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The mate choice mind: studying mate preference, aversion and social cognition in the female poeciliid brain

Molly E. Cummings*

Department of Integrative Biology, University of Texas, Austin, TX, U.S.A.

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Male phenotypes vary across mating systems, but what about the female mind? In poeciliid fishes, we observe that female response towards males varies, both at inter- and intraspecific levels. By using the natural variation in poeciliid male reproductive phenotypes, we can probe female responses in different social contexts to isolate the neuromolecular components associated with mate choice. Female *Xiphophorus nigrensis* exhibit differential nonapeptide (*isotocin*, *vasotocin*) gene expression between social contexts that differ by social affiliation; while differential expression of synaptic plasticity genes (*neuroserpin*, *neuroligin-3*, *NMDAR*) is more strongly predictive of social contexts that differ by mate preference discrimination. Gene expression and pharmacological manipulation with *X. nigrensis* females suggests that the social cognition task of mate choice involves neuromolecular processes linked to learning at the cellular (synaptic plasticity genes) and regional (amygdala and hippocampus) levels. Comparative assays between two poeciliid species with different mating systems provide the first hint of a shared neuromolecular pathway underlying female mate preference response. Yet, it is still unclear how specific components of this neuromolecular pathway (nonapeptides and synaptic plasticity processes) interact to coordinate behavioural tasks associated with mate choice encounters (vigilance, affiliation, evaluation and discrimination). Nevertheless, this collection of studies, coupled with the natural diversity of poeciliid mating systems, pave the way for exciting new insights into the social cognition of mate choice.

Mating systems are often defined by male reproductive behaviour (e.g. Emlen & Oring, 1977), and great evolutionary insight has been gained in understanding the mechanisms that maintain diversity in male reproductive phenotypes (Brockmann & Taborsky, 2008; Gross, 1985; Henson & Warner, 1997; Lim et al., 2004; Shuster & Wade, 1991). In reality, however, mating systems are the product of the interplay between the sexes; and we are becoming increasingly aware that female behaviour can contribute to variation in mating systems (van Schaik & Kappeler, 1997). If one sex initiates an action, the other sex responds, and the interplay between male and female behaviour and physiology can lead to shifts in mating systems (Arnqvist & Rowe, 2005; Holland & Rice, 1999). Determining the mechanisms that underlie female responses towards males, and specifically towards the diversity of reproductive phenotypes, may help to uncover some of the coevolutionary dynamics between the sexes that contribute to mating system diversity.

For decades, variation in female responses towards male traits has been examined at the level of the sensory system (Boughman, 2001; Cummings, 2007; Cummings, Rosenthal, & Ryan, 2003; Ender, 1992; Fisher, Wong, & Rosenthal, 2006; Fuller, 2002; Maan, Hofker, Alphen, & Seehause, 2006; Rodd, Hughes, Grether, & Baril, 2002; Ryan & Rand, 1990; Seehausen et al., 2008). More recently, we are recognizing that cognitive processes, specifically mate choice learning, contribute to the variation in female response (ten Cate & Rowe, 2007; Ryan & Cummings, 2013; Verzijden et al., 2012). Studies with birds and fishes show that many female preferences are not static, but rather emerge from social experiences (Breden, Novinger, & Schubert, 1995; ten Cate & Vos, 1999; Kodric-Brown & Nicoletto, 2001; Kozak, Head, & Boughman, 2011; Verzijden & ten Cate, 2007; Verzijden & Rosenthal, 2011; Verzijden et al., 2012; Walling, Royle, Lindström, & Metcalfe, 2008). These studies suggest that mate preference is, in part, a product of learning. Yet it remains unknown whether the learning pathways in the brain associated with mate preference are shared across species (e.g. deep homologies; Hofmann et al., 2014; Pearson, Watson, &

* Correspondence: M. E. Cummings, Department of Integrative Biology, University of Texas, Austin, TX 78712, U.S.A.
E-mail address: mcummings@austin.utexas.edu.

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Platt, 2014), or whether differences in the cognitive hardware involved for mate preference differs by species or by interactions with different reproductive phenotypes.

We can start to investigate these questions by working with a system that has natural variation in both male behavioural phenotypes and female responses towards them. Poeciliidae, a viviparous family of freshwater fish, provides ample behavioural diversity in mating systems, male reproductive phenotypes and female responses. Poeciliid fish have traditionally been classified into mating systems based on whether males use only coercive mating tactics (copulatory thrust) or whether males exhibit some combination of copulatory thrust with courtship display (Langerhans, 2011; Martin, Albert, & Leberg, 2010; Rosen & Tucker, 1961). The diversity of male reproductive phenotypes is extensive within some species and constrained in others. For example, in the northern El Abra pygmy swordtail, *Xiphophorus nigrensis*, there are three genetically determined male size classes with discrete behavioural repertoires (large males court, small males coerce and intermediate-sized males exhibit a mixed strategy; Ryan & Rosenthal, 2001; Zimmerer & Kallman, 1989). Whereas in other taxa, females are exposed to a single male phenotype with either limited (e.g. coercive-dominant *Gambusia* sp.; Bisazza, 1993; Farr, 1989) or extensive (mixed courting and coercive, *Poecilia reticulata*; Godin, 1995; Rodd & Sokolowski, 1995) behavioural repertoires.

Poecilliid female response to these different male phenotypes varies by taxa. In some taxa with only coercive males, female preferences are absent (e.g. *Gambusia holbrooki*: Bisazza, Vaccari, & Pilastro, 2001; *Phallichthys quadripundtactaus*: Kolluru & Joyner, 1997). Meanwhile, in other taxa with multiple male phenotypes, female preference for the courting phenotype over the coercive phenotype grows stronger with age (*Xiphophorus multilineatus*: Rios-Cardenas, Tudor, & Morris, 2007; *X. nigrensis*: Wong, So, & Cummings, 2011). Controlled manipulation studies with adult poeciliid females have shown that relatively short social exposure (<4 days) to different male stimuli (e.g. heterospecifics) can alter female preference functions (Marler, Foran, & Ryan, 1997). These results suggest that female mate choice processes in poeciliids are not simple by-products of sensory biases, but rather are dynamic processes that involve learning about social stimuli.

