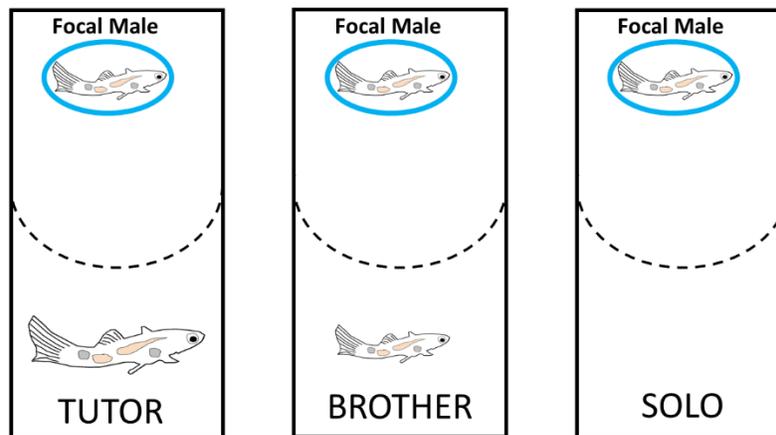


Figure 3.2: Focal males were reared in one of three environments after 6 weeks of age. *Tutor* males were reared with a sexually experienced older male. *Brother* males were reared with their naïve brother. *Solo* males were reared in social isolation starting at 4 weeks.

Reproductive behavioral assays

We performed the behavioral trials once the males were at least 12-weeks old. All males experienced the same procedure. We anesthetized males with MS-222 and photographed them. We waited until full recovery from anesthesia before placing males in individual 2.5-gallon glass tanks in the experimental room over night to acclimate.

We tattooed females from the same Garden Grove population using elastomer (Northwest Marine Technologies, Inc.) in either pink or green. These colors allowed us to identify virgin and

non-virgin females in the videos. To prevent color bias, we tattooed all females as virgins and used them once as virgins, then we housed them tanks with another male until used later as a recently mated female. We interpret females left in tanks with males as recently mated because of previous work shows mating with virgin females happens rapidly upon introduction of males (reviewed in Houde, 1997; Magurran, 2005).

We presented males simultaneously with one virgin and one recently mated female and allowed them to interact freely for 1 hour. We recorded behaviors using a video camera to minimize observer effects. We removed the females after the 1 hour and placed them back on the recirculating system. The males remained in their experimental tanks and were fed there. After 24 hours, we repeated the same procedure with novel females. This was repeated on a third day, and then we removed the males and euthanized them with rapid decapitation per our IACUC protocol (#16-651AA).

We scored behaviors using Jwatcher (Blumstein, Evans, & Daniel, 2006). We scored the male behaviors toward both females at the same time using their tattoo colors as identifiers. We subsequently re-scored the female behaviors for each female independently. Behaviors scored for both males and females are described in Table 3.1. We scored female interest based on “eye contacts” which are the act of the female facing the male and actively tracking his movements. Female interest is usually quantified through the “glide” behavior, which includes swimming with primarily the pectoral and caudal fins with attention tracking the male (Liley, 1966). We validated female interest and eye contacts through associations between eye contact and successful copulations. Successful copulations can be identified by jerky swimming by the male immediately after a sigmoid or forced copulation attempt with a female (Liley, 1966).

Table 3.1: Male and female behavior descriptions

Sex	Behavior	Definition	Example citations
Male	Sigmoid	Body is in “S” shape and begins vibrating while circling around female	Houde 1997, magurran 2005, liley 1966
	Forced Copulation	Swims underneath female rapidly with gonopodium extended	Houde 1997, Magurran 2005, liley 1966
Female	Eye Contact	Active tracking with body position of male is performed from a short distance.	Adopted from “glides” Liley 1966
	Avoiding	Active movement away from male when being pursued.	
	Ignoring	General behaviors, such as foraging, where female is not actively avoiding male behaviors.	

Analysis

We analyzed the summary output data from Jwatcher using SAS enterprise guide (SAS Institute Inc. v.7.11 HFE) with GLMMIX using a Poisson distribution and a Kenward-Rodger degrees of freedom method. We treated behaviors in Table 1 as response variables in separate models with factors rearing treatment, female receptivity, and day of experience and their interactions as predictors. We also included ID of both the male and females as random effect variables to account for repeated measures. We nested male ID within family to account for relatedness between brothers.

To assess how males modify their behaviors in relationship to females behaviors over multiple experiences, we evaluated models of associations between male behaviors and females behaviors, specifically comparing male sigmoid displays and forced copulation attempts with paired females’ numbers of eye contacts, total time avoiding, and total time ignoring. The 6 models included all interaction terms between the female behavior, male rearing experience, day

of male experience, and receptivity of the female as predictor terms for the male behavior. If there was no significant four-way interaction (Female behavior* Rearing* Day* Receptivity), then we re-ran the model while removing highest order interactions. We used models defining the male behaviors of “sigmoid” and “forced copulations” as a response to the female behaviors of “eye contact”, “avoid”, and “ignore”. For definitions of these behaviors see Table 1. With all models we began analysis with the largest interaction of all variables and then removed higher level interactions if their F-tests yielded p-values below 0.05. Because lengths of the male and female fish had no effect on the model (results not shown), we present models without length covariates.

We validated associations between eye contact and female interest by performing correlations using `cor.test` in R (R Core Team, 2019) with Pearson’s product moment.

For post-hoc analyses, we looked at effect slices to investigate the differences within treatments as independent variables.

Results

Male Behavior

Our results showed that males from different developmental treatments altered their numbers of sigmoid displays over the course of the three acute experiences differently based on female receptivity (rearing*day*receptivity $F[4,164.9]=3.29$, $p=0.0126$) (Fig. 3.3). *Tutor* males adjusted the number of sigmoids depending on receptivity of female and the day of their experience (rearing* receptivity $F[5, 170]=5.58$, $p<0.001$), but *Brother* (rearing* receptivity

F[5, 106.7]=1.89, p=0.1013) and *Solo* (rearing* receptivity F[5, 101.8]=0.67, p=0.65) males did not show this interaction.

Rearing treatment, day of experience and female receptivity influenced use of forced copulations as well (rearing*day*receptivity F[4,170]=4.12, p=0.0032) (Fig. 3.4). Unlike sigmoid behaviors, in forced copulations *Tutor* males did not adjust their use of forced copulations in response to day of experience and receptivity of females (rearing* receptivity F[5, 170]=2.03, p=0.08), while *Brother* (rearing* receptivity F[5, 145]=2.63, p=0.026) and *Solo* (rearing* receptivity F[5, 170]=3.78, p=0.003) males did adjust their use of forced copulations in response to day of experience and receptivity of females.

The majority of males did not mate, and there were only seven successful copulations through out of all the trials. Of the successful copulations, six out of seven were with virgin females (Fig. 3.5).

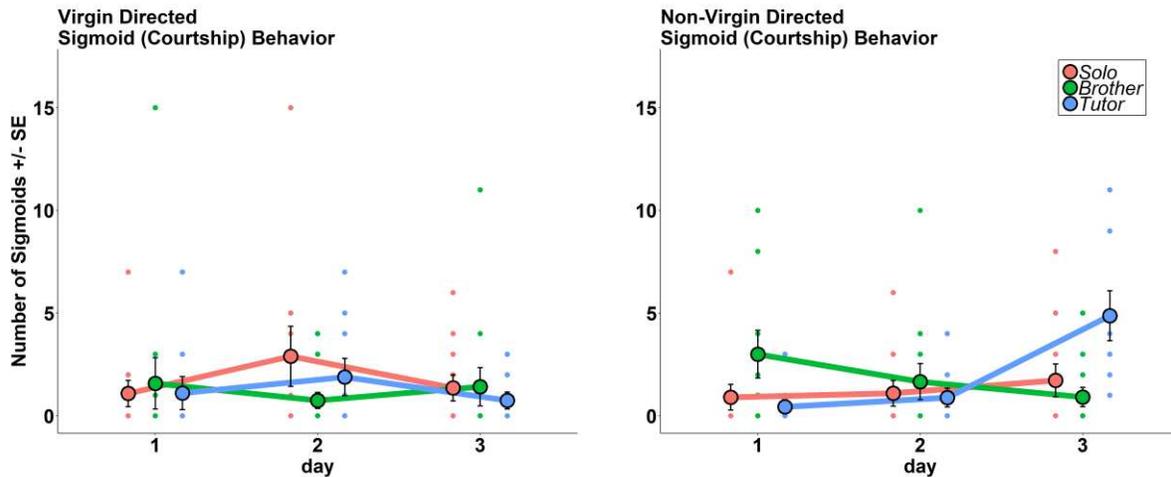


Figure 3.3: Developmental experiences influenced how males allocated sigmoid behaviors depending on receptivity of females in their first three mating opportunities. Individuals varied greatly in the number of sigmoids within a treatment (differentiated by color). Small points indicate raw counts for each individual and large circles represent group mean +/- standard error.

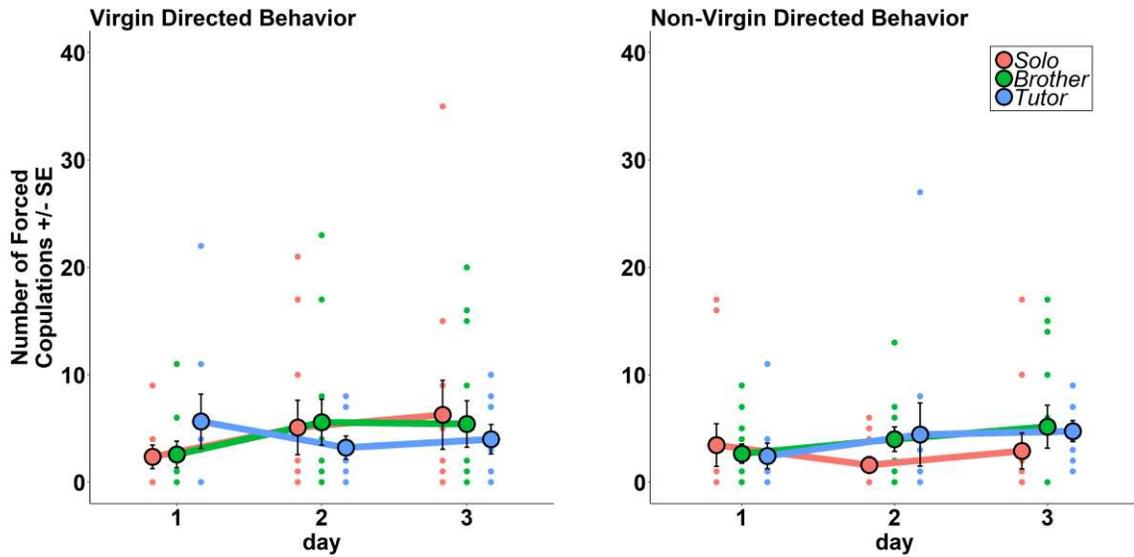


Figure 3.4: Interactions between the rearing treatment of the male and the day of experiences with females show how dynamic the use of forced copulations can be in this system. As with sigmoids, individuals varied greatly in the number of forced copulations within a treatment (indicated by color). Small points indicate raw counts for each individual and large circles represent group mean +/- standard error.

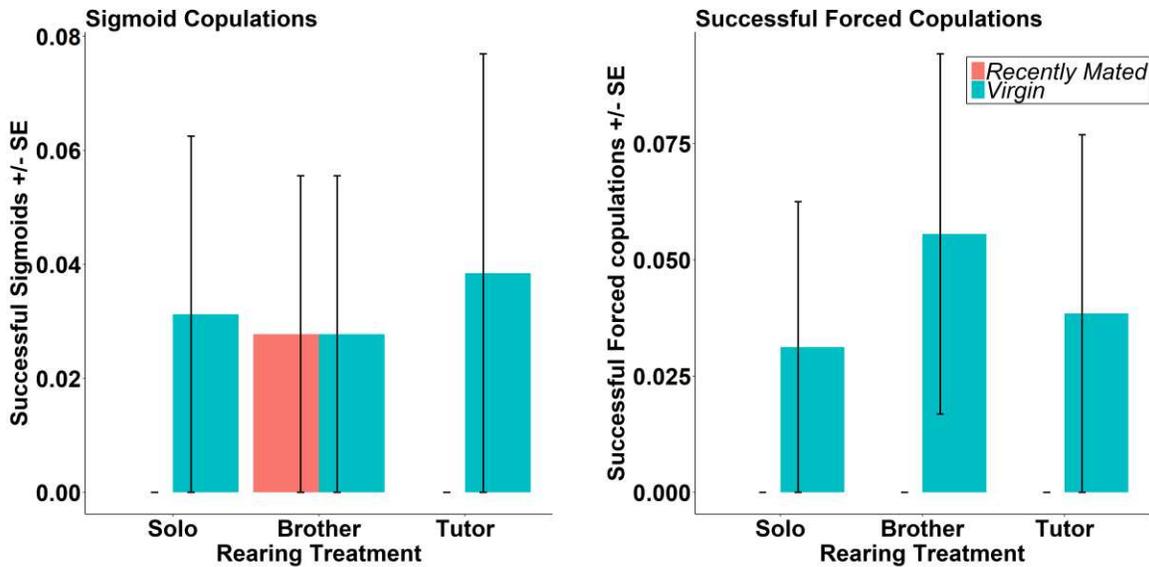


Figure 3.5: Average numbers of successful matings across treatment groups, with colored bars representing the mating experience of the mated female. There were very few successful copulations across all trials, but 6 out of 7 were with virgin females.

Female behaviors

We validated our measure of eye contact as a proxy of female interest based on the positive correlation between the number of eye contacts and successful copulations (Pearson correlation=0.15 $T=2.07$ $p=0.039$). Number of eye contact was also positively correlated with the number of glides (Pearson correlation=0.31 $T=4.53$ $p<0.001$), which is a common measure of female interest (Magurran, 2005, Liley 1966). Because eye contact was unambiguous in our videos and glides were not, we used eye contacts in our analyses of female behavior. There was no three way interaction between rearing treatment, day of experience, and receptivity of female (rear*day*receptivity $F[4,170]= 1.46$, $p=0.217$), so we ran the model with all lower level interactions. Eye contact behaviors of females varied across the day of experience of the male as well as the rearing treatment of the male, but not with female mating status (Fig. 3.6, rear*day $F[4,174]= 2.78$, $p=0.028$).

