

Swarthmore College

Works

Biology Faculty Works

Biology

5-14-2021

Social Communication Across Reproductive Boundaries: Hormones And The Auditory Periphery Of Songbirds And Frogs

M. D. Gall

Alexander T. Baugh
Swarthmore College, abaugh1@swarthmore.edu

J. R. Lucas

See next page for additional authors

Follow this and additional works at: <https://works.swarthmore.edu/fac-biology>



Part of the [Biology Commons](#)

[Let us know how access to these works benefits you](#)

Recommended Citation

M. D. Gall, Alexander T. Baugh, J. R. Lucas, and M. A. Bee. (2021). "Social Communication Across Reproductive Boundaries: Hormones And The Auditory Periphery Of Songbirds And Frogs". *Integrative And Comparative Biology*. DOI: 10.1093/icb/icab075
<https://works.swarthmore.edu/fac-biology/624>

This work is brought to you for free by Swarthmore College Libraries' Works. It has been accepted for inclusion in Biology Faculty Works by an authorized administrator of Works. For more information, please contact myworks@swarthmore.edu.

Authors

M. D. Gall, Alexander T. Baugh, J. R. Lucas, and M. A. Bee

1
2
3 **Title:** Social communication across reproductive boundaries: hormones and the auditory
4
5 periphery of songbirds and frogs
6

7
8 **Title:** Hormones, the auditory periphery, and social communication
9

10 **Megan D. Gall^{1†}, Alexander T. Baugh², Jeffrey R. Lucas³, Mark A. Bee^{4,5}**
11

12 ^{1†} Department of Biology, Vassar College, 124 Raymond Ave, Poughkeepsie, NY, 12604, USA
13

14 ² Department of Biology, Swarthmore College, 500 College Avenue, Swarthmore, PA, 19081,
15
16 USA
17

18 ³Department of Biological Sciences, Purdue University, West Lafayette, IN 65203
19

20 ⁴ Department of Ecology, Evolution, and Behavior, University of Minnesota, 1479 Gortner Ave,
21
22 St. Paul, MN, 55108, USA
23

24 ⁵Graduate Program in Neuroscience, University of Minnesota, 321 Church Street SE,
25
26 Minneapolis, MN, 55455, USA
27

28
29
30
31
32
33 † Corresponding Author email: megall@vassar.edu, phone: 845-437-7115
34

35 36 **Acknowledgements:**

37
38 We would like to acknowledge the contributions of Walter Wilczynski to the field, as well as his
39
40 mentorship and inspiration. Funding was provided by an NSF doctoral dissertation improvement
41
42 grant (IOS-1109677), an Animal Behavior Society graduate student research award, the Society
43
44 for Integrative and Comparative Biology, and the Company of Biologists. All experiments were
45
46 approved under Purdue IACUC # 1111000125.
47
48
49
50
51
52
53
54
55
56

ABSTRACT

Most animals experience reproductive transitions in their lives; for instance, reaching reproductive maturity or cycling in and out of breeding condition. Some reproductive transitions are abrupt, while others are more gradual. In most cases, changes in communication between the sexes follow the time course of these reproductive transitions and are typically thought to be coordinated by steroid hormones. We know a great deal about hormonal control of communication behaviors in birds and frogs, as well as the central neural control of these behaviors. There has also been significant interest in the effects of steroid hormones on central nervous system structures that control both the production and reception of communication signals associated with reproductive behaviors. However, peripheral sensory structures have typically received less attention, although there has been growing interest in recent years. It is becoming clear that peripheral sensory systems play an important role in reproductive communication, are plastic across reproductive conditions, and, in some cases, this plasticity may be mediated by steroid hormones. In this paper, we discuss recent evidence for the role of peripheral auditory structures in reproductive communication in birds and frogs, the plasticity of the peripheral auditory system, and the role of steroid hormones in mediating the effects of the peripheral auditory system on reproductive communication. We focus on both seasonal and acute reproductive transitions, introduce new data on the role of hormones in modulating seasonal patterns, and make recommendations for future work.

Keywords: seasonality, reproduction, communication, hearing, anurans, birds

INTRODUCTION

Communication systems show seasonal plasticity (within-individual variation in behavior or physiology, irrespective of the possible functional implications of that variability) in many seasonally breeding animals. This within-individual plasticity is evidenced in both the production and reception of communication signals (songbirds: Catchpole and Slater 2008; fish: Webb et al. 2008; frogs: Ryan 2001). Temperate songbirds and frogs have served as the two main models for investigations of vocal communication. In these taxa, male production of mate attraction vocalizations increases during the breeding season and is accompanied by hormonal and neural changes (Kroodsma and Miller 1982; Itoh and Ishii 1990). Female responses to male vocalizations in both birds and frogs also show plasticity and are tightly correlated with current reproductive condition (Arch and Narins 2009; Maney and Pinaud 2011). Animals can also experience acute reproductive transitions, such as those associated with oviposition, where females rapidly (< 24 hours) transition from a breeding to a non-breeding condition. These transitions are often accompanied by dramatic changes in the receptivity of females to male communication signals (Lynch et al. 2005; Gall et al. 2019). Mounting evidence suggests that these behavioral changes are accompanied by plasticity in peripheral auditory processing in birds and frogs (Lucas et al. 2002; 2007; Henry and Lucas 2009; Caras et al. 2010; Zhang et al. 2012; Gall et al. 2013). However, our understanding of the mechanisms responsible for these reproductively-related changes in auditory processing is relatively limited. The role of steroid hormones in modulating other aspects of communication, as well as a strong body of work in midshipman and cichlid fish, suggests that steroid hormones may be implicated in modulating peripheral auditory processing (Forlano et al. 2016). In this review, we discuss the current evidence for plasticity in peripheral auditory processing across seasonal and acute reproduction

1
2
3 transitions. We focus primarily on songbirds and frogs, the role of steroid hormones in
4
5 modulating this plasticity (including new data on recapitulation of seasonal patterns by
6
7 exogenous steroid hormones), and possible mechanisms through which hormones may influence
8
9 auditory processing.
10

11
12 Our review covers three aspects of peripheral auditory processing: sensitivity, frequency
13
14 selectivity and temporal resolution. Sensitivity can be described by either the lowest amplitude
15
16 signal that can be detected (e.g. threshold) or the magnitude of the response to signals above this
17
18 threshold. Frequency selectivity, which can be measured in a number of ways, represents the
19
20 ability of the peripheral auditory system to discriminate between two tones close together in
21
22 frequency. Finally, temporal resolution, which can again be measured in many ways, describes
23
24 the ability of the auditory system to discriminate between two sounds that are close together in
25
26 time or the ability to follow rapid temporal fluctuations in sounds. Together, these parameters
27
28 play a role in an animal's ability to detect and discriminate among communication signals and
29
30 are likely important in determining the salience of these signals.
31
32