Understanding the neuromolecular pathways underlying the cognitive processes mediating female responses towards males allows us to identify which pathways regulate (and represent selective targets of) this important evolutionary interaction between the sexes. Here, I review an initial exploration into the molecular mechanisms within the brain underlying dynamic female responses towards males. This body of work highlights the utility of the candidate gene approach when candidate genes for a behaviour of interest are unknown (Fitzpatrick et al., 2005). All of the studies reviewed here stem from discovery of gene associations in mate choice contexts as determined with microarray analysis (Cummings et al., 2008; Fig. 1a) and the subsequent examination of these candidate genes using whole-brain qPCR, in situ hybridization, pharmacological manipulation and comparative approaches to identify the critical components involved in mate choice behaviour. The data suggest that while poeciliid females experience different male phenotypes, their responses may be regulated by the same neuromolecular pathway and that this pathway is associated with learning and social cognition.

MATE CHOICE AND THE SOCIAL COGNITION PATHWAY

Social cognition refers to the neuronal processes involved in acquisition, retention and use of information during social interactions that enable an appropriate context-specific behavioural output (Barrett, Henzi, & Rendall, 2007; Dukas, 2004; Jensen et al., 2011; Oliveira, 2013; Taborsky & Oliviera, 2012; Weitekamp & Hofmann, 2014; Zuberbühler & Byrne, 2006). Social cognition is the differential recognition of, and the adaptive response towards, social agents. Identifying social cognition in the laboratory can be challenging as it requires inferring 'adaptive' or 'appropriate' behavioural response in artificial settings and is often quantified by a single behavioural variable (e.g. association time or approach behaviours; O'Connell & Hofmann, 2011). Inferring the intent of these actions in laboratory experiments, and therefore the adaptiveness of response, can be particularly difficult (Insel & Fernald, 2004).

Poeciliids represent a promising taxonomic group to identify the social cognition components associated with mate choice behaviour distinct from other social interactions. First, by employing noncontact experimental designs where association time predicts mating intent (*Xiphophorus helleri*; Walling, Royle, Lindström, & Metcalfe, 2010), we can isolate mate choice behaviour from the act of mating itself. Second, by using male phenotypes with discrete behavioural repertoires, we are able to isolate female responses relating to specific male interactions. Third, by pairing females with different male phenotypes or with other females, we can disentangle general social responses from those specific to mate preference. We took advantage of these features with *X. nigrensis*, where we exposed females to four different social contexts: two large courting males (LL), a large courter and small coercive male (LS), two small coercive males (SS) and two females (FF). We then quantified a diversity of behaviours to characterize the behavioural complexity associated with each social context including measures that characterize preference (biased responses towards individuals), affiliation or prosociality (association time), avoidance (transits away from individuals) and sociosexual (receptivity display) behaviours; followed by whole-brain qPCR analyses to compare expression of candidate genes associated with these behaviours (Ramsey, Maginis, Wong, & Cummings, 2012).

We used standard multivariate statistical tools to show that females exhibit characteristic combinations of behaviours in each social context (Fig. 1b). Females differed in combinations of behaviours defined by two axes: one defined mainly by preference behaviours, and a second defined by general sociality and activity. For instance, the *X* axis of Fig. 1b, the primary multidimensional behaviour axis, is defined by mate preference social groups (groups with courting males, LL, LS) on the left with non-mate-preference groups on the right (females or coercive males only, FF, SS). The secondary axis captures variation in prosociality between social environments characterized by social affiliation or avoidance (defined by social groups with high affiliation, FF, LL, LS, versus the group with low affiliation and high avoidance behaviours, SS). Hence, in *X. nigrensis*, we have a system where (1) different social agents evoke unique behavioural responses from females, (2) female responses fit 'adaptive' a priori assumptions (e.g. affiliation towards noncoercive phenotypes; avoidance of coercive ones) and (3) general social affiliation can be extracted from the specific affiliation associated with mate preference.

From a neurogenomics point of view, it is important to distinguish general social affiliation from mate preference behaviour in order to characterize the molecular processes associated with each social task. In theory, molecular pathways that mediate social cognition should enable organisms to rapidly recognize social agents, update information and initiate appropriate responses for specific social interactions. The molecular components involved in social cognition are likely to be part of the same neuromachinery that animals use to process decision making for any task. Decision making components that have evolved to coordinate nonsocial discrimination processes are commonly found to be recruited for

