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

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3 **Title:** Social communication across reproductive boundaries: hormones and the auditory
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5 periphery of songbirds and frogs
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8 **Title:** Hormones, the auditory periphery, and social communication
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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

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3 transitions. We focus primarily on songbirds and frogs, the role of steroid hormones in
4 modulating this plasticity (including new data on recapitulation of seasonal patterns by
5 exogenous steroid hormones), and possible mechanisms through which hormones may influence
6 auditory processing.
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11 Our review covers three aspects of peripheral auditory processing: sensitivity, frequency
12 selectivity and temporal resolution. Sensitivity can be described by either the lowest amplitude
13 signal that can be detected (e.g. threshold) or the magnitude of the response to signals above this
14 threshold. Frequency selectivity, which can be measured in a number of ways, represents the
15 ability of the peripheral auditory system to discriminate between two tones close together in
16 frequency. Finally, temporal resolution, which can again be measured in many ways, describes
17 the ability of the auditory system to discriminate between two sounds that are close together in
18 time or the ability to follow rapid temporal fluctuations in sounds. Together, these parameters
19 play a role in an animal's ability to detect and discriminate among communication signals and
20 are likely important in determining the salience of these signals.
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35 **SEASONAL AND HORMONE-MEDIATED PLASTICITY IN PERIPHERAL** 36 37 **AUDITORY PROCESSING**

38 *Seasonal differences in the auditory periphery of songbirds*

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40 An understanding of the plasticity in auditory processing has the potential to
41 fundamentally change our understanding of communication, particularly with respect to what
42 information is extracted from signals, how that information is extracted, and the functional
43 implications of changes in information processing. Seasonal variation in the auditory periphery
44 of birds was first reported by Lucas et al. in 2002 when they found species-specific seasonal
45 changes in the response amplitude of auditory evoked potentials to broadband clicks in three
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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
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6 (*Zonotrichia leucophrys*), kept under induced-breeding conditions (i.e. implanted with either
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8 testosterone in males or estradiol in females and kept on a long-day light cycle), had auditory
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10 thresholds that were higher than birds kept in non-breeding condition (Caras et al. 2010). This
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12 study suggests a role for estrogen-mediated changes in the auditory periphery. However, it is
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14 difficult to extrapolate these results to naturally-occurring seasonal changes because no auditory
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16 threshold data are currently available for white-crowned sparrows in natural breeding and non-
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18 breeding conditions. Furthermore, it is not clear whether steroid hormones are involved in the
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20 plasticity of other aspects of auditory processing in females, such as frequency selectivity or
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22 temporal resolution. Testosterone did not induce plasticity in frequency selectivity or temporal
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24 resolution in white-crowned sparrow males, and hormone-manipulated females were not tested
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26 for these traits (Caras et al. 2010).
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33 *Breeding condition induced by exogenous hormones can recapitulate seasonal patterns*

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36 Gall et al. (2013) previously demonstrated that the frequency selectivity (i.e. auditory
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38 filter bandwidths) and temporal resolution of the peripheral auditory system in house sparrows
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40 varies seasonally in a sex-specific manner (Figure 1). Specifically, they showed that female
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42 house sparrows have enhanced frequency resolution (auditory filter bandwidths narrowed) and
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44 diminished temporal resolution (as measured by response to paired clicks) in the breeding season
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46 relative to the non-breeding season, while males did not exhibit changes in their auditory
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48 processing. Previously unpublished work from two of the authors, Gall and Lucas, suggests that
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50 the reproductive condition induced by steroid hormones may play a role in this seasonal pattern.
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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.
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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).
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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
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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 Perhaps more importantly, the hormone manipulations, and thus induced breeding
13 condition, described here resulted in auditory plasticity that largely mirrored the natural seasonal
14 variation Gall et al. (2013) had previously found, suggesting that breeding condition is linked to
15 auditory processing. For frequency selectivity, both males and females with hormone implants
16 showed greater frequency selectivity after treatment. Animals with placebo implants did not
17 exhibit auditory plasticity (Figure 2). Moreover, there were no significant differences between
18 the placebo and hormone groups prior to treatment; however, post-treatment animals with
19 hormone implants had greater frequency selectivity than placebo animals. Temporal resolution
20 mirrored seasonal changes even more closely. Placebo animals did not show plasticity, nor were
21 there differences between the sexes. However, animals treated with hormones showed sex-
22 specific responses, with no plasticity in males and a decrease in temporal resolution following
23 hormone implantation in females (See ESM for full statistical model results).