33 **SEASONAL AND HORMONE-MEDIATED PLASTICITY IN PERIPHERAL** 34 35 **AUDITORY PROCESSING** 36 37

38 *Seasonal differences in the auditory periphery of songbirds* 39

40
41 An understanding of the plasticity in auditory processing has the potential to
42
43 fundamentally change our understanding of communication, particularly with respect to what
44
45 information is extracted from signals, how that information is extracted, and the functional
46
47 implications of changes in information processing. Seasonal variation in the auditory periphery
48
49 of birds was first reported by Lucas et al. in 2002 when they found species-specific seasonal
50
51 changes in the response amplitude of auditory evoked potentials to broadband clicks in three
52
53
54
55

1
2
3 species that form mixed-species flocks during the fall and winter. Specifically, white-breasted
4 nuthatches (*Sitta carolinensis*) had greater response amplitudes (i.e. sensitivity) in the winter and
5
6 Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) had greater
7
8 sensitivity in the spring. Subsequent studies of these three species found similar patterns in the
9
10 processing of the onsets and sustained portions of tones, as well as temporally modulated signals
11
12 (Lucas 2007; Velez et al. 2015). These results suggest that auditory processing abilities reflect
13
14 seasonal changes in the types and information content of vocalizations. Velez et al. (2015) found
15
16 that seasonal processing of both temporally modulated signals and the fine structure of tones was
17
18 sex-specific in chickadees and titmice, suggesting that it may be of particular importance for
19
20 mate choice in females. Songs in both of these species tend to be tonal whereas the call system
21
22 consists of more complex elements - patterns that match season-specific changes in auditory
23
24 processing. Additionally, Henry and Lucas (2009) found that house sparrows (*Passer*
25
26 *domesticus*) showed seasonal differences in their frequency sensitivity, with the greatest effects
27
28 at and above 2 kHz, in the frequency range of male vocalizations. While these studies
29
30 demonstrated seasonal differences in auditory processing, the mechanisms generating these
31
32 differences were not investigated.

33 34 35 36 37 38 39 40 41 *Evidence for steroid hormone effects in the avian auditory periphery*

42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
There has been ample speculation that steroid hormones are involved in the peripheral auditory plasticity of songbirds, but little published work on the subject. The discovery of estrogen receptors and aromatase in the inner ear of zebra finches (*Taeniopygia guttata*, Noirot et al. 2009), suggests that estrogen (either circulating or locally synthesized from testosterone) potentially influences peripheral auditory function. However, only one published study has

1
2
3 explicitly linked the level of circulating sex hormones to the peripheral processing of auditory
4 stimuli in birds (See Caras et al. 2010). The authors found that white-crowned sparrows
5
6 (*Zonotrichia leucophrys*), kept under induced-breeding conditions (i.e. implanted with either
7
8 testosterone in males or estradiol in females and kept on a long-day light cycle), had auditory
9
10 thresholds that were higher than birds kept in non-breeding condition (Caras et al. 2010). This
11
12 study suggests a role for estrogen-mediated changes in the auditory periphery. However, it is
13
14 difficult to extrapolate these results to naturally-occurring seasonal changes because no auditory
15
16 threshold data are currently available for white-crowned sparrows in natural breeding and non-
17
18 breeding conditions. Furthermore, it is not clear whether steroid hormones are involved in the
19
20 plasticity of other aspects of auditory processing in females, such as frequency selectivity or
21
22 temporal resolution. Testosterone did not induce plasticity in frequency selectivity or temporal
23
24 resolution in white-crowned sparrow males, and hormone-manipulated females were not tested
25
26 for these traits (Caras et al. 2010).
27
28
29
30
31

32 33 *Breeding condition induced by exogenous hormones can recapitulate seasonal patterns*

34
35
36 Gall et al. (2013) previously demonstrated that the frequency selectivity (i.e. auditory
37
38 filter bandwidths) and temporal resolution of the peripheral auditory system in house sparrows
39
40 varies seasonally in a sex-specific manner (Figure 1). Specifically, they showed that female
41
42 house sparrows have enhanced frequency resolution (auditory filter bandwidths narrowed) and
43
44 diminished temporal resolution (as measured by response to paired clicks) in the breeding season
45
46 relative to the non-breeding season, while males did not exhibit changes in their auditory
47
48 processing. Previously unpublished work from two of the authors, Gall and Lucas, suggests that
49
50 the reproductive condition induced by steroid hormones may play a role in this seasonal pattern.
51
52
53
54
55
56
57
58
59
60

1
2
3 In the following section we will present the results from this previously unpublished work
4 examining the relationship between exogenous hormone-induced reproductive condition on
5 auditory plasticity, compare the results to the published work on natural seasonal patterns of
6 auditory plasticity (Gall et al. 2013), and discuss these results in the context of the literature on
7 auditory plasticity (Gall et al. 2013), and discuss these results in the context of the literature on
8 house sparrow behavior and endocrinology. The goal of this study was not to determine the
9 specific effects of estradiol, or testosterone, on auditory processing, but rather to recapitulate the
10 seasonal transition in reproductive condition and auditory processing previously found in wild
11 house sparrows. While the administration of hormones did successfully induce a reproductive
12 condition, the hormone levels induced by the manipulation were somewhat different than those
13 found in naturally breeding animals (see Table 1), thus care should be taken with the
14 interpretation of the data, particularly for males. However, as they are currently the only data
15 investigating whether hormone administration can recapitulate season patterns, we feel they are
16 important to discuss.
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32

33 Male and female house sparrows were captured in the non-breeding season and their
34 frequency selectivity and temporal resolution was measured using auditory evoked potentials.
35 Animals were then randomly assigned to a placebo or systemic hormone implant group (males:
36 testosterone; females: 17β -estradiol), housed for three weeks on a 14:10 light cycle, and then re-
37 tested for frequency selectivity and temporal resolution (See ESM for methodological details).
38
39
40
41
42
43
44

45 Implants were successful in elevating hormone levels. Testosterone levels increased in
46 both placebo and testosterone males; however, the increase in testosterone was much greater in
47 males given supplemental testosterone (Table 1). Estradiol levels were elevated in females that
48 were given supplemental hormones but did not increase in females given a placebo implant
49 (Table 1). Secondary sexual characteristics suggested that the hormone manipulation
50
51
52
53
54
55
56
57
58
59
60

1
2
3 successfully brought the animals into breeding condition. All males given supplemental
4 testosterone developed jet-black bills and showed a cloacal protuberance. Bill color in placebo
5 birds ranged from horn to light black. In particular, the bills of males caught earlier in the season
6 (October) did not appear to darken as much as males caught in November, which suggests that
7 individuals with exposure to more short days are more physiologically responsive to the
8 transition to long days in the lab. Males that received a placebo implant showed no sign of
9 cloacal protuberance. All females given supplemental estrogen lost feathers from their lower
10 abdomen (brood patch) while none of the females given a placebo implant lost feathers.
11
12
13
14
15
16
17
18
19
20
21