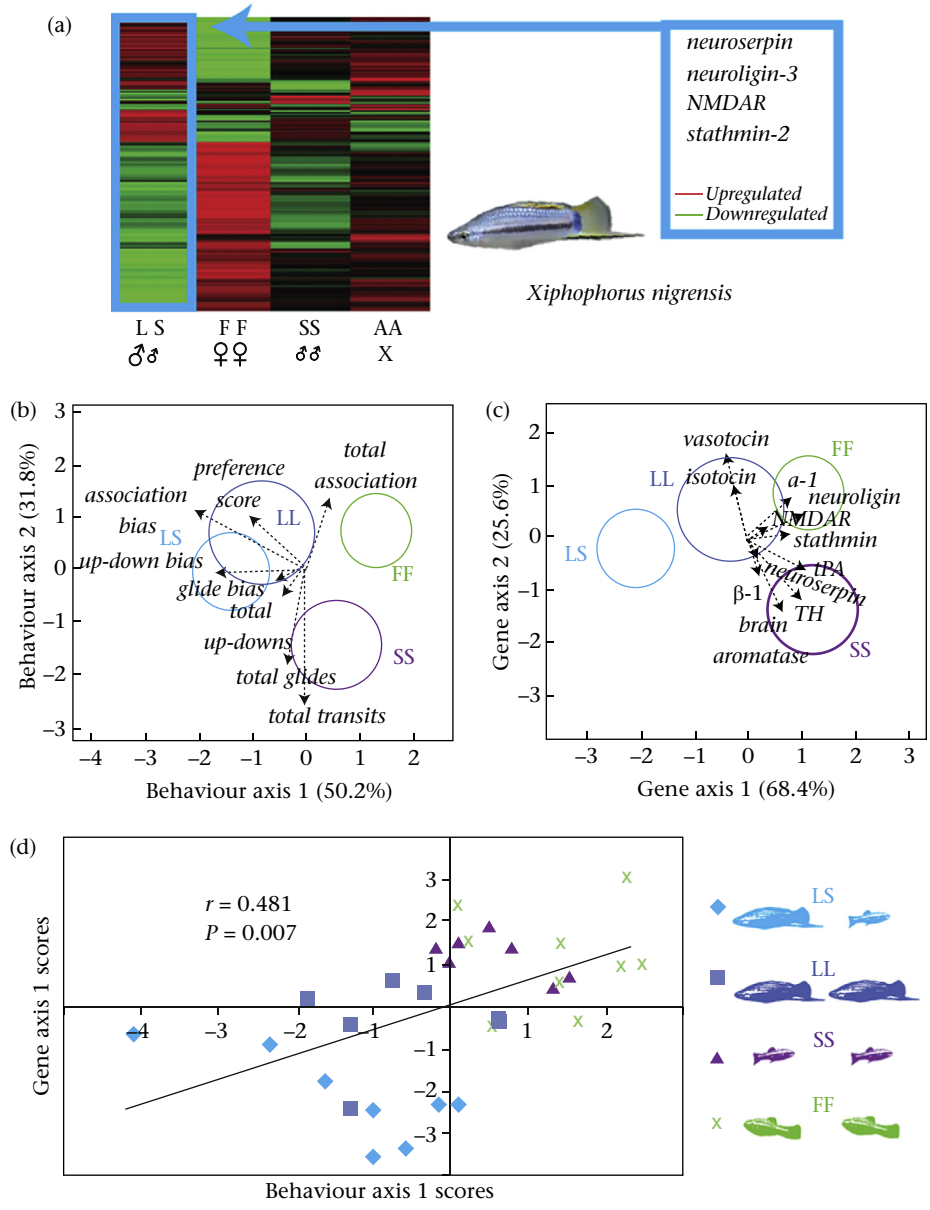

Figure 1. Whole-brain gene expression and behaviour responses from female *Xiphophorus nigrensis* following 30 min noncontact social exposure assays. (a) Heat map of microarray expression analyses identifying different brain-based patterns of downregulation (green) and upregulation (red) of gene transcripts in females experiencing mate choice conditions (large courter male, L (shown) versus small coercive male, S) relative to social controls (females only, FF; two small males, SS; asocial conditions, AA), with some of the synaptic plasticity genes (*neuroserpin*, *neuroligin-3*, *NMDAR and stathmin-2*) that exhibited statistically unique expression levels in the simple mate choice (LS) condition (Cummings et al., 2008). *Xiphophorus nigrensis* female response to social contexts in multidimensional space for (b) behaviour, (c) genes and (d) the correlation between gene and behaviour multidimensional scores (data from Ramsey et al. (2012)). Multiple discriminant analyses were evaluated across four social treatments (LL: two large courting males (dark blue); LS: large courter versus small coercive conspecific males (light blue); SS, two coercive small males (purple); FF, two conspecific females (green)). Circles represent the 95% confidence ellipses around each multivariate centroid and vectors represent the orientation in multidimensional space along the two primary axes. (b) Multiple discriminant analyses of eight input behaviours scored across four social treatments (total association time; association bias; preference score; up–down bias; glide bias; total glides; total transits away from stimuli). (c) Multiple discriminant analyses of 11 gene variables (whole-brain gene expression directly following 30 min exposure to each social context, LL, LS, SS and FF) including genes associated with social affiliation (*vasotocin*, *isotocin*), synaptic plasticity preference behaviour (*neuroserpin*, *neuroligin-3*; *NMDAR*, *tPA*, *Stathmin-2*) and sexual receptivity (β-1, β-adrenergic receptor; *a*-1,α-adrenergic receptor; *Tyrosine hydroxylase*, TH1, and brain aromatase). (d) Pearson correlation between the multiple discriminant analyses (MDA) scores of the two main axes: primary behaviour axis 1 and primary gene axis 1.

social-specific tasks (Pearson et al., 2014). Hence, it should be unsurprising that the molecular elements that have thus far been identified with social affiliation (prosociality) and mate preference responses are those involved in neural activity (e.g. immediate-early genes: Hoke et al., 2004; Sockman, Gentner, & Ball, 2002; Wong, Ramsey, & Cummings, 2012; Woolley & Doupe, 2008), synaptic processes (genes associated with synaptic plasticity: Cummings et al., 2008; Lynch, Ramsey, & Cummings, 2012; see Fig. 1a), and neuropeptides (oxytocin and vasopressin: McGraw & Young, 2010; GnRH: Okuyama et al., 2014). These types of molecular responses imply that social cognition tasks require (1) activation of neurons in critical brain regions associated with sensory processing and decision making, (2) updating neural pathways and/or accessing memories of previous encounters with specific social agents via plasticity processes and (3) modulating responses based on recognition of social agents via neuropeptides. How

neuropeptides and neuron processes (activation or plasticity) interact to coordinate prosocial behaviour in one context and selecting mates in another, however, is not yet clear as few studies have directly compared the neurogenomic responses between these social contexts.

In our initial assay comparing the behavioural neurogenomics of social affiliation from that of mate preference (Ramsey et al., 2012), we examined whole-brain expression levels of candidate genes for fish prosociality (nonapeptides: isotocin, vasotocin: Donaldson & Young, 2008; Goodson & Thompson, 2010; Thompson & Walton, 2004), sociosexual responses (e.g. brain aromatase: Forlano & Bass, 2011) and mate preference behaviour (synaptic plasticity genes, e.g. *neuroligin-3*, *neuroserpin*; NMDAR: Cummings et al., 2008; Lynch et al., 2012) in female *X. nigrensis* as they experienced distinct social contexts. The distinct social contexts that evoked unique behavioural responses from female *X. nigrensis* (Fig. 1b) also evoked unique expression levels of different candidate genes (Fig. 1c). By using composite gene suite scores alone we recapitulated the same major axes as produced by behavioural analyses (a primary axis representing a preference continuum and a secondary axis representing a prosociality continuum), but with even greater statistical signal (Ramsey et al., 2012). This result suggests that unique combinations of genes are expressed within the female brain as she encounters distinct social demands, suggesting that they may be involved in orchestrating the appropriate level of preference, affiliation and avoidance for each social context. Specifically, it suggests that there are gene suites more directly involved in regulating one of the major axes of social cognitive response (e.g. nonapeptides *isotocin* and *vasotocin* along the affiliation/avoidance axis in Fig. 1c) while other gene suites (e.g. synaptic plasticity genes) are differentially engaged in social contexts that involve discrimination between social agents of different valences (e.g. courting versus coercive males in LS; the preference axis in Fig. 1c).

