

SHORT COMMUNICATION

D2 dopamine receptor activation induces female preference for male song in the monogamous zebra finch

Nancy F. Day¹, David Saxon^{2,*}, Anastasia Robbins², Lily Harris², Emily Nee², Naomi Shroff-Mehta², Kaeley Stout², Julia Sun², Natalie Lillie², Mara Burns², Clio Korn^{2,‡} and Melissa J. Coleman^{2,§}

ABSTRACT

The evolutionary conservation of neural mechanisms for forming and maintaining pair bonds is unclear. Oxytocin, vasopressin and dopamine (DA) transmitter systems have been shown to be important in pair-bond formation and maintenance in several vertebrate species. We examined the role of dopamine in formation of song preference in zebra finches, a monogamous bird. Male courtship song is an honest signal of sexual fitness; thus, we measured female song preference to evaluate the role of DA in mate selection and pair-bond formation, using an operant conditioning paradigm. We found that DA acting through the D2 receptor, but not the D1 receptor, can induce a song preference in unpaired female finches and that blocking the D2 receptor abolished song preference in paired females. These results suggest that similar neural mechanisms for pair-bond formation are evolutionarily conserved in rodents and birds.

KEY WORDS: Monogamy, Social behavior, Mate choice, Operant conditioning, Song bird, Birdsong

INTRODUCTION

Forming monogamous pairs is important in many social animals for survival and reproductive success. The prairie vole has given clues to some of the neurotransmitter systems that are critical for pair-bond formation (McGraw and Young, 2010; Young et al., 2011; Young and Wang, 2004). In general, nonapeptides such as oxytocin and vasopressin are important for pair-bond formation in females and males, respectively (McGraw and Young, 2010). Activation of D2 dopamine receptors (D2Rs) in the nucleus accumbens can induce a partner preference in both males and females (Aragona et al., 2003; Liu and Wang, 2003), whereas D1 dopamine receptors (D1Rs) block partner formation and contribute to selective aggression (Aragona et al., 2003; Hostetler et al., 2011). Although much has been gleaned from prairie voles, the specific mechanisms by which DA and nonapeptides influence neural circuits that underlie partner preference are still unknown, in part because

manipulation of specific neurons and receptors in the mesolimbic reward system and social behavior network is difficult. Oxytocin, vasopressin and dopamine have also been implicated in pair-bond formation in humans and titi monkeys (Bales et al., 2017; Feldman, 2017; Hostetler et al., 2017), suggesting conserved neurotransmitter systems, although the neural circuitry may differ (Hostetler et al., 2017; Young et al., 2019). Social monogamy is more common in birds; >85% of avian species are classified as socially monogamous (Cockburn, 2006; Lack, 1968) compared with ~9% in mammals (Lukas and Clutton-Brock, 2013). Therefore, comparing mechanisms of affiliative behavior in birds with those in other vertebrates is critical to understanding the conserved neural underpinnings (Banerjee et al., 2013; O'Connell and Hofmann, 2011a,b).

The zebra finch (*Taeniopygia guttata*) provides an excellent avian system to understand the neural mechanisms of pair bonding. In addition to the formation of monogamous pairs, their courtship behavior is well described (Zann, 1994, 1996), much of the circuitry involved in social behaviors is known (O'Connell and Hofmann, 2011b; Prior and Soma, 2015; Wild and Botelho, 2015) and the system is becoming more accessible to specific neural manipulations (Heston et al., 2018; Murugan et al., 2013; Xiao et al., 2018; Yazaki-Sugiyama et al., 2015). Additionally, previous studies in zebra finches have identified that partner preference is dependent on many neurotransmitters and other signaling molecules, including oxytocin (Klatt and Goodson, 2013; Pedersen and Tomaszycki, 2012), vasopressin (Goodson et al., 2004), cortisol (LaPlante et al., 2014), hormones (Prior and Soma, 2015) and dopamine (Adkins-Regan, 2009; Banerjee et al., 2013; Goodson et al., 2009; Iwasaki et al., 2014; Tokarev et al., 2017).

Female song birds use male song as an honest signal of sexual fitness and song is important for forming affiliative bonds (Gil and Gahr, 2002; Tomaszycki and Adkins-Regan, 2005). In zebra finches, only the males sing and females exhibit a preference for their mate's song (Woolley and Doupe, 2008). To test whether neural mechanisms are evolutionarily conserved in the formation and maintenance of partner preference, we evaluated female preference for male song. Dopamine, acting through D2Rs, can induce partner preference in prairie voles (Wang et al., 1999); thus, we tested whether activation or blockage of D2Rs altered song preference. We predicted that, in female zebra finches, a D2R agonist would induce a song preference in females and that a D2R antagonist would reduce song preference in pair-bonded females.