22 Perhaps more importantly, the hormone manipulations, and thus induced breeding
23 condition, described here resulted in auditory plasticity that largely mirrored the natural seasonal
24 variation Gall et al. (2013) had previously found, suggesting that breeding condition is linked to
25 auditory processing. For frequency selectivity, both males and females with hormone implants
26 showed greater frequency selectivity after treatment. Animals with placebo implants did not
27 exhibit auditory plasticity (Figure 2). Moreover, there were no significant differences between
28 the placebo and hormone groups prior to treatment; however, post-treatment animals with
29 hormone implants had greater frequency selectivity than placebo animals. Temporal resolution
30 mirrored seasonal changes even more closely. Placebo animals did not show plasticity, nor were
31 there differences between the sexes. However, animals treated with hormones showed sex-
32 specific responses, with no plasticity in males and a decrease in temporal resolution following
33 hormone implantation in females (See ESM for full statistical model results).
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48

49 Overall, we found that supplemental hormones that induced changes in reproductive
50 condition could induce auditory plasticity over the course of three weeks. Increased photoperiod
51 alone was insufficient to induce reproductive condition and did not result in an increase in
52
53
54
55
56
57
58
59
60

1
2
3 frequency selectivity or a reduction in temporal resolution in the auditory system over the course
4
5 of three weeks, while administration of supplemental hormones produced a reproductive
6
7 condition and sex-specific plasticity in temporal resolution that matched natural sex-specific
8
9 seasonal plasticity (Gall et al. 2013). However, the changes in frequency selectivity found here
10
11 did not show the sex-specificity that we previously found in natural breeding populations.
12
13

14 Previous cross-sectional data investigating natural seasonal variation in frequency selectivity
15
16 suggested that frequency selectivity increases in females during the breeding season but does not
17
18 change in males. In contrast, data reported herein suggest hormone-induced plasticity occurred
19
20 in both sexes. It is possible that males treated with supplemental testosterone had a surfeit of
21
22 testosterone, beyond the normal breeding levels, which permitted the peripheral auditory system
23
24 to produce a greater amount of estradiol than would usually be produced, resulting in plasticity.
25
26 Alternatively, the combination of hormone treatment and captive housing may have interacted to
27
28 induce plasticity. Our data do not allow us to evaluate these hypotheses, which require further
29
30 testing. Functionally, these changes in peripheral auditory processing may gate the salience of
31
32 conspecific signals or make it easier for females to discriminate between conspecific and
33
34 heterospecific signals, as estradiol has been shown to decrease responsiveness of central auditory
35
36 processing areas to heterospecific signals (Lattin et al. 2017).
37
38
39
40
41

42 The patterns found here likely reflect the reproductive biology of house sparrows in
43
44 temperate regions. Following the breeding season, house sparrows have a short non-breeding
45
46 period (generally September – October) in which gonad development is photorefractory. During
47
48 this time, individuals go through their prebasic molt (Anderson 2006). Photorefractoriness is
49
50 broken after prebasic molt. House sparrows (males in particular) then enter a prolonged slow
51
52 gonadal growth phase (Hegner and Wingfield 1986a-c) in which animals are sensitive to
53
54
55
56
57
58
59
60

1
2
3 stimulatory photoperiods; however, animals are not fully reproductively active during this time.
4
5 Following prebasic molt there is a small surge in gonadal steroid levels and the gonads begin a
6
7 very slow increase in size (generally November – February) that is accompanied by increased
8
9 nest site attendance by males. This increase in testosterone also triggers a slow increase in the
10
11 darkness of male bills. As the spring equinox approaches there is a second and much larger spike
12
13 in steroid hormones that initiates rapid growth of the gonads, after which animals are fully
14
15 reproductively active.
16
17
18

19 In the fall and winter months, steroid hormone levels are still quite low, and, from a
20
21 communication perspective, animals are primarily using signals in flocking, foraging and anti-
22
23 predator contexts. Housing animals caught immediately post-molt on a stimulatory photoperiod
24
25 results in a slow increase in steroid hormones and gonadal growth, such that full reproductive
26
27 condition would not be recovered in three weeks (Riley 1936; Anderson 2006). Indeed, although
28
29 we found evidence of moderately elevated plasma testosterone in placebo males, we did not find
30
31 an increase in estradiol levels in placebo females (as seen in Table 1). Furthermore, secondary
32
33 sexual characteristics did not emerge (cloacal protuberance, brood patch) or show changes
34
35 consistent with the breaking of photorefractoriness (bill color; Hegner and Wingfield 1986a-c). It
36
37 may not be surprising, therefore, that auditory plasticity was not induced by a stimulatory
38
39 photoperiod alone but was induced when exogenous hormones were supplied. However, we
40
41 would expect that prolonged housing on a stimulatory light cycle would be sufficient to induce
42
43 auditory plasticity, if longer exposure to a stimulatory light cycle was sufficient to increase
44
45 circulating levels of gonadal steroids to reproductive levels.
46
47
48
49

50
51 *Seasonal and steroid-related changes in the auditory periphery of anurans*
52
53
54
55
56
57
58
59
60

1
2
3 There is perhaps even less evidence for seasonal changes in the auditory periphery of
4 anuran amphibians. Zhang et al. (2012) found that frequency sensitivity was greater in the
5 breeding season relative to the non-breeding season in Emei music frogs (*Babina daunchina*).
6
7 However, frogs were all captured during the breeding season and held in captivity until the non-
8 breeding season, so it is difficult to determine whether the observed plasticity was due to
9 breeding condition, captivity or both. In green treefrogs (*Hyla cinerea*), seasonal plasticity in
10 peripheral auditory processing has not yet been documented. However, sensitivity to tones and
11 to call-like stimuli masked by preceding calls increases in green treefrogs that have 10 days of
12 experience with conspecific signals, but not random tones (Gall and Wilczynski 2015; 2016),
13 suggesting the peripheral auditory system is plastic. This type of exposure to conspecific signals
14 also elevates circulating levels of steroid hormones in several species of frogs (Wilczynski and
15 Burmeister 2016), suggesting that hormones could play a role in this peripheral plasticity.
16
17 Steroid hormones have been implicated in sex-specific peripheral auditory sensitivity to the
18 spectral features of conspecific calls in African clawed frogs, *Xenopus* (Hall et al. 2016).
19
20 Females in four species of *Xenopus* had greater peripheral sensitivity than males.
21
22 Ovariectomized *X. laevis* females had male-like tuning, while ovariectomized females treated
23 with dihydrotestosterone retained female-like tuning. Although these results do not directly
24 implicate steroid hormones in seasonal or reproductively-related plasticity, they do suggest that
25 peripheral auditory tuning is sensitive to endocrine state in some frogs.
26
27