While we have been able to tease apart some of the behavioural and neurogenomic responses associated with important social contexts that female poeciliids encounter (courting males, harassing males, shoaling females), we have also found descriptive evidence that these differences lie on a continuum (Ramsey et al., 2012). The significant correlation between the composite behavioural and gene scores (Fig. 1d) lends limited support for a general social cognition pathway in the brain that mediates appropriate context-dependent behaviours by coordinating differential expression of polygenic suites from different functional groups (e.g. nonapeptides and synaptic plasticity pathways). Importantly, these different neuromolecular components (e.g. synaptic plasticity genes) are not uniquely devoted to social discrimination tasks, but rather are elements of general learning processes that the brain employs to encode associations between stimuli and response (e.g. NMDAR-dependent long-term potentiation; Bliss & Collingridge, 2013). However, our finding of a social context continuum of this polygenic suite suggests they are uniquely engaged by context to coordinate responses involving social interactions. Taken as a whole, this descriptive behavioural neurogenomics work with *X. nigrensis* females suggests that a general social cognition module in the brain is differentially engaged by specific social agents, resulting in distinct coordination of neuropeptide and synaptic plasticity responses, and that these distinct subunits subserve the unique behavioural demands of each social context (avoidance, affiliation, mate preference).

Nonapeptides and Synaptic Plasticity Pathways Inform Female Mate Choice Responses

Our finding that expression levels of nonapeptides (*isotocin* and *vasotocin*) are more strongly aligned along an axis defined by contexts ranging from affiliative-prone (females and courting males, FF, LL) to harassment-prone (small coercive males, SS) social agents (gene axis 2 in Fig. 1c) is not surprising given the proposed role of oxytocin in mediating social vigilance in mammals (Ebitz & Platt, 2014). Mammalian researchers have noted that oxytocin does not uniformly increase prosociality behaviours, but rather can enhance prosociality in one context and suppress sociality in another (Bartz, Zaki, Bolger, & Ochsner, 2011). An emerging hypothesis that takes into account these context-specific effects ('the adaptive component process model'; Ebitz & Platt, 2014) suggests that oxytocin release as a result of affiliative interactions can lead to changes in specific component processes (e.g. increased social memory in the hippocampus, reduced anxiety in amygdala regions) that ultimately lead to reduced social vigilance. Our swordtail behavioural neurogenomic data set shown in Fig. 1, while purely descriptive, is consistent with this model, as we see the behaviour axis modulating social vigilance (coercive versus noncoercive groups) is strongly associated with isotocin.

While nonapetide genes are more strongly associated with the prosociality behaviour axis, synaptic plasticity genes (e.g. NMDAR, *neuroligin*) are more strongly aligned along an axis defined by mate preference (gene axis 1 in Fig. 1b; contexts with preferred (LS, LL) versus nonpreferred (FF, SS) social agents for mating). Synaptic plasticity, the broad category of neural functions involved in the genesis, remodelling, transmission and strengthening of neuronal synapses, is the underlying cellular process that enables learning and memory in animals (Li et al., 2013). These results confirm our initial microarray work with *X. nigrensis* females that identified synaptic plasticity gene suites associated with exposure to mate choice encounters (large courting versus small coercive males) relative to other social contexts (asocial, two females, or two small coercive males; Fig. 1a). Furthermore, our data suggest that active updating of neural hardware occurs more often under some social contexts than others. It suggests that synaptic plasticity processes may mediate how females evaluate social agents and determine the adaptive response (to mate or not to mate).

If synaptic plasticity processes are part of the social cognition pathway involved in evaluating social agents and rapidly updating stimulus–outcome associations, then we might expect to see quantitative variation in expression levels of synaptic plasticity genes in females as social agents vary. Quantitative variation in neural responses is an expected feature of decision-making processes to encode variation in value or context (Pearson et al., 2014); and studies in mammalian brains find quantitative differences between brain regions as task-related variables change (Wallis & Kennerley, 2010). We see some evidence for this hypothesis when examining patterns of expression of synaptic plasticity genes across brain regions within the social decision-making network (SDMN, O'Connell & Hofmann, 2011, 2012) of female *X. nigrensis* experiencing social environments with different male phenotypes (Wong & Cummings, 2014; Wong et al., 2012; Fig. 2). The SDMN is a large, conserved network that combines brain regions responsive to steroid stimulation (social behaviour network; Goodson, 2005; Newman, 1999) with the mesolimbic reward circuitry and coordinates nonsocial learning as well as appropriate social cognition responses (Weitekamp & Hofmann, 2014).

Our examination of the expression of *neuroligin*-3 and *neuroserpin* genes across the SDMN of female *X. nigrensis* experiencing different mate choice contexts revealed distinctive scaling of gene expression by social complexity and/or male phenotypic characteristics (Fig. 2). Specifically, we observed that the significant correlation of synaptic plasticity gene expression between brain regions scaled in a progressive fashion from minimal in coercive environments with unornamented harassing males (SS; Fig. 2a, d), intermediate in simple mate choice conditions with a single

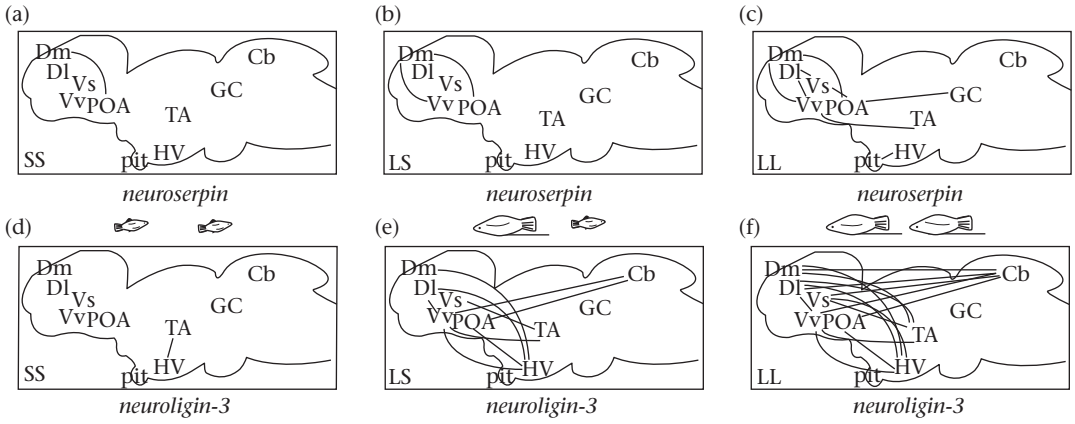

Figure 2. Network of synaptic plasticity gene expression by social context in *Xiphophorus nigrensis* female brains. Significant positive pairwise correlations of *neuroserpin* (a–c, from Wong et al. (2012)) or *neuroligin-3* (d–f, from Wong and Cummings (2014)) gene expression between social decision-making network (SDMN) brain regions. These teleost brain regions (and their putative tetrapod homologue) in a schematic sagittal section include the following: Dm: area dorsomedialis telencephali (basolateral amygdala); Dl: area dorsolateralis telencephali (pallial hippocampus); POA: nucleus preopticus (preoptic nucleus); HV: hypothalamus ventralis (ventral hypothalamus); pit: pituitary; GC: central grey (periaqueductal grey); TA: nucleus tuberis anterioirs (ventraomedial hypothalamus); Vs: ventralis supracommissuralis telencephali (medial amygdala); Vv: area ventroventralis telencephali (lateral septum); Cb: cerebellum (not an SDMN node). Each line represents a significant positive pairwise correlation between brain regions unique to male-exposed social contexts, SS (a, d), LS (b, e) or LL (c, f) relative to nonmate choice social contexts (e.g. female–female, FF, or home tank, HT, controls).

