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Behavioural and morphological effects of 5α-dihydrotestosterone and oestradiol-17β in the prepubertally castrated boar

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Summary. Three groups of 5 prepubertally castrated boars received twice weekly subcutaneous injections from 16 to 28 weeks of age of 5α-dihydrotestosterone propionate (1 mg/kg), oestradiol-17β dipropionate (0·1 mg/kg), or a combination of the two steroids. The pigs were tested each week for sexual behaviour with an oestrogen-treated ovariectomized gilt. 5α-Dihydrotestosterone did not induce copulatory behaviour whereas oestradiol initiated mounting, although this behaviour was not maintained. However, the combined hormonal treatment induced the full pattern of copulation, including ejaculation, in 4/5 pigs. Oestrogen-treated animals also showed champing and salivation. None of the pigs treated with 5α-dihydrotestosterone showed lordosis when exposed to a mature boar. Increases in the size of the penis, the ischio- and bulbocavernosus muscles, seminal vesicles and bulbourethral glands were produced by 5α-dihydrotestosterone, and, with the exception of the penis, this hypertrophy was further enhanced by additional treatment with oestradiol. Increases in the weight of the prostate and muscular urethra were due mainly to the effects of oestrogen; this steroid caused extensive development of fibromuscular tissue and also increased mammary teat length. In the submaxillary salivary glands, synergism between 5α-dihydrotestosterone and oestradiol resulted in hypertrophy of the serous cells.

Introduction

The conversion of 4-ene-unsaturated androgens, such as testosterone, to oestrogen (aromatization) takes place in the brain of many vertebrates (Naftolin *et al.*, 1975; Callard, Petro & Ryan, 1978) and there is evidence in laboratory mammals that the aromatization of testosterone is necessary for male sexual behaviour. For example, in the castrated male rat, aromatase enzyme inhibitors block the behavioural effects of testosterone (Christensen & Clemens, 1975) whereas non-aromatizable 5α-reduced androgens are incapable of inducing copulatory activity (Beyer, Larsson, Peréz-Palacios & Morali, 1973). However, although oestrogen will support sexual behaviour (Davidson, 1969), it is more effective when administered in conjunction with the 5α-reduced androgen 5α-dihydrotestosterone (Baum & Vreeburg, 1973; Larsson, Sodersten & Beyer, 1973). This facilitatory action of 5α-dihydrotestosterone is probably related to its ability to maintain sensory feedback (Parrott, 1975) by supporting normal penile morphology (Read, Lloyd, Eisenberg & Devine, 1976) because 5α-dihydrotestosterone itself does not induce sexual behaviour (McDonald *et al.*, 1970). Nevertheless, the possibility that 5α-dihydrotestosterone may also synergize centrally with oestrogen (Larsson *et al.*, 1973) cannot be ruled out.

Oestrogen stimulates various amounts of sexual activity in castrated stags (Fletcher & Short, 1974), stallions (Thompson, Pickett, Squires & Nett, 1980), bulls (Dykeman, Katz & Foote, 1982) and rams (D'Occhio & Brooks, 1976; Mattner 1976; Parrott, 1978). Oestrogen alone induces mounting in castrated rams, but oestrogen plus 5α-dihydrotestosterone stimulates intromission and ejaculation (D'Occhio & Brooks, 1980). In the pig, the mating performance of boars castrated when sexually mature and treated with testosterone is enhanced by additional administration of oestrogen (Joshi & Raeside, 1973). Furthermore, in prepubertally castrated boars, oestrone induces champing of saliva and mounting with thrusting, but no penile extrusion (Booth, 1983). However, the behavioural effects of 5α-dihydrotestosterone either alone, or in combination with oestrogen, have not been examined in this species.

In the rat, a species with a vascular penis, copulatory efficiency is related to the density of the penile spines which are maintained by 5α-dihydrotestosterone (Parrott, 1975). In the sheep, which has a fibroelastic penis like that of the pig, peripherally administered 5α-dihydrotestosterone produces erections in wethers sexually motivated by hypothalamic testosterone implants (Parrott & Baldwin, 1984). Therefore, in the boar, 5α-dihydrotestosterone might affect both the development of the penis and the musculature involved in erection and ejaculation. Furthermore, 5α-dihydrotestosterone either by itself, or in combination with oestrogen, is likely to influence the growth of the accessory sex organs, since previous work has shown that both androgens and oestrogen have stimulatory effects on these structures in pigs (Booth, 1980, 1983).