28 **ACUTE REPRODUCTIVE TRANSITIONS AND HORMONE-MEDIATED**

29 **PLASTICITY IN PERIPHERAL AUDITORY PROCESSING**

30
31 Although seasonal changes have been the primary focus of work on auditory plasticity,
32 one of the most dramatic changes in behavioral responses to acoustic communication signals
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

occurs during the rapid transition from a breeding to non-breeding condition that occurs following oviposition (Lynch et al. 2005; Gall et al. 2019). Following oviposition, female response to conspecific calls decreases dramatically. In the tropical túngara frog (*Physalaemus pustulosus*) both receptivity (i.e. likelihood of approaching an advertisement signal) and permissiveness (i.e. likelihood of approaching a heterospecific signal) increase dramatically at reproductive competence (Baugh and Ryan 2010) and decrease in post-mated females, although a small number of post-mated females continue to respond to male calls (Lynch et al. 2005). In the temperate Cope's gray treefrog (*Hyla chrysoscelis*) all post-mated females failed to respond to conspecific male calls or discriminate between conspecific and heterospecific calls (Gall et al. 2019). Similarly, circulating levels of gonadal and adrenal steroid hormones decline dramatically following breeding (Harvey et al. 1997; Lynch and Wilczynski 2005; Gall et al. 2019), which appears to cause rapid post mating behavior shifts. Based on these previous findings, it would be natural to predict that peripheral sensitivity should decrease following oviposition. However, in two recent studies of Cope's gray treefrogs, we found that peripheral auditory sensitivity was greater in post-oviposition females than in pre-oviposition females (Gall et al. 2019, Baugh et al. 2019). First, we found that post-oviposition females had lower threshold and greater suprathreshold responses to tonebursts designed to mimic the population average spectral components of conspecific calls (Gall et al. 2019). Circulating levels of estradiol, testosterone and corticosterone were also significantly lower in the post-oviposition females as compared to the pre-oviposition females. We found some evidence that circulating hormone levels were correlated with suprathreshold responses, but not thresholds. In particular, we found that in pre-oviposition females, suprathreshold sensitivity decreased with increasing levels of estradiol, while in post-oviposition females sensitivity increased with increasing levels of estradiol. This

1
2
3 may suggest that there is a non-linear relationship between auditory sensitivity and circulating
4 levels of estradiol, with intermediate levels leading to the greatest sensitivity. Second, we found
5 frequency-specific changes in frequency sensitivity, with post-oviposition females being more
6 sensitive than pre-oviposition females, particularly at frequencies corresponding to the
7 amphibian papilla, one of the two sensory organs in the frog's inner ear sensitive to airborne
8 sound (Baugh et al. 2019). Again, thresholds did not appear to be correlated with circulating
9 levels of hormones, but we found that suprathreshold sensitivity was positively correlated with
10 increasing levels of testosterone.
11
12
13
14
15
16
17
18
19
20

21
22 There are at least three explanations for these findings. First, both reproductive condition
23 and circulating hormone level were included in the statistical model, so reproductive condition
24 may explain some of the same variance in auditory sensitivity that is explained by circulating
25 hormone levels. The second is that peripheral auditory sensitivity may vary in a non-linear or
26 asymptotic manner that was not captured in our linear model. Finally, changes in peripheral
27 processing associated with oviposition may not result from acute changes in circulating levels of
28 steroid hormones. For instance, the changes we found are consistent with temporary threshold
29 shifts resulting from high levels of noise (such as those encountered in a chorus environment)
30 although anurans seem more resistant to this phenomenon than mammals (Zelick and Narins
31 1985; Penna and Narins 1989; Simmons et al. 2014). It is also possible that other hormones or
32 neuromodulators may mediate these rapid changes in peripheral sensitivity. Pharmacological
33 experiments, sound exposure experiments, or ideally a combination of both would allow us to
34 further investigate these alternative hypotheses. Functionally, it is intriguing to consider the
35 speculative hypothesis that these paradoxical results reflect an adaptive plasticity; for example,
36 female auditory sensitivity during peak reproductive competence may be dampened because it
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55

1
2
3 mitigates against a hyper-stimulated proceptivity and resultant impulsivity during mate choice in
4
5 favor of a more protracted mate sampling effort (c.f. sexual conflict).
6
7

8 9 10 **MECHANISMS THROUGH WHICH STEROID HORMONES MAY ALTER** 11 12 **PERIPHERAL AUDITORY FUNCTION** 13

14
15 Steroid hormones may act directly on the auditory system to induce plasticity, or steroid
16 hormones may act on auditory plasticity indirectly through some intermediate physiological
17 mechanism. In frogs and songbirds, we do not yet have any experimental investigations of the
18 mechanisms by which steroid hormones might mediate peripheral auditory plasticity. However,
19 work on hormonally-mediated plasticity of the central auditory system of songbirds and frogs, as
20 well as work on the hormonally-mediated plasticity of the peripheral auditory system of fish,
21 suggest several possibilities.
22
23
24
25
26
27
28
29

30
31 In the central auditory system, estradiol can influence auditory function over several time
32 scales (Caras and Remage-Healey 2016). Estradiol has rapid neuromodulatory function in the
33 auditory cortex (NCM) of zebra finches, increasing responsiveness to conspecific signals.
34
35 Conversely, local levels of neuroestradiol are elevated by stimulation with conspecific song
36 (Tremere et al. 2009, Remage-Healey et al. 2010, 2012). These rapid effects are thought to be
37 regulated by non-traditional estrogen receptors on neuronal membranes (Yoder and Vicario
38 2011). Systemic estrogen can also alter neural function, presumably acting through nuclear
39 estrogen receptors (e.g. ER α) to produce genomic effects (Maney et al. 2006, Yoder and Vicario
40 2011). For instance, female white-throated sparrows implanted with estradiol show increased
41 activation of cortical auditory areas in response to conspecific song compared to females
42 implanted with a placebo (Maney et al. 2008). In several species of frog, seasonal changes have
43
44
45
46
47
48
49
50
51
52
53
54
55

1
2
3 been documented in the torus semicircularis, a midbrain auditory center with a high density of
4 gonadal hormone receptors (Chakraborty and Burmeister 2010; O'Connell et al. 2011), including
5 fire bellied toads (*Bombina bombina*; Walkowiak 1980), Cope's gray treefrogs (Hillary 1984)
6 and northern leopard frogs (*Rana pipiens*; Goense and Feng 2005). In green treefrogs, there are
7 differences in multi-unit responses from the torus semicircularis in mated and unmated females,
8 as well as differences that result from the administration of testosterone (Miranda and
9 Wilczynski 2009a; b). Furthermore, treatment with hCG or estrogen enhances the expression of
10 the immediate early gene *egr-1* in the torus semicircularis of female túngara frogs, both to
11 conspecific vocalizations and in silence (Lynch and Wilczynski 2008; Chakraborty and
12 Burmeister 2015). This pattern in response to hormone manipulation recapitulates the
13 ontogenetic pattern in behavior and *egr-1* activation in this species (Baugh and Ryan 2010;
14 Baugh et al. 2012)