MATERIALS AND METHODS

Animals and housing

A total of 46 adult female (>90 days post-hatch) and 44 adult male zebra finches, *Taeniopygia guttata* (Vieillot 1817), were used in this

¹Department of Integrative Biology and Physiology, University of California Los Angeles, Los Angeles, CA 90095-7246, USA. ²W.M. Keck Science Department of Claremont McKenna, Pitzer and Scripps Colleges, Claremont, CA 91711-5916, USA.

*Present address: Georgetown University School of Medicine, Washington, DC 20007, USA.

‡Present address: Department of Psychiatry, University of California San Francisco, San Francisco, CA 94143, USA.

§Author for correspondence (mcoleman@kecksci.claremont.edu)

© N.F.D., 0000-0001-5367-9473; D.S., 0000-0002-6430-8835; A.R., 0000-0002-8921-3365; L.H., 0000-0003-3499-9003; E.N., 0000-0001-9148-356X; N.S., 0000-0001-7169-3164; K.S., 0000-0001-8991-3540; J.S., 0000-0001-6198-3491; N.L., 0000-0002-7545-2082; M.B., 0000-0002-1841-4952; C.K., 0000-0001-6328-6876; M.J.C., 0000-0001-6600-7510

study. All birds were subject to a 12 h:12 h light:dark cycle and had access to food and water *ad libitum*. All experiments were approved by the W.M. Keck Science Department IACUC, in accordance with NIH guidelines.

Experimental design

Birds were divided into two groups: pair-bonded and unpaired females. Pair-bonded females were housed with a male for at least 2 weeks, which is long enough to form pair bonds (Zann, 1996), and unpaired females were housed with other females. Prior to the behavioral experiment, each female was isolated for 24–48 h in a sound-isolation chamber with her partner in the pair-bonded group or with a novel male partner in the unpaired group (Fig. 1A). During this time, females were injected twice, 6–24 h apart, with a drug (see below) or saline given by a 50 μ l subcutaneous injection in the inguinal fold, at the base of each leg. All drugs (Sigma) were dissolved in 0.9% saline at a dose of 1 mg kg⁻¹ body mass (Balthazart et al., 1997; Kabelik et al., 2010), with an average body mass of 13 g. To test the role of each dopamine receptor, we used (\pm)-SKF-38393 (D1R) and (-)-quinpirole-hydrochloride (D2R) as agonists, and SCH 23390 (D1R) and raclopride (D2R) as antagonists.

During the isolation period, male courtship song was collected with a microphone (Shure SM94), digitized at 44100 Hz (PreSonus, AudioBox) and stored on a PC using Sound Analysis Pro 2011 (Tchernichovski et al., 2000).

Behavioral test

Immediately following isolation with a single male, females were tested for their song preference using an operant testing cage (Fig. 1B) modeled after Woolley and Doupe (2008). This testing cage was composed of identical chambers (400×400×440 mm) connected by a window (100×140 mm). Each chamber included a single perch with an infrared beam (Banner Engineering) set at the level of the perch and a speaker (Pioneer TS-F1643R) positioned at either end of the two chambers. When a subject landed on a perch, the infrared beam was interrupted and a song playback was triggered, using the Matlab software ARTSy (Gess et al., 2011) or Sound Analysis Pro 2011.

For an hour before each test, the chamber bias of the female was determined by recording the number of perch triggers, with no song played (silence). During the preference test, song from the male that was isolated with the female (partner song) was played through the speaker in the non-preferred chamber for 1 h (see

Fig. 1B). The other chamber played back a female-directed song from an unfamiliar male. The same unfamiliar male song was used for all experiments to reduce variability of perceived song complexity. To calculate chamber and song preference, the number of triggers on the partner's side of the cage was divided by the total number of triggers.

Statistics

All statistical tests were performed in Prism (GraphPad, version 8.01). Paired *t*-tests were used to determine whether a treatment changed the chamber preference from silence to song playback, where data are presented as means \pm s.d. To compare the overall change in preference from silence to song playback (mean \pm s.e.m.), a one-way ANOVA with a *post hoc* Tukey's test for multiple comparisons was used. Sample size ($N=7$ to 8 birds per group) was determined using the 'pwr' package in R (3.5.1) for a desired effect size of 0.8.

