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Effects of Sex Steroids on Calling, Locomotor Activity, and Sexual Behavior in Castrated Male Japanese Quail

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Castrated male Japanese quail were implanted with Silastic capsules containing testosterone (T), estradiol-17β (E_2), 5β-dihydrotestosterone (5β-DHT), Δ_4-androstenedione (Δ_4), 5α-androstanedione (A), 5α-dihydrotestosterone (5α-DHT) or with empty capsules. Calling, monitored continuously and automatically, was induced significantly by T and Δ_4. Locomotor activity, also monitored continuously by floor deflection, was enhanced by T, Δ_4, and E_2. Additional data concerning heterosexual and homosexual behavior were obtained from castrated quails after implantation of T, Δ_4, E_2, or 5α-DHT. T and Δ_4 restored hetero- and homosexual behavior as did E_2 but to a lesser extent. 5α-DHT did not induce either sexual behavior. Growth of the cloacal protrusion was induced in birds implanted with T, Δ_4, A, and 5α-DHT but not with 5β-DHT and E_2. These results indicate that calling and locomotor activity enhancement (including sexual behavior) are two different components of reproductive behavior which require different androgens or their metabolites to be activated.

It is well documented that androgens induce masculine sexual behavior in males of vertebrate species (see for review Larsson, 1979; Silver, O'Connell, and Saad, 1979; Crew, 1979; for amphibian species see Kelley and Pfaff, 1976; Moore and Zoeller, 1979; Wada and Gorbman, 1977). It is now widely accepted that testosterone is converted in the central nervous system to estradiol which activates masculine sexual behavior in mammals (Christensen and Clemens, 1974; Edwards and Burge, 1971; Fletcher and Short, 1974; Södersten, 1973, but see Yahr and Gerling, 1978) and in birds (Adkins, 1975; Adkins, 1977; Adkins and Adler, 1972; Adkins and Pniewski, 1978). However, we know little concerning the hormonal dependence of male vocalization in birds. Adkins and Pniewski (1978) showed that in Japanese quail 5α-dihydrotestosterone and testosterone could induce calling but estradiol did not. On the other hand, the "bow-coo," a vocalization of ring doves and pigeons, is stimulated by testosterone but not by estradiol and dihydrotestosterone (Cheng and Lehrman, 1975; Hutchison, 1970; Pietras and Wenzel, 1974). So far a

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mechanism of induction of male vocalization by steroid hormones has not been investigated fully.

Recently, Wada (1981) established an apparatus to record the numbers of calls emitted by a quail and its locomotor activity, and showed that these behaviors are androgen dependent. Since the method used in the study allowed full recording of both calling and locomotor activity without any disturbance of the animals, it is useful to investigate how testosterone and its metabolites affect these behaviors and whether these behaviors are comparable with other behaviors such as mating and aggressive behavior. This report provides the results concerning these two points.

MATERIALS AND METHODS

Male Japanese quail (*Coturnix coturnix japonica*), purchased from a commercial source, were kept in recording cages enclosed in light-tight boxes described elsewhere (Wada, 1981). Briefly, the box was designed to record the number of calls (crows) made by a quail, and locomotor activity as the number of floor deflections. Each event was counted, recorded, and printed out for every clock hour. Inside the box illumination was provided by a fluorescent lamp, and a 24-hr light–dark cycle was regulated by an external timer. Birds were given pelletized quail food and water *ad libitum*.

Six photostimulated quail under 16L:8D (lights on from 0900 to 0100) for 20 days beginning from 5 weeks of age were castrated and remained under the long day. After 2 weeks, they were implanted with two subcutaneous Silastic capsules (30 mm in length including sealing at the both ends) containing testosterone (T). Two weeks after implantation, the capsules were removed. Implantation and removal of implants were carried out without anesthesia. Thereafter, two capsules containing one of the following were implanted in and removed from each bird every 2 weeks: estradiol-17β (E_2), 5β-dihydrotestosterone (5β-DHT), nothing (empty), Δ_4 androstenedione (Δ_4), 5α-androstanedione (A), 5α-dihydrotestosterone (5α-DHT), and T. T was implanted again to check effects of long-term castration. Capsules were made of Silastic medical-grade tubing (3.18 mm o.d. × 1.57 mm i.d.) filled with the free form of the steroid hormones mentioned above (Sigma Chemical Co., St. Louis, Mo.) and sealed with Silastic adhesive Type A. The capsules were incubated overnight in saline solution at room temperature before implantation. Before implantation and after removal of implants, they were weighed to the nearest 0.1 mg to estimate weight loss during implantation.