15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31 Estradiol may also be important in modulating auditory function at the periphery, as ER α
32 (estrogen receptor alpha) and aromatase have been found in the inner ear of songbirds (Noirot et
33 al. 2009), although it is currently unknown whether these receptors are present in the auditory
34 end organs of frogs. It is also not currently known whether estrogen receptors (nuclear or non-
35 traditional) are present in the auditory nerve or brainstem of songbirds, so it is unclear what role
36 estrogen action could have on these areas. Gonadal hormone receptors have not typically been
37 found in the auditory forebrain or hindbrain of frogs (Wilczynski and Burmeister 2016).
38 Similarly, some songbird auditory forebrain and midbrain areas appear to be lacking estrogen
39 receptors and aromatase (Maney and Pinaud 2011). Yet, neural function in these areas is altered
40 by systemic estrogen implants, suggesting estrogen-mediated feed-forward effects from the
41 auditory periphery or descending effects from higher-order auditory areas that are sensitive to
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 estrogen (Maney and Pinaud 2011). Therefore, even if steroid hormone receptors are not found
4
5 in the auditory end organs, there may still be efferent modulation that is sensitive to endocrine
6
7 state.
8
9

10 There are several mechanisms by which hormones have been shown to regulate
11
12 peripheral auditory processing in fish, which could potentially operate in songbirds and frogs.
13
14 Plainfin midshipman fish (*Porichthys notatus*), for example, show enhanced phase-locking in
15
16 their auditory nerve during the breeding season and this effect can be mimicked with estrogen
17
18 manipulations (Sisneros et al. 2004; Sisneros 2009). Hair cells also show steroid-dependent
19
20 sensitivity to tones (Rohmann and Bass 2011). These changes in sensitivity may be due to the
21
22 addition of hair cells to the saccule during the breeding season (Coffin et al. 2012). Songbirds are
23
24 capable of regenerating hair cells after damage (Marean et al. 1998; Woolley and Rubel 2002),
25
26 but it is not yet known whether the addition or replacement of hair cells is a feasible mechanism
27
28 underlying seasonal plasticity in the avian auditory periphery.
29
30
31
32

33 Peripheral auditory plasticity could also be induced by hormone-mediated expression of
34
35 ion channels in hair cells. For instance, splice variants of voltage-gated calcium and calcium
36
37 sensitive big potassium (BK) ion channels play an important role in determining the electrical
38
39 tuning of hair cells in fish (Sugihara and Furukawa 1989; Steinacker and Romero 1992),
40
41 amphibians (Ashmore 1983), reptiles (Jones et al. 1999) and birds (Fuchs et al. 1988). The
42
43 expression of splice variants appears to be influenced by estrogen responsive elements involved
44
45 in transcription of the α -subunit (Zhu et al. 2005; Kundu et al. 2007). Seasonal changes in
46
47 hormone levels could alter estrogen-mediated transcriptional regulation, thereby altering the
48
49 expression of ion channels in the hair cells. This in turn would alter the functional properties of
50
51 the hair cells in response to acoustic stimulation.
52
53
54
55

CONCLUSIONS AND FUTURE DIRECTIONS

There are many open questions to be explored about plasticity of the auditory periphery of songbirds and frogs. Although this review has focused primarily on gonadal steroid hormones, there may be other modulators of peripheral auditory function such as adrenal steroid hormones, catecholamines, serotonin, or oxytocin as observed in other taxa (Caras and Ramage-Healey 2016; Forlano et al. 2016). Manipulative studies that alter hormone levels both systemically and locally in the periphery at both acute as well as prolonged time frames are needed in a greater number of species and across a wider swath of reproductive time points. It also remains unknown to what extent various receptors are present in auditory end organs and to what degree their expression is plastic across reproductive conditions, which may most easily be addressed through quantitative PCR or transcriptomic approaches, as immunohistochemistry approaches can be challenging in non-model organisms. Finally, the functional consequences of plasticity in peripheral processing are generally unknown. Within-individual approaches may be used to evaluate potential correlations between communication behaviors and individual differences in auditory processing, hormonal state or both.

LITERATURE CITED

- Anderson T. 2006. *Biology of the ubiquitous house sparrow: from genes to populations*. New York: Oxford University Press.
- Arch VS, Narins PM. 2009. Sexual hearing: The influence of sex hormones on acoustic communication in frogs. *Hear Res* 252:15–20. doi: 10.1016/j.heares.2009.01.001.
- Ashmore J F. 1983 Frequency tuning in a frog vestibular organ. *Nature* 304, 536–38.
- Baugh AT, Ryan MJ. 2010. The development of sexual behaviour in túngara frogs. *J Comp Psychol* 124:66–80.
- Baugh AT, Hoke KL, Ryan MJ. 2012. Development of communication behaviour: receiver ontogeny in túngara frogs and a prospectus for a behavioural evolutionary development. *Sci World J*, 2012:1–10.
- Baugh AT, Bee M, Gall M. 2019. The paradox of hearing at the lek: auditory sensitivity increases after breeding in female gray treefrogs (*Hyla chrysoscelis*). *J Comp Physiol A* 205:629–639.
- Caras ML, Brenowitz E, Rubel, EW. 2010. Peripheral auditory processing changes seasonally in Gambel’s white-crowned sparrow. *J Comp Physiol A* 196: 581-599.
- Caras ML, Ramage-Healey L. 2016. Modulation of peripheral and central auditory processing by estrogens in birds. In: Bass AH, Sisneros JA, Popper AN and Fay RR, editors. *Hearing and hormones*. Springer handbook of auditory research, Vol. 57. New York: Springer Science+Business Media, LLC. p. 77-99.
- Catchpole CK, Slater PJB. 2008. *Bird song: biological themes and variations*. 2nd edn. Cambridge, UK: Cambridge University Press.

- 1
2
3 Chakraborty M, Burmeister SS. 2010. Sexually dimorphic androgen and estrogen receptor
4 mRNA expression in the brain of túngara frogs. *Hormone Behav* 58: 619–627. doi:
5 10.1016/j.yhbeh.2010.06.013 .
6
7
8
9
10 Chakraborty M, Burmeister SS. 2015. Effects of estradiol on neural responses to social signals in
11 female túngara frogs. *J Exp Biol* 218: 3671–3677.
12
13
14 Coffin AB, Mohr RA, Sisneros JA. 2012 Saccular-specific hair cell addition correlates with
15 reproductive state-dependent changes in the auditory saccular sensitivity of a vocal fish. *J*
16 *Neurosci* 32: 1366-1376.
17
18
19
20
21 Forlano PM, Maruska KP, Sisneros JA, Bass AH. 2016. Hormone-dependent plasticity of
22 auditory systems in fishes. In: Bass AH, Sisneros JA, Popper AN and Fay RR, editors.
23 *Hearing and Hormones*. Springer Handbook of Auditory Research, Vol. 57. New York:
24 Springer Science+Business Media, LLC. p. 15-51.
25
26
27
28
29
30
31 Fuchs PA, Nagai T, Evans MG. 1988 Electrical tuning in hair cells isolated from the chick
32 cochlea. *J Neurosci* 8: 2460–67.
33
34
35
36 Gall MD, Salameh TS, Lucas JR. 2013. Songbird frequency selectivity and temporal resolution
37 vary with sex and season. *Proc Roy Soc B* 280: 20122296
38
39
40
41 Gall MD, Wilczynski W. 2015. Hearing conspecific vocal signals alters peripheral auditory
42 sensitivity. *Proc Roy Soc B*, 282: 20150749.
43
44
45
46 Gall MD, Wilczynski W. 2016. The effects of call-like masking diminish after nightly exposure
47 to conspecific choruses in green treefrogs (*Hyla cinerea*). *J Exp Biol* 219: 1295:1302.
48
49
50
51 Gall MD, Bee MA, Baugh AT. 2019. The difference a day makes: breeding remodels hearing,
52 hormones and behavior in female Cope’s gray treefrogs (*Hyla chrysoscelis*). *Hormones*
53 *Behav* 108:62–72
54
55
56
57
58
59
60