RESULTS AND DISCUSSION

Female finches prefer their partner's song

Pair-bonded females prefer their partner's song (Woolley and Doupe, 2008). To validate the operant conditioning paradigm (Gess et al., 2011) for song preference, we tested saline-injected females that were unpaired (isolated with an unfamiliar partner for 24–48 h prior to testing) or pair-bonded (housed with a partner for >2 weeks). After a female's chamber bias was determined by recording the number of perch landings triggering no song playback (silence), female song choice was compared with her chamber preference (Fig. 2A). As expected, we found that paired females preferred their partner's song to an unfamiliar song (side preference: silence, 0.35 \pm 0.15; partner song, 0.62 \pm 0.20; $P=0.003$, $t=4.59$, d.f.=7, $n=8$), and unpaired females showed no preference for their partner's song (side preference: silence, 0.35 \pm 0.12; partner song, 0.38 \pm 0.26; $P=0.63$, $t=0.50$, d.f.=7, $n=8$).

Induction of song preference is mediated by D2R

To determine the effect of D1R or D2R on induction of song preference, we tested unpaired females that were injected twice with 1 mg kg⁻¹ of either a D1R agonist (SKF-38392) or a D2R agonist (quinpirole). Females injected with the D2R agonist showed a significant preference for their partner's song (Fig. 2B; side preference: silence, 0.22 \pm 0.11; partner song, 0.76 \pm 0.13; $P<0.0001$, $t=9.26$, d.f.=7, $n=8$). However, females injected with the D1R agonist did not show a preference for their partner's song (side

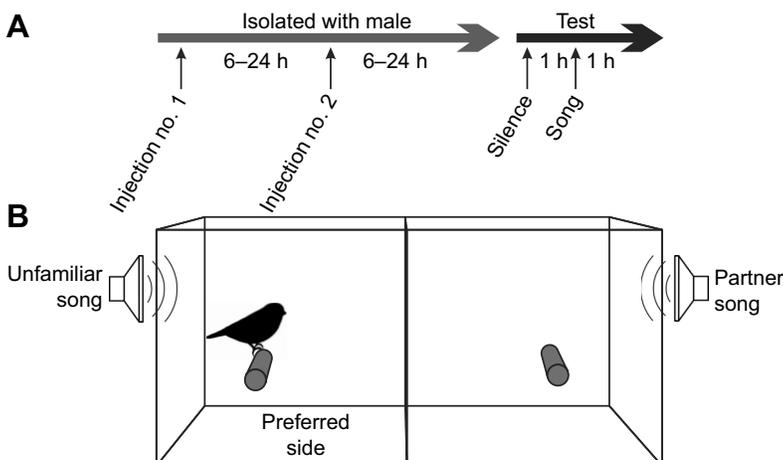


Fig. 1. Schematic diagram of the experimental design to test the song preference of female zebra finches. (A) Each female was isolated with a partner during the injection of either saline or a D1 or D2 dopamine receptor (D1R or D2R) agonist or antagonist. Two injections (1 mg kg⁻¹) were delivered during the co-housing period (gray arrow). After isolation with a male, females were placed in the testing arena and their side bias (Silence) was determined prior to their song preference (Song) by counting the number of perch landings on each side of the chamber in 1 h. (B) Schematic diagram of the operant testing cage. The side of the chamber with fewer perch landings during silence was paired with the partner song. When the bird landed on a perch, song playback from a speaker on that side of the cage was triggered.

