The photoperiodic control circuit in euthyroid American tree sparrows (*Spizella arborea*) is already programmed for photorefractoriness by week 4 under long days

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The aim of this investigation was to determine whether spontaneous testicular regression in male American tree sparrows (*Spizella arborea*) that were thyroidectomized at week 4 of photostimulation manifests photorefractoriness, as it does in chronically photostimulated euthyroid controls. On the basis of our demonstration that exogenous thyroxine stimulates the gonads only when recipient birds are photosensitive, male tree sparrows were thyroidectomized at week 4 of photostimulation (20 h light:4 h dark) and given thyroxine periodically to assay for photosensitivity. When initiated at weeks 4, 7, 10, 13 and 16 of photostimulation, thyroxine replacement therapy had no effect on testis size until week 16, when most recipient birds showed robust testicular growth. The inductive effect of exogenous thyroxine at week 16 confirms that chronic thyroidectomy dissipates photorefractoriness and simulates the effect of short days. The failure of replacement thyroxine to halt spontaneous testicular regression between week 7 and week 13 establishes that spontaneous testicular regression after thyroidectomy manifests photorefractoriness. Moreover, the failure of replacement thyroxine to induce testicular growth between week 4 and week 7 indicates that by week 4 of photostimulation, at least 3 weeks before photoinduced testicular growth ends, male tree sparrows are programmed for photorefractoriness. This conclusion is strengthened by the finding that thyroidectomy at week 4 of photostimulation does not uncouple photorefractoriness and postnuptial moult, which in euthyroid tree sparrows are tightly linked. In another experiment, photosensitive thyroid-intact tree sparrows were moved from 8 h light:16 h dark to 20 h light:4 h dark and given exogenous thyroxine or vehicle through week 6 of photostimulation. Exogenous thyroxine augmented testicular growth.

Introduction

Photorefractoriness, a reversible state of unresponsiveness to daylengths gonadostimulatory, terminates seasonal breeding in many photoperiodic species of bird (for reviews, see Farner *et al.*, 1983; Nicholls *et al.*, 1988). Although significant progress has been made, the aetiology of photorefractoriness is unknown. The most promising work addressing this phenomenon has explored the role of the thyroid gland in European starlings (Goldsmith and Nicholls, 1984a, b; Dawson, 1989a, b; Boulakoud *et al.*, 1991), Japanese quail (Follett and Nicholls, 1985, 1988; Follett *et al.*, 1988; Chaturvedi and Meier, 1989; Hall *et al.*, 1993; Wada, 1993), turkeys (Lien and Siopes, 1989a, b, 1993a, b), and American tree sparrows (Wilson and Reinert, 1993). The role of the thyroid gland in the seasonal inhibition of breeding has also been explored in several mammals, including sheep (Moenter *et al.*, 1991; Webster *et al.*, 1991a, b; Dahl *et al.*, 1994; Parkinson and Follett, 1994) and red deer (Shi and Barrell, 1992).

American tree sparrows (*Spizella arborea*) are obligately photoperiodic and exhibit absolute photorefractoriness. In males, a testosterone-independent reduction in photoperiodic drive triggers photorefractoriness (Wilson, 1985, 1986), and a simulated annual testicular cycle, complete with growth, regression, photorefractoriness, and the recovery of photosensitivity, can be generated in the absence of the eyes and/or the pineal gland (Wilson, 1989, 1991). Wilson and Reinert (1993) showed that thyroidectomy 30 days before photostimulation inhibits (but does not block) photoinduced testicular growth and later prevents spontaneous testicular regression. Such birds remain in a persistent state of photosensitivity and do not moult until given exogenous thyroxine. However, when thyroidectomy is performed 4 weeks after photostimulation, testicular collapse is not immediately induced, and spontaneous testicular regression is not later blocked; moult is only temporarily delayed. Thus, while thyroid hormones do not initiate seasonal breeding (rather, they appear to expedite it by facilitating the expression of photoperiodic drive), either thyroid hormones or thyroid hormone-dependent ligands may play an essential role in the mechanism that terminates seasonal

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breeding, perhaps by programming the photoperiodic control mechanism for photorefractoriness early during photostimulation. This latter suggestion is based on the presumption that spontaneous testicular regression in tree sparrows that are thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark manifests photorefractoriness. However, this presumption could be erroneous, for when birds thyroidectomized at week 4 are challenged with exogenous thyroxine at week 33, they show robust testicular growth, thus confirming their photosensitivity. It is not clear when photosensitivity is restored before week 33, as the transition is not signalled by spontaneous testicular recrudescence. Now that it has been demonstrated that thyroxine-induced testicular growth constitutes a qualitative assay for photosensitivity (Wilson and Reinert, 1993), it is possible to determine whether spontaneous testicular regression in tree sparrows that are thyroidectomized at week 4 of photostimulation manifests photorefractoriness and, if it does, when photosensitivity is later restored. Resolving these issues is the primary goal of the experiments reported here.