During the whole experimental period, the numbers of calls and activity counts were recorded and the area of the cloacal protrusion of each quail was measured with a ruler every 2 or 3 days.

For estimation of sexual behavior, intact photostimulated male birds (20–25 days of photostimulation under 16L:8D), castrates (2 weeks after

castration), and castrates with implants (10–13 days after implantation of two Silastic capsules containing Δ_4, T, E_2, or 5α-DHT) were used. Observations were carried out between 1030 and 1300. For heterosexual interaction, a receptive, egg-laying female quail was placed in an observation cage (35 × 39 × 39 cm high) covered with kraft paper and illuminated from above. A small cage (15 × 30 × 16 cm high) was attached to the observation cage but the two cages were separated by a partition. Each experimental bird was placed in the small cage for 1 min and then the partition was removed. During the next 3 min, duration of head grabbing and the number of cloacal contact movements were observed through a one-way glass and recorded. For homosexual interaction, a castrated male bird was placed in the observation cage instead of a female bird and observed for 2 min.

Statistical analyses were carried out by Student's *t* test, Mann–Whitney *U* test, or Fischer's exact probability test.

RESULTS

Figure 1 shows the effects of various steroid hormone treatments on calling, locomotor activity, and growth of the cloacal protrusion during the whole experimental period in a group of six birds. The effects of photostimulation, castration, and T replacement on calling and locomotor activity have already appeared elsewhere (Wada, 1981), and a part of the results are repeated here for comparison. Both T and Δ_4 effectively induced calling in the castrated birds. As for activity enhancement, T, Δ_4, and E_2 were effective (Fig. 1). Failure of A and 5α-DHT to induce calling and enhancement of activity was not due to effects of long-term castration, since a second T implantation again induced both behaviors.

The numbers of calls and locomotor activity, respectively, during each period of steroid hormone treatment, were combined for each bird to obtain recovery rates against those of the first T session. Then the means of the group were calculated for calling and locomotor activity (Fig. 2). T and Δ_4 were the hormones to induce calling in castrated quail. The birds implanted with Δ_4 called most frequently during the first hour after the lights were turned on as in T-implanted birds (Wada, 1981). Other than T and Δ_4, only E_2 significantly enhanced locomotor activity (Fig. 2).

T, Δ_4, A, and 5α-DHT were equivalently effective in any individual in stimulating growth of the cloacal protrusion (Fig. 1).

Amounts of steroid hormones released from the implanted capsules during 2 weeks are shown in Table 1. There were differential rates of release in different steroid hormones.

In both heterosexual and homosexual interactions, similar bouts of behavior, which included head grabbing, mounting, and cloacal contact movement, were observed. Since it was difficult to discriminate between

