

Sex steroids modulate changes in social and sexual preference during juvenile development in zebra finches

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Abstract

Zebra finches, like many other animals, have close social relationships mainly with the family at young ages but begin to express interest in opposite-sex extra-family animals as they enter the late juvenile period and sexual maturity. This experiment tested a set of hypotheses that sex steroids are involved in this developmental transition. At 25–30 days, subjects were implanted subcutaneously with Silastic tubes that were empty (controls), filled with testosterone propionate, filled with estradiol benzoate, or filled with a combination of ATD (an aromatization inhibitor) and flutamide (an anti-androgen). Once a week between ages 30 and 90 days, they were given three-choice tests where the three stimulus types were the family members, unpaired males, or unpaired females. The preferred category was defined as the one adjacent to the proximity zone in which the subject spent the most time. Control males were more likely to prefer females and less likely to prefer the family as they got older, and control females were increasingly likely to prefer males. Males treated with testosterone or estradiol showed a premature increase in preferences for females. Females treated with ATD plus flutamide failed to show the normal increase in preferences for males shown by controls. These results indicate an involvement of sex steroids in the maturation of sexual preferences in a socially monogamous species that relies on visual and auditory, rather than olfactory, cues for sexual or other social behavior.

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Introduction

In many species of mammals, birds, and other animals with parental care, the young initially interact mainly or exclusively with their family members (parents and siblings). Later in development, these social bonds may cease to exist. When this coincides with the onset of sexual maturity, it is logical to hypothesize that activational effects of sex steroid hormones might be involved in the change in social interest from family members to non-family members, especially potential mating partners. There appear to have been few positive experimental tests of this hypothesis. In chickens, it has been shown that male chicks imprinted to a rubber ball (a hen surrogate) increasingly detach from it beginning at age 5–7 weeks because of an increase in circulating testosterone (Gvoryahu et al., 1986).

Observations of zebra finches (*Taeniopygia guttata*) in both laboratory and field suggest an interesting shift in social preferences and relationships during juvenile development (Immelmann, 1972; Zann, 1996). This species is gregarious and breeds colonially. Adults are socially monogamous, forming a behaviorally exclusive relationship with an opposite-sex bird at the onset of sexual maturity, which occurs at 60–90 days post-hatching age depending on sex, genotype, and environmental conditions (Zann, 1996). This relationship is characterized by constant physical proximity (the pair is never very far apart), frequent vocal interaction, and several contact behaviors, including clumping (perching in contact), allopreening (mutual grooming), and spending long periods of time in a nest box together. The young remain dependent on parental feeding until at least 35 days, continue to roost with the parents until at least 48 days, and engage in the same contact behaviors with them as do paired adults (Zann, 1996). Thereafter the young spend more time roosting with other young birds. Thus, young birds transition from a nearly exclusive close relationship with the family to an increasing interest in opposite-sex birds and soon

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thereafter to an adult pair relationship. Much of the contact behavior remains the same, but the objects for it change from the parents and siblings to the pair bond partner. In the language of attachment theory, social development is marked by a change in the attachment objects, not the attachment process itself (Zeifman and Hazan, 1997). The new attachment object is a female in the case of a male bird and a male in the case of a female bird, the sex-typical adult sexual and pairing preferences.

Again, it is logical to hypothesize that changing sex hormone levels during late juvenile development as sexual maturity approaches might be producing these developmental changes in social and sexual preference. Nonetheless, there are reasons to be cautious in assuming that this hypothesis is correct. First, in zebra finches that have already reached adulthood (birds that are 100 days old or more), the preference for opposite-sex partners (sexual partner preference) does not seem to be very sensitive to changes in sex steroid levels. Adults that are gonadectomized and given hormone implants consisting of estradiol (for males) or testosterone (for females) still show the normal sex-typical preferences (Adkins-Regan and Ascenzi, 1987). In other species as well, there is little evidence that sexual partner preference is subject to significant activational hormone effects (Adkins-Regan, 1988). For example, male rats in approach tests with a choice of male or female stimuli begin to show a preference for females as they become sexually mature, but so do neonatally castrated males, though their preference is less strong (Eliasson and Meyerson, 1981). Sexual partner preference is strongly sexually dimorphic, but hormonal organization earlier in development seems to be responsible (Bakker, 2003). Second, experimentally elevating or reducing sex steroid action in unpaired adult zebra finches has no effect on their pairing behavior, interest, or success (Hill et al., 2005; Tomaszycski et al., 2006). Third, during zebra finch development circulating sex steroid levels (testosterone, dihydrotestosterone, estradiol) are substantial (close to adult levels), show little change between fledging and age 54 days, and are similar in the sexes during this period (Adkins-Regan et al., 1990). It is unclear if there is an increase in estradiol in either sex between 54 days and sexual maturity, but Pröve (1983) did report a rise in testosterone in males at age 74 days.