Materials and Methods

Animals

American tree sparrows were captured in mist nets from an overwintering flock near Manhattan, Kansas, during February 1993 and maintained in the laboratory under a photoperiod of 8 h light:16 h dark (lights on 08:30–16:30 h). Captive birds were housed four or six per cage in cages measuring 23 cm × 25 cm × 41 cm or 27 cm × 27 cm × 51 cm, respectively, and provided with water and food (a vitamin- and mineral-enriched 20% protein crumble produced by the Department of Grain Science and Industry, Kansas State University) *ad libitum*. Illumination, provided by cool white fluorescent bulbs, was ≥ 100 lux at cage level, and room temperature fluctuated a few degrees around 21°C. After acclimatizing to laboratory conditions, each bird was laparotomized under lidocaine-induced local anaesthesia (Wilson, 1989), and testis length was measured *in situ* to the nearest 0.01 mm with digital callipers fitted with angular pin-like tips. Animal care was governed by protocols approved by the Animal Facilities and Care Panel of Kansas State University and was monitored by a veterinarian.

Experiment 1

At week 0, photosensitive male tree sparrows were transferred from a photoperiod of 8 h light:16 h dark to 20 h light:4 h dark (lights on 08:30–04:30 h), laparotomized to determine testis length, and scored for moult (0–5 per primary remex) according to Newton (1966). Thereafter, testis length was measured and moult scored at weeks 3, 7, 10, 13 and 16. The score for a fully moulted tree sparrow is 90.

Birds were thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark by injecting 0.31–0.33 mCi Na^{131}I in 0.05 ml phosphate-buffered saline (pH 7.5–9.0; Syncor Corporation, Kansas City, MO) s.c. into the nape (Wilson and

Reinert, 1993). Six thyroid-intact control birds were injected in the same way with 0.05 ml 0.85% (w/v) NaCl.

At weeks 4, 7, 10, 13 and 16 under a photoperiod of 20 h light:4 h dark, groups of 4–6 thyroidectomized birds were given, in lieu of drinking water, 10 mg L-thyroxine sodium salt pentahydrate (Sigma, St Louis, MO) in 1 mmol NaOH l^{-1} for 3 weeks to assay for photosensitivity (Wilson and Reinert, 1993). In addition, from week 4, thyroidectomized birds not given thyroxine, as well as thyroidectomized and thyroid-intact control groups, were given 1 mmol NaOH l^{-1} . Drinking solutions were prepared three times a week according to Boulakoud and Goldsmith (1991). In view of the failure to observe thyroxine-induced testicular growth in known photorefractory birds (Wilson and Reinert, 1993), thyroxine was not administered to thyroid-intact birds, thereby minimizing the number of experimental animals.

Experiment 2

Chronically photosensitive male tree sparrows were transferred from a photoperiod of 8 h light:16 h dark to 20 h light:4 h dark and given 10 mg thyroxine in 1 mmol NaOH l^{-1} or 1 mmol NaOH l^{-1} in lieu of drinking water for 6 weeks to determine whether exogenous thyroxine enhances the gonadostimulatory effect of long days in thyroid-intact birds. Laparotomy was performed, and testis length measured, at weeks 0, 3 and 6.

Statistical analyses

Data were analysed by repeated-measures parametric or nonparametric analysis of variance (either one-way or two-way, as appropriate). Missing data were handled using a general linear model approach. Pairwise multiple comparisons were made using Student-Newman-Keuls' test. Computations were performed using SIGMASTAT (version 1.01). Significance was defined as $P < 0.05$.

Results

Experiment 1

When five tree sparrows were thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark and not given thyroxine, no deleterious effect on the testicular cycle was observed (Fig. 1a, b). However, when a larger group of thyroidectomized birds not yet given thyroxine replacement therapy (Fig. 1c) was compared with thyroid-intact birds (Fig. 1a), a significant difference in mean testis length was detected at week 7. Thus, thyroidectomy at week 4 under a photoperiod of 20 h light:4 h dark slowed testicular growth, but did not immediately induce testicular collapse, or later block spontaneous testicular regression.