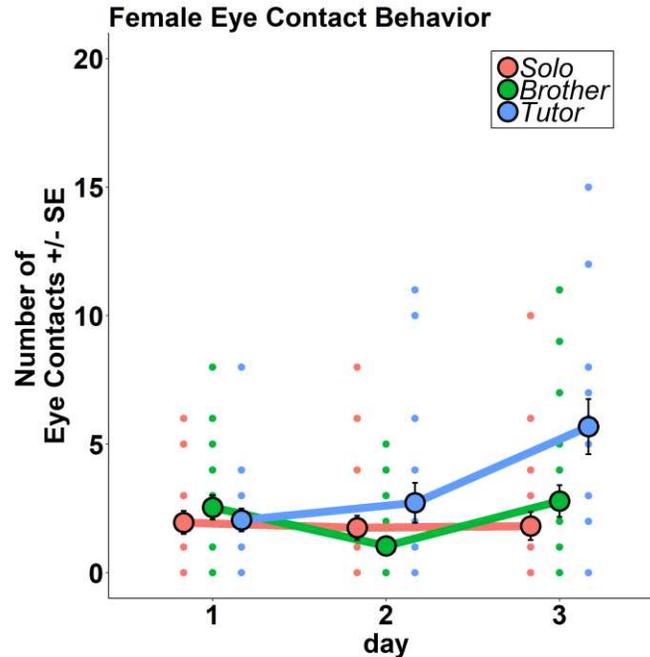


Figure 3.6: Females responded to male treatment (indicated by color) and the day of the males' experience, regardless of the female's mating status. Trials varied greatly in the number of eye contacts by females within each treatment. Small points indicated raw counts and large circles represent group mean +/- standard error.

Influence of females on male reproductive behavior

We did not find a four-way interaction between female eye contact, day, male treatment, and female receptivity for male sigmoids (eye contact* day * rearing treatment*receptivity, $F[4,152]=1.42$, $p=0.2284$). However, when we re-ran the model with lower level interactions we found associations between male sigmoids and female eye contacts varied across not only day, but also depended on the rearing treatment of the male (Fig. 3.7, eye contact* day * rearing treatment, $F[4,146.7]=3.13$, $p=0.0167$). The way the relationships between these behaviors changed over days were opposite our predictions. Males reared with tutors decreased in positive associations between sigmoids and eye contacts over the course of the three experiences, and solo reared males showed an increase (Fig. 3.7). We did not find a four-way interaction between

total time (TT) a female spent avoiding a male, day, male treatment, and female receptivity for male sigmoids (TTavoiding* day * rearing treatment*receptivity, $F[4,152]=1.52$, $p=0.1988$). Male sigmoid behaviors varied in association with the total time the female spent avoiding him depending on the male's rearing treatment and the female's mating status (Fig. 3.8, total time avoiding* treatment* receptivity, $F[2,148.6]=3.08$, $p=0.0491$). *Tutor* males had a positive association with the total time a virgin spent avoiding him and the number of sigmoids he performed, but *solo* males had a positive association with the total time a non-virgin female spent avoiding him (Fig. 3.8). We did not find a four-way interaction between total time (TT) a female spent ignoring a male, day, male treatment, and female receptivity for male sigmoids (TTignoring* day * rearing treatment*receptivity, $F[4,150.9]=1.47$, $p=0.2145$). We found male sigmoid displays were associated with male treatment and total time a female spent ignoring the male (Fig. 3.9A, TTignoring*treatment, $F[2,132.6]=3.73$, $p=0.026$) as well as an interaction between female mating status and total time a female spent ignoring the male (Fig. 3.9B, TTignoring*receptivity, $F[1,138.5]=8.23$, $p=0.005$). *Tutor* males had a negative association between the total time a female spent ignoring the male and their use of sigmoids (Fig. 3.9A) and there was a negative association between virgin females' total time spent ignoring the male and the number of sigmoid behaviors (Fig. 3.9B).

We found associations between male forced copulations and female eye contacts depend on day of mating experience, male treatment, and female receptivity (Fig. 3.10, eye contact* day * rearing treatment*receptivity, $F[4,152]=3.80$, $p=0.0057$). Associations between male forced copulations and total time the female spent avoiding the male did not show a four-way interaction (TTavoiding* day * rearing treatment*receptivity, $F[4,146.8]=1.79$, $p=0.133$), but rather depended on the day of experience only (Fig.3.11, TTavoiding* day, $F[2,168]=15.54$,

$p < 0.0001$). On day one of males' experiences with mating opportunities there was a positive association between the number of forced copulations and the total time a female spent avoiding the male (Fig. 3.11). We found a similar pattern for the association between male forced copulations and total time the female spent ignoring the male, with no four-way interaction (TTignoring* day * rearing treatment*receptivity, $F[4,138.3]=1.45$, $p=0.222$), but also depended on the day of experience only (Fig. 3.12, TTavoiding* day, $F[2,168]=12.42$, $p < 0.0001$). On day one of males' experiences with mating opportunities there was a negative association between the total time a female spent ignoring the male and the number of forced copulation attempts by the male (Fig. 3.12)

For both sigmoids and forced copulations, males tended to have negative associations with the total time a female was ignoring the male (Fig. 3.9 and 3.12 respectively) and positive associations with eye contacts (Fig. 3.7 and 3.10) and the total time she spent avoiding the male (Fig. 3.8 and 3.11).

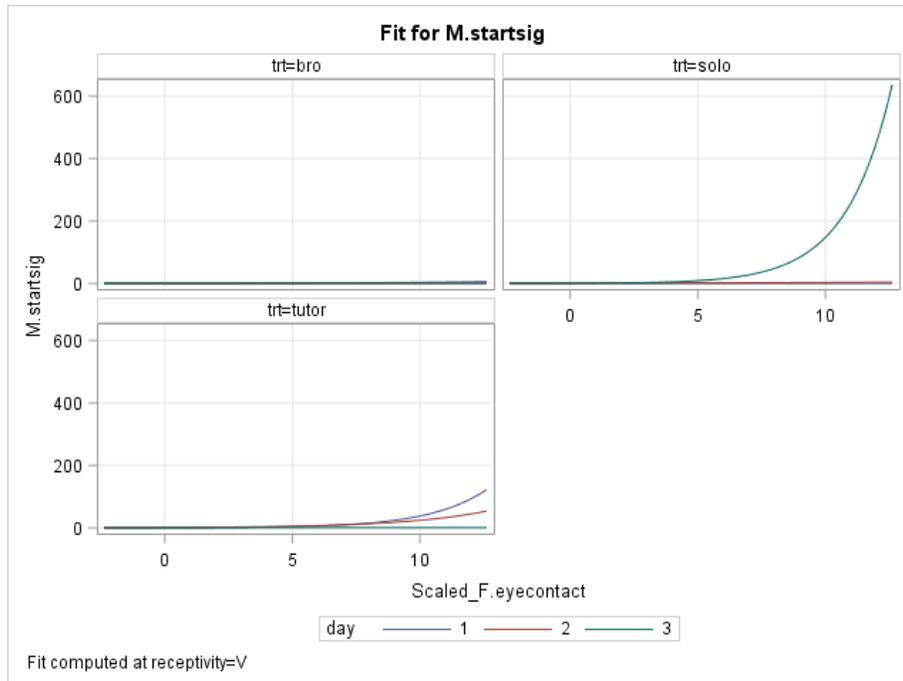


Figure 3.7: Rearing treatment (each panel) and the day of experience (color of line) of the male influenced the association between the number of female eye contacts and the number of sigmoids the male performed. Males reared with a tutor decreased their positive associations between eye contact and sigmoids over the course of the three days, but solo reared males increased the association between sigmoid behaviors and female eye contact.

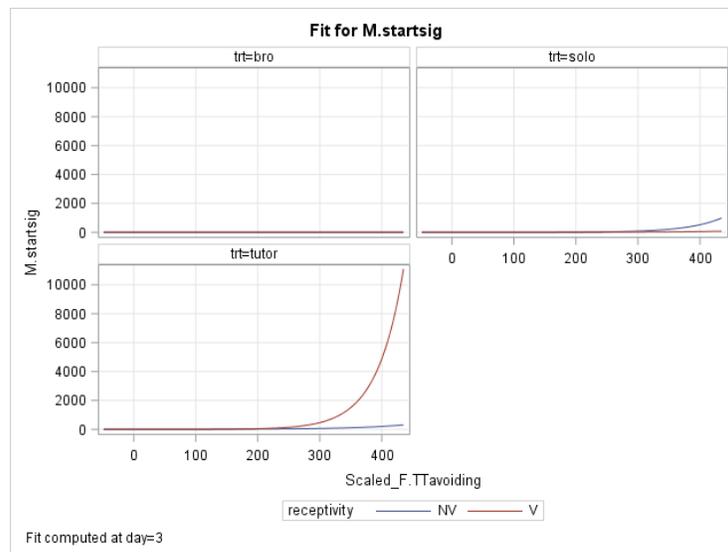


Figure 3.8: Rearing treatment of the male and the mating status of the female interacted in predicting the association between the total time a female spent avoiding the male and the number of sigmoids the male performed. Males reared with a tutor had a positive association between the male and female behaviors but only with virgin females, whereas solo-reared males had produced slightly more sigmoid attempts toward the non-virgin females that spent more time avoiding the male.

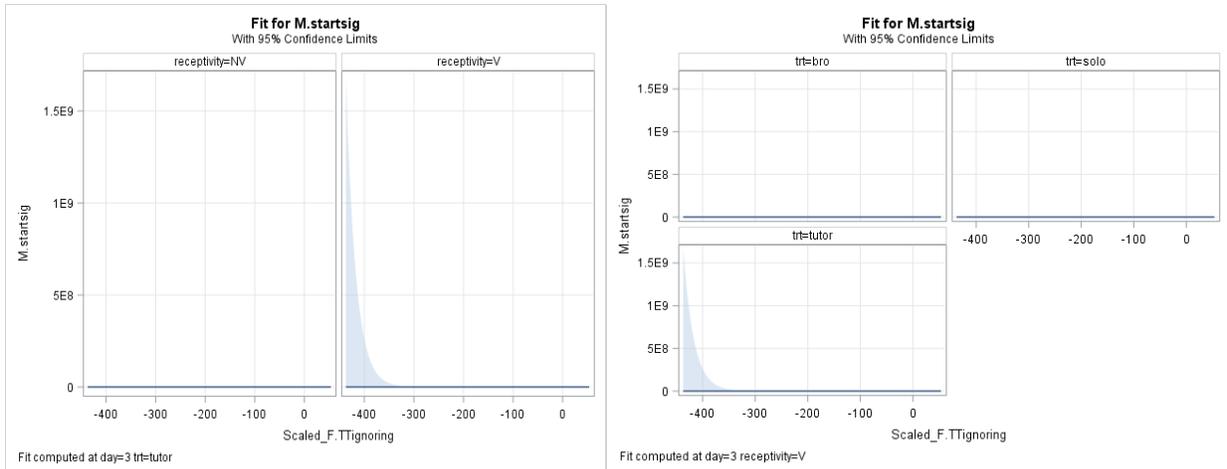


Figure 3.9: Both mating status of the female (A) and (B) predicted the association between the total time a female spent ignoring the male and the number of sigmoids the male performed. Males reared with a tutor produced fewer sigmoid displays toward females that spent more time ignoring him and in particular that negative association between the behaviors was stronger for virgin females.

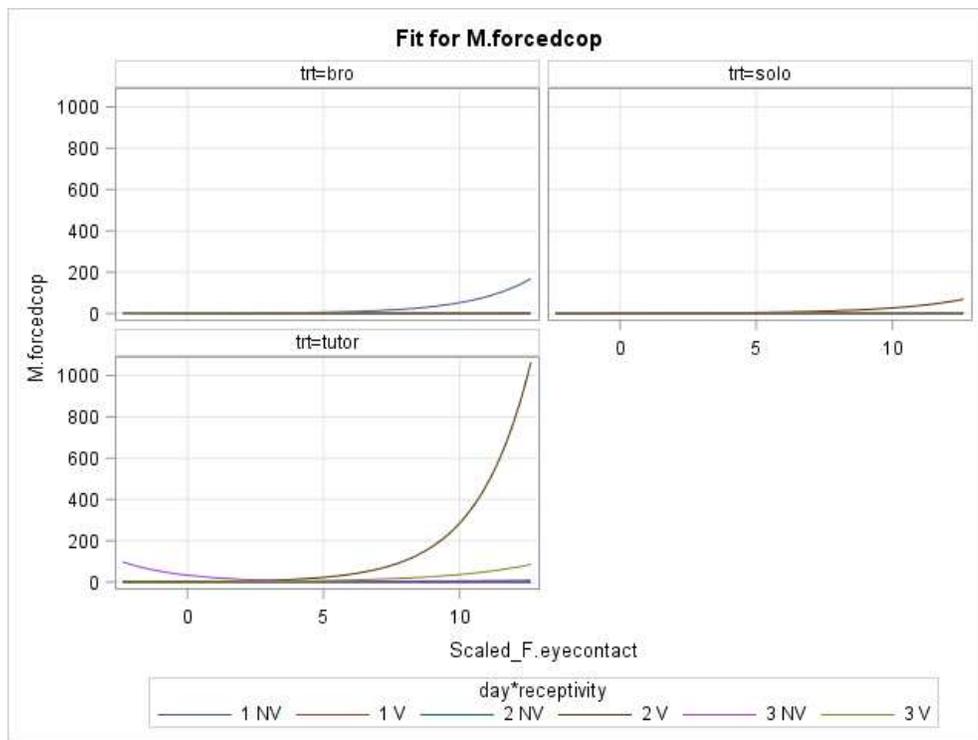


Figure 3.10: Rearing treatment of the male, the mating status of the female, and the day of experience interacted in predicting the association between the number of female eye contacts and the number of forced copulations the male performed. Males reared with a tutor attempted more forced copulations toward females that made more eye contacts, but only with virgin females on the second and third days. Males reared with their brothers had a similar positive association on the first day toward non-virgin females, and solo reared males had a slight positive association toward non-virgin females on the second day.