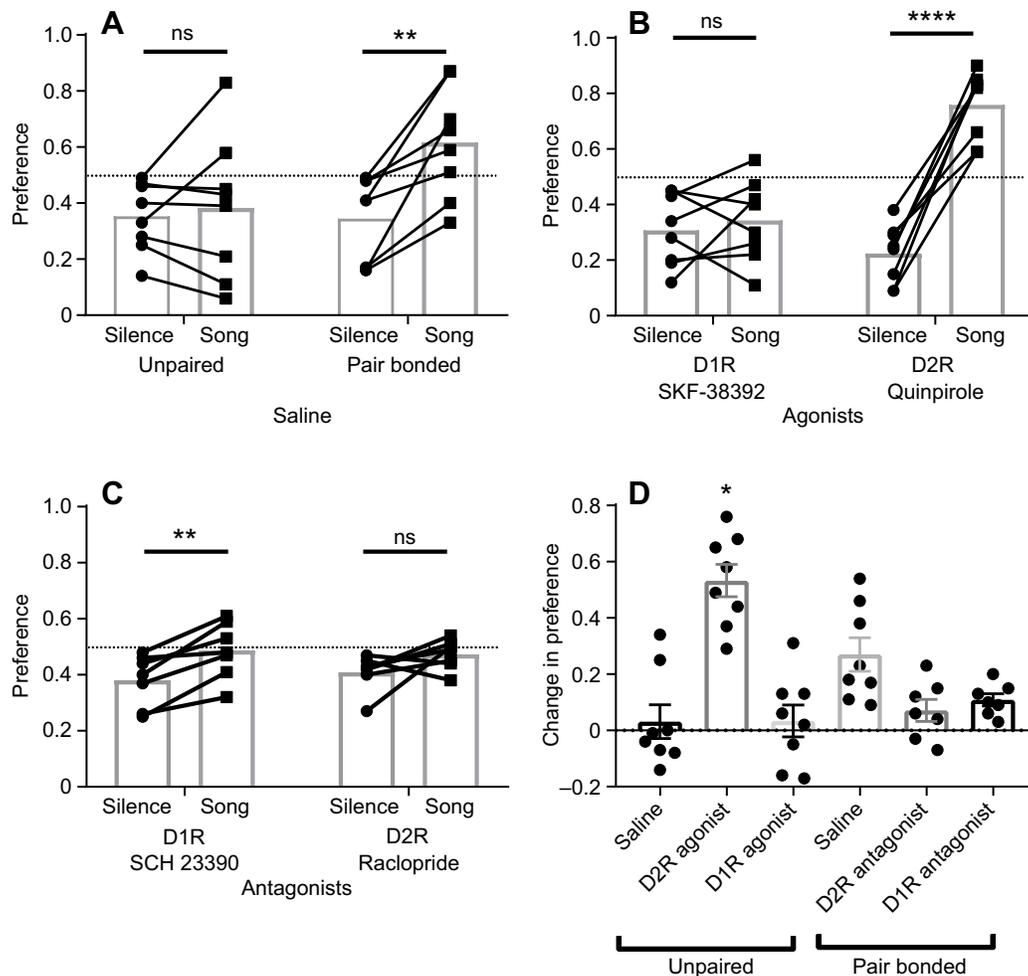


Fig. 2. Ratio of perch triggers during operant testing indicates preference for songs produced by conspecific males. Each female's side preference was tested initially by playing 'silence' when she landed on a perch. Her partner's song was then played when she landed on a perch in the non-preferred chamber. Connected symbols are changes in preference for each individual; bars represent the mean for each group. (A) Saline-injected unpaired females do not have a preference for song produced by a 'partner' male following 48 h of cohabitation, but pair-bonded females prefer the song of their partner to an unfamiliar male song. ** $P < 0.01$. (B) Following injection of a D2R agonist (quinpirole), unpaired females significantly prefer the song of their partner. Preference for partner song is not observed following injection of a D1R agonist (SKF-38392). **** $P < 0.0001$. (C) In pair-bonded females, delivery of a D2R antagonist (raclopride) is sufficient to abolish partner song preference. Pair-bonded females injected with a D1R antagonist (SCH 23390) retain a preference for their partner's song. ** $P < 0.01$. (D) Change in preference (playback – silence) for each group of females (means \pm s.e.m.). *Unpaired females given the D2R agonist showed a significant increase in song preference compared with all other groups (see Results and Discussion for details). Dots indicate changes in preference for each individual.

preference: silence, 0.31 ± 0.13 ; partner song, 0.34 ± 0.15 ; $P = 0.55$, $t = 0.63$, d.f. = 7, $n = 8$). These data indicate that activation of the D2R, but not the D1R, is sufficient to induce a song preference in female finches.

D2Rs are required for maintaining partner preference

In order to determine whether D2Rs are necessary to maintain partner preference, we used D1R and D2R antagonists in paired females (Fig. 2C). We found that females injected with the D2R antagonist raclopride did not have a song preference (side preference: silence, 0.41 ± 0.07 ; partner's song, 0.47 ± 0.05 ; $P = 0.14$, $t = 1.72$, d.f. = 6, $n = 7$). The paired females injected with the D1R antagonist SCH 23390 retained a preference for their partner's song (side preference: silence, 0.38 ± 0.09 ; partner's song, 0.49 ± 0.10 ; $P = 0.003$, $t = 4.87$, d.f. = 6, $n = 7$). These data suggest that D2Rs, but not D1Rs, are necessary to maintain song preference in paired female finches.