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25 Overall, we found that supplemental hormones that induced changes in reproductive
26 condition could induce auditory plasticity over the course of three weeks. Increased photoperiod
27 alone was insufficient to induce reproductive condition and did not result in an increase in

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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).
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20 Females in four species of *Xenopus* had greater peripheral sensitivity than males.
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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.
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28 **ACUTE REPRODUCTIVE TRANSITIONS AND HORMONE-MEDIATED**

29 **PLASTICITY IN PERIPHERAL AUDITORY PROCESSING**

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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
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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

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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.
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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
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3 mitigates against a hyper-stimulated proceptivity and resultant impulsivity during mate choice in
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5 favor of a more protracted mate sampling effort (c.f. sexual conflict).
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8 9 10 **MECHANISMS THROUGH WHICH STEROID HORMONES MAY ALTER** 11 12 **PERIPHERAL AUDITORY FUNCTION** 13

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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.
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31 In the central auditory system, estradiol can influence auditory function over several time
32 scales (Caras and Ramage-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, Ramage-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
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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)

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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
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3 estrogen (Maney and Pinaud 2011). Therefore, even if steroid hormone receptors are not found
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5 in the auditory end organs, there may still be efferent modulation that is sensitive to endocrine
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7 state.
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10 There are several mechanisms by which hormones have been shown to regulate
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12 peripheral auditory processing in fish, which could potentially operate in songbirds and frogs.
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14 Plainfin midshipman fish (*Porichthys notatus*), for example, show enhanced phase-locking in
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16 their auditory nerve during the breeding season and this effect can be mimicked with estrogen
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18 manipulations (Sisneros et al. 2004; Sisneros 2009). Hair cells also show steroid-dependent
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20 sensitivity to tones (Rohmann and Bass 2011). These changes in sensitivity may be due to the
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22 addition of hair cells to the saccule during the breeding season (Coffin et al. 2012). Songbirds are
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24 capable of regenerating hair cells after damage (Marean et al. 1998; Woolley and Rubel 2002),
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26 but it is not yet known whether the addition or replacement of hair cells is a feasible mechanism