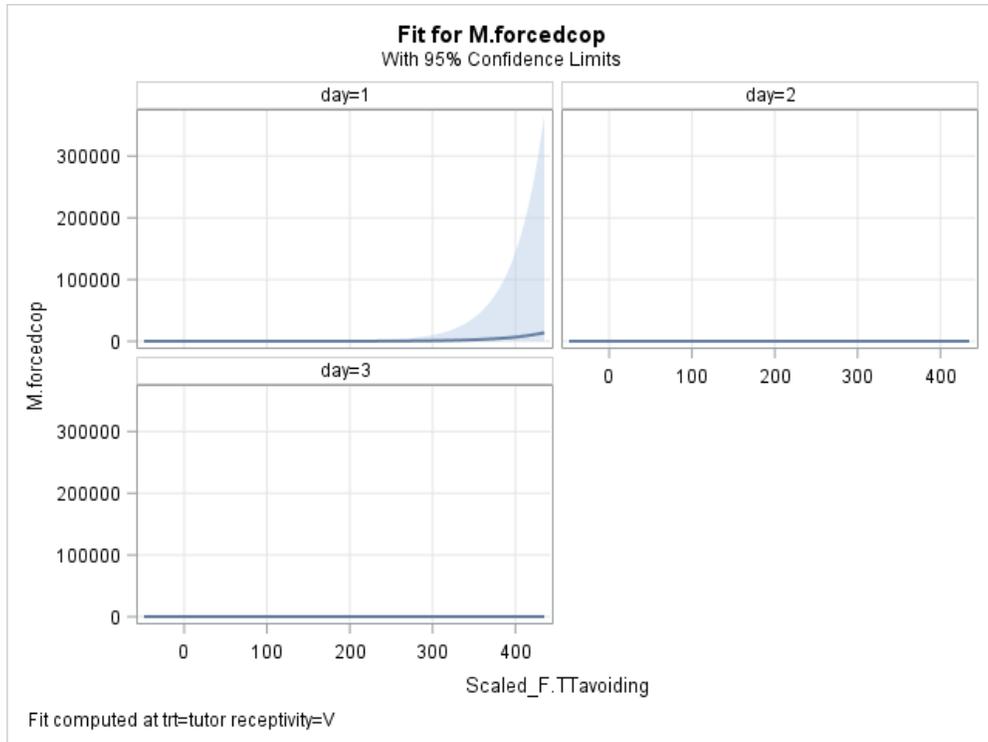


Figure 3.11: Day influenced the association between the number of male forced copulation attempts and the total time the female spent avoiding the male. On day 1, males attempted more forced copulations toward females that spent more time avoiding them, but the association was weaker on days 2 and 3.

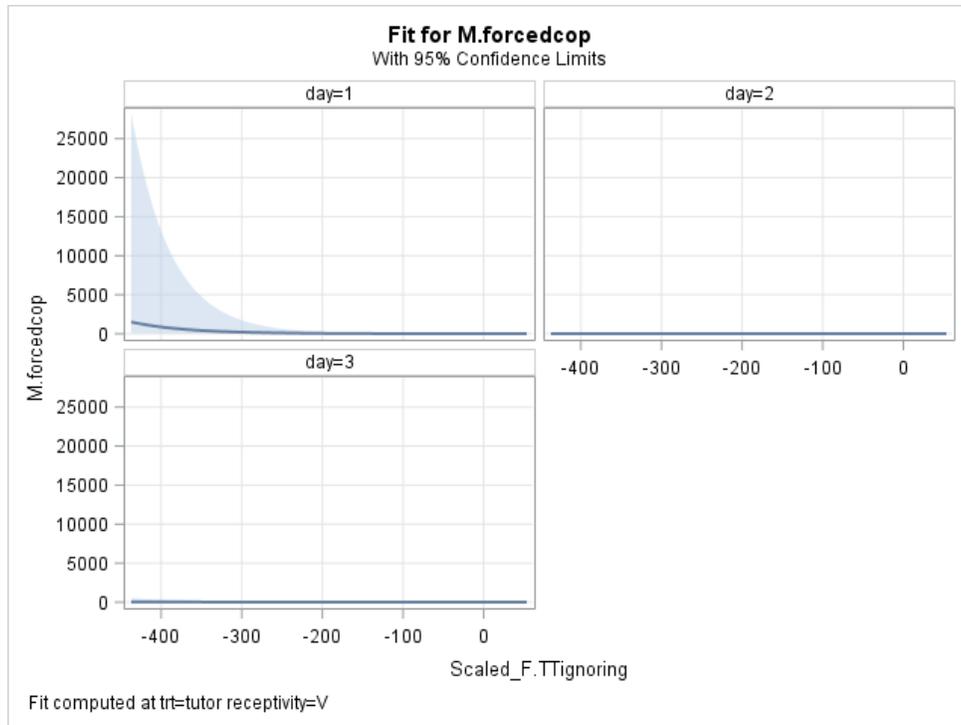


Figure 12: Day of experience influenced the association between the number of male forced copulation attempts and the total time the female spent ignoring the male. On day males attempted fewer forced copulations toward females that spent more time ignoring them, but the negative association was weaker on days 2 and 3.

Discussion

We hypothesized that previous experiences during development would influence how adults are able to modify their mating strategies over multiple experiences with females. We found that both developmental experiences with conspecific males and acute experiences with females influenced male mating strategies. Males modified how many sigmoid and forced copulation behaviors they performed over the course of multiple experiences with females, and that refinement depended on their rearing environment (Fig.3.3 and 3.4). However, these behaviors were not directed toward the virgin females, typically found to be more receptive. We demonstrated that female mating history does not always predict female interest, and that male

mating attempts are associated with female behavioral patterns. Moreover, associations between male and female behaviors changed over the course of multiple experiences.

Surprisingly, we did not find males directed more sigmoid displays toward virgin females as predicted (Cole & Endler, 2016; Guevara-Fiore, Skinner, & Watt, 2009). In contrast males reared with a tutor directed sigmoids at non-virgin females (Fig. 3.3). Females are often still considered receptive for three days after mating (Liley & Wishlow, 1974; Magurran, 2005), and some of our females were within this time frame when they were used in the recently mated group. However, we see that females from both categories of receptivity performed the same numbers of eye contact behaviors (Fig. 3.6), so female interest levels is not sufficient to explain the sigmoids specifically directed at the recently mated females particularly because successful matings were predominately with the virgin females as expected (Fig. 3.5). Virgin females will reduce responsiveness to males over the course of several experiences regardless of mating success (Liley & Wishlow, 1974), so female interest may not be a reliable signal of female fertility for males. We found that *Tutor* males reduced the positive associations between the number of sigmoids performed by the males and the number of eye contacts by females over the course of three mating experiences (Fig.3.7), although these males produced relatively high levels of sigmoid displays on that third day (Fig. 3.3). These results suggest that males with social priming may learn to base sigmoid behaviors off more reliable signals. Furthermore, *Tutor* males also had a negative association between total time a female spends ignoring him and the number of sigmoids he performed (Fig. 3.9A) and this association is stronger for virgin females (Fig. 3.9B). The female ignoring behavior was recorded when the female was performing other behaviors, so demonstrates high levels of uninterest. Conversely, the female avoiding behavior reflected actively swimming away from the male, typically after mating attempts. Total time

ignoring the male is thus likely a better measure of uninterest by the female, and males using that behavior as an indicator of uninterest may explain why we see expected negative relationship between sigmoids and ignoring (Fig. 3.9 and 3.12), whereas the positive association between total time avoiding and mating attempts (Fig. 3.8 and 3.11) is consistent with the possibility that avoiding is triggered by unwanted mating attempts. Based on a social competency hypothesis, we predicted males would refine their strategies based on female behaviors over the course of multiple experiences. Interested females (more eye contact behavior) should attract more sigmoid behaviors from the males, and we see this pattern in *Tutor* males on day 1 and in *Solo* males on day 3 (Fig.3.7). However, the developmental experiences of the males shift how males update those strategies over the course of their first three mating experiences, so it is difficult to parse out if one rearing group is demonstrating greater social competency.

Other studies that have also found complex interactions between developmental social environments and acute social environments. For example, male guppies reared with an older experienced male or in mixed tanks spent more time performing sigmoid behaviors than males reared with adult females, although the number of sigmoid displays did not differ (Guevara-Fiore, 2012). Our results mirror these results with complex interactions between rearing treatment and behaviors, but we extended previous findings by following the progression of male behaviors through multiple experiences to characterize changing strategies. Our findings that males update strategies over the course of their first three reproductive encounters builds on previous work showing males update their strategies based on experiences with females. Males reared with exposure to adult conspecifics were faster to initiate mating behaviors than males reared in isolation from birth to adulthood or isolated starting at six weeks, but all males performed similar mating behaviors by the end of a 30-minute trial with females (Barbosa et al.,

2013). Our results demonstrate that developmental experiences continue to influence male strategies over the course of multiple experiences with females. However, we did not find that adult experience was able to override rearing environment experience as in other studies (e.g. Guevara-Fiore, Svensson, & Endler, 2012). Barbosa et al. (2013) used two males with four females or four males with two females in their studies, and Guevara-Fiore et al. (2012) used a single male and female in their behavior assays. The differences we found in our result compared to theirs may be explained by the different social contexts in our assays. Male guppies will shift their behavioral strategies based on sex biases (Barbosa et al., 2013; Barrett, Evans, & Gasparini, 2014; Jirotkul, 1999), and our assays may indicate the importance of recent experiences with conspecific males in the regulation of mating strategies. Moreover, we had very few successful matings in our study, and the act of successfully mating may also be vital for the refinement of mating strategies to overcome developmental experiences (as in Guevara-Fiore, Svensson, & Endler, 2012). Future work should work to resolve these discrepancies; however, our results clearly support that rearing conditions can influence how males modify their strategies based on experiences with females as adults.

When animals can learn through trial and error, including social learning, you expect to see fine-tuning of strategies (Dukas, 2013; Mery & Burns, 2010). For example, reinforcement can create strong assumptions in animals about expected responses to behaviors, as in a Bayesian framework of behavioral plasticity (J. McNamara & Houston, 1980; Richerson, 2018; Stamps & Frankenhuis, 2016). Under the social competency hypothesis, we had predicted that social competency would make males more responsive to the receptive behaviors demonstrated by females and would result in stronger associations between female interest behaviors and male mating strategies as males gained experience. Males reared with a tutor increased the number of

sigmoids they performed by day three (Fig. 3.3), which aligns with previous results on age-related distributions of mating strategies and potential evidence for learning (e.g. Rodd & Sokolowski, 1995). However, counter to our hypothesis we found that males reared with a tutor did not have stronger associations between their behaviors and female behaviors over multiple experiences. We largely saw a breakdown of associations between female behaviors and male forced copulations over the course of three experiences (Fig. 3.10-3.12) and mixed associations over time with male sigmoid behaviors (Fig. 3.7-3.9). For example, we found female interest (eye contact) was initially positively associated with sigmoids but decreased over three experiences in tutor males but the association increased in solo males by day three as would be predicted in a social competency learning framework (fig. 3.6). We interpret these results as demonstrating that being raised with adult conspecifics does not improve social competency compared to isolation, counter to our predictions. However, due to small sample sizes, we may have lacked sufficient power to measure associations between male and female behaviors. Further, males may shift strategies based on information gathered during experiences with females based on cues we did not measure. For example, males may gauge receptivity using pheromones (Guevara-Fiore et al., 2009). We also did not incorporate successful matings into our models, which may also influence behaviors on subsequent days (Guevara-Fiore & Endler, 2018), because too few males were successful for analysis. While we cannot detail male learning based on specific interactions with females, our results clearly demonstrate that males use previous experiences to influence their strategies, as predicted by the developmental priming refinement hypothesis, although rearing condition does influence that updating in ways inconsistent with the proposal that a rich social environment produced greater social competency.

We provide evidence that sigmoid behaviors and forced copulation behaviors are independent rather than acting as a modular “mating strategy” unit (e.g. Endler, 1987; Fischer, Ghalambor, & Hoke, 2016; Ojanguren & Magurran, 2004). We have found male mating strategies are not simply inversely correlated as expected (e.g. Godin, 1995), but rather fluctuate in complex patterns depending on rearing treatments and seemingly independently, in line with previous studies (e.g. Dill et al., 1999; Fischer et al., 2016, Dolphin chapter 2). For example, light levels influence sigmoid propensity but not forced copulations (Endler, 1987), whereas forced copulation numbers increase toward recently mated compared to virgin females, but males did not differentially direct sigmoid displays (Guevara-Fiore et al., 2009). Barbosa et al. (2013) conclude that female behaviors influence sigmoids but not forced copulations, and high-speed water flow influenced sigmoid behaviors and not forced copulations (Head et al., 2010). Males will decrease both sigmoids and forced copulatory behaviors when exposed to predators and in response to females who have recently been exposed to predators (Dill et al., 1999). Moreover, Rodd and Sokolowski (1995) found little evidence for genetic underpinnings of the relative allocation of the mating strategies, except in the forced copulation numbers. These results were further supported by Miller and Brooks (2005) who found a family effect on the number of forced copulations but not sigmoid numbers (Miller & Brooks, 2005). Further evidence of these behaviors not being directly linked is found in studies which show water pollutants will often affect forced copulation numbers but not sigmoids behaviors (e.g. Bertram, Saaristo, Ecker, Baumgartner, & Wong, 2018; Zhang et al., 2019). Sigmoid behaviors are higher risk and more metabolically costly than forced copulation behaviors and are only successful with receptive females (reviewed in Magurran 2005), which may lead to different selection pressures on the two behaviors. This independence potentially allows for greater plasticity in behavioral

repertoire (E. K. Fischer et al., 2016) with each behavior elicited by different cues, and thus may allow greater flexibility in learning and adaptation to complex cues.

A Bayesian framework predicts that animals use previous social experiences to refine their responses (J. McNamara & Houston, 1980; Polverino et al., 2019; Stamps & Frankenhuis, 2016), with naïve expectations (priors) updated through experience. Animals in which priors were established in isolation may face greater challenges in updating to refine decisions. Our results determined how developmental experiences influence the priors established early in life that are subsequently built upon in a Bayesian updating framework. *Solo* males may have established priors that were ambiguous and not informative for later life reproductive decisions. *Solo* males were able to update their strategies over three mating interactions, so isolation does not necessarily result in poor social competency but rather a different naïve prior than socially reared males that is built upon later. Future work is needed to further understand how animals respond to developmental social situations, and how many experiences may be necessary to overcome unexpected responses in a social competency context.