The song preference of females across treatments was compared by calculating the change in chamber preference (playback–silence) (Fig. 2D). We found that administration of the D2R agonist quinpirole significantly increased the preference for partner song compared with all other groups (one-way ANOVA, $F_{5,40} = 14.3$, $P < 0.0001$; Tukey *post hoc*, D2R agonist versus unpaired saline, D1R agonist, D2R antagonist and D1R antagonist, $P < 0.0001$; D2R agonist versus paired saline, $P = 0.01$). In addition, paired finches given saline had a significantly stronger preference for their partner's song than unpaired females given saline ($P = 0.03$) and unpaired females given the D1R agonist SKF-38392 ($P = 0.03$). Taken together, these data indicate that D2Rs are both necessary and sufficient for song preference in female finches.

Drug application does not change finch activity

The increase in song preference could be due to a change in motor activity in females as D2R can result in increased motor behavior

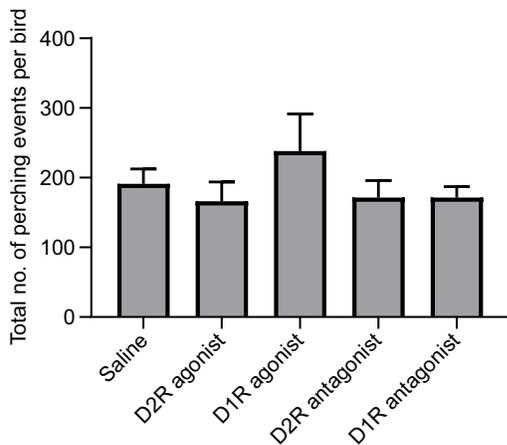


Fig. 3. Drug injection does not change the number of perching events.

The total number of times (mean ± s.e.m.) females in each treatment group landed on the two perches during the 2 h test trial (no song playback+song playback). The saline group includes both unpaired and paired females injected with saline.

(Cousins and Salamone, 1996; Gadagkar et al., 2016; Howe and Dombeck, 2016). To test whether injection of any drug changed motor activity in females, we compared the total number of times each female landed on the two perches during the operant task, combining the number of perching events in both silence and playback (Fig. 3). Overall, there was no significant difference in the average number of perching events per bird between any group (one-way ANOVA, $F_{4,41}=0.82$, $P=0.52$), suggesting the increase in song preference after injection of the D2R agonist was not due to an increase in motor activity.

Taken together, we found that systemic injection of a D2R agonist, but not a D1R agonist, induced a song preference in unpaired females. In addition, injection of a D2R antagonist abolished song preference in paired female finches. Paired females injected with a D1R antagonist still showed a preference for their partner's song, presumably as a result of the continued activation of D2Rs. Taken together, these data indicate that D2Rs are both necessary and sufficient for song preference in female finches. These results are similar to those seen in other monogamous species, including voles and titi monkeys (Hostetler et al., 2017; Walum and Young, 2018; Young and Wang, 2004). Both voles and titi monkeys show an increase in D1Rs in paired animals; however, there may be some differences in the mechanisms of maintenance of partner preference across species (Walum and Young, 2018). Future studies will need to more directly test the role of D1R activation in partner formation in finches. Our song preference behavioral assay provides a robust experimental framework in which to examine the mechanisms by which dopamine and other neurotransmitter and/or neurohormone systems contribute to song preference and mate selection.

Location of dopamine action in formation of song preference

In male finches, D2Rs are primarily localized to the striatum, ventral tegmental area, substantia nigra pars compacta and midbrain central gray (Kubikova et al., 2010). The anatomical distribution of dopamine receptors in female finches has not been well characterized. Using positron-emission tomography (PET), Tokarev et al. (2017) found activation of D2Rs in the striatum of female finches in response to presentation of their partner's song.

Banerjee et al. (2013) measured an increase in dopamine and its metabolite 3,4-dihydroxyphenylacetic acid (DOPAC) in the ventral medial striatum in newly paired female finches. These studies and others (Alger et al., 2011; Goodson et al., 2009; Iwasaki et al., 2014) suggest that dopamine influences female song preference via striatal circuitry.