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28 underlying seasonal plasticity in the avian auditory periphery.
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33 Peripheral auditory plasticity could also be induced by hormone-mediated expression of
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35 ion channels in hair cells. For instance, splice variants of voltage-gated calcium and calcium
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37 sensitive big potassium (BK) ion channels play an important role in determining the electrical
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39 tuning of hair cells in fish (Sugihara and Furukawa 1989; Steinacker and Romero 1992),
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41 amphibians (Ashmore 1983), reptiles (Jones et al. 1999) and birds (Fuchs et al. 1988). The
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43 expression of splice variants appears to be influenced by estrogen responsive elements involved
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45 in transcription of the α -subunit (Zhu et al. 2005; Kundu et al. 2007). Seasonal changes in
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47 hormone levels could alter estrogen-mediated transcriptional regulation, thereby altering the
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49 expression of ion channels in the hair cells. This in turn would alter the functional properties of
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51 the hair cells in response to acoustic stimulation.
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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
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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
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3 frequency selectivity plasticity. Pre-treatment animals in the two treatment conditions did not
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5 differ. Animals with a placebo implant did not show plasticity in their frequency resolution
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7 (females: $F_{1,182} = 0.68$, $p = 0.41$, males: $F_{1,182} = 0.68$ $p = 0.41$), but animals given a hormone
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9 implant showed enhanced frequency resolution after three weeks (females: $F_{1,182} = 5.7$, $p = 0.018$,
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11 males: $F_{1,182} = 3.74$ $p = 0.04$). (b) Similarly, neither sex exhibited plasticity in temporal
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13 resolution when given a placebo implant (females: $F_{1,665} = 0.98$, $p = 0.32$, males: $F_{1,665} = 0.3$ $p =$
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15 0.59). (c) Females, but not males, showed diminished temporal resolution when given a hormone
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17 implant (females: $F_{1,665} = 21.7$, $p < 0.001$, males: $F_{1,665} = 1.62$ $p = 0.20$). LSMEANS (\pm S.E.)
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19 were generated in SAS 9.2.
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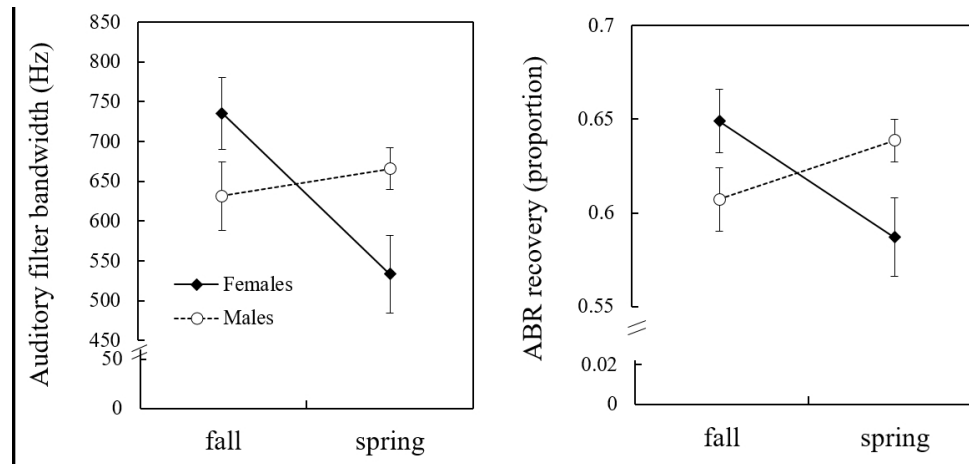


Figure 1. Effects of sex and season on frequency selectivity and temporal resolution in the house sparrow (*Passer domesticus*, N=36 total, 9 per group). Frequency selectivity was measured using a notched-noise protocol to determine auditory filter bandwidth. Note that bandwidths are averaged across 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.

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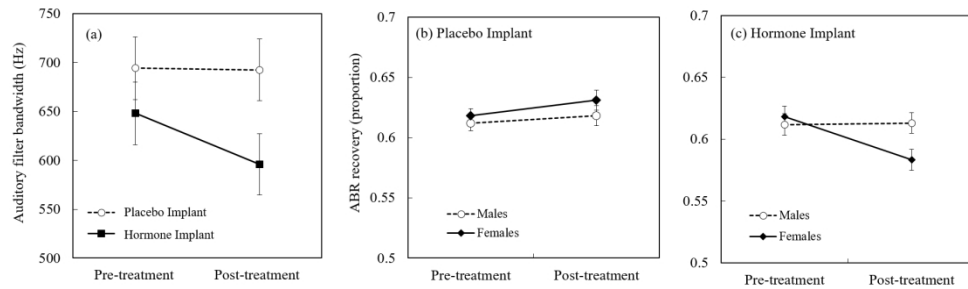


Figure 2. (a) Frequency selectivity and (b,c) temporal resolution in house sparrows (*Passer domesticus*) treated with either a placebo or hormone implant (N total = 36, N per group = 9). Frequency selectivity was measured using a notched-noise protocol to determine auditory filter bandwidth. Note that 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.

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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