- 1
2
3 Goense J, Feng AS. 2005. Seasonal changes in frequency tuning and temporal processing in
4
5 single neurons in the frog auditory midbrain. *J Neurobiol* 65: 22–36.
6
7
8 Hall IC, Woolley SMN, Kelley DB. 2016. Sex differences and endocrine regulation of auditory-
9
10 evoked, neural responses in African clawed frogs (*Xenopus*). *J Comp Physiol A* 202: 17–
11
12 34. doi:10.1007/s00359-015-1049-9.
13
14
15 Harvey LA, Propper CR, Woodley SK, Moore MC. 1997. Reproductive endocrinology of the
16
17 explosively breeding desert spadefoot toad, *Scaphiopus couchii*. *Gen Comp Endocrinol*
18
19 105: 102-113.
20
21
22 Hegner RE, Wingfield JC. 1986a. Behavioral and endocrine correlates of multiple brooding in
23
24 the semicolonial house sparrow *Passer domesticus*. I. males. *Hormone Behav* 20: 294-
25
26 312.
27
28
29 Hegner RE, Wingfield JC. 1986b. Behavioral and endocrine correlates of multiple brooding in
30
31 the semicolonial house sparrow *Passer domesticus*. II. Females. *Hormone Behav* 20: 313-
32
33 326.
34
35
36 Hegner RE, Wingfield JC. 1986c. Gonadal development during autumn and winter in house
37
38 sparrows. *Condor* 88:269-278.
39
40
41 Henry KS, Lucas JR. 2009. Vocally-correlated seasonal auditory variation in the house sparrow
42
43 (*Passer domesticus*). *J Exp Biol* 212: 3817-3822.
44
45
46 Hillary CM. 1984. Seasonality of two midbrain auditory responses in the treefrog, *Hyla*
47
48 *chrysoscelis*. *Copeia* 1984: 844–852.
49
50
51 Itoh M, Ishii S. 1990. Changes in plasma levels of gonadotropins and sex steroids in the toad,
52
53 *Bufo japonicus*, in association with behavior during the breeding season. *Gen Comp*
54
55 *Endocrinol* 80: 451-464.
56
57
58
59
60

- 1
2
3 Jones EM, Gray-Keller M, Fettiplace R. 1999. The role of Ca²⁺-activated K⁺ channel spliced
4 variants in the tonotopic organization of the turtle cochlea. *J Physiol* 518: 653–665.
5
6
7
8 Kundu P, Alioua A, Stefani E, Toro L. 2007 Regulation of mouse Slo gene expression: multiple
9 promoters, transcription start sites, and genomic action of estrogen. *J Biol Chem* 282:
10 27478–27492.
11
12
13
14 Kroodsma DE, Miller EH. 1982. Acoustic communication in birds, Vol 2. New York: Academic
15 Press.
16
17
18
19 Lattin CR, Stabile FA, Carson RE. 2017. Estradiol modulates neural response to conspecific and
20 heterospecific song in female house sparrows: An in vivo positron emission tomography
21 study. *PLoS One*: e0182875.
22
23
24
25
26 Lucas JR, Freeberg TM, Krishnan A, Long GR. 2002. A comparative study of avian auditory
27 brainstem responses: correlations with phylogeny and vocal complexity, and seasonal
28 effects. *J Comp Physiol A* 188: 981-992.
29
30
31
32
33 Lucas JR, Freeberg TM, Long GR, Krishnan A. 2007. Seasonal variation in avian auditory
34 evoked responses to tones, a comparative analysis of Carolina chickadees, tufted titmice,
35 and white-breasted nuthatches. *J Comp Physiol A* 192: 201-215.
36
37
38
39
40 Lynch KS, Wilczynski W. 2005. Gonadal steroid fluctuations in a tropically breeding female
41 anuran. *Gen Comp Endocrinol* 43:51–56.
42
43
44
45 Lynch KS, Rand AS, Ryan MJ, Wilczynski W. 2005. Plasticity in female mate choice associated
46 with changing reproductive states. *Anim Behav* 69:689–699
47
48
49
50 Lynch KS, Wilczynski W. 2008. Reproductive hormones modify reception of species- typical
51 communication signals in a female anuran. *Brain Behav Evol* 71:143–150. doi:
52 10.1159/000111460 .
53
54
55

- 1
2
3 Maney DL, Cho E, Goode CT. 2006. Estrogen-dependent selectivity of genomic responses to
4 birdsong. *E J Neurosci* 23: 1523–1529. doi:10.1111/j.1460-9568.2006.04673.x
5
6
7
8 Maney DL, Goode CT, Lange HS, Sanford SE, Solomon BL. 2008. Estradiol modulates neural
9 responses to song in a seasonal songbird. *J Comp Neurol* 511: 173–186.
10
11
12 Maney DL, Pinaud R. 2011. Estradiol-dependent modulation of auditory processing and
13 selectivity in songbirds. *Front Neuroendocrin* 32: 287–303.
14
15
16
17 Marean GC, Burt JM, Beecher MD, Rubel EW. 1998. Auditory perception following hair cell
18 regeneration in European starling (*Sturnus vulgaris*): frequency and temporal resolution. *J*
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
- Miranda JA, Wilczynski W. 2009a. Sex differences and androgen influences on midbrain
auditory thresholds in the green treefrog, *Hyla cinerea*. *Hear Res* 252:79–88. doi:
10.1016/j.heares.2009.04.004.
- Miranda JA, Wilczynski W. 2009b. Female reproductive state influences the auditory midbrain
response. *J Comp Physiol A* 195: 341–349. doi: 10.1007/s00359-008-0410-7.
- Noirot IC, Adler HJ, Cornil CA, Harada N, Dooling RJ, Balthazart J, Ball GF. 2009. Presence of
aromatase and estrogen receptor alpha in the inner ear of zebra finches. *Hear Res* 252:
49-55.
- Penna M, Narins PM. 1989. Effects of acoustic overstimulation on spectral and temporal
processing in the amphibian auditory nerve. *J Acoust Soc Am* 85:1617–1629
- O’Connell LA, Ding JH, Ryan MJ, Hofmann HA. 2011. Neural distribution of the nuclear
progesterone receptor in the túngara frog, *Physalaemus pustulosus*. *J Chem Neuroanat*
41: 137–147. doi: 10.1016/j.jchemneu.2011.01.002.