The mechanisms by which dopamine might act in the striatum to influence song preference are not known. The mesolimbic dopamine system is implicated in salience and reward-based processes, particularly reward learning (Goodson et al., 2009; Schultz, 2004). Dopamine, acting through D2Rs in the striatum, could act as a reinforcement signal and attach a positive association to the male's song as the pair bond develops. Consistent with this idea, we found that blocking D2Rs, but not D1Rs, in paired females blocked song preference. D2R blockade could disrupt the rewarding association that the female had developed for her partner's song, resulting in this lack of song preference. Additional experiments will test the combinatorial effects of D1Rs and D2Rs, and the influence of different drug concentrations on song induction. In addition, future work will identify specific regions within the mesolimbic dopamine pathway or social behavior network critical for song preference and pair bonding. With this behavioral test we can deliver D1R or D2R agonists or antagonists (separately or together) directly to identified brain regions to test their role in the induction and maintenance of song preference.

Induction versus maintenance of song preference

Although we have shown that antagonizing D2Rs reduces song preference, the contribution of dopamine to the maintenance of song preference most likely differs from the induction of preference. For example, in voles, D1Rs have been implicated in the maintenance of partner preference by increasing selective aggression, perhaps to prevent additional pair formation (Aragona et al., 2006). Future experiments will address the neural mechanisms by which dopamine and other neurotransmitter systems influence the maintenance of song preference. Untangling this important and complex behavior will require understanding not only of the individual neural networks but also of the interaction between the networks.

In conclusion, we used an operant conditioning paradigm to show that activation of D2Rs is important for the formation and maintenance of song preference for a mate. These data will contribute to our understanding of the evolution and mechanisms of a social behavior network shared by most vertebrates (O'Connell and Hofmann, 2011b; Young et al., 2019).

Acknowledgements

We thank Petra Grutzik for construction of the behavioral cage, Isaiah Alba and Amelia Gagliuso for help with data collection, Drs E. Ferree and D. Smith for help with statistical analyses, Dr Zachary Burkett for comments on the manuscript, and Dr Stephanie White for her generous support.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.S., A.R., C.K., M.J.C.; Methodology: N.F.D., D.S., A.R.; Formal analysis: N.F.D., D.S., L.H., M.J.C.; Investigation: D.S., A.R., L.H., E.N., N.S.-M., K.S., J.S., N.L., M.B.; Resources: M.J.C.; Writing - original draft: N.F.D., D.S., M.J.C.; Writing - review & editing: N.F.D., C.K., M.J.C.; Visualization: N.F.D., M.J.C.; Supervision: N.F.D., M.J.C.; Funding acquisition: M.J.C.

Funding

Funding was provided by a Howard Hughes Medical Institute undergraduate summer research grant [HHMI no. 30052007536 to D.S. and L.H.].

Data availability

Data are available from the Dryad Digital Repository (Day et al., 2019): <https://doi.org/10.5061/dryad.pc27th6>.