The object of this study, therefore, was to investigate the effects of 5α-dihydrotestosterone and oestradiol-17β, administered separately or together, on the development of sexual behaviour, the genitalia and the accessory sex organs of prepubertally castrated pigs.

Materials and Methods

Animals and treatments. Fifteen Large White pigs were castrated at 3 weeks of age and kept under normal husbandry conditions until 15 weeks of age, when they were randomly assigned to 3 groups (A, B and C) of 5 pigs in each group. Between 16 and 28 weeks of age, the pigs were weighed weekly and given twice-weekly (Monday and Thursday) subcutaneous injections of 5α-dihydrotestosterone propionate (DHTP) (1 mg/kg) dissolved in arachis oil (40 mg/ml) (Group A), or oestradiol dipropionate (ODP) (0·1 mg/kg) dissolved in arachis oil (4 mg/ml) (Group B), or a combination of both steroids as above (DHTP + ODP) (Group C). The steroids were purchased from Steraloids Ltd, Croydon, U.K.

An ovariectomized gilt was used as a mating partner in the behavioural tests. This animal was the same age as the males and was injected twice weekly with oestradiol benzoate (5 μg/kg) dissolved in arachis oil (0·5 mg/ml) to keep it in continuous oestrus. The oestradiol benzoate was obtained from Intervet Laboratories, Ltd, Cambridge, U.K.

Behavioural tests. Observations were made in a large covered pen (3·4 × 2·9 m) on the same day (Wednesday) each week. The female stayed in the pen for the duration of the test session and individual males were introduced for 5-min periods. The 3 groups of pigs were tested in a rotating order each week and individual animals within a group were tested in random order. During each 5-min test the following behavioural indices were scored on a chart recorder: (1) head contact—the male rubs or touches the female's head with his snout; (2) genital sniffing—the male sniffs the female's vulva and perineum; (3) body nosing—the male nudges the female's flank and abdomen with his snout; (4) mounting—the male stands astride the female's back; (5) mounting and thrusting—the male's mounts are associated with rhythmical pelvic thrusting; (6) erection—the penis is fully extruded from the sheath; (7) intromission—the penis is inserted into the vagina and ejaculation takes place.

The above measures were scored as frequencies, i.e. the number of times they were exhibited within an individual test. However, certain other activities were recorded on a presence or absence

basis within an individual test. These were as follows: (1) aggression—tests in which fighting occurred, regardless of which partner initiated the attack; (2) champing—tests in which the male showed rhythmical opening and closing of the jaws; (3) salivation—tests in which champing produced copious quantities of frothy saliva.

At the end of the experiment each group of pigs (A, B & C) was exposed on 3 separate occasions to a fully mature boar placed in an adjoining pen which permitted visual, olfactory and limited tactile communication. Each pig was tested to see whether it would stand in response to back pressure in this situation, and whether such behaviour could be facilitated with an aerosol preparation of boar pheromone ('Boarmate': Antec International, Sudbury, Suffolk, U.K.).

Morphology. At the end of the experiment the castrated boars were killed and the following organs were removed, measured and weighed: the penis shaft, ischiocavernosus and bulbocavernosus muscles, the muscular portion of the urethra, the bulbourethral glands, prostate, seminal vesicle and also the submaxillary salivary glands; the mean length of the mammary teats were determined for each animal. Samples of tissue from the prostate, seminal vesicles and submaxillary glands were fixed in Bouin's fluid for histology. Histomeric analysis of submaxillary gland sections was carried out as described by Booth, Hay & Dott (1973). The seminal vesicles were stored at $-70°C$ pending the analysis of zinc as described by Booth & Baldwin (1980).

Statistics. The effect of treatments on the various morphological indices was examined using analysis of variance (ANOVA). A statistical analysis was not considered appropriate for the behavioural data because the number of animals responding in a given treatment group was not consistent from week to week.