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CHAPTER 4: NEUROMODULATORY RESPONSES TO REPRODUCTIVE CONTEXTS

Introduction

The ability to modify behaviors in response to a changing acute environment is vital to many animal systems and is often tightly linked with fitness consequences (reviewed in Taborsky & Oliveira, 2012). Circuits within the brain that control behaviors interact with physiological state of the individual (endogenous cues), and sensory input from the external environment (exogenous cues) (e.g. Hau et al., 2017; Kennedy et al., 2014) to inform decisions (Stamps & Frankenhuis, 2016). Neuromodulatory cell groups are key integrators of the endogenous and exogenous cues that produce flexible behavioral responses (reviewed in Oliveira, 2009). Neuromodulators are molecules within the brain that bind to receptors in the cell membrane and trigger signaling cascades that have lasting effects from seconds to weeks (reviewed in Libersat & Pflueger, 2004). Neuromodulator responses are highly specific to sensory cues, environmental contexts, and physiological states (reviewed in Oliveira, 2009). Neuromodulators influence behaviors on multiple timescales and through multiple mechanisms (Marder, 2012), and neuromodulators may influence neural responses differently depending on the current physiological state (Marder, O’Leary, & Shruti, 2014). A first step in linking neuromodulatory responses to cues at different timescales with their lasting behavioral consequences, we need to first uncover the network of multiple neuromodulators active in the relevant environmental context.

Reproductive contexts directly link behavioral responses to exogenous and endogenous cues with fitness effects. Sexually dimorphic species often have male-specific reproductive

behaviors, which are regulated by different neuromodulators (reviewed in Chen & Hong, 2018; McKinsey, Ahmed, & Shah, 2018; Yang & Shah, 2014). Previous works demonstrates that neuromodulators influences reproductive behaviors, such as male courtship (e.g. Chen & Hong, 2018; Gil, Bhatt, Picotte, & Hull, 2011; McKinsey et al., 2018; Shahjahan, Kitahashi, & Parhar, 2014; Yang & Shah, 2014). For example, dopamine has been implicated in mating drive and can directly influence the initiation of mating behaviors (Creighton, Satterfield, & Chu, 2013; Forlano & Bass, 2011; Lenschow & Lima, 2020; S. X. Zhang, Rogulja, & Crickmore, 2016), serotonin influences sensitivity of sensory systems to different cues (reviewed in Sizemore, Hurley, & Dacks, 2020) and may help prime males to better sense and respond to females behaviors during courtship (Keesom & Hurley, 2016), and gonadotropin releasing hormone may also influence sensory systems during courtship (Eisthen, Delay, Wirsig-Wiechmann, & Dionne, 2000) while also directly influencing reproductive behaviors (Arch & Narins, 2009).

Neuromodulatory control over the integration of exogenous and endogenous cues and signals helps animals to use the same sensory information to produce wildly different behavioral strategies (reviewed in Chen & Hong, 2018). There is a mosaic of different neural circuits facilitating the production and decisions between reproductive behaviors, but studies investigating the influence of neuromodulators often only focus on one or two of the many potential mechanisms underlying behavioral decisions. Identifying the players within the mosaic underlying reproductive behaviors will help us disentangle how the same cue leads to dramatically different behaviors in individuals and between sexes.

To more holistically investigate cell groups associated with acute reproductive contexts, we evaluated transcripts being translated in recently activated. Using a phosphoTRAP procedure (Knight et al., 2012), we compared the identities of cells activated in a male Trinidadian guppy

Poecilia reticulata) to the presence of a female. Male guppies are highly motivated in mating contexts, and individual males differ in mating strategy depending on endogenous and exogenous cues (Houde, 1997; Liley, 1966; Magurran, 2005). We allowed virgin males to interact freely with females for one hour while recording their behaviors. We selectively sequenced transcripts associated with activated ribosomes in these reproducing males and compared those to males who were alone in a tank. We identified the biochemical identities of cells active during reproductive opportunities using the results of the differential expression analysis. Our study identifies neuromodulator components activated within a reproductive context, as well as providing evidence for critical sensory system responses. The multiple pathways that interact during a social encounter establish hypotheses for future studies.

Methods

Husbandry and rearing

Fish were raised in the lab for two generations the Aripo source population in Trinidad. We maintained fish in a freshwater recirculating system in 0.5-gallon tanks. We maintained fish at approximately 23° C on a 12:12 light: dark cycle and fed them each morning with measured Tetramin™ fish flakes. We raised fish in family groups until they were at 6 weeks old then housed males in individual tanks until 12 weeks of age. Fish were able to see conspecifics between tanks but not interact directly. All fish reach adulthood before the behavioral trials and were virgins because they were housed alone after sexual maturity.

Behavior

To determine how reproductive contexts influence neuromodulatory cells, we compared males that freely interacted with females for 1 hour (female treatment) with males that were left alone in a tank (control).

We placed males into individual 2.5-gallon glass experimental tanks with rocks along the bottom 24 hours before the assay. On the day of the assay, we turned on the lights manually at 7am and allowed 1 hour of acclimation. We added the stimulus to the first tank at 8 am and then subsequent tanks at 5-minute intervals. Males in the female treatment were given a virgin female as a stimulus and males in the control treatment had the net tapped on the top of the water of their tank. Males remained in their tanks for 1 hour during which we recorded behaviors using a video camera. After 1 hour, we euthanized males and females with ice water and rapid decapitation per our IACUC protocol (#16-651AA). Brains were dissected and flash frozen in liquid nitrogen within approximately 2 minutes of removing the male from the experimental tank. We stored the brains in a -80 °C freezer until processing.

PhosphoTRAP

Immunoprecipitation of mRNAs associated with phosphorylated S6 ribosomal subunit allows us to identify the mRNAs being translated in recently active cells. We evaluated immunoprecipitated mRNAs in each sample compared to the total mRNA present in the cell to look for enrichment and suppression.

We prepared phosphoTRAP libraries for immunoprecipitated (IP) and total (TOT) RNA from each individual separately using modified methods described by (Knight et al. 2012) and (Fischer et al. 2019). We homogenized whole in 2-mL beadbug tubes (Sigma-Aldrich, St Louis,

MO, USA) in BeadBug homogenizer buffer for 3 min at 4 °C. We clarified the supernatant by adding 70 µL of 10% NP40 and 70 µL DHPC from 300nM stock per 1.0 mL of supernatant. After clarification, we combined 50 µL of the sample with 350 µL buffer RLT (Qiagen RNeasy Micro kit) and stored at -80°C for our total mRNA (TOT) samples. The rest of the clarified lysate was incubated with Protein A Dynabeads (Invitrogen, Carlsbad, CA, USA) loaded with pS6 antibody (Phospho-S6 (Ser244, Ser247) Polyclonal Antibody; Thermo Fisher Scientific, catalog # 44-923G Invitrogen, Carlsbad, CA, USA) for 10 min at 4 °C and then washed four times with cold 0.35M KCl wash buffer. This immunoprecipitated (IP) RNA was resuspended in buffer RLT from the Qiagen RNeasy Micro kit (Qiagen cat #74004). Both the IP and total RNA were purified with the RNeasy Micro kit before amplification with the SMART-Seq v4 Ultra Low Input RNA Kit for Sequencing (Takara cat# 634896, Mountain View, CA, USA) and library preparation with the Nextera XT DNA Library Prep kit (Illumina, San Diego, CA, USA), both according to manufactures' instructions. For both TOT and IP samples we assumed very low levels of RNA (~10pg), we maximized the amount of sample used to 10.5 µL while preparing our samples for First-strand cDNA synthesis and ran 18 PCR cycles. We normalized our libraries to 0.2ng/µL as measured using a Qubit and then diluted to ~1.5 pM before 100-bp paired end sequencing on Illumina HiSeq 2500. We combined all 24 samples per lane for four lanes.

Analysis

Mapping

We trimmed our data using Trim galore (Krueger 2015) with the Nextera specification. We used FastQC (Andrews 2010) to inspect for any irregularities. We mapped our trimmed reads to the guppy genome (Kunstner et al. 2016) from Ensemble (GCA_000633615.2) using

STAR (Dobin et al. 2013) with BAM specification to get our gene count estimates. We adjusted `outFilterScoreMinOverLread` and `outFilterMatchNminOverLread` in STAR to 0.3 because many of our reads were dropped for being too short and this increased our mapping. One sample had very poor mapping and very few reads using FastQC (Andrews 2010), so we removed it and its paired library from further analysis. This left us with a sample size of n=7 female treatment with 79.7% mapped reads and n=4 control treatment with 82.5% mapped reads. We then used `featureCounts` (Liao et al. 2014) to get our mapped count matrix from the BAM files outputted from STAR. We normalized our IP and Total counts separately with the DESeq2 (Love et al. 2014) package in R (R Core Team, 2019 v. 3.5.1).

GO enrichment and TOT differential expression analyses

We performed a differential expression analysis on our TOT samples using DESeq2 (Love, Huber, & Anders, 2014) and edgeR (Robinson, McCarthy, & Smyth, 2009) in R (R Core Team v. 3.5.1, 2019), with independent filtering and an alpha of 0.05. We then used Shiny GO v0.061 (Ge, Jung, & Yao, 2019) to inspect for GO term enrichment within genes that were found to be differentially expressed at alpha 0.05.

Statistics

To determine how IP counts vary with treatment, while accounting for total mRNA abundances of each gene, we applied a linear model with an offset.

We rounded our IP counts to the nearest whole number to keep them within the assumptions of a negative binomial distribution. We used the `glmmTMB` (Brooks et al. 2017) package in R (R Core Team v. 3.5.1) with a negative binomial distribution. Our model included IP counts as the response variable, treatment as the independent variable, and total RNA counts

as an offset. Using an offset allows us to account for differences in total RNA counts for each gene across brain. We found some opsin and retinal gene contamination, so we removed these genes from our analysis based on key word search within gene descriptions (“opsin” and “retina”). We ran a separate model for each gene and adjusted for multiple hypothesis testing using the *fdr* method in the *p.adjust* package in R (R Core Team, 2019).

Results

PhosphoTRAP

We found 1188 genes significantly enriched (adjusted p value ≤ 0.05) in the courtship context, and we found 1408 genes significantly inhibited. A GO analysis showed no significant enrichment for any groups within our enriched group of genes, however our downregulated genes were significantly enriched across many metabolic processes (table 4.1).

We inspected the annotations of the inhibited and enriched genes to identify genes associated with neuromodulator signaling, then searched for other pathway members in the dataset to examine evidence for groups of related genes. We found evidence downregulation of *gnrh-3* in the mating context, but no other *gnrh* isoforms were differentially expressed (Fig. 4.1). The neuromodulators dopamine (Fig. 4.2) and serotonin (Fig. 4.3) signaling pathways both differentially responded to a reproductive context.

Further inspection of the differentially immunoprecipitated gene lists noted several olfactory receptor genes upregulated in the mating context (Fig. 4.4).

We also investigated neural plasticity because of an *a priori* interest in how male’s first mating experience alters the brain. We found limited evidence of a neural plasticity response based on the expression of a subset of 23 genes we chose from previous RNAseq studies in

teleosts that found differential expression related to social interactions (Bloch et al., 2018; K. Maruska, Soares, Lima-maximino, Henrique de Siqueira-Silva, & Maximinod, 2019; Teles, Cardoso, & Oliveira, 2016; Wang, Ramsey, & Cummings, 2014), with only *neuromod2* enriched and *egr1* and *fosab* reduced in association with activated ribosomes in the presence of a female (Fig. 4.5).

Table 4.1: GO enrichment of significantly down regulated genes

Enrichment FDR	Genes in list	Total genes	Functional Category
0.0002	29	161	Drug metabolic process
0.0050	18	90	Ribonucleoside triphosphate metabolic process
0.0053	18	93	Nucleoside triphosphate metabolic process
0.0055	18	99	Nucleoside monophosphate metabolic process
0.0055	17	89	Purine nucleoside triphosphate metabolic process
0.0055	17	89	Purine ribonucleoside triphosphate metabolic process
0.0055	9	28	Electron transport chain
0.0066	17	93	Purine nucleoside monophosphate metabolic process
0.0066	17	93	Purine ribonucleoside monophosphate metabolic process
0.0100	17	97	Ribonucleoside monophosphate metabolic process
0.0100	15	80	ATP metabolic process
0.0100	17	98	Generation of precursor metabolites and energy
0.0186	4	6	Response to alcohol
0.0186	10	43	Cellular respiration
0.0186	44	407	Carbohydrate derivative metabolic process
0.0230	21	148	Ribonucleotide metabolic process
0.0247	7	23	Oxidative phosphorylation
0.0248	59	607	Small molecule metabolic process
0.0269	20	144	Purine ribonucleotide metabolic process
0.0269	11	56	Energy derivation by oxidation of organic compounds
0.0269	40	371	Organophosphate metabolic process
0.0269	21	154	Ribose phosphate metabolic process
0.0269	5	12	Drug catabolic process
0.0269	30	255	Nucleobase-containing small molecule metabolic process
0.0269	11	55	Proton transmembrane transport
0.0293	22	167	Purine-containing compound metabolic process
0.0336	6	19	Granulocyte differentiation
0.0395	3	4	Response to ethanol
0.0428	17	120	Myeloid cell differentiation
0.0428	5	14	Mitochondrial ATP synthesis coupled electron transport

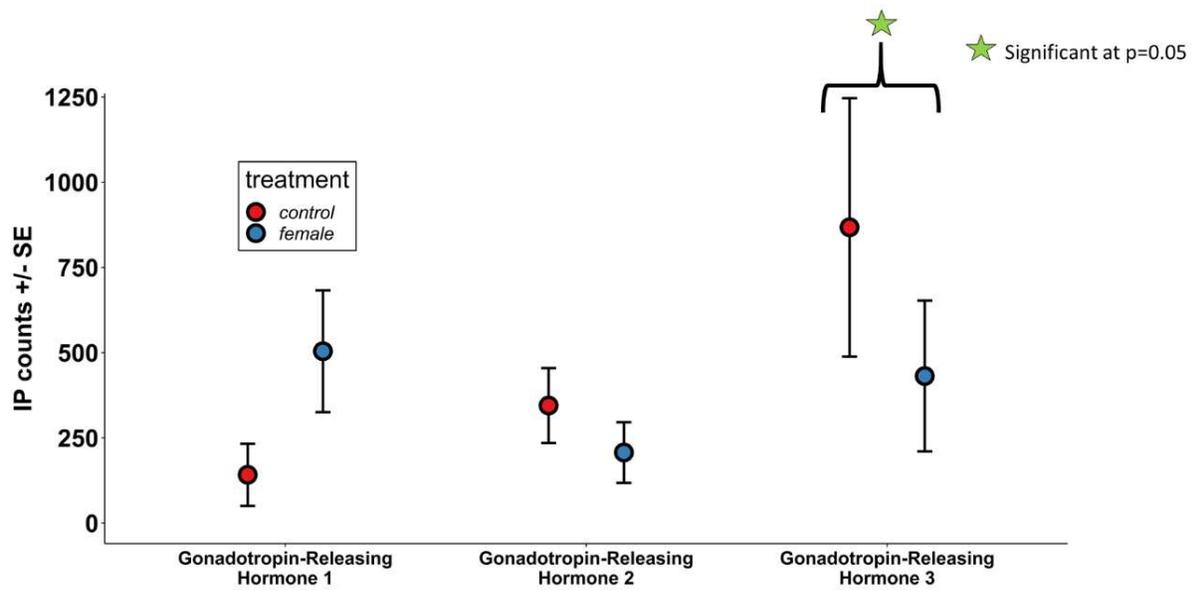


Figure 4.1. Mating influences the association of one GnRH isoforms with active ribosomes. Points indicate average IP counts in brains of males in control (red) and female (blue) treatments. PhosphoTRAP provides evidence that mating context influences *gnrh-3* (FDR adjusted $p=0.0013$) translation, but not other *gnrh* isoforms (*gnrh-1* or *gnrh-2*). Error bars indicate the standard error (SE).