courting phenotype paired with a coercive male (LS; Fig. 2b, e) to highest in the most complex mate choice condition, where females experienced two ornamented courting male phenotypes (LL; Fig. 2c, f). This variation in synaptic plasticity gene expression observed here in swordtails may relate to the downregulation of synaptic plasticity genes during avoidance learning (e.g. Ressler, Paschal, Zhou, & Davis, 2002), while evaluation and assessment of courting phenotypes with different ornaments and behavioural displays may demand greater synaptic plasticity processes in specific brain regions. Manipulative studies on specific brain regions or synaptic plasticity pathways across social contexts may further test these hypotheses.

Exploring the Mate Choice Neuromolecular Response Beyond X. nigrensis

Greater co-expression of synaptic plasticity genes across many of the nodes in the SDMN circuit (Fig. 2) in social contexts that involve mate preference expression and behavioural discrimination (LS, LL) over environments with aversive stimuli present (SS) suggests that the cognitive processing of mate discrimination may be reliant on synaptic plasticity processes. We observe further support that synaptic plasticity processes are part of the social cognition pathway mediating mate preference responses, in our findings of covariation in *X. nigrensis* female preference responses and whole-brain expression of synaptic plasticity genes (Fig. 3a, b; Cummings et al., 2008; Lynch et al., 2012).

Exploratory analysis of the involvement of these synaptic plasticity genes in mediating female responses towards males in a coercive-prone poeciliid species, *Gambusia affinis*, provided interesting and unexpected results. Although males of this species are largely nonornamented and all sizes of males engage in coercive matings (Farr, 1989), females exhibit a modest bias for associating with larger male conspecifics (Lynch et al., 2012). Large males may be favoured in this system as they are less successful at sneaky copulations than smaller males because they are more visible to females when approaching from behind (Pilastro, Giacomello, & Bisazza, 1997). Given that the behavioural bias for larger males is considerably more muted in *G. affinis* than in *X. nigrensis* (Lynch et al., 2012), we expected to observe a more muted correlation (e.g. shallower slope) or no correlation between female behaviour towards males and these preference-associated synaptic plasticity genes. Instead, we observed a negative relationship between expression of synaptic plasticity genes and association time bias with the larger male conspecific (Fig. 3c, d; Lynch et al., 2012).

The opposing pattern of genetic covariation with behaviour in these two poeciliid species with different mating systems suggests either that the two species evolved divergent neuromolecular responses involved in mating interactions, or that the neuromolecular pathway was shared but differentially engaged by male phenotypes. We could not differentiate between these two hypotheses because females from these species experienced different kinds of conspecific males (*X. nigrensis* have both courting and coercive males; whereas *G. affinis* have only coercive males). To disentangle these hypotheses, we exposed *G. affinis* females to coercive and courting males of a heterospecific, the sailfin molly, *Poecilia latipinna*. When interacting with the courting *P. latipinna* males, *G. affinis* females exhibited a positive relationship between synaptic plasticity gene expression and preference behaviour (Fig. 3e), similar to patterns observed in the courtship-prominent *X. nigrensis* (Fig. 3a, b). Conversely, when we exposed *G. affinis* females to coercive *P. latipinna* males, we found a negative relationship between preferences and expression of genes involved in synaptic plasticity, similar to the pattern observed with their own conspecific males (Fig. 3c–e). Hence, the covariation of synaptic plasticity gene expression and female preference behaviour exhibited a plastic response, and one that was differentiated by the male mating type (coercive versus courting). This demonstration that female interactions with specific male phenotypes evoke the same gene-by-behaviour response from both coercive- and courtship-dominant poeciliid species is an early suggestion of a shared neuromolecular pathway underlying female mate choice responses (Wang, Ramsey, & Cummings, 2014).

Brain Regions Underlying Mate Preference: Fear and Learning on the Mate Choice Front

To determine whether mate preference responses were a product of arousal-related mechanisms, as well as to identify key brain regions associated with the neuromolecular pathway of mate choice, we conducted behaviour assays with *X. nigrensis* females