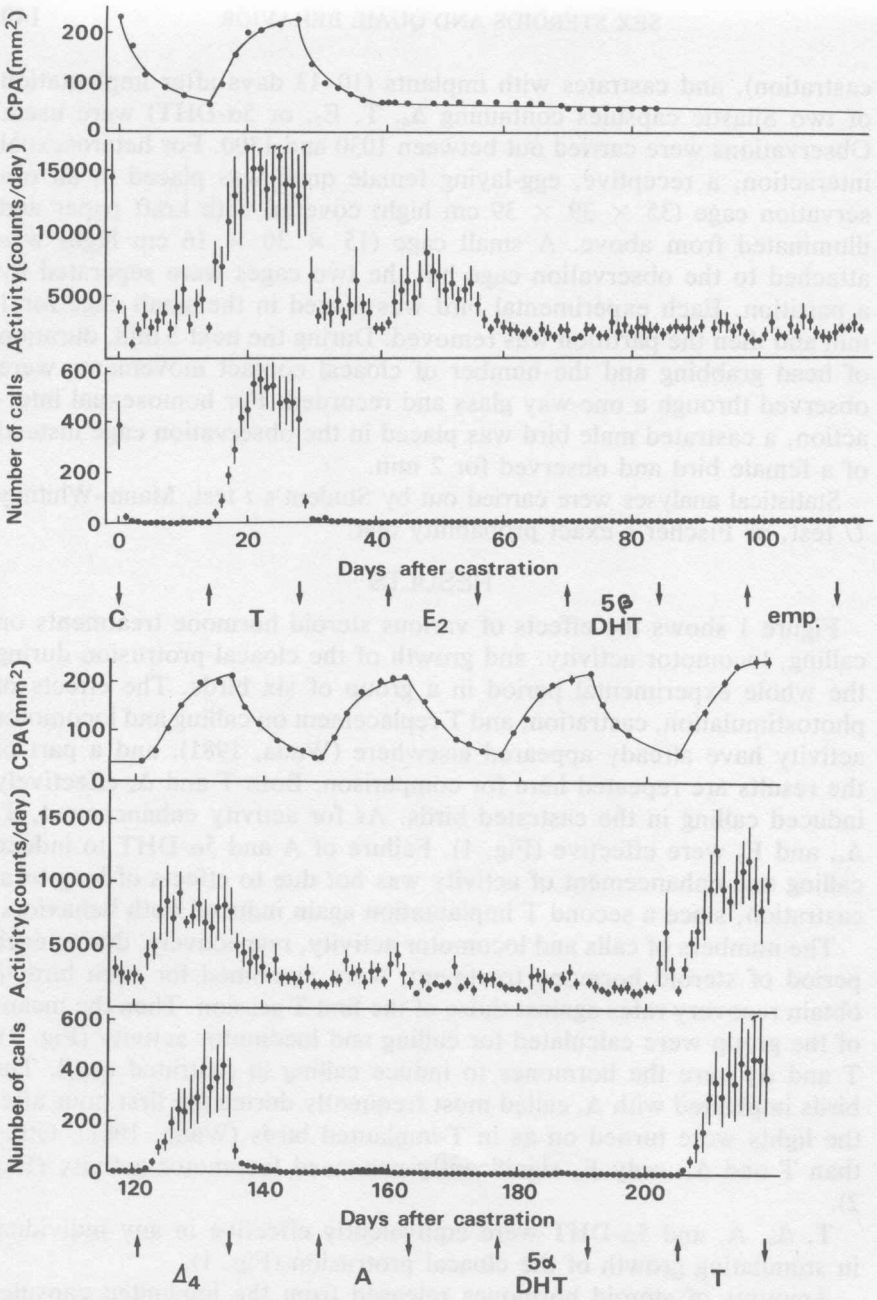

FIG. 1. Changes in numbers of calls, locomotor activity, and area of the cloacal protrusion (CPA) during the whole experimental period in a group of six birds. The C with a down arrow indicates the day of castration. Up arrows and down arrows thereafter indicate the day that Silastic capsules, containing steroid hormones mentioned below, were implanted and removed, respectively. T, testosterone; E_2, estradiol-17β; 5β-DHT, 5β-dihydrotestosterone; emp., without any steroid hormone; Δ_4, androstenedione; A, 5α-androstanedione; 5α-DHT, 5α-dihydrotestosterone. T was implanted again at last.

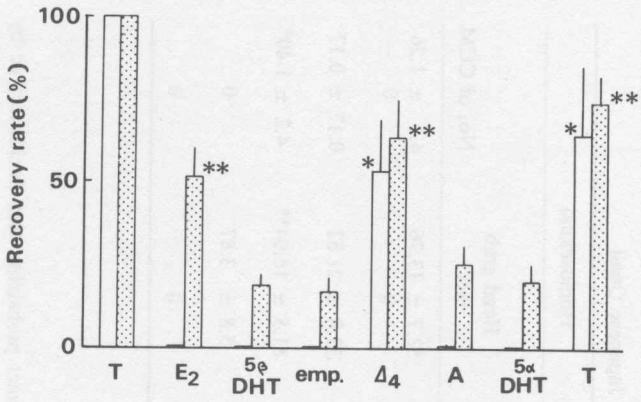

FIG. 2. Effects of various steroid hormones on calling (white columns) and locomotor activity (dotted columns). The data are expressed as percentage recovery rates during the treatment considering the value of the first T session as 100%. The values are the means of six birds with standard errors indicated by bars. Significant differences from the value for the empty capsule session are shown: $*P < 0.05$ and $**P < 0.01$ (t test). Abbreviations are the same as in Fig. 1.

male copulatory behavior to the male and male aggressive behavior to the male in these observations, the words homosexual and heterosexual behavior were used for description of the behavior observed in homosexual interaction and heterosexual interaction.

Table 2 shows the behavioral frequencies of hetero- and homosexual behavior in intact photostimulated, castrated, and implanted castrated birds. Almost all the intact photostimulated birds showed hetero- and

TABLE 1
Amounts of Hormones Released From the Silastic Capsules During 2-Week Implantation[a]

	Hormone implanted (mg)	Hormone released (mg)
Testosterone		
(First session)	36.3 ± 0.29[b]	3.2 ± 0.32[c]
(Last session)	33.1 ± 0.43	2.2 ± 0.08
Estradiol-17β	50.6 ± 2.28	0.6 ± 0.16
5β-Dihydrotestosterone	22.3 ± 0.90	4.2 ± 0.32
Δ_4-Androstenedione	44.0 ± 0.92	7.9 ± 0.36
5α-Androstanedione	37.1 ± 1.01	19.1 ± 0.47
5α-Dihydrotestosterone	43.8 ± 0.90	0.6 ± 0.21

[a] After removal, the capsules were dried for 2 weeks at room temperature, and weight loss was calculated.