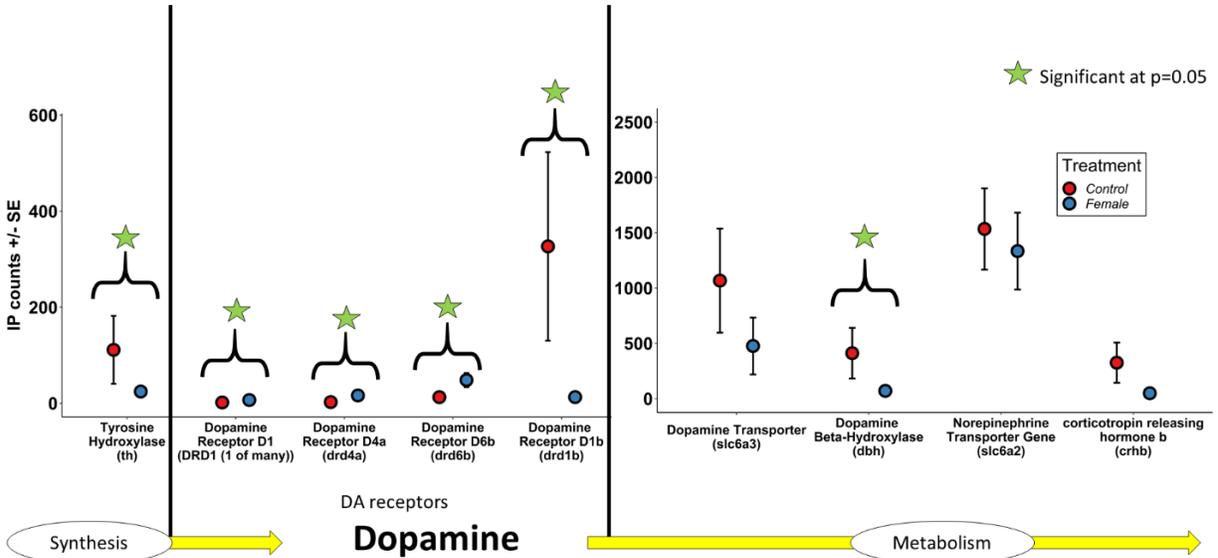


Figure 4.2: Multiple components of the dopamine (DA) pathway are differentially associated with activated ribosomes in the reproductive context compared to the control. Points represent average IP counts in the female (blue) or control (red) treatment for each dopamine-associated gene. PhosphoTRAP results demonstrate strong evidence for synthesis and use of dopamine in a courtship context. Out of eight genes specifically annotated as dopamine receptors three dopamine receptors (*drd1* FDR adjusted $p=0.0077$; *drd4a* FDR adjusted $p=0.0011$; *drd6b* FDR adjusted $p=0.0031$) transcripts are enriched and one was inhibited (*drd1b* FDR adjusted $p<0.0001$) in the female courtship context compared to the solo control context. The enzyme that synthesizes dopamine and norepinephrine, tyrosine hydroxylase, was inhibited (*th* FDR adjusted $p<0.0001$), as was DA Beta-Hydroxylase (*dbh* FDR adjusted $p=0.0143$). Dopamine transporter (*slc6a3*) was not differentially expressed, nor were several genes associated with norepinephrine or other metabolites of dopamine, with *slc6a2* and *crhb* serving as examples. Error bars indicate the standard error (SE).

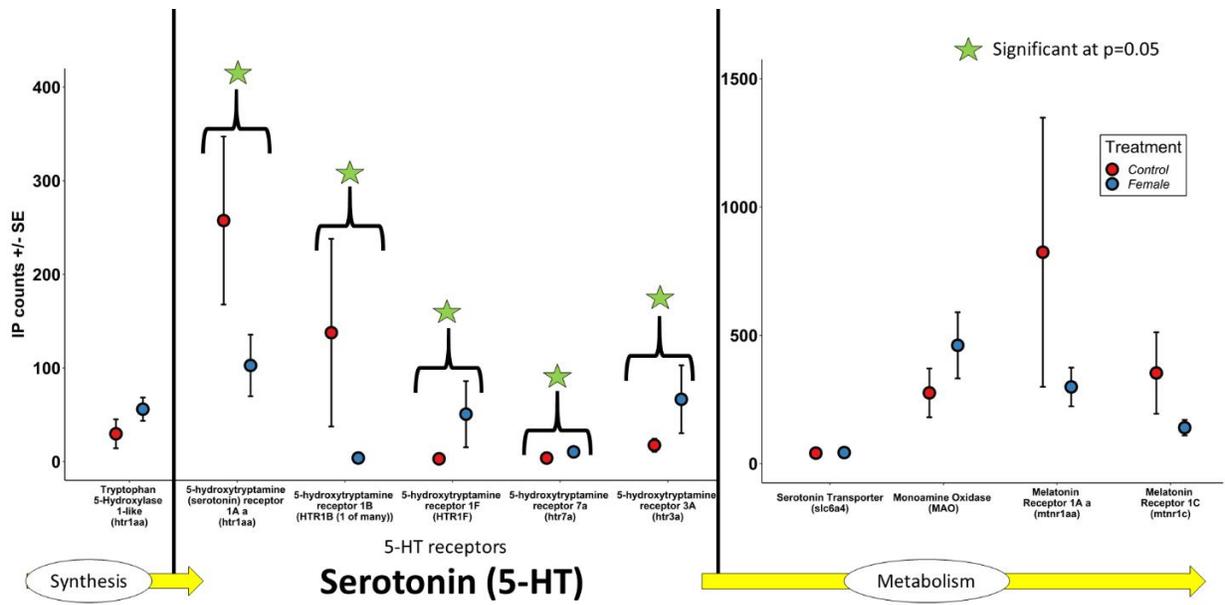


Figure 4.3: Multiple components of the serotonin (5-HT) pathway show enriched or reduced association with active ribosomes in the reproductive context. Points represent average IP counts of genes from the 5-HT pathway in mating (blue) and control (red) contexts. Of 19 genes specifically annotated as 5-HT receptors, two serotonin receptor transcripts were inhibited in the courtship context (*htr1aa* FDR adjusted $p=0.0003$ and *htr1b* FDR adjusted $p=0.0014$), and three serotonin receptor transcripts enriched in the courtship context (*htr1f* FDR adjusted $p=0.0042$, *htr7a* FDR adjusted $p=0.0070$, and *htr3a* FDR adjusted $p=0.0446$). Other components of the 5-HT pathway were not differentially expressed. Tryptophan 5-hydroxylase 1-like, MAO, and two out of the four melatonin receptor genes are graphed for examples. Tryptophan 5-hydroxylase 1-like was the only ortholog of tryptophan 5-hydroxylase in our list of expressed genes. Error bars indicate the standard error (SE)

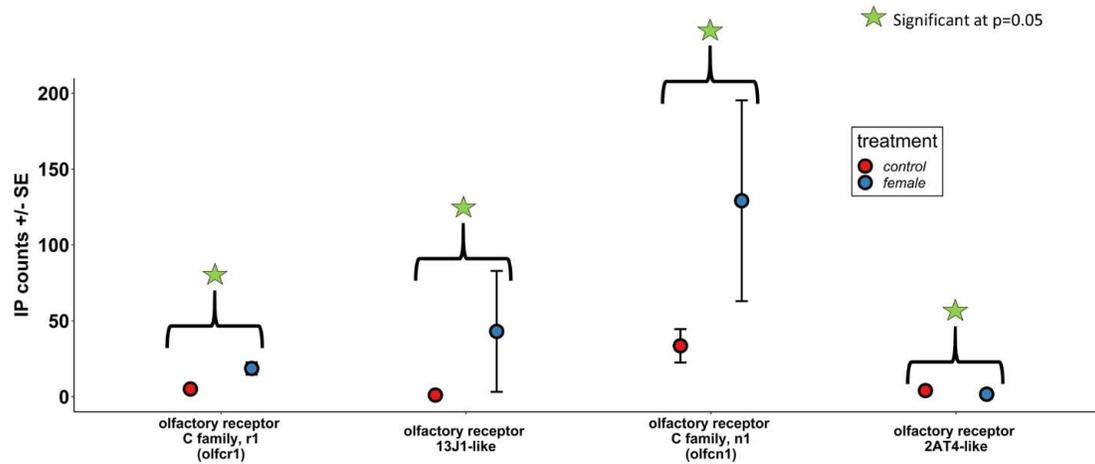


Figure 4.4. Average IP counts of four olfactory receptor genes are differentially associated with active ribosomes in female vs. control treatments. Out of 38 genes annotated as olfactory receptors, three olfactory receptors were significantly enriched (*olfcr1* (FDR adjusted $p=0.0006$), OR 13J1-like (FDR adjusted $p=0.0324$), *olfcn1* (FDR adjusted $p=0.0430$)) while one was inhibited (OR 2AT4-like (FDR adjusted $p=0.0008$)). No other olfactory-associated genes in our analysis were significantly differentially expressed between treatments. Error bars indicate the standard error (SE)

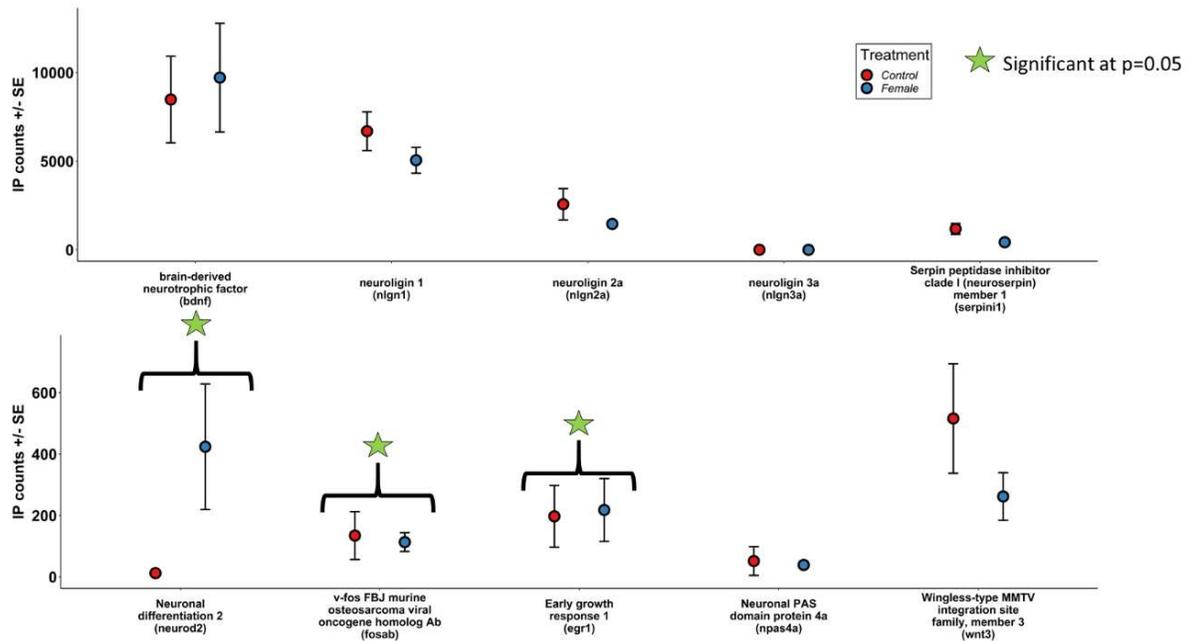


Figure 4.5: We chose a subset of 23 genes that have been previously implicated in neural activity during social interactions in teleost fish (Bloch et al., 2018; K. Maruska et al., 2019; Teles et al., 2016; Wang et al., 2014) to investigate translation in acute courtship context (Table below). Points represent the average IP counts of each gene in the female (blue) or control (red) treatment. Our phosphoTRAP results show *neurod2* was enriched (FDR adjusted $p=0.0001$), whereas *fosab* (FDR adjusted $p=0.0423$) and *egr1* (FDR adjusted $p=0.0001$) were inhibited in the reproductive context. However, none of the other twenty genes differed between treatments. Error bars indicate the standard error (SE).

Table 4.2: Complete list of 23 gene names and descriptions of neural plasticity associated genes we chose for analysis. Significance is noted with *.