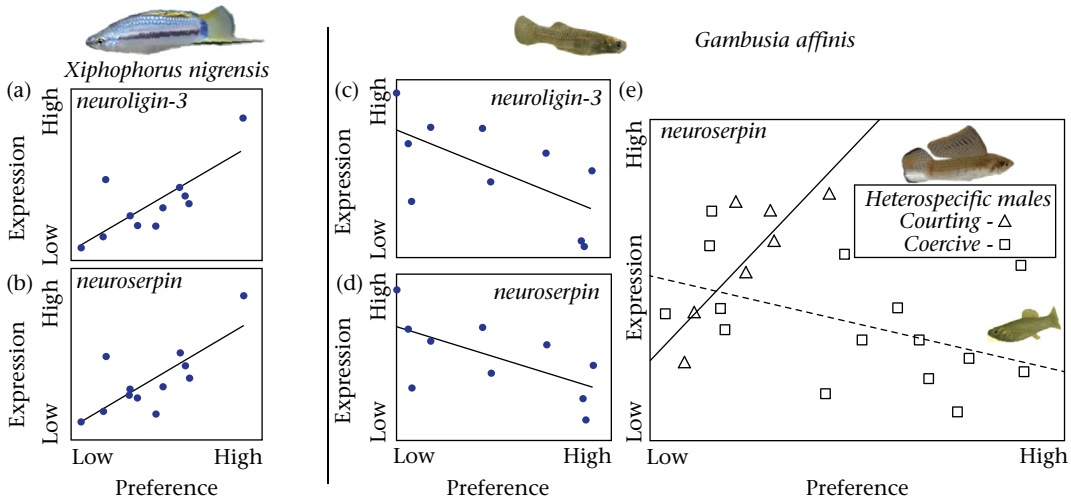

Figure 3. Whole-brain gene expression responses from female *Xiphophorus nigrensis* (a, b; image of large courting male) and *Gambusia affinis* (c–e; image of coercive male above panel (c)) following 30 min exposure to mate choice assays with conspecifics (a–d) or heterospecifics (e). (a) Whole-brain gene expression of (a) *neuroligin-3* and (b) *neuroserpin* from female *X. nigrensis* significantly covary with female preference behaviour in male-exposed trials (LS + SS; Cummings et al., 2008; a pattern also found in Lynch et al., 2012). Whole-brain gene expression of (c) *neuroligin-3* and (d) *neuroserpin* from female *G. affinis* to conspecific males (LS, both coercive; Lynch et al. 2012). (e) Female *G. affinis* exhibit opposing patterns of whole-brain gene expression (*neuroserpin*) by female preference behaviour when exposed to heterospecific (*Poecilia latipinna*) males that engage in either courting or coercive behaviours (from Wang et al. (2014)).

with localized expression of genes involved in reward, synaptic plasticity and neural activation (Wong & Cummings, 2014; Wong et al., 2012). Using in situ hybridization (Fig. 4a), we quantified preference-dependent gene expression of *tyrosine-hydroxylase* (TH1, a rate-limiting enzyme in dopamine biosynthesis), *neuroligin-3*, *neuroserpin* and *egr-1* across 10 brain regions in *X. nigrensis* females. While we found no context-dependent expression of TH1 in any brain region, we found significant differences in expression of synaptic plasticity genes in four brain regions between females exhibiting high and low levels of mate preference behaviour (Fig. 4b) with three of these brain regions (each a node in the SDMN) exhibiting a positive covariance between preference behaviour and gene expression (Fig. 4c–f). These specific brain regions (Dm, area dorsomedialis telencephali; Dl, area dorsolateralis telencephali; POA, nucleus preopticus) are the putative fish homologues to the mammalian basolateral amygdala, pallial hippocampus and preoptic area, respectively. Additional experiments with *egr-1* (an immediate-early gene used as a marker for neural activity) in female swordtails, also revealed positive correlations between female preference behaviour and *egr-1* expression in Dm and Dl brain regions (Wong et al., 2012).

Studies from mammals to fish have linked amygdalar and hippocampal brain regions and their nonmammalian homologues to learning and emotional processing (Broglio et al., 2005; Iordanova, Good, & Honey, 2011; Ressler et al., 2002), while the hypothalamic POA region has been strongly linked to sexual behaviour and reproduction (Burmeister, Jarvis, & Fernald, 2005). The fish homologues to the mammalian amygdala and hippocampus (Dm and Dl) are sensory integration centres (Northcutt, 2008) and are associated with fear modulation and spatial learning (Broglio et al., 2005). Fear conditioning in rats has shown extensive synaptic plasticity gene expression in amygdala and hippocampus regions (Ressler et al., 2002); and the fish homologue to the amygdala (Dm) has been shown to influence avoidance behaviour in zebrafish (Lau, Mathur, Gould, & Guo, 2011). Dm and Dl project to the POA (Northcutt, 2008), a region that governs reproductive physiology in vertebrates via GnRH neurons and can be modulated by social information. For instance, in female cichlids, social information about mates (observing a winning or losing male partner) leads to differential POA activation (Desjardins, Klausner, & Fernald, 2010). In swordtail females, we hypothesize that telencephalic Dm and Dl regions are involved in evaluating the social valence of different male stimuli and relay this information to the POA to coordinate sexual receptivity. Telencephalic gating of sexual receptivity has been recently identified in other teleosts. Specifically, terminal nerve GnRH neurons (TN-GnRH3), which have widespread projections throughout the brain including the telencephalon (Von Bartheld, 2004), gate female medaka mate preference and receptivity responses to familiar males (Okuyama et al., 2014). These neurons appear to represent a critical component of social cognition: recognizing individuals or classes of individuals (male phenotypes) of specific valence and regulating a context-specific response.

FUNCTIONAL TESTS OF SYNAPTIC PLASTICITY IN MATE PREFERENCE PATHWAY

While associations between synaptic plasticity gene expression at whole-brain and within brain regions of the social decision-making network suggest that these neuromolecular pathways are involved in coordinating a mate preference response, these associations remain tentative until functional tests can confirm their role. While direct manipulation of gene expression coupled with testing behavioural consequences is an ideal approach (e.g. Lim et al., 2004), we have initially applied a more general (e.g. sledgehammer) approach to testing the neural components involved in processes in mate choice behaviour by using pharmacology to block the function of one of the synaptic plasticity genes associated with mate choice contexts (N-methyl-D-aspartate receptor, NMDAR; Fig. 1a). NMDA receptors (a class of glutamate receptors), play an essential role in memory formation (long-term potentiation; Bliss & Collingridge, 2013) and are critical gate keepers in social cognition pathways (Gao, Elmer, Adams-Huet, & Tamminga, 2009; Gunduz-Bruce, 2009; Reidel, Platt, & Micheau, 2003). NMDA receptors are important in experience-dependent synaptic plasticity as they have been shown to be critical in both imprinting (Bock & Braun, 1999; Heinrich, Singh, Sohrabji, Nordeen, & Nordeen, 2002; McCabe & Horn, 1991, 1994) and classical associative