[b] Mean ± SEM.

[c] The values are not corrected for the changes observed in the empty capsules (0.18 ± 0.216 mg gain).

TABLE 2
Effects of Sex Steroid Hormones on Hetero- and Homosexual Behavior in Male Japanese Quail

	Heterosexual			Homosexual		
	Incidence[a] (%)	Head grab (sec)	No. of CCM[b]	Incidence (%)	Head grab (sec)	No. of CCM
Photostimulated (7) (3 weeks)	85.7	30.9 ± 10.62[c]	4.3 ± 1.43	85.7	52.7 ± 13.76	4.1 ± 1.26
Castrated (6)	0	0	0	0	0	0
Castrated with androstenedione capsules (6)	83.3**	33.0 ± 10.13**	3.5 ± 1.02**	50.0	33.8 ± 21.82	0.17 ± 0.17
Castrated with testosterone capsules (6)	83.3**	78.2 ± 31.30**	5.7 ± 2.11**	100**	81.5 ± 16.04**	4.2 ± 1.40*
Castrated with estradiol capsules (6)	50.0	13.5 ± 12.12	0.7 ± 0.49	66.7*	5.8 ± 3.87	0
Castrated with 5α-dihydrotestosterone capsules (6)	0	0	0	0	0	0

Note. The numbers in parentheses are the numbers of birds.

[a] Incidence means percentage of animals which showed any head grabbing or CCM.

[b] Cloacal contact movement.

[c] Mean ± SEM.

* $P < 0.05$ or ** $P < 0.01$, significantly different compared with castrated group by Fisher's exact probability test (incidence) or by Mann–Whitney U test (duration of head grabbing and number of CCM).

homosexual behavior. However, castrated control birds never showed any sexual behavior. T restored both hetero- and homosexual behavior in castrated birds to the level of the intact photostimulated birds. Δ_4 also induced heterosexual behavior, but was not so effective on homosexual behavior. E_2 activated heterosexual behavior in three out of six birds but frequencies of behavior were less than those of T- and Δ_4- implanted birds. E_2 was also partially effective in inducing homosexual behavior.

DISCUSSION

These results demonstrate that calling and enhancement of motor activity (together with homo- and heterosexual behavior) are activated by different steroid hormones. Calling is induced by T and Δ_4, but increased activity is induced by E_2 as well as T and Δ_4, suggesting that expression of the latter behavior needs aromatization of T to E_2. This aromatization hypothesis was first presented by Naftolin, Ryan, and Petro (1972), and it has been well documented that E_2 is the active metabolite to induce male sexual behavior in mammals (Christensen and Clemens, 1974; Edwards and Burge, 1971; Fletcher and Short, 1974; Södersten, 1973) and also in birds (Adkins, 1975; Adkins and Adler, 1972; Adkins and Pniewski, 1978). Thus, androgens which can be converted to E_2 are behaviorally effective, whereas androgens incapable of such conversion when administered alone are not (mammals: Beyer, Larsson, Pérez-Palacious, and Morali, 1973; Beyer and Rivaud, 1973; McDonald, Beyer, Newton, Brien, Baker, Tan, Sampson, Kitching, Greenhill, and Pritchard, 1970; birds: Adkins, 1977). Activation of quail mating behavior by TP was blocked by concurrent administration of the antiestrogens (Adkins and Nock, 1976). These studies all indicate that E_2 is the active metabolite of T in the central nervous system. E_2 was also effective in enhancing general motor activity as shown in this experiment. Roy and Wade (1975) have also shown that E_2 but not DHT is effective in increasing spontaneous activity in rats. In this sense, enhancement of locomotor activity is in the same behavioral category of steroid specificity with sexual behavior. Enhancement of locomotor activity in this species might be one of the reproductive behaviors, since Watson (1970) showed that testosterone implantation in red grouse resulted in birds becoming more aggressive and more exploratorily active, resulting in the enlargement of a territory. On the other hand, calling does not require aromatization, but is activated directly by T and Δ_4, indicating that calling is different from mating and aggressive behavior. Two components might possibly be different in specificity of steroid receptors.