Tree sparrows thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark did not respond to thyroxine replacement therapy initiated at week 4, 7, 10 or 13 under a photoperiod of 20 h light:4 h dark (Fig. 1d–g). Although mean testis length did increase significantly between week 4 and

Fig. 1. Tests for photosensitivity in the American tree sparrow (*Spizella arborea*) under a photoperiod of 20 h light:4 h dark after thyroidectomy at week 4. (a) Testis lengths of thyroid-intact controls given 1 mmol NaOH l⁻¹ between weeks 4 and 16. Testis lengths of thyroidectomized birds given (b) 1 mmol NaOH l⁻¹ between weeks 4 and 16; (c) 1 mmol NaOH l⁻¹ from week 4 until the onset of replacement therapy (10 mg thyroxine in 1 mmol NaOH l⁻¹) at week 7, 10, 13 or 16; (d) 10 mg thyroxine in 1 mmol NaOH l⁻¹ between weeks 4 and 7; (e) 10 mg thyroxine in 1 mmol NaOH l⁻¹ between weeks 7 and 10; (f) 10 mg thyroxine in 1 mmol NaOH l⁻¹ between weeks 10 and 13; (g) 10 mg thyroxine in 1 mmol NaOH l⁻¹ between weeks 13 and 16; or (h) 10 mg thyroxine in 1 mmol NaOH l⁻¹ between weeks 16 and 19. Group c declined in size over time as groups d, e, f, g and h were recruited from it. Data are means $\pm$ SEM. Dotted line: time of thyroidectomy; $\square$: thyroxine replacement therapy; and numbers are the sample sizes. * $P < 0.05$ (c versus a). Within treatment groups, values with common letters are not significantly different ($P > 0.05$).

week 7 under a photoperiod of 20 h light:4 h dark in tree sparrows given thyroxine beginning on the day of thyroidectomy (Fig. 1d), the increase cannot be attributed to thyroxine, because mean testis length also increased significantly between week 4 and week 7 in thyroidectomized birds given no thyroxine (Fig. 1b, c). The administration of thyroxine between weeks 7 and 10, 10 and 13, and 13 and 16 neither induced testicular growth nor halted spontaneous testicular regression. However, when thyroxine replacement therapy was initiated at week 16 under a photoperiod of 20 h light:4 h dark, 12 weeks after thyroidectomy, three of four birds showed robust testicular growth (Fig. 1h).

Although thyroidectomy at week 4 of photostimulation temporarily delayed the onset of postnuptial moult, it had no lasting effect, as moult was about 80% complete at week 16 in both thyroid-intact and thyroidectomized birds (Table 1).

Experiment 2

When chronically photosensitive tree sparrows were moved from a photoperiod of 8 h light:16 h dark to 20 h light:4 h dark and given no thyroxine, testicular growth was rapidly induced (Fig. 2). By week 6, when the experiment ended, mean testis length was near the maximum for captive euthyroid birds in our laboratory. Exogenous thyroxine enhanced the gonadostimulatory effect of long days (Fig. 2).

Discussion

The results of the study reported here confirm that thyroidectomy of American tree sparrows at week 4 of photostimulation neither immediately induces testicular collapse nor later blocks spontaneous testicular regression (Wilson and Reinert, 1993). The hypothesis that spontaneous testicular regression in birds thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark manifests photorefractoriness, as it does in thyroid-intact birds, was tested by administering thyroxine at intervals after thyroidectomy at week 4. Previous observations suggested that replacement thyroxine would induce testicular growth only when recipient birds were photosensitive. Accordingly, thyroidectomized birds that failed to respond to thyroxine replacement therapy (that is, showed testicular regression, no change in testis length, or thyroxine-independent testicular growth during the period of thyroxine replacement) were judged to be either photorefractory or programmed for photorefractoriness. Testicular growth between week 4 and week 7 of photostimulation was independent of thyroxine replacement therapy. Thus, male tree sparrows thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark were already programmed for photorefractoriness at thyroidectomy. Thyroxine replacement therapy failed to halt testicular regression between weeks 7 and 10, 10 and 13, and 13 and 16. Thus, male tree sparrows thyroidectomized at week 4 under a

Table 1. Moulting scores (means $\pm$ SEM (*n*)) of thyroid-intact (THI) and thyroidectomized (THX) male American tree sparrows under a photoperiod of 20 h light:4 h dark during a simulated testicular cycle