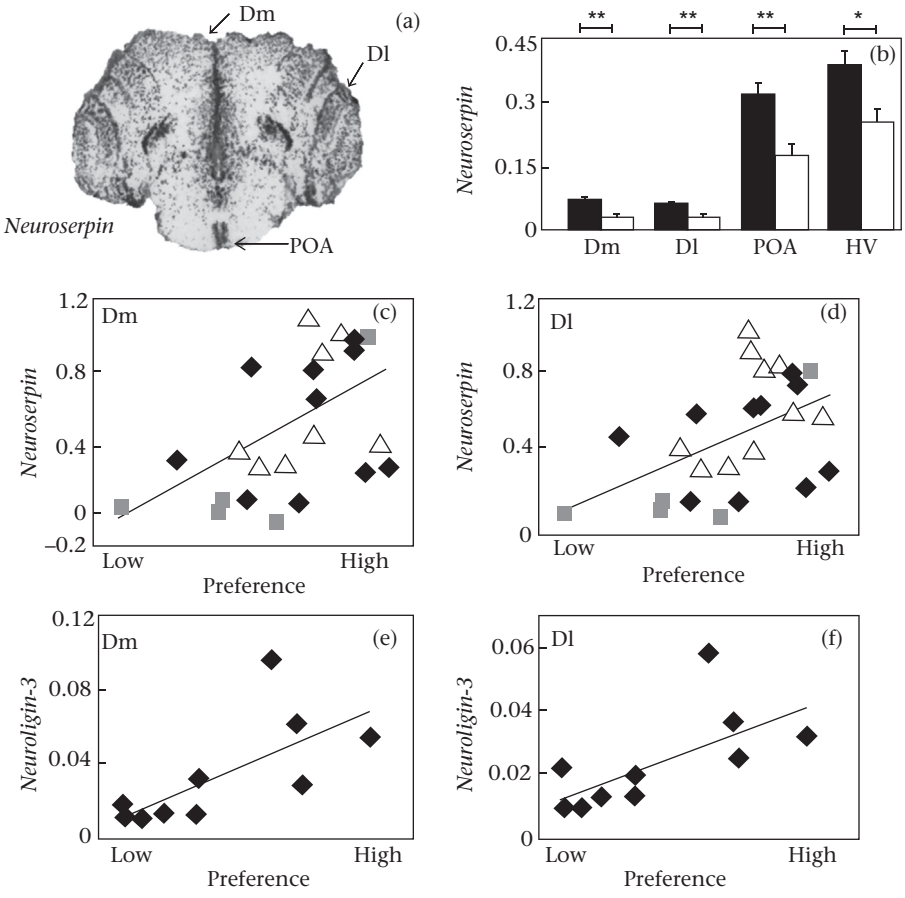

Figure 4. Localized brain expression of synaptic plasticity genes (*neuroserpin*, *neurologin-3*) in female *Xiphophorus nigrensis* following mate choice trials. Data in (a–d) from Wong et al. (2012), and data in (e–f) from Wong and Cummings (2014). (a) Representative *neuroserpin* in situ hybridization cross-section of a female *X. nigrensis* following a mate choice trial. (b) Female *X. nigrensis* exhibiting above-median levels of preference behaviour (black bars) had significantly greater *neuroserpin* expression in four brain regions (Dm: area dorsomedialis telencephali; Dl: area dorsolateralis telencephali; POA: nucleus preopticus; HV: hypothalamus ventralis) than females exhibiting below-median levels of preference behaviour (white bars). Females exhibited a significant correlation between preference behaviour and synaptic plasticity gene expression (*neuroserpin* (c, d) and *neuroligin-3* (e, f) in Dm (c, e), Dl (d, f) and POA (data not shown)) when exposed to a range of mate choice contexts including minimal (SS: two small coercive males; squares), simple (LS: large courting and small coercive; diamonds) and complex (LL: two large courting males; triangles).

learning processes (Iordanova et al., 2011). We treated female *X. nigrensis* with an NMDAR antagonist (MK-801) prior to placing them in simple mate choice environments (LS, large versus small male condition) and found that the NMDAR blockade disrupted preference behaviour without disrupting other activities (Fig. 5a; Ramsey, Vu, & Cummings, 2014).

Given that female swordtails with NMDAR disruption were not able to differentiate between aversive (coercive small male, S) and nonaversive (courting large male, L) social agents, we hypothesized that the NMDAR blockade altered preference behaviour by disrupting a female's learned avoidance response to aversive stimuli. To test this, we conducted additional scototaxis (Maximo, Marques de Brito, Dias, Gouveia, & Morato, 2010) experiments to examine the role of NMDAR in mediating fear/aversion responses. Small fish typically show an aversion to high-light environments, and scototaxic trials (exposing fish to experimental chambers with both black and white regions) have been used to examine anxiolytic effects of different pharmacological agents (Riehl et al., 2011; Rujescu et al., 2006; Sison & Gerlai, 2011). We used the scototaxis trial to determine whether females with NMDAR disruption alter their response to aversive environments (Ramsey et al., 2014). Swordtail females showed a dramatic decrease in aversion to the high-light (white) portion of the scototaxis chamber following NMDAR blockade (Fig. 5b). This finding suggests that NMDAR may be gating an avoidance response towards aversive social agents in swordtails. It is important to note that mate choice does not always involve discrimination between aversive and nonaversive stimuli. Does the NMDA receptor play an important role in mate choice discrimination when females are discriminating between nonaversive stimuli such as two ornamented or courting phenotypes? Further manipulative tests in social contexts that do not involve aversive stimuli (e.g. comparing LS to LL male conditions) may help elucidate this issue.

An examination of the dynamically expressed gene profiles from the brains of female swordtails treated with the NMDAR antagonist (MK-801) revealed distinctly different nonopeptide (*isotocin*, *vasotocin*) expression patterns from those of untreated female controls (Fig. 5c). It is not clear at this point whether NMDAR regulates nonapeptide expression in these swordtails or whether nonapeptides are regulating NMDAR. While future research should ascertain this, the current snapshot suggests that they are both involved in coordinating expression of mate preference behaviour. Our gene expression snapshot of the swordtail brain suggests that these gene modules were differentially engaged following disruption of appropriate approach/avoid responses towards specific social agents during mate choice interactions. This hypothesis is consistent with the natural variation in gene expression and behaviour we observed across unmanipulated control females. In