In the present experiment, E_2 did not fully enhance locomotor activity, nor did it fully restore hetero- and homosexual behavior (Figs. 1, 2, and Table 2). This might be due to lack of enough E_2 in circulation in the E_2-implanted birds to activate these behaviors. Table 1 shows that E_2

is difficult to release from the implanted Silastic capsules. In fact, Tsutsui and Ishii (1981) showed that injection of a sufficient amount of E_2 was more effective in inducing aggressive behavior than T and Δ_4 in male Japanese quail.

Adkins and Pniewski (1978) showed that 5α-DHT was a more potent stimulator of calling than T in Japanese quail. This was not found in the present experiment. I cannot explain the reason for the different results between two experiments with the same species. Several differences in the experimental designs are apparent, however. Adkins and Pniewski (1978) observed calling only for 10 min during the first 2-hr period after lights were turned on. This period is certainly the time when quail call most frequently (Guyomarc'h and Thiboult, 1969; Wada, 1981). However, in both the TP and DHTP treatment groups, but especially in the TP groups, calling was not so extensive in their experimental birds. There may have been some suppressive factors during observations which happened to cause the differences. On the other hand, the design of the present experiment allowed quail to call without any suppressive effects, and also calling was observed for the whole experimental period. It is true that calling was observed during 5α-DHT as well as A and E_2 treatments, but the numbers of counts were very low compared with those of T and Δ_4 (Figs. 1 and 2). Another difference was in the method and dose of the steroid hormones administered. In this experiment, the hormones were administered by implantation of Silastic capsules instead of by injection. As is shown in Table 1, the amounts of hormones released from the capsules were different for each steroid and very small compared with the amounts of hormones given in the injection experiments. This differential rate of release through Silastic capsules has already been demonstrated by Balthazart and Hirschberg (1979a) in chicks. 5α-DHT was a very slow penetrator, about one-fifth as fast as T. However, 5α-DHT implants could induce full growth of the cloacal protrusion (Fig. 1), indicating that enough hormone was present in the circulation. Androstanedione, a 5α metabolite of Δ_4 which had the highest release rate in this experiment, also had no effect on calling and enhancement of locomotor activity. In male ring doves and pigeons, 5α-DHT had no effect on the "bow-coo," a vocalization of these species (Cheng and Lehrman, 1975; Hutchison, 1970; Hutchison, 1971; Martinez-Vegas, 1974; Murton, Thearle, and Lofts, 1969; Pietras and Wenzel, 1974; Saad and Silver, 1979). Therefore, failure of 5α-DHT to induce calling was not due to a lower concentration of hormone; rather it indicated that 5α-DHT, which is the active metabolite for peripheral tissues, was not involved in expression of the behavior in this species.

However, among mammalian species, there is a great species variation in the responsiveness to 5α-DHT (see Larsson, 1979). Thus, in rats, rabbits, hamsters, and one strain of mice, DHT has a weak stimulatory

effect on male sexual behavior. In the rhesus monkey, DHT is potent, but less so than T; in the guinea pig it is as potent as T.

On the other hand, 5α-DHT restores the growth of the cloacal protrusion in castrated birds, and this gland of the male Japanese quail is known for its dependence on circulating androgens (Sachs, 1969; Adkins and Adler, 1972; Adkins, 1977). T, Δ_4, and A, as well as 5α-DHT, were all effective in inducing growth of the gland. Furthermore, T, Δ_4, and A are all capable of being metabolized to 5α-DHT. Therefore, 5α-DHT should be the active metabolite of the androgens for stimulation of glandular growth.

5β-DHT had essentially no effect on quail behavior or peripheral androgen-dependent tissues, as is also the case in rats (Beyer *et al.*, 1973). In avian species, however, 5β-DHT is the dominant metabolite in the hypothalamus (chicken: Nakamura and Tanabe, 1974; starling: Massa, Cresti, and Martini, 1977) and 5β metabolites of T were effective in inducing juvenile copulatory behavior in chicks (Balthazart and Hirschberg, 1979b). These results in chicks are contrary to those of Adkins (1977) and of the present experiment in Japanese quail. This might be due to species differences and ages, together with differences in behavioral test procedures. The former study employed observations with an anesthetized female or the hand-thrust test, whereas one of the latter investigations employed observations with conscious, receptive females and the other observed calling and locomotor activity, which are spontaneous. We have to be cautious when extrapolating to mature behavior from the results obtained in juvenile individuals. Furthermore, results obtained by the hand-thrust test are not necessarily assumed to be a reflection of adult copulatory behavior. There are still conflicts, but 5β-DHT might have a role in the central nervous system other than induction of sexual behavior, at least in this species.

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