- 1
2
3 Ramage-Healey L, Coleman ME, Oyama RK, Schlinger BA. 2010. Brain estrogens rapidly
4 strengthen auditory encoding and guide song preference in a songbird. *Proc Natl Acad*
5
6 *Sci USA* 107:3852-7
7
8
9
10 Ramage-Healey L, Dong SM, Chao A, Schlinger BA. 2012. Sex-specific, rapid neuroestrogen
11 fluctuations and neurophysiological actions in the songbird auditory forebrain. *J*
12 *Neurophysiol* 107:1621-31.
13
14
15
16
17 Riley GM. 1936. Light regulation of sexual activity in the male house sparrow (*Passer*
18 *domesticus*). *Proc Soc Exp Biol Med* 34:331-332.
19
20
21 Rohmann KN, Bass AH. 2011. Seasonal plasticity of auditory hair cell frequency sensitivity
22 correlates with plasma steroid levels in vocal fish. *J Exp Biol* 214: 1931-1942.
23
24
25
26 Ryan, M.J. 2001. *Anuran Communication*. Smithsonian Institution Press. Washington, D.C.
27
28
29 Simmons DD, Lohr R, Wotring H, Burton MD, Hooper RA, Baird RA. 2014. Recovery of
30 otoacoustic emissions after high-level noise exposure in the American bullfrog. *J Exp*
31 *Biol* 217:1626–1636. <https://doi.org/10.1242/jeb.09009>
32
33
34
35 Sisneros JA, Forlano PM, Deitcher DL, Bass AH. 2004. Steroid-dependent auditory plasticity
36 lead to adaptive coupling of sender and receiver. *Sci* 305: 404-407.
37
38
39
40 Sisneros JA. 2009. Adaptive hearing in the vocal plainfin midshipman fish, getting in tune for
41 the breeding season and implications for acoustic communication. *Int Zool* 4: 33-42.
42
43
44
45 Steinacker A, Romero A. 1992. Voltage-gated potassium current and resonance in toadfish
46 saccular hair cells. *Brain Res* 574: 229–36.
47
48
49 Sugihara I, Furukawa T. 1989. Morphological and functional aspects of two different types of
50 hair cells in the goldfish sacculus. *J Neurophysiol* 62:1330–43.
51
52
53
54
55
56
57
58
59
60

- 1
2
3 Tremere LA, Jeong JK, Pinaud R. 2009. Estradiol shapes auditory processing in the adult brain
4 by regulating inhibitory transmission and plasticity-associated gene expression. *J*
5
6 *Neurosci* 29:5949–5963
7
8
9
10 Velez A, Gall MD, Lucas JR. 2015. Seasonal plasticity in auditory processing of the envelope
11 and temporal fine structure of sounds in three songbirds. *Anim Behav* 103: 53-63.
12
13
14 Walkowiak W. 1980. The coding of auditory signals in the torus semicircularis of the fire-
15 bellied toad and the grass frog: Responses to simple stimuli and to conspecific calls. *J*
16
17 *Comp Physiol* 138: 131–148. doi: 10.1007/BF00680437 .
18
19
20
21 Webb JF, Fay RR, Popper AN. 2008. *Fish bioacoustics*. New York: Springer-Verlag.
22
23
24 Wilczynski W, Burmeister SS. 2016. Effects of steroid hormones on hearing and communication
25 in frogs. In: Bass AH, Sisneros JA, Popper AN and Fay RR, editors. *Hearing and*
26
27 *hormones*. Springer handbook of auditory research, Vol. 57. New York: Springer
28
29 Science+Business Media, LLC. p. 53-75.
30
31
32
33 Woolley SMN, Rubel EW. 2002. Vocal memory and learning in adult Bengalese finches with
34 regenerated hair cells. *J Neurosci* 22:7774-7787.
35
36
37
38 Yoder KM, Vicario DS. 2011. To modulate and be modulated: estrogenic influences on auditory
39 processing of communication signals within a socio-neuro-endocrine framework. *Behav*
40
41 *Neurosci* 126: 17–28.
42
43
44
45 Zelick R, Narins PM. 1985. Temporary threshold shift, adaptation, and recovery characteristics
46 of frog auditory nerve fibers. *Hear Res* 17:161–176
47
48
49
50 Zhang D, Cui J, Tang Y. 2012. Plasticity of peripheral auditory frequency sensitivity in Emei
51 music frog. *PLoS ONE* 7: e45792. <https://doi.org/10.1371/journal.pone.0045792>
52
53
54
55
56
57
58
59
60

1
2
3 Zhu N, Eghbali M, Helguera G, Song M, Stefani E, Toro L. 2005. Alternative splicing of Slo
4 channel gene programmed by estrogen, progesterone and pregnancy. FEBS Lett 579:
5
6 4856–4860.
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4
5
6
7
8 Figure 1. Effects of sex and season on frequency selectivity and temporal resolution in the house
9 sparrow (*Passer domesticus*; N=36 total, 9 per group). Frequency selectivity was measured using
10 a notched-noise protocol to determine auditory filter bandwidth. Note that bandwidths are
11 averaged across center frequencies (CF=2, 3, or 4 kHz) and that frequency selectivity is inversely
12 related to filter bandwidth. Temporal resolution was measured with a paired click paradigm
13 (inter-click intervals 0.7-25 ms). ABR (auditory brainstem response) recovery is the amplitude of
14 the onset response to the second click divided by the amplitude of the onset response to a single
15 click. Males and females did not differ in the fall and males did not change across the seasons.
16 However, female frequency selectivity increased and temporal resolution decreased in the spring,
17 leading to a difference between males and females in the spring. Note that data are averaged
18 across all inter-click intervals. LSMEANS (\pm S.E.) were generated in SAS 9.2. From Gall et. al
19 2013.
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37

38 Figure 2. (a) Frequency selectivity and (b,c) temporal resolution in house sparrows (*Passer*
39 *domesticus*) treated with either a placebo or hormone implant (N total = 36, N per group = 9).
40 Frequency selectivity was measured using a notched-noise protocol to determine auditory filter
41 bandwidth. Note that bandwidths are averaged across center frequencies (CF=2, 3, or 4 kHz) and
42 that frequency selectivity is inversely related to filter bandwidth. Temporal resolution was
43 measured with a paired click paradigm (inter-click intervals 0.7-25 ms). ABR (auditory
44 brainstem response) recovery is the amplitude of the onset response to the second click divided
45 by the amplitude of the onset response to a single click. (a) We did not find an effect of sex on
46
47
48
49
50
51
52
53
54
55