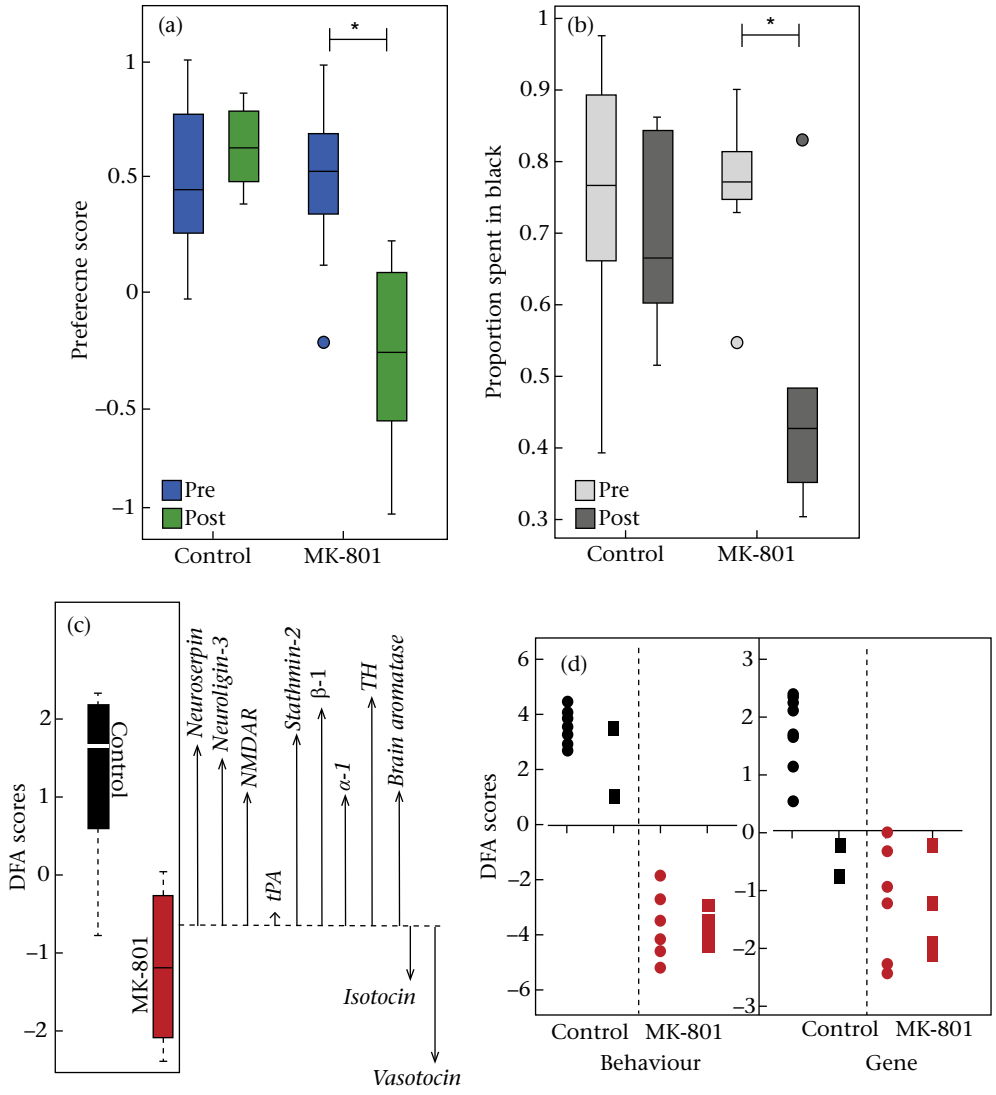

Figure 5. Pharmacological blockade of NMDAR (via MK-801) in female *Xiphophorus nigrensis* disrupts (a) preference behaviour, (b) scototaxis response and (c) whole-brain nonopeptide expression levels typically associated with preference for large courting male phenotypes (d), all data from Ramsey et al. (2014). (a) Control ($N = 10$) and treated ($N = 10$) female *X. nigrensis* were tested for preference behaviour in an LS (large courting vs small coercive) mate choice trial on day 1 (pre) and day 6 (post) following treatment with either vehicle (control) or a noncompetitive NMDAR antagonist (20 μM of MK-801) for 1 h each day (days 2–5). Treated females exhibited a significant decrease in preference behaviour ($P < 0.005$) without a change in total activity ($P > 0.05$; data not shown). (b) Subsequent trials with 16 additional female *X. nigrensis* ($N = 8$ controls; $N = 8$ MK-801 treated) followed the same subchronic MK-801 protocol as in (a), but subjects were behaviourally tested in a scototaxis chamber. Control females exhibited normal white/light-aversive responses in pre- and post-trials, whereas MK-801 females showed a significant increase in time spent in the white portion of the tank ($P < 0.05$). (c) Discriminant function analysis scores (DFA) for multivariate (11 gene inputs) comparison between control and MK-801 females in (a) (gene names as Fig. 1). (d) Discriminant function analysis behaviour and gene scores between control and MK-801 females by preference for large males (circles) or small males (squares) in post (day 6) behaviour trial.

general, swordtail females prefer large courting males over small coercive males; however, some females prefer to associate with smaller males. In our NMDAR manipulation study (Ramsey et al., 2014), two of the control females exhibited a preference for the small male in the LS paradigm, and these females had brain multivariate gene expression profiles that were similar to females experiencing NMDAR disruption (Fig. 5d), indicating that the presence or absence of aversion towards the small male may be mediated through NMDAR signalling. Did these females have different social experiences than the others that differentially shaped their synaptic plasticity and social affiliation pathways and consequently their preference behaviours towards males? These questions are worth pursuing and may provide insight not only into the mechanisms underlying variation between females within this species, but may also provide insight into between-taxa variation in female responses towards different male phenotypes.

CONCLUSION

The social interactions that females engage in while experiencing different male phenotypes in the poeciliids varies considerably. Yet, the neuromolecular pathways that poeciliid females use to respond to these different social cognition tasks may be shared across lineages. While far more extensive comparative data is required before substantiative conclusions can be made, this early data set provocatively points to the presence of a shared neuromolecular pathway mediating mate preference responses. Importantly, these initial studies suggest that the shared genomic tool-kit that poeciliids may draw from include neuromolecular pathways that involve learning, allow them to differentiate between social stimuli, and are differentially engaged to mediate approaching or avoiding specific social agents. Such a finding makes sense in light of the breadth of conserved neuromolecular pathways mediating

social behaviour across vertebrates (O'Connell & Hofmann, 2011, 2012; Pearson et al., 2014; Weitekamp & Hofmann, 2014). Yet, further experimentation is required to test the specific roles of some of the shared neuromolecular components (nonapeptides, synaptic plasticity genes) in mediating specific subtasks required for each social context. Do interactions with courting males demand greater synaptic plasticity activation due to the increased assessment, or memory storage requirements associated with processing the neural representation of male display or ornamentation features? Does the suppression or inhibition of synaptic plasticity pathways during social interactions with coercive stimuli represent a cognitive switch from evaluation to aversion? Are poeciliid females gathering information in the presence of courting males or experiencing real-time rewiring of neural circuitry? At this point, we simply do not know. Direct tests of learning in mate choice, with specific manipulation of social agent and neuromolecular components (e.g. synaptic plasticity genes), will better elucidate the mechanisms of learning and rapid updating that occurs during social cognition tasks. Furthermore, the specific relationship between *isotocin* and synaptic plasticity in mediating avoidance of some social agents and the act of selecting others for mating events is still very murky. Nevertheless, the diversity of social agents and contexts that poecillids have to offer provides ample promise that many of these questions will be revealed.

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