Week	THI + $T_4(0)_{4-16}$	THX + $T_4(0)_{4-16}$	THX + $T_4(0)_{4-n}$
0	0 (5)	0 (5)	0 (26)
3	0 (5)	0 (5)	0 (26)
7	0 (5)	0 (5)	0 (20)
10	$8.6^a \pm 4.4$ (5)	0^a (5)	0^a (15)
13	$49.4^b \pm 3.6$ (5)	$23.0^a \pm 3.0$ (5)	$17.8^a \pm 3.1$ (10)
16	$73.2^a \pm 6.1$ (5)	$75.8^a \pm 4.8$ (5)	$69.0^a \pm 6.4$ (4)

Group designations signify thyroid status and exposure to $1 \text{ mmol NaOH l}^{-1}$ (that is, no thyroxine-replacement therapy ($T_4(0)$) between weeks 4 and 16 or weeks 4 and *n*). Groups correspond to groups a, b and c, respectively, in Fig. 1. Beginning at week 10, between-group means that share common superscript letters do not differ ($P > 0.05$).

Fig. 2. Testicular growth in photosensitive, thyroid-intact American tree sparrows (*Spizella arborea*) moved from a photoperiod of 8 h light:16 h dark to 20 h light:4 h dark and given 10 mg thyroxine in $1 \text{ mmol NaOH l}^{-1}$ (●) or $1 \text{ mmol NaOH l}^{-1}$ (○) for 6 weeks. Data are means $\pm$ SEM. Sample sizes were 3, 2 and 2 (●) and 3, 3 and 2 (○). * $P < 0.05$ ((●) versus (○)). Letters (c, b, a) apply to means within treatment groups. Within each treatment group, all means are significantly different ($P < 0.05$).

photoperiod of 20 h light:4 h dark were already photorefractory when replacement therapy was initiated at weeks 7, 10 and 13. Thyroxine replacement therapy initiated at week 16 under a photoperiod of 20 h light:4 h dark induced robust testicular growth in three of four birds. Thus, most birds thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark had regained photosensitivity 12 weeks later, despite chronic photostimulation. That change in physiological state is not manifested by spontaneous testicular recrudescence (Wilson and Reinert, 1993).

Therefore, by week 4 of photostimulation, endogenous thyroid hormones, either directly or indirectly via thyroid

hormone-dependent ligands, have programmed the photoperiodic control circuit for photorefractoriness. Thereafter, thyroid hormones are not required, and spontaneous testicular regression, a latent, peripheral manifestation of photorefractoriness, both begins and proceeds independently of them. Precedents for early programming of photorefractoriness derive from methodologically independent studies (that is, those involving neither exogenous thyroxine nor thyroidectomy) on photostimulated euthyroid white-throated sparrows (Harris and Turek, 1982), white-crowned sparrows (Moore *et al.*, 1983) and starlings (Dawson *et al.*, 1985a). Moulting is also programmed early during photostimulation (cf. Dawson, 1994). Thyroidectomy at week 4 of photostimulation delays moulting only temporarily, whereas thyroidectomy before photostimulation prevents it (Wilson and Reinert, 1993).

Although the data presented here do not exclude other interpretations (for example, that programming is an indirect effect of thyroid hormones), they are consistent with the hypothesis that thyroid hormones exert a direct, organizational action on one or more components of the photoperiodic control circuit. Viewed from that conceptual perspective, there is striking parallelism between the physiological transition from photosensitivity to photorefractoriness in American tree sparrows and a developmental transition in *Xenopus laevis*. French *et al.* (1994) reported that triiodothyronine programmes larval epidermal cells of *Xenopus* for terminal differentiation. Thereafter, terminal differentiation proceeds independently of triiodothyronine. The data indicate that there is basal (triiodothyronine-independent) expression of a set of control genes in premetamorphic tadpoles, triiodothyronine-induced upregulation during metamorphosis, and triiodothyronine-independent expression in adults. In American tree sparrows, thyroidectomy before photostimulation impedes, but does not block, photoinduced testicular growth (Wilson and Reinert, 1993). Thus, testicular growth is initiated by a thyroid hormone-independent process, and in the absence of thyroid hormones, testicular growth is slow (cf. basal). Because thyroid hormones accelerate early photoinduced testicular growth, they may be viewed as enhancing (cf. upregulating) a process previously activated by a thyroid hormone-independent stimulus, namely long days. The fact that testis length is greatest at week 7 under a photoperiod of 20 h light:4 h dark after thyroidectomy at week 4 indicates that testicular growth proceeds independently of endogenous thyroid hormones during that interval. Moreover, early during photostimulation (before week 4 under a photoperiod of 20 h light:4 h dark), thyroid hormones directly or indirectly programme the photoperiodic control circuit for photorefractoriness. Later, photorefractoriness plays out as spontaneous testicular regression in chronically photostimulated birds, whether thyroid hormones are present or absent (thyroid hormone-independent expression of spontaneous testicular regression). These parallels between metamorphosis and seasonal breeding raise the possibility that both direct- and delayed-response genes function in the control of the annual testicular cycle. It is possible that, by inducing the synthesis of appropriate transcription factors, thyroid hormones upregulate the expression of different sets of delayed-response genes previously activated by long days and, in doing so, both accelerate testicular growth and programme the photoperiodic