1
2
3 frequency selectivity plasticity. Pre-treatment animals in the two treatment conditions did not
4
5 differ. Animals with a placebo implant did not show plasticity in their frequency resolution
6
7 (females: $F_{1,182} = 0.68$, $p = 0.41$, males: $F_{1,182} = 0.68$ $p = 0.41$), but animals given a hormone
8
9 implant showed enhanced frequency resolution after three weeks (females: $F_{1,182} = 5.7$, $p = 0.018$,
10
11 males: $F_{1,182} = 3.74$ $p = 0.04$). (b) Similarly, neither sex exhibited plasticity in temporal
12
13 resolution when given a placebo implant (females: $F_{1,665} = 0.98$, $p = 0.32$, males: $F_{1,665} = 0.3$ $p =$
14
15 0.59). (c) Females, but not males, showed diminished temporal resolution when given a hormone
16
17 implant (females: $F_{1,665} = 21.7$, $p < 0.001$, males: $F_{1,665} = 1.62$ $p = 0.20$). LSMEANS (\pm S.E.)
18
19 were generated in SAS 9.2.
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

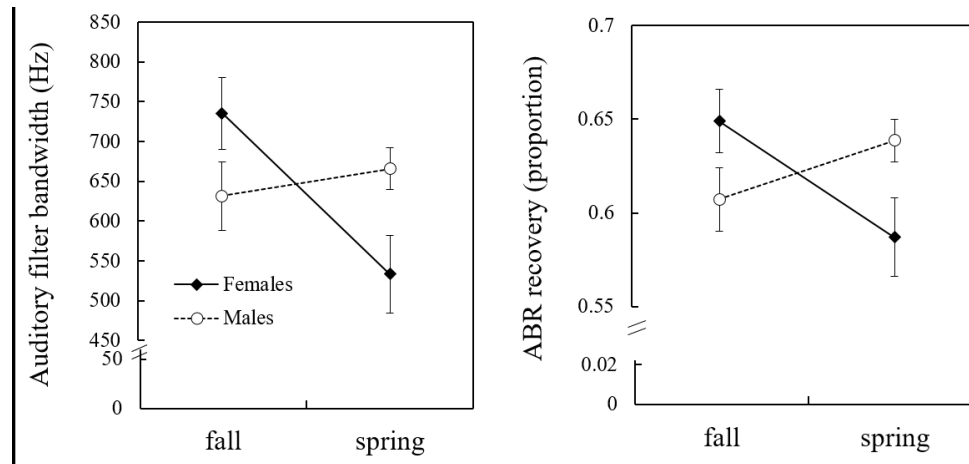


Figure 1. Effects of sex and season on frequency selectivity and temporal resolution in the house sparrow (*Passer domesticus*, N=36 total, 9 per group). Frequency selectivity was measured using a notched-noise protocol to determine auditory filter bandwidth. Note that bandwidths are averaged across center frequencies (CF=2, 3, or 4 kHz) and that frequency selectivity is inversely related to filter bandwidth. Temporal resolution was measured with a paired click paradigm (inter-click intervals 0.7-25 ms). ABR recovery is the amplitude of the onset response to the second click divided by the amplitude of the onset response to a single click. Males and females did not differ in the fall and males did not change across the seasons. However, female frequency selectivity increased and temporal resolution decreased in the spring, leading to a difference between males and females in the spring. Note that data are averaged across all inter-click intervals. LSMEANS (\pm S.E.) were generated in SAS 9.2. From Gall et. al 2013.

203x93mm (150 x 150 DPI)

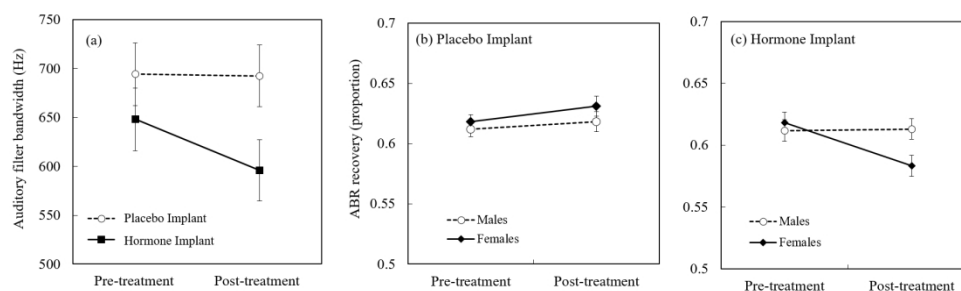


Figure 2. (a) Frequency selectivity and (b,c) temporal resolution in house sparrows (*Passer domesticus*) treated with either a placebo or hormone implant (N total = 36, N per group = 9). Frequency selectivity was measured using a notched-noise protocol to determine auditory filter bandwidth. Note that bandwidths are averaged across center frequencies (CF=2, 3, or 4 kHz) and that frequency selectivity is inversely related to filter bandwidth. Temporal resolution was measured with a paired click paradigm (inter-click intervals 0.7-25 ms). ABR (auditory brainstem response) recovery is the amplitude of the onset response to the second click divided by the amplitude of the onset response to a single click. (a) We did not find an effect of sex on frequency selectivity plasticity. Pre-treatment animals in the two treatment conditions did not differ. Animals with a placebo implant did not show plasticity in their frequency resolution (females: $F_{1,182} = 0.68$, $p = 0.41$, males: $F_{1,182} = 0.68$, $p = 0.41$), but animals given a hormone implant showed enhanced frequency resolution after three weeks (females: $F_{1,182} = 5.7$, $p = 0.018$, males: $F_{1,182} = 3.74$, $p = 0.04$). (b) Similarly, neither sex exhibited plasticity in temporal resolution when given a placebo implant (females: $F_{1,665} = 0.98$, $p = 0.32$, males: $F_{1,665} = 0.3$, $p = 0.59$). (c) Females, but not males, showed diminished temporal resolution when given a hormone implant (females: $F_{1,665} = 21.7$, $p < 0.001$, males: $F_{1,665} = 1.62$, $p = 0.20$). LSMEANS (\pm S.E.) were generated in SAS 9.2.

336x113mm (150 x 150 DPI)

Table 1. Pre-treatment and post-treatment plasma testosterone (male) and estradiol (female) levels in house sparrows (ng ml^{-1}). All plasma samples were collected between 1100 and 1300 EST. All animals were housed on a long day (14:10) light cycle. Values given are mean \pm S.E.

	Pre-treatment	Post-treatment	t	p	n
Males (Placebo)	2.01 \pm 0.27	4.97 \pm 0.84	2.85	0.022	9
Males (T)	2.14 \pm 0.29	33.77 \pm 4.26	7.68	< 0.001	9
Females (Placebo)	0.23 \pm .08	0.25 \pm 0.11	0.24	0.82	9
Females (E2)	0.21 \pm 0.07	0.60 \pm 0.11	2.92	0.019	9

T = Testosterone, E2 = Estradiol