If sex steroid hormones have any activational role in pairing interest and sexual partner preference, the most likely time for it would be during the late juvenile period when this interest begins. That is the hypothesis tested here. The predictions are as follows: (1) experimentally elevating sex steroid levels in juvenile males will cause a premature interest in females and possibly a reduction of interest in the family as well; (2) elevating sex steroid levels in juvenile females will cause a premature interest in males and possibly a reduction of interest in the family; and (3) lowering sex steroid action in juveniles will prevent the onset of sexual partner preference and may cause preferences to remain family-oriented beyond the normal age.

To test these predictions, birds were treated via implants and tested beginning at an early age (25 to 30 days), to give the treatment time to work and to allow detection of a premature change in preference. Treatment continued throughout the juvenile period. The method chosen to lower sex steroid action

was to administer a combination of ATD (1,4,6-androstatrien-3,17-dione), an estrogen synthesis inhibitor, and flutamide, an anti-androgen, interfering with both of the established pathways for sex steroid action on behavior. This combination has been used successfully in a diverse array of birds to reduce sex steroid modulated behavior (e.g., Canoine and Gwinner, 2002; Hau et al., 2000; Van Duyse et al., 2005), and both ATD and flutamide are effective in zebra finches (Bottjer and Hewer, 1992; Tomaszycski et al., 2006; Walters and Harding, 1988). Although fadrozole is a more effective estrogen synthesis inhibitor than ATD in this species (Wade et al., 1994), it is water soluble and not well suited to methods of administration that need to last for weeks. Birds were not gonadectomized because gonadectomy does not change the level of circulating estradiol, which is produced in the brain, is substantial in males as well as females throughout development, and is critical for male reproductive behavior (Adkins-Regan et al., 1990; Schlinger and Arnold, 1992; Walters and Harding, 1988).

Preferences for conspecifics were assessed weekly from 30 to 90 days in three-choice proximity tests with males, females, and the family as the three choices. Proximity is a valid indicator of family and sexual/pairing interest in this species, because these relationships are marked by close physical proximity (Clayton, 1990).

Methods

Animals

All subjects were hatched in the laboratory colony in wire cages (61 × 36 × 41 cm) each containing a single breeding pair that produced one clutch. Subjects lived with their parents and siblings in this cage throughout the experiment. Those that developed white or pied plumage were not included in the experiment. Birds used as unpaired male and female stimuli also had wild-type plumage, were currently unpaired, and were housed in all-male or all-female cages. They had previously been stimuli in other experiments, gaining sexual experience for periods of one or more weeks.

All birds were housed on a 14L:10D light:dark cycle and fed mixed seeds supplemented with hard-boiled egg and greens. All animal procedures were approved by the Cornell University IACUC.

Juvenile treatments

At 25–27 days of age, each subject was banded (avoiding band colors that are preferred or avoided by other birds; Burley et al., 1982), assigned to one of four treatment groups, and implanted accordingly. The groups were: (1) control, (2) testosterone, (3) estradiol, or (4) ATD plus flutamide (ATD+F). Birds in the same clutch were assigned to different treatment groups such that across clutches group assignment was unrelated to hatching order. All subjects were given two subcutaneous Silastic implants (2 mm outer diameter, 1.5 mm inner diameter), one on each side near the flank. Prior to making the small incisions for inserting the implants, the skin at each implant site was numbed with an injection of 4 µl of 2% lidocaine HCl. Birds in the control group received two 10-mm long empty implants. Birds in the testosterone group received one empty 10-mm long implant and one 8-mm implant filled with testosterone propionate (Sigma Chemical Co.). Birds in the estradiol group received one empty 10-mm implant and one 2-mm implant filled with estradiol benzoate diluted 1:2 with cholesterol (Sigma Chemical Co.). Birds in the ATD+F group received one 10-mm implant filled with ATD (1,4,6-androstatrien-3,17-dione, ResearchPlus) and one 10-mm implant filled with flutamide (both from Sigma Chemical Co.). Implants were soaked in saline for 24 h before insertion. Implants were checked once a week to confirm that they were still in place (and replaced, if one had fallen out), and all

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