Gene	Full name from citation	Citation	PhosphoTRAP analysis gene	Guppy annotation description	estimate	FDR_A djP	*Sig
bdnf	brain-derived neurotrophic factor	Teles et al. 2016, Bloch et al. 2018	bdnf	brain-derived neurotrophic factor	-0.2923	0.6913	
npas4	neuronal PAS domain protein 4a	Teles et al. 2016	npas4a	neuronal PAS domain protein 4a	-1.1678	0.2101	
nlgn1	neuroligin 1	Teles et al. 2016	nlgn1	neuroligin 1	-0.4393	0.3058	
nlgn2	neuroligin 2	Teles et al. 2016	nlgn2a	neuroligin 2a	-0.6155	0.1026	
			nlgn2b	neuroligin 2b	-0.3424	0.6913	
nlgn3	neuroligin 3	Wong and Cummings 2014	nlgn3a	neuroligin 3a	-2.2162	0.3701	

			nlgn3b	neuroligin 3b	-0.3900	0.6561	
wnt3	wingless-type MMTV integration site family, member 3	Teles et al. 2016	wnt3	wingless-type MMTV integration site family, member 3	-0.3859	0.7583	
neurod1	neuronal differentiation 1	Teles et al. 2016	neurod1	neuronal differentiation 1	0.3433	0.5894	
neurod2	neuronal differentiation 2	Bloch et al. 2018	neurod2	neuronal differentiation 2	5.1931	0.0001	*
egr1	egr-1	Wang et al. 2014	egr1	early growth response 1	-5.1660	0.0001	*
egr2b		Bloch et al. 2018	egr2b	early growth response 2b	0.6711	0.6270	
neuroserpin		Wang et al. 2014	serpini1	serpin peptidase inhibitor, clade I (neuroserpin), member 1	-1.1983	0.0942	
early B		Wang et al. 2014	NA	NA	NA	NA	
grin1		Bloch et al. 2018	grin1a	glutamate receptor, ionotropic, N-methyl D-aspartate 1a	-0.6575	0.3564	
march8		Bloch et al. 2018	march8	membrane-associated ring finger (C3HC4) 8	-0.6238	0.3852	
thoc6		Bloch et al. 2018	thoc6	THO complex 6	2.6363	0.0575	
cant1		Bloch et al. 2018	cant1a	calcium activated nucleotidase 1a	-0.9974	0.4708	
			cant1b	calcium activated nucleotidase 1b	-1.4080	0.0412	
thap6		Bloch et al. 2018	thap6-like	THAP domain-containing protein 6-like	1.8965	0.1451	
smarcc1		Bloch et al. 2018	smarcc1b	SWI/SNF related, matrix associated, actin dependent regulator of chromatin, subfamily c, member 1b	1.9871	0.0865	
c-fos		Bloch et al. 2018	fosab	v-fos FBJ murine osteosarcoma viral oncogene homolog Ab	-2.1119	0.0423	*
inhba		Bloch et al. 2018	inhbaa	inhibin subunit beta Aa	2.4572	0.1067	

Of these 58 differentially expressed genes, 25 were also enriched or inhibited in the phosphoTRAP analysis of actively translated genes. None of the neurotransmitters, olfactory receptors, or hormones we found with our analysis were present in the total mRNA analysis results. One neuropeptide was unique to the DE analysis of the total mRNA. Isotocin (fish homolog to oxytocin, Urano and Ando 2011, but annotated as oxytocin in guppy genome) was upregulated in total mRNA from brains of males in reproductive contexts compared to isolated males ($\log_2\text{FoldChange}=3.363$, Adjusted $P=0.0089$) but was not enriched in phosphorylated ribosomes (FDR adjusted $p=0.7689$) (Fig.4.7). None of the associated receptors were enriched in either the total mRNA analysis or the phosphoTRAP analysis (not shown). A GO analysis of the genes implicated by the total mRNA analysis found no enrichment in the downregulated genes, but upregulated genes were enriched for genes annotated as involved in endosomal transport (enrichment FDR = 0.019).

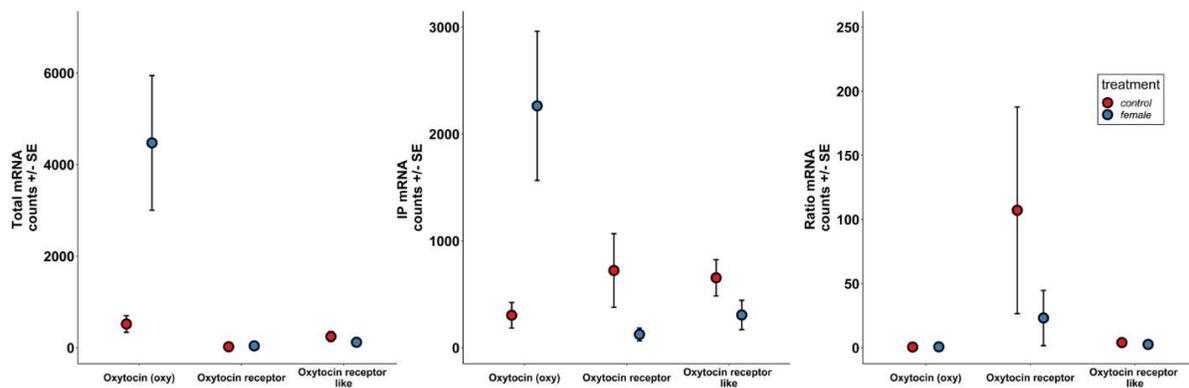


Figure 4.7: Analyses of differential expression based on total mRNA and differential association with activated ribosomes based on IP mRNA differed dramatically. We use the three isotocin (annotated as oxytocin) related annotated genes as an example to demonstrate how phosphoTRAP results differ from those using the standard total mRNA procedure. Points represent X. DEseq2 found *oxy* was enriched in the presence of a female (adjusted $p=0.008932$), however analysis of the IP dataset did not find this pattern. None of the other isotocin-related genes were differentially expressed or differentially translated. Error bars indicate the standard error (SE)

Table 4.4: Annotation and statistics of the 58 differentially expressed genes from standard analysis on total mRNA counts

Gene ID	Gene description	Gene name	Base Mean	log2FoldChange	lfcSE	stat	P value	P adj
ENSPREG00000000445	O-GlcNAcase like [Source:ZFIN;Acc:ZDB-GENE-110914-153]	ogal	67.06623	3.834453	0.95097	4.032147	5.5E-05	0.0260
ENSPREG00000000867	cocaine- and amphetamine-regulated transcript protein-like [Source:NCBI gene;Acc:103463151]		15.16946	-4.89501	1.276671	-3.8342	1.3E-04	0.0424
ENSPREG00000001428			511.8039	2.437734	0.584314	4.17196	3.0E-05	0.0164
ENSPREG00000002445	nebulin [Source:ZFIN;Acc:ZDB-GENE-041111-216]	neb	405.1105	-2.68185	0.598909	-4.47789	7.5E-06	0.0089
ENSPREG00000002783			27.94798	-4.90854	1.018637	-4.81873	1.4E-06	0.0042
ENSPREG00000003156	7-dehydrocholesterol reductase [Source:ZFIN;Acc:ZDB-GENE-030912-9]	dher7	142.5885	4.490723	1.136548	3.951196	7.8E-05	0.0307
ENSPREG00000003547			94.87593	-3.4573	0.825024	-4.19055	2.8E-05	0.0161
ENSPREG00000004093	cytochrome P450 2J2-like [Source:NCBI gene;Acc:103461257]		26.39795	4.062684	0.951751	4.268642	2.0E-05	0.0132
ENSPREG00000004283			32.55229	-5.09566	1.107914	-4.59932	4.2E-06	0.0063
ENSPREG00000004346	SPARC-like 1 [Source:ZFIN;Acc:ZDB-GENE-060130-6]	sparcl1	82.99195	-4.32681	0.791164	-5.46892	4.5E-08	0.0005
ENSPREG00000004985	Rap guanine nucleotide exchange factor (GEF) 4 [Source:ZFIN;Acc:ZDB-GENE-070912-385]	rapgef4	98.07617	-2.30537	0.580281	-3.97285	7.1E-05	0.0289
ENSPREG00000005383	claudin domain-containing protein 1-like [Source:NCBI gene;Acc:103466270]		31.30653	-3.60941	0.950693	-3.79661	1.5E-04	0.0481
ENSPREG00000006048	large 60S subunit nuclear export GTPase 1 [Source:ZFIN;Acc:ZDB-GENE-030131-2184]	lsg1	65.52384	-3.08821	0.775104	-3.98426	6.8E-05	0.0287

ENSPREG0000007166			16.79196	-6.43876	1.6036 11	- 4.01516	5.9E-05	0.026 5
ENSPREG0000007386	interphotoreceptor matrix proteoglycan 2a [Source:ZFIN;Acc:ZDB-GENE-140106-217]	impg 2a	59.67544	-4.04981	0.8189 93	- 4.94486	7.6E-07	0.004 0
ENSPREG0000008338	Usher syndrome 1Gb (autosomal recessive) [Source:ZFIN;Acc:ZDB-GENE-110411-55]	ush1g b	44.39008	4.474488	1.1477 28	3.89856 1	9.7E-05	0.036 4
ENSPREG0000008506	complement C1q like 2 [Source:HGNC Symbol;Acc:HGNC:24181]	C1QL 2	17.45493	-4.57727	1.2141 36	- 3.76998	1.6E-04	0.049 0
ENSPREG0000009163	transmembrane channel-like 2b [Source:ZFIN;Acc:ZDB-GENE-060526-262]	tmc2b	29.27362	-4.96778	1.1414 13	- 4.35231	1.4E-05	0.010 6
ENSPREG0000009658			10.39886	-6.64644	1.5378 99	- 4.32176	1.6E-05	0.011 2
ENSPREG0000010057	sarcoglycan, alpha [Source:ZFIN;Acc:ZDB-GENE-041111-121]	sgca	24.03822	-4.65674	1.0512 55	- 4.42969	9.4E-06	0.009 0
ENSPREG0000010110	STT3 oligosaccharyltransferase complex catalytic subunit A [Source:ZFIN;Acc:ZDB-GENE-021015-3]	stt3a	491.0396	3.37501	0.8903 19	3.79078 9	1.5E-04	0.048 4
ENSPREG0000010133	cyclin Pas1/PHO80 domain containing 1 [Source:ZFIN;Acc:ZDB-GENE-030131-6808]	cnppd 1	145.571	4.150717	0.8769 39	4.73319	2.2E-06	0.004 7
ENSPREG0000010221	transmembrane p24 trafficking protein 8 [Source:ZFIN;Acc:ZDB-GENE-050522-283]	tmed8	12.92463	-5.75931	1.2190 31	-4.7245	2.3E-06	0.004 7
ENSPREG0000010432	transmembrane serine protease 2 [Source:ZFIN;Acc:ZDB-GENE-041212-48]	tmprs s2	43.78091	-3.48215	0.7117 14	- 4.89262	1.0E-06	0.004 0
ENSPREG0000011072	cytidine and dCMP deaminase domain containing 1 [Source:ZFIN;Acc:Z	cdadc 1	51.6278	-2.14516	0.5516 51	- 3.88863	1.0E-04	0.036 5

	DB-GENE-041114-163]							
ENSPREG00000011166	leupaxin [Source:ZFIN;Acc:Z DB-GENE-081105-159]	lpxn	38.15928	-4.0665	0.8828 41	- 4.60615	4.1E-06	0.006 3
ENSPREG00000011461	DP-Gal:betaGlcNAc beta 1,4- galactosyltransferase, polypeptide 1, like [Source:ZFIN;Acc:Z DB-GENE-061013-84]	b4galt 11	16.68767	4.553028	1.0881 52	4.18418 2	2.9E-05	0.016 1
ENSPREG00000012860			44.00956	5.542407	1.1756 67	4.71426 6	2.4E-06	0.004 7
ENSPREG00000012923	tRNA methyltransferase 11 homolog [Source:ZFIN;Acc:Z DB-GENE-040426-953]	trmt1 1	75.13262	-2.69165	0.6328 05	- 4.25352	2.1E-05	0.013 6
ENSPREG00000012964	sorting nexin 1a [Source:ZFIN;Acc:Z DB-GENE-060302-3]	snx1a	276.0051	2.86428	0.7212 53	3.97125 5	7.2E-05	0.028 9
ENSPREG00000013866			615.9158	-5.42776	1.2853 37	- 4.22283	2.4E-05	0.014 5
ENSPREG00000014084	Jupiter microtubule associated homolog 2 [Source:ZFIN;Acc:Z DB-GENE-030131-599]	jpt2	51.03078	3.53409	0.7993	4.42148	9.8E-06	0.009 0
ENSPREG00000014205	leucine rich repeat containing 4.2 [Source:ZFIN;Acc:Z DB-GENE-030131-7997]	lrrc4. 2	17.10721	5.347313	1.3310 98	4.01722	5.9E-05	0.026 5
ENSPREG00000014342			23.43104	-6.51967	1.2039 75	- 5.41512	6.1E-08	0.000 5
ENSPREG00000015204	oxytocin [Source:ZFIN;Acc:Z DB-GENE-030407-1]	oxt	2723.751	3.363347	0.7518 81	4.47324 3	7.7E-06	0.008 9
ENSPREG00000015940			44.46881	-3.65655	0.8964 78	-4.0788	4.5E-05	0.023 9
ENSPREG00000016768			13.65347	3.205351	0.7936 67	4.03866 1	5.4E-05	0.026 0
ENSPREG00000016818	WD repeat and coiled coil containing [Source:ZFIN;Acc:Z DB-GENE-050320-107]	wdcp	16.64106	3.848816	0.9946 95	3.86934 5	1.1E-04	0.038 7
ENSPREG00000017457	Niemann-Pick disease, type C1 [Source:ZFIN;Acc:Z	npc1	111.7457	-2.66475	0.7055 38	-3.7769	1.6E-04	0.049 0