control circuit for photorefractoriness. In *Xenopus*, triiodothyronine changes the larval programme to the adult programme during a 2-day lag period (French *et al.*, 1994). For tree sparrows, we have no estimate of the putative lag period, but it probably exceeds 2 days.

Our observations shed no light on where in the photo-neuroendocrine machinery thyroid hormones or thyroid hormone-dependent ligands exert their effects. Follett and Nicholls (1988) argued that thyroxine does not act on pituitary gonadotropes, GnRH neurones, or encephalic photoreceptors and speculated that the thyroxine-dependent component is located somewhere between photoreceptors and neuroendocrine cells. Thus, likely candidates include the photoperiodic clock and interconnecting neural circuits. In this context, Parry and Goldsmith (1993) found no ultrastructural/immunocytochemical evidence for a change in glial ensheathment of, or neural input to, GnRH perikarya in photostimulated European starlings at the time of spontaneous testicular regression. Although this finding from a narrowly focused study does not support the suggestion of Follett and Nicholls, neither does it invalidate it. In view of recent reports suggesting that thyroid hormone may regulate the timing of oligodendrocyte differentiation *in vivo* (Barres *et al.*, 1994), the search for changes in glial ensheathment and synaptic innervation should not be abandoned, but redirected toward the perikarya of clock cells or interneurons. However, a lack of knowledge of their anatomical locations thwarts a productive search. In an unrelated study, Kubokawa *et al.* (1994) demonstrated a significant decline in pituitary LH β -subunit mRNA in white-crowned sparrows that had been photostimulated for 60 days. Finding greater expression of the gene for LH β -subunit at day 30 of photostimulation (by which time both starlings and tree sparrows have been programmed for photorefractoriness) suggests that the downregulation observed at day 60 may be an effect, rather than a cause, of photorefractoriness.

As confirmed by the thyroxine-induced testicular growth, most American tree sparrows thyroidectomized at week 4 under a photoperiod of 20 h light:4 h dark had regained photosensitivity 12 weeks later, despite chronic photostimulation. This finding is consistent with the observation that tree sparrows thyroidectomized during photorefractoriness (at week 18 under a photoperiod of 20 h light:4 h dark) show testicular growth when thyroxine replacement therapy is initiated at week 30 (Wilson and Reinert, 1993) and with earlier reports both on the restorative effect of thyroidectomy (Dawson *et al.*, 1985b; Creighton, 1988) and on the anti-restorative effect of exogenous thyroxine (Boulakoud *et al.*, 1991; Wilson and Reinert, 1993). Under natural conditions, chronic exposure to short days, as experienced during autumn and winter, dissipates photorefractoriness. By an unknown mechanism, but perhaps because thyroid hormones are deficient or inactive, short days create an internal milieu that is inappropriate for maintaining the photoperiodic control circuit in a refractory mode. Thus, in photorefractory birds exposed to short days, the photoperiodic control mechanism is rejuvenated, and photosensitivity is gradually restored (Dawson, 1991; Wilson, 1992; Boulakoud and Goldsmith, 1994). If thyroid hormones play a regulatory role in the timing of differentiation and facilitate the programming of the photoperiodic control circuit for seasonal reproduction, as the data

from the study reported here suggest, and if the programme calls for loss of neurones, for which there is direct evidence in adult avian brains (Kirn and Nottebohm, 1993), or for dysfunctional changes in neuronal or synaptic morphology, then proliferation of replacement components or morphological restoration of existing components may be facilitated by the absence or inaction of thyroid hormones, as after thyroidectomy or perhaps during chronic exposure to short days.

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