References

- Adkins-Regan, E.** (2009). Neuroendocrinology of social behavior. *ILAR J.* **50**, 5-14.
- Alger, S. J., Juang, C. and Ritters, L. V.** (2011). Social affiliation relates to tyrosine hydroxylase immunolabeling in male and female zebra finches (*Taeniopygia guttata*). *J. Chem. Neuroanat.* **42**, 45-55.
- Aragona, B. J., Liu, Y., Curtis, J. T., Stephan, F. K. and Wang, Z.** (2003). A critical role for nucleus accumbens dopamine in partner-preference formation in male prairie voles. *J. Neurosci.* **23**, 3483-3490.
- Aragona, B. J., Liu, Y., Yu, Y. J., Curtis, J. T., Detwiler, J. M., Insel, T. R. and Wang, Z.** (2006). Nucleus accumbens dopamine differentially mediates the formation and maintenance of monogamous pair bonds. *Nat. Neurosci.* **9**, 133-139.
- Bales, K. L., Arias Del Razo, R., Conklin, Q. A., Hartman, S., Mayer, H. S., Rogers, F. D., Simmons, T. C., Smith, L. K., Williams, A., Williams, D. R. et al.** (2017). Titi monkeys as a novel non-human primate model for the neurobiology of pair bonding. *Yale J. Biol. Med.* **90**, 373-387.
- Balthazart, J., Castagna, C. and Ball, G. F.** (1997). Differential effects of D1 and D2 dopamine-receptor agonists and antagonists on appetitive and consummatory aspects of male sexual behavior in Japanese quail. *Physiol. Behav.* **62**, 571-580.
- Banerjee, S. B., Dias, B. G., Crews, D. and Adkins-Regan, E.** (2013). Newly paired zebra finches have higher dopamine levels and immediate early gene Fos expression in dopaminergic neurons. *Eur. J. Neurosci.* **38**, 3731-3739.
- Cockburn, A.** (2006). Prevalence of different modes of parental care in birds. *Proc. R. Soc. B* **273**, 1375-1383.
- Cousins, M. S. and Salamone, J. D.** (1996). Involvement of ventrolateral striatal dopamine in movement initiation and execution: a microdialysis and behavioral investigation. *Neuroscience* **70**, 849-859.
- Day, N. F., Saxon, D., Robbins, A., Harris, L., Nee, E., Shroff-Mehta, N., Stout, K., Sun, J., Lillie, N., Burns, M., Korn, C. and Coleman, M. J.** (2019). Data from: D2 dopamine receptor activation induces female preference for male song in the monogamous zebra finch. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.pc27th6>.
- Feldman, R.** (2017). The neurobiology of human attachments. *Trends Cogn. Sci.* **21**, 80-99.
- Gadagkar, V., Puzerey, P. A., Chen, R., Baird-Daniel, E., Farhang, A. R. and Goldberg, J. H.** (2016). Dopamine neurons encode performance error in singing birds. *Science* **354**, 1278-1282.
- Gess, A., Schneider, D. M., Vyas, A. and Woolley, S. M. N.** (2011). Automated auditory recognition training and testing. *Anim. Behav.* **82**, 285-293.
- Gil, D. and Gahr, M.** (2002). The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* **17**, 133-141.
- Goodson, J. L., Lindberg, L. and Johnson, P.** (2004). Effects of central vasotocin and mesotocin manipulations on social behavior in male and female zebra finches. *Horm. Behav.* **45**, 136-143.
- Goodson, J. L., Kabelik, D., Kelly, A. M., Rinaldi, J. and Klatt, J. D.** (2009). Midbrain dopamine neurons reflect affiliation phenotypes in finches and are tightly coupled to courtship. *Proc. Natl. Acad. Sci. USA* **106**, 8737-8742.
- Heston, J. B., Simon, J. T., Day, N. F., Coleman, M. J. and White, S. A.** (2018). Bidirectional scaling of vocal variability by an avian cortico-basal ganglia circuit. *Physiol. Rep.* **6**, e13638.
- Hostetler, C. M., Harkey, S. L., Krzywosinski, T. B., Aragona, B. J. and Bales, K. L.** (2011). Neonatal exposure to the D1 agonist SKF38393 inhibits pair-bonding in the adult prairie vole. *Behav. Pharmacol.* **22**, 703-710.
- Hostetler, C. M., Hinde, K., Maninger, N., Mendoza, S. P., Mason, W. A., Rowland, D. J., Wang, G. B., Kukis, D., Cherry, S. R. and Bales, K. L.** (2017). Effects of pair bonding on dopamine D1 receptors in monogamous male titi monkeys (*Callicebus cupreus*). *Am. J. Primatol.* **79**, e22612.
- Howe, M. W. and Dombeck, D. A.** (2016). Rapid signalling in distinct dopaminergic axons during locomotion and reward. *Nature* **535**, 505.
- Iwasaki, M., Poulsen, T. M., Oka, K. and Hessler, N. A.** (2014). Sexually dimorphic activation of dopaminergic areas depends on affiliation during courtship and pair formation. *Front. Behav. Neurosci.* **8**, 210.
- Kabelik, D., Kelly, A. M. and Goodson, J. L.** (2010). Dopaminergic regulation of mate competition aggression and aromatase-Fos colocalization in vasotocin neurons. *Neuropharmacology* **58**, 117-125.
- Klatt, J. D. and Goodson, J. L.** (2013). Oxytocin-like receptors mediate pair bonding in a socially monogamous songbird. *Proc. R. Soc. B* **280**, 20122396.