0017116	DB-GENE-030131-3161]								
ENSPREG00000017617	excision repair cross-complementation group 6-like [Source:ZFIN;Acc:ZDB-GENE-060531-56]	ercc6l	36.22626	-5.0277	1.0942	-4.59486	4.3E-06	0.0063	
ENSPREG00000018387	RUNX family transcription factor 1 [Source:ZFIN;Acc:ZDB-GENE-000605-1]	runx1	60.08406	-3.24593	0.833499	-3.89434	9.9E-05	0.0364	
ENSPREG00000018718	Rh family, B glycoprotein (gene/pseudogene) [Source:ZFIN;Acc:ZDB-GENE-030131-9542]	rhbg	45.58263	2.884367	0.75254	3.832842	1.3E-04	0.0424	
ENSPREG00000019537	v-fos FBJ murine osteosarcoma viral oncogene homolog Ab [Source:ZFIN;Acc:ZDB-GENE-031222-4]	fosab	404.6991	2.235675	0.488885	4.573008	4.8E-06	0.0064	
ENSPREG00000019587	zgc:123010 [Source:ZFIN;Acc:ZDB-GENE-051120-15]	zgc:123010	33.1013	-2.88308	0.680349	-4.23766	2.3E-05	0.0140	
ENSPREG00000019819	sodium/bile acid cotransporter-like [Source:NCBI gene;Acc:103458516]		17.56083	5.676285	1.308342	4.338531	1.4E-05	0.0108	
ENSPREG00000019889			19.69592	-4.81813	1.080659	-4.45851	8.3E-06	0.0090	
ENSPREG00000020088	centrosomal protein 135 [Source:ZFIN;Acc:ZDB-GENE-041210-325]	cep135	56.97199	-3.51126	0.867148	-4.04921	5.1E-05	0.0255	
ENSPREG00000020339			63.58572	-4.1675	0.968554	-4.3028	1.7E-05	0.0117	
ENSPREG00000020970	centrosomal protein 72 [Source:ZFIN;Acc:ZDB-GENE-101115-1]	cep72	30.34562	-3.87349	0.951593	-4.07053	4.7E-05	0.0240	
ENSPREG00000021530	transgelin 2 [Source:ZFIN;Acc:ZDB-GENE-020802-2]	tagln2	153.0422	4.704455	1.244625	3.779817	1.6E-04	0.0490	
ENSPREG00000021530	ADP-ribosylhydrolase like 1	adprh11	15.05779	-3.76326	0.854604	-4.40352	1.1E-05	0.0093	

0021533	[Source:ZFIN;Acc:ZDB-GENE-041010-126]								
ENSPREG00000022045	microcephalin 1 [Source:ZFIN;Acc:ZDB-GENE-060421-6122]	mcp1	117.3825	-2.45829	0.613247	-4.00864	6.1E-05	0.0266	
ENSPREG00000022531	histone-lysine N-methyltransferase SETDB2 [Source:NCBI gene;Acc:103457816]		95.66055	3.205781	0.835707	3.836011	1.3E-04	0.0424	
ENSPREG00000022625	trypsin-like [Source:NCBI gene;Acc:103464362]		10.12603	-5.84052	1.548449	-3.77185	1.6E-04	0.0490	
ENSPREG00000022647	FA complementation group E [Source:ZFIN;Acc:ZDB-GENE-060510-5]	fance	37.9931	-4.26726	1.087323	-3.92455	8.7E-05	0.0336	
ENSPREG00000022680	methylcrotonoyl-CoA carboxylase 1 (alpha) [Source:ZFIN;Acc:ZDB-GENE-050208-450]	mccc1	29.4975	3.524665	0.807767	4.36347	1.3E-05	0.0106	
ENSPREG00000022788			11.05897	-5.29546	1.197702	-4.42135	9.8E-06	0.0090	
ENSPREG00000023184	glycine cleavage system protein H (aminomethyl carrier), b [Source:ZFIN;Acc:ZDB-GENE-040718-319]	gcsb	63.58647	5.767225	1.185871	4.863283	1.2E-06	0.0040	

Discussion

This study provides a well-rounded picture of many interacting neural systems activated during a mating opportunity. Neuromodulators influence a wide range of reproductive behaviors (e.g. Chen & Hong, 2018; Gil, Bhatt, Picotte, & Hull, 2011; McKinsey, Ahmed, & Shah, 2018; Shahjahan, Kitahashi, & Parhar, 2014; Yang & Shah, 2014). Our results highlight dopaminergic and serotonergic systems in males' responses to females, as well as potentially important olfactory responses in a mating context. The coordinated responses of multiple components of

specific signaling pathways to mating opportunities provide strong evidence that specific cell groups are strongly modulated during mating. This contrasts with the differential expression patterns from the total mRNA samples, which had few differentially expressed genes and no evidence for widespread expression changes related to specific cell types. Our results provide a holistic look at multiple systems that may play a role in acute responses to reproductive contexts.

Our study measures mRNAs bound to recently activated ribosomes to identify neural cell groups activated in a reproductive context. PhosphoTRAP differs from standard mRNA studies in how dynamic changes in gene expression are captured. Social interactions elicit very different gene expression patterns across timescales (Bukhari et al., 2017). The analysis with total mRNA found only found 58 differentially expressed genes between reproductive context and our control, and 33 of these genes were unique in comparison to the phosphoTRAP analysis. Previous studies of the differential expression of genes in reproductive contexts researcher typically find more than 150 DE genes (e.g. Bloch et al., 2018; Tripp, Feng, & Bass, 2018), although occasionally researchers identify fewer than 50 DE genes associated with mating (e.g. Ellis & Carney, 2010). A major difference between these DE studies, other than the taxa, is the time point when samples were taken. Studies range from 10 min (e.g. Bloch et al. 2018) and 30 min (Tripp et al. 2018) to over 2 hours (e.g. Ellis and Carney 2010) after experiences. Gene expression depends on external cues and intrinsic molecular properties of specific genes (De Jong, Moshkin, & Guryev, 2019). Acute transcriptional responses to experiences can be difficult to interpret because they may be span a gradient of slow and fast time courses (Rittschof & Hughes, 2018). Therefore, the time point at which a study occurs has direct influence on the expression profiles measured and may explain why analysis of the total mRNA in our study revealed few DE genes. In contrast, phosphoTRAP leverages the short term (ca. 30-90 minute)

(e.g. Baran & Streelman, 2020; Fischer, Westrick, Hartsough, & Hoke, 2018; Knight et al., 2012) phosphorylation of ribosomal proteins in active neurons to identify which proteins are being translated (Knight et al. 2012). Phosphorylation of the S6 ribosomal subunit depends on biochemical stimulation such as the secondary messenger cascades that typify responses to neuromodulator or metabotropic neurotransmitter receptor binding (Biever, Valjent, & Puighermanal, 2015; Knight et al., 2012). Hence, phosphoTRAP identifies transcripts in a specific subset of highly active neurons, allowing us unique insights into cell groups participating in behavior. Our phosphoTRAP results identify functionally similar transcripts and multiple pathway components responding, providing confidence in our interpretation of transcript dynamics as reflecting specific neural responses in male guppies to a reproductive context.

Gonadotropin releasing hormone (GnRH) is implicated across vertebrates in reproductive functions from maturation of gametes to reproductive behaviors (Umatani & Oka, 2019). Extensive research has identifies three isoforms of GnRH, with teleosts having two or three forms, each with unique distributions in the brain and specific influence on behaviors (reviewed in Hofmann, 2006). When all three isoforms are present in a fish, GnRH-1 is predominantly located in the preoptic area with a major role in the hypophysiotropic control of reproduction (reviewed in Abe & Oka, 2011; Hofmann, 2006). GnRH-2 and GnRH-3 are located in the midbrain tegmentum and the terminal nerve (TN) respectively (reviewed in Abe & Oka, 2011; Hofmann, 2006), and have received a considerable amount of attention for their potential non-hypophysiotropic role in influencing reproductive behaviors (Abe & Oka, 2011; Umatani & Oka, 2019). We found no differences in *gnrh-1* nor *gnrh-2* between treatments, but *gnrh-3* association with phosphorylated ribosomes was reduced in the reproductive context (Fig. 4.1). GnRH-3 in

the TN (TN-GnRH3) modulates multiple sensory systems including visual, olfactory, and somatosensory processing centers (Umatani & Oka, 2019). TN-GnRH3 alters visual processing through suppression of membrane excitability in the retino-tectal pathway (Umatani et al. 2015). GnRH from the TN has also increases the excitability of olfactory receptors neurons (Eisthen et al., 2000; Kawai, Abe, Akazome, & Oka, 2010). Behavioral data suggest TN-GnRH3 may have strong influences on not only mating behaviors but also other motivational state dependent behaviors (Karigo & Oka, 2013). We cannot confirm the direct role of inhibition of *gnrh-3* in our study, but the enrichment of several olfactory receptors in males in a reproductive context (Fig. 4.4) suggests *gnrh-3* might interact with olfactory processing. GnRH isoforms are linked to many other neuromodulatory systems (Karigo & Oka, 2013; Prasad, Ogawa, & Parhar, 2015; Umatani & Oka, 2019), with still unanswered questions specifically about the interaction between dopaminergic interplexiform cells and TN-GnRH3 neurons (Abe & Oka, 2011). The GnRH-3 response to reproductive contexts we have described warrants further study into possible functions of *gnrh-3* in courtship and mating behaviors.

Dopamine is a highly conserved neuromodulator in form and function that is present in many taxa and is synthesized directly in the brain (reviewed in Dufour et al., 2019). The dopaminergic pathway is defined by the D1 and D2 family of receptors, where D1 family is excitatory and D2 is inhibitory. Several D2 receptor subtypes may act as potential autoreceptors (D2, D3, and D4), but the strongest evidence based on studies in mice is that D2 acts as an autoreceptor (reviewed in Sulzer, Zhang, Benoit-Marand, & Gonon, 2010). The rate-limiting enzyme of dopamine biosynthesis is tyrosine hydroxylase (TH), and regulation of DA comes in the modulation of synthesis, reuptake by *slc6a3* (DAT), and storage (reviewed in Sulzer et al. 2010). The primary enzyme needed for DA metabolism is dopamine beta-hydroxylase (dbh),

which is the rate limiting step between DA and norepinephrine synthesis (Joh & Hwang, 1987). In bony fish DA has 9 subtypes with D1 family receptors include subtypes D1, D5, D6, and D7 and D2 family include subtypes D2, D3, D4, D8, and D9 (Yamamoto, Fontaine, Pasqualini, & Vernier, 2015). Dopamine (DA) is commonly associated with social decision-making and reward responses (Braver et al., 2014; Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Schroeder & Ritters, 2006). We found an inhibition of TH and DBH in the presence of female (Fig. 4.3), but recycling and reuptake of DA has been shown to play a strong role in the maintenance of usable DA (reviewed in Sulzer et al. 2010), so these decreases may not be entirely surprising. Out of 8 annotated DA receptor genes, we found enrichment of three dopamine receptor subtypes (D1, D4a, and D6b), and the inhibition of D1b in the reproductive context treatment of males (Fig. 4.2). The enrichment of D1 and D6b imply increased excitatory properties of some dopaminergic pathways, while the enrichment of D4a and inhibition of D1b demonstrate the modulation and down regulation of other components of the DA pathway. DA properties are highly specific to brain regions they are in (see O'Connell & Hofmann, 2011), so it is unsurprising that we are seeing both excitatory and inhibitory properties in the DA pathway response to a reproductive context by analyzing a whole brain.

DA also has complex interactions with other receptors types as putative heteroreceptors (e.g. GABA(B)(Sulzer et al. 2010) and GnRH-1(S. Dufour, Sebert, Weltzien, Rousseau, & Pasqualini, 2010; Sylvie Dufour et al., 2019, 2005). DA is linked as a key regulator of male sexual behaviors in mice and mammals (reviewed in Sylvie Dufour et al., 2019; Hull, Muschamp, & Sato, 2004), birds (Schroeder & Ritters, 2006), amphibians (Creighton et al., 2013), insect (S. X. Zhang et al., 2016) and teleosts (S. Dufour et al., 2010; Ghahramani, Timothy, Varughese, Sisneros, & Forlano, 2018). Our results further supported the role of cells

in line with previous studies (e.g. Ghahramani et al., 2018; Monier, Nöbel, Danchin, & Isabel, 2019; Zhang et al., 2016). DA generally is considered to have an inhibitory role in reproductive functions across taxa through inhibition of GnRH (reviewed in Dufour et al. 2019), but also has important excitatory functions for motivated behaviors and reinforcement learning as you would see in courtship contexts (reviewed in Scaplen & Kaun, 2016). Future work will help disentangle how D1 and D2 families of receptors are influencing behaviors while interacting with other neuromodulators like *gnrh3* and serotonin.

Serotonin is also a neuromodulator that is highly conserved in form and function across many taxa (Herculano & Maximino, 2014; reviewed in Nichols & Nichols, 2008). Vertebrates have seven recognized 5-HT receptor subtypes (Bockaert, Claeysen, Dumuis, & Marin, 2010; Katz & Lillvis, 2014; Nichols & Nichols, 2008). Functional studies are largely limited to mammalian models, despite complex receptor-specific physiological responses in fish bodies and brains (e.g. Velarde, Delgado, & Alonso-Gómez, 2010). Serotonin synthesis is limited by the enzyme tryptophan hydroxylase, and removal of tryptophan hydroxylase reduces serotonin driven behaviors in diverse taxa (Scaplen & Kaun, 2016). We found no difference between treatments in expression of tryptophan hydroxylase (annotated as tryptophan 5-hydroxylase 1-like), but we did find differential expression of genes associated with several serotonin receptors. We found reduced binding of 5-HT1a and 5-HT1B mRNA with phosphorylated ribosomes. 5-HT1a and 5-HT1B receptors have been found to act as autoreceptors and inhibit 5-HT release in mammals (Adell et al., 2010; Nichols & Nichols, 2008; Sharp, 2010) and at least one teleost (Norton, Folchert, & Bally-Cuif, 2008), however this inhibitory role may be brain-region and cell-specific (reviewed in Barnes & Sharp, 1999). We also found enrichment of 5-HT1F, 5-HT7a, and 5-HT3a receptors in the presence of females (Fig. 4.3). Receptors 5-HT1F, 5-HT7a,

and 5-HT_{3a} are implicated with release and response to serotonin in mammals (Barnes & Sharp, 1999; Bockaert et al., 2010). Specifically, 5-HT_{3a} has been identified as a potential heteroreceptor that may regulate non 5-HT neurotransmitter release (Barnes and Sharp, 1999). We found no differences in the primary serotonin transporter (*slc6a4*) nor in the primary metabolizing enzyme monoamine oxidase (MOA). Serotonin is metabolized to melatonin, which is known to influence reproduction and behavioral responses in teleosts (Falcón, Migaud, Muñoz-Cueto, & Carrillo, 2010), but we found no evidence for responses by melatonin receptor genes.