- Kubikova, L., Wada, K. and Jarvis, E. D.** (2010). Dopamine receptors in a songbird brain. *J. Comp. Neurol.* **518**, 741-769.
- Lack, D. L.** (1968). *Ecological Adaptations for Breeding in Birds*. Chapman & Hall.
- LaPlante, K. A., Huremovic, E. and Tomaszycki, M. L.** (2014). Effects of acute corticosterone treatment on partner preferences in male and female zebra finches (*Taeniopygia guttata*). *Gen. Comp. Endocrinol.* **199**, 33-37.
- Liu, Y. and Wang, Z. X.** (2003). Nucleus accumbens oxytocin and dopamine interact to regulate pair bond formation in female prairie voles. *Neuroscience* **121**, 537-544.
- Lukas, D. and Clutton-Brock, T. H.** (2013). The evolution of social monogamy in mammals. *Science* **341**, 526-530.
- McGraw, L. A. and Young, L. J.** (2010). The prairie vole: an emerging model organism for understanding the social brain. *Trends Neurosci.* **33**, 103-109.
- Murugan, M., Harward, S., Scharff, C. and Mooney, R.** (2013). Diminished FoxP2 Levels Affect Dopaminergic Modulation of Corticostriatal Signaling Important to Song Variability. *Neuron* **80**, 1464-1476.
- O'Connell, L. A. and Hofmann, H. A.** (2011a). Genes, hormones, and circuits: an integrative approach to study the evolution of social behavior. *Front. Neuroendocrinol.* **32**, 320-335.
- O'Connell, L. A. and Hofmann, H. A.** (2011b). The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. *J. Comp. Neurol.* **519**, 3599-3639.
- Pedersen, A. and Tomaszycki, M. L.** (2012). Oxytocin antagonist treatments alter the formation of pair relationships in zebra finches of both sexes. *Horm. Behav.* **62**, 113-119.
- Prior, N. H. and Soma, K. K.** (2015). Neuroendocrine regulation of long-term pair maintenance in the monogamous zebra finch. *Horm. Behav.* **76**, 11-22.
- Schultz, W.** (2004). Neural coding of basic reward terms of animal learning theory, game theory, microeconomics and behavioural ecology. *Curr. Opin. Neurobiol.* **14**, 139-147.
- Tchernichovski, O., Nottebohm, F., Ho, C. E., Pesaran, B. and Mitra, P. P.** (2000). A procedure for an automated measurement of song similarity. *Anim. Behav.* **59**, 1167-1176.
- Tokarev, K., Hyland Bruno, J., Ljubicic, I., Kothari, P. J., Helekar, S. A., Tchernichovski, O. and Voss, H. U.** (2017). Sexual dimorphism in striatal dopaminergic responses promotes monogamy in social songbirds. *eLife* **6**, e25819.
- Tomaszycki, M. L. and Adkins-Regan, E.** (2005). Experimental alteration of male song quality and output affects female mate choice and pair bond formation in zebra finches. *Anim. Behav.* **70**, 785-794.
- Walum, H. and Young, L. J.** (2018). The neural mechanisms and circuitry of the pair bond. *Nat. Rev. Neurosci.* **19**, 643-654.
- Wang, Z., Yu, G., Cascio, C., Liu, Y., Gingrich, B. and Insel, T. R.** (1999). Dopamine D2 receptor-mediated regulation of partner preferences in female prairie voles (*Microtus ochrogaster*): a mechanism for pair bonding? *Behav. Neurosci.* **113**, 602-611.
- Wild, J. M. and Botelho, J. F.** (2015). Involvement of the avian song system in reproductive behaviour. *Biol. Lett.* **11**, 20150773.
- Woolley, S. C. and Doupe, A. J.** (2008). Social context-induced song variation affects female behavior and gene expression. *PLoS Biol.* **6**, e62.
- Xiao, L., Chatree, G., Oscos, F. G., Cao, M., Wanat, M. J. and Roberts, T. F.** (2018). A basal ganglia circuit sufficient to guide birdsong learning. *Neuron* **98**, 208-221.e5.
- Yazaki-Sugiyama, Y., Yanagihara, S., Fuller, P. M. and Lazarus, M.** (2015). Acute inhibition of a cortical motor area impairs vocal control in singing zebra finches. *Eur. J. Neurosci.* **41**, 97-108.
- Young, L. J. and Wang, Z.** (2004). The neurobiology of pair bonding. *Nat. Neurosci.* **7**, 1048-1054.
- Young, K. A., Gobrogge, K. L., Liu, Y. and Wang, Z.** (2011). The neurobiology of pair bonding: Insights from a socially monogamous rodent. *Front. Neuroendocrinol.* **32**, 53-69.
- Young, R. L., Ferkin, M. H., Ockendon-Powell, N. F., Orr, V. N., Phelps, S. M., Pogany, A., Richards-Zawacki, C. L., Summers, K., Szekely, T., Trainor, B. C. et al.** (2019). Conserved transcriptomic profiles underpin monogamy across vertebrates. *Proc. Natl. Acad. Sci. USA* **116**, 1331-1336.
- Zann, R.** (1994). Reproduction in a zebra finch colony in south-eastern Australia: the significance of monogamy, precocial breeding and multiple broods in a highly mobile species. *Emu* **94**, 285-299.
- Zann, R.** (1996). *Zebra Finch: A Synthesis of Laboratory and Field Studies*. New York: Oxford University Press.