Serotonin has been associated with social behaviors including aggression and parental behaviors (Filby, Paull, Hickmore, & Tyler, 2010), reproduction (Sylvie Dufour et al., 2019; Hull et al., 2004), and is associated with social hierarchy status (Loveland, Uy, Maruska, Carpenter, & Fernald, 2014; Prasad et al., 2015; Teles, Dahlbom, Winberg, & Oliveira, 2013). Serotonin is also implicated in social learning (Soares, Paula, & Bshary, 2016), and neural plasticity in this system that indicate rapid changes in receptor presence or cell numbers in response to acute social contexts (Loveland et al., 2014). Serotonin pathways have received increased attention as a potential region of effects by selective serotonin reuptake inhibitor (SSRI) pollutants in water ways on important behaviors, such as aggression and foraging (Kreke & Dietrich, 2008; León-Olea et al., 2014) and courtship strategies (Fursdon, Martin, Bertram, Lehtonen, & Wong, 2019). Serotonin has been shown to interact with many other neuromodulatory pathways, including GnRH (Sylvie Dufour et al., 2019; Groves & Batten, 1986) and DA (Adell et al., 2010; Sylvie Dufour et al., 2019; Monier et al., 2019). Future work is needed to confirm evolutionary relationships between these receptors across vertebrates and their roles in behavior (Prasad et al., 2015). Our results demonstrate an intriguing clue that serotonin

plays a role in responses by males to a reproductive context. Future studies should investigate the time course and potential downstream effects of altered 5-HT receptor abundances within the 5-HT pathway as well as potential interacting pathways.

Neural plasticity includes processes such as synaptogenesis, neurogenesis, biochemical switches, and changes in the sensitivity of the neurons that alter the brain in response to experience (Sweatt, 2016). Specifically, plasticity within the brain structures and functions in fish allows updating or learning of behavioral strategies in novel environments (Salvanes et al., 2013) and social contexts (K. Maruska et al., 2019; Teles et al., 2016), and in some cases repair to neural systems after damage (Ghosh & Hui, 2016). There are many genes associated with different aspects of neural plasticity, for example neurotrophins are responsible for regulating many neural plasticity processes (Levy et al., 2018). However, there are over 2,000 genes annotated a some type of neurotrophic factor alone in the guppy genome (<https://uswest.ensembl.org/>), and the full list of genes related to neural plasticity in guppies is unknown. In order to narrow down the scope of potential genes associated with neural plastic we chose to use a subset with promising responses to social stimuli specifically in teleosts. Teles et al. (2016) found that *bdnf*, *npas4*, *nlgn1*, *nlgn2*, *wnt3*, and *neurod1* showed different expression depending on social hierarchy and aggression experiences, Wong and Cummings (2014) found *nlgn3* had high expression in some brain regions in the presence of mate choice by females (Wong & Cummings, 2014), Wang et al (2014) found expression patterns of *egr-1*, *neuroserpin*, and *early B* in females were associated with mating strategies by males, and Bloch et al. (2018) found that *grin1*, *march8*, *bdnf*, *thoc6*, *cant1*, *thap6*, *inhba*, *neurod2*, *smarcc1*, *egr2b* and *c-fos* were differentially expressed between social contexts. We found no differential expression in a reproductive context in most of these genes (Fig. 4.5). However, we did find high enrichment of

neurod2 but reduced associations with active ribosomes of *egr-1* and *fosab* (encodes for *c-fos*) in our reproductive context. The *neurod2* gene facilitates neurogenesis by increasing differentiation in zebrafish (Ghosh & Hui, 2016), and increased in a mating context with a colorful male regardless of preference in female guppies (Bloch et al., 2018). The genes that had reduced associations are both examples of immediate early genes (IEGs) or transcription factors that can influence expression of other downstream genes (reviewed in Oliveira 2012), and also commonly found to have associations with neural plasticity (*egr1* (Wang et al., 2014) and *c-fos* (R. F. Oliveira, 2012)), but also aggression and stress responses (e.g. Malki et al., 2016; Matsumoto, Ono, Ouchi, Tsushima, & Murakami, 2012; Oliveira, 2012; Rodriguez-Barreto et al., 2019). One possible reason we did not identify more robust neuroplasticity patterns is because brain regions differ in the expression of these genes (e.g. K. P. Maruska, Becker, Neboori, & Fernald, 2013) and hence our whole-brain studies may have precluded discovery of plasticity-related genes. Nonetheless, our results show differential expression by a small number of genes associated with neural plasticity in response to a reproductive context. Future work is needed to understand how context and time after experience alter neural plasticity processes in social contexts.

Our results present new hypotheses about how males respond to reproductive contexts, but also allow us to speculate about potential effects of novel environments on reproductive strategies. Out of the 1562 genes that were differentially expressed in a reproductive context with a female, we chose to focus on the responses by GnRH, DA, and 5-HT pathways because of their rich history in the literature demonstrating their vital roles in reproduction and behaviors, but this is far from exhaustive and many other systems are undoubtedly interacting to influence behavioral strategies during reproduction. We used virgin males with relatively little social

experiences, so our results may reflect mechanisms that facilitate rapid learning (Chapter 3). Our results provide evidence that multiple neuromodulatory systems interact as males encounter females. Future work is needed to investigate how interacting neuromodulatory systems shape acute behaviors and how these initial responses shape experience-dependent changes in behaviors.

CHAPTER 4 WORKS CITED

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CHAPTER 5: CONCLUSION

Cognition is the mental function of acquiring, processing, and acting on information in the environment. Decision making is ubiquitous cognitive function across animal species, and those decisions often have direct fitness consequences. Decisions often may appear to be suboptimal in a one-off event, however may be considered ecologically rational, or good enough in the environment in which that animal evolved (reviewed in Fawcett et al., 2014). Theory proposes experiences on evolutionary, developmental, and acute timescales influence decisions (Stamps & Frankenhuis, 2016). In a Bayesian framework, animals start with an initial assumption of the state of their world (termed a prior) and after experiences they apply new information to update their assumptions (termed posterior) (J. M. McNamara, Green, & Olsson, 2006). This framework requires some component of learning and mental algorithms that may not be feasible across all taxa (Lange & Dukas, 2009). Many models predict that animals do not use a true Bayesian updating framework, but rather use previous experiences to produce a Bayesian approximation strategy that often can perform nearly as well as a true Bayesian analysis of environmental information (Castellano, 2015; Lange & Dukas, 2009; Trimmer et al., 2011). However, the costs and risks associated with iterative sampling may also influence the ability of animals to collect information to update priors (reviewed in Mery & Burns, 2010). An alternative are decision rules, which could apply to there is either a fixed rule that produces consistent innate responses to a stimulus over time or a flexible rule that can update within some constraints to changing conditions. Decision rules tend to be good enough on average despite the strong decision biases they often create with novel stimuli (J. McNamara & Houston, 1980).

When animals use decision rules versus Bayesian updating strategies is still an outstanding question. Specific environments promote learning (Dunlap, Austin, & Figueiredo, 2019; Dunlap & Stephens, 2016) or that promote rule-based decision-making strategies (Fawcett et al., 2013). For example, innate or decision rule-based behaviors may be more likely to evolve when environmental conditions are stable across multiple generations, while learning-based strategies may be more likely to evolve when environmental heterogeneity is present and predictable within an individual's lifetime (reviewed in Mery & Burns, 2010). The level of uncertainty or ambiguity in cues and how risky a decision is in a context (Trimmer et al., 2011) may also cause a shift in which strategy an animal relies on to make decisions and how it samples information, as could the personality of the animal (Mathot et al., 2012). Environmental pressures (e.g. elevation (Morand-Ferron, Hermer, Jones, & Thompson, 2019), predation (Beri, Patton, & Braithwaite, 2014)) and physiological limitations (e.g. perceptual biases (Santacà, Busatta, Lucon-Xiccato, & Bisazza, 2019)) may influence the evolution of cognitive strategies and abilities. We have shown that ancestral differences have influenced responses to specific cues, and reproductive behaviors are being independently influenced by experiences across multiple timescales. Sigmoids and forced copulations differ in costs and benefits, so we propose they may provide an opportunity to investigate how animals may use behavior and context specific decision strategies.

In humans, psychology has long been interested in when a heuristic or decision rule is used in decision making compared to a Bayesian analysis framework (Bossaerts & Murawski, 2015; Gigerenzer & Brighton, 2009). For example, in humans there is evidence that lack of sleep will lead to more heuristic based decision-making strategies (Dickinson & McElroy, 2019), low glucose levels indirectly influence decision-making by reducing response times (Dickinson,

McElroy, & Stroh, 2014), and computational complexity of the decision itself will influence the type of strategy used to make decisions (Bossaerts & Murawski, 2017). Similar to aforementioned research in cognitive ecology of animals, psychological reviews are now also considering how human brains may be performing Bayesian approximations (e.g. Zhu, Sanborn, & Chater, 2020). Using theories from human psychology may help facilitate our understanding of the complexity and irrationality seen in animal decision making (reviewed in Hutchinson & Gigerenzer, 2005). The literature on the cognitive ecology of animals does not consider whether cognitive strategies are holistic across all decisions, or if, like humans, behavior and context shape strategies. Animals are likely applying different strategies for making decisions based on contexts and their own condition. Each behavior may have different risks and ambiguity of cues, so we should expect that selection for different decision-making strategies may evolve. This idea presents testable hypotheses about how decision-making strategies evolve, as well as presents an exciting bridge to human cognition that does not seem to be present.

The previous chapters showed that previous experiences during evolutionary and developmental timescales interact to shape the decisions guppies make between mating strategies. In the second chapter, evolutionary history shaped how developmental contexts influence the resulting behavioral phenotypes across multiple acute contexts. However, the influence of experiences across timescales were not consistent between behaviors; for example, sigmoid displays were influenced by developmental exposure to predator cues and forced copulation behaviors were not. Social experiences during developmental timescales also had distinct influences on the expression of the two reproductive strategies in chapter three. We showed that males modulated and refined mating strategies relatively independently of each other in relationship to their rearing experiences. These two chapters provide evidence that

sigmoid behaviors and forced copulation behaviors are independent rather than acting as a modular “mating strategy” unit (e.g. Endler, 1987; Fischer, Ghalambor, & Hoke, 2016; Ojanguren & Magurran, 2004). Independence between behaviors may potentially allow for greater plasticity in behavioral repertoire (E. K. Fischer et al., 2016) with each behavior regulated differently depending on specific experiences across timescales.

Plasticity in the Trinidadian guppy has been well established across many contexts and environments. For example, guppies are plastic in their mate choices (Lynch, Rand, Ryan, & Wilczynski, 2005), their shoaling strategies (Hasenjager & Dugatkin, 2017), and even whether they will use social versus private information (Leris & Reader, 2016). Fischer et al. (2016) showed a breakdown of correlations between behaviors when guppies were raised in environments that did not match their ancestral predator level, implying less of a constraint on the ability of these fish to adapt to novel environments (E. K. Fischer et al., 2016). With their adaptability to novel environments, guppies are considered an invasive species and are able to establish populations with a single pregnant female (Deacon, Ramnarine, & Magurran, 2011). We demonstrated males’ may be plastic in the cues that influence behaviors the most, in chapter 2 evolutionary and developmental cues influenced sensitivity to acute social cues, and in chapter 3 developmental experiences directly influenced male responses to female behaviors. Together, our results may present new avenues of plasticity expressed in this system that have not been considered earlier.

Which cues animals use is the first step for the decision toward an action (Mendelson et al., 2016). We demonstrated that ancestral selection pressures may help define which cues have the largest impact on behavior, and selection may directly influence the type of cognitive strategy that is employed. Moreover, our finding that that male developmental experiences

influence the associations between male and female behaviors may indicate that some males are more likely than others to use female behaviors to gauge interest and even to learn from previous experiences. Previous studies on population differences in cognitive performance by guppies speculated that predation pressures drive differences in cue use (e.g. Brown & Braithwaite, 2005). The type of information an animal integrates may depend on the task at hand, which then may change the cognitive processes needed (reviewed in Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). For example, social contexts are extremely complex and involve a dynamic conspecific, so integrating cues may be very complex (Taborsky & Oliveira, 2012), while the effects of the presence of a predator may be much more binary. Ancestral and developmental experiences directly influence not only the responses to cues, but also which cues influence behavioral strategies (Kasumovic & Brooks, 2011). We were able to demonstrate evidence of shifts in cue use based on evolutionary and developmental histories because we integrated cognitive ecology and multiple social contexts into our study, presenting a more well-rounded understanding of decision-making strategies.

While the cognitive mechanisms underlying decisions in animals is important to understand the evolution of behavioral plasticity, cognitive processes emerge from the neural pathways that respond to salient cues. For example, endogenous cues influencing “affect” (emotion) may represent the priors from previous experiences that bias mechanisms in decision-making contexts (e.g. animals: (Giske et al., 2013; Kennedy et al., 2014), humans: (Kusev et al., 2017; Loewenstein & Lerner, 2003; Mendl, Burman, Parker, & Paul, 2009)). For a complete picture of the evolution of cognitive mechanisms we need to also incorporate the neural responses to cues in our studies. For example, chapter four provides evidence that the dopamine pathway responds to cues in a reproductive context, which could point to constraints on

evolution. Dopamine is often considered for its role in motivation and aversive learning, but it also has been associated with modulation of sensitivity in sensory systems (reviewed in Bromberg-Martin, Matsumoto, & Hikosaka, 2010). Dopamine is a highly conserved neurotransmitter, but its role in behavioral regulation can vary across taxa (reviewed in Katz & Lillvis, 2014), and it is associated with many other complex pathways such as serotonin (Adell et al., 2010) and gonadotropin releasing hormone (GnRH) (Zohar, Muñoz-Cueto, Elizur, & Kah, 2010), all of which have complex interactions on behavior and long lasting associations with affect (e.g. dopamine (Libersat & Pflueger, 2004; Mendl et al., 2009), serotonin (Ansorge, Morelli, & Gingrich, 2008; Canli & Lesch, 2007; Crockett & Cools, 2015), and GnRH (Wojniusz et al., 2011)). By highlighting the role of dopamine in the reproductive context we can make hypotheses about how not only this pathway influences decisions in reproductive contexts, but also how it may influence the evolvability of the decision-making strategy.

In sum, this dissertation used an integrative approach to understand how experiences across multiple timescales influence decisions. We bridged several fields that can help provide insight into the evolution of decision-making processes and allow us to make future hypotheses about influences of multiple experiences with complex cues. Neural responses that make up cognitive mechanisms are influenced by genetics and experiences during development, so by integrating neuroethology, cognition, and evolution principles we can begin to understand how animals make decisions in acute contexts.

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