Results

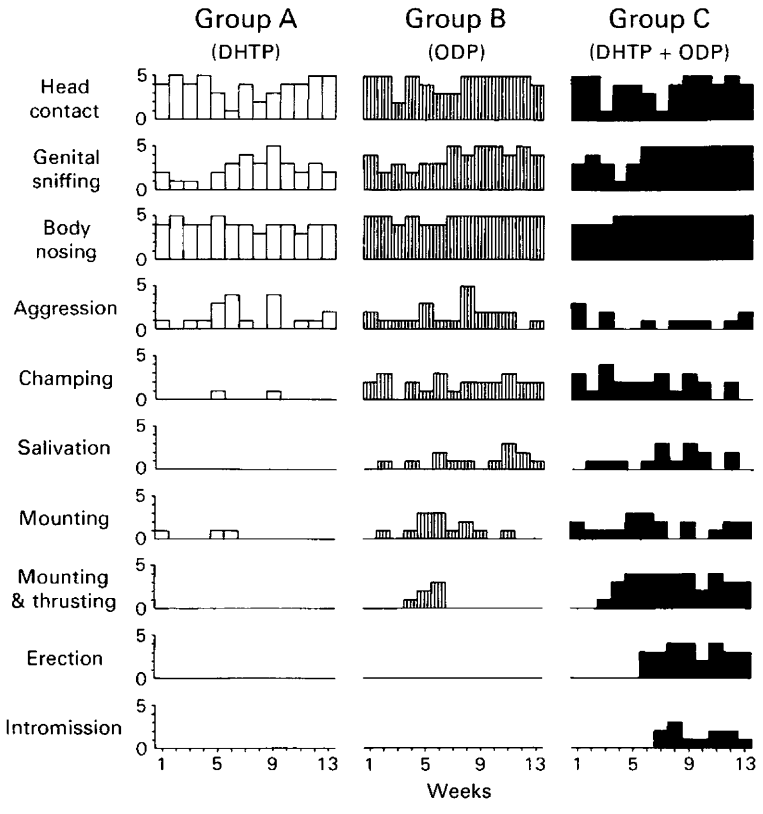
Behaviour

Text-figure 1 shows the number of pigs in each treatment group that engaged in a particular behaviour during each of the 13 weeks of observation. Head contact, genital sniffing and body nosing were displayed by every pig in at least one, and usually in several, tests (Text-fig. 1). The number of animals showing head contact throughout the experiment was similar in the 3 treatment groups. In some tests, every pig in a particular treatment group exhibited genital sniffing or body nosing. With regard to genital sniffing, this happened once in pigs in Group A, 4 times in pigs in Group B and in 8 consecutive tests in pigs in Group C. Similarly, body nosing was displayed by all 5 pigs in 2/13, 9/13 and 10/13 tests in pigs in Groups A, B and C, respectively.

Text-figure 1 also illustrates tests in which aggression, champing and salivation were observed. All pigs in Group B showed aggression on occasions throughout the 13-week period, and 4/5 animals in each of Groups A and C engaged in aggressive exchanges. However, there was a tendency for aggression to be lowest in pigs in Group C. Two Group A pigs showed champing on a single occasion but no animals in this group were seen to salivate. In contrast, champing was exhibited from time to time by all the pigs in Groups B and C and salivation by 4/5 animals in both of these groups.

Behavioural measures relating to copulation are also shown in Text-fig. 1. Three pigs in Group A mounted the gilt on a single occasion but animals in this group did not display thrusting or erections and consequently never achieved intromission. Three pigs in Group B also mounted the gilt, with most activity occurring between the 4th and 9th week of the experiment. These animals showed thrusting but this behaviour was not maintained after the 6th week and no erections or intromissions were seen. All Group C animals except one exhibited mounting, mounting with thrusting, erection, intromission and ejaculation.

Text-figure 2 indicates the mean number of events recorded each week for the three treatment groups. Head contact was most frequent in the first weeks of testing and thereafter was maintained



Text-fig. 1. Total number of prepubertally castrated boars from groups (5 animals per group) treated with 5α-dihydrotestosterone propionate (DHTP, Group A), oestradiol dipropionate (ODP, Group B) or DHTP + ODP (Group C) that, each week, displayed various aspects of sexual and related behaviours during the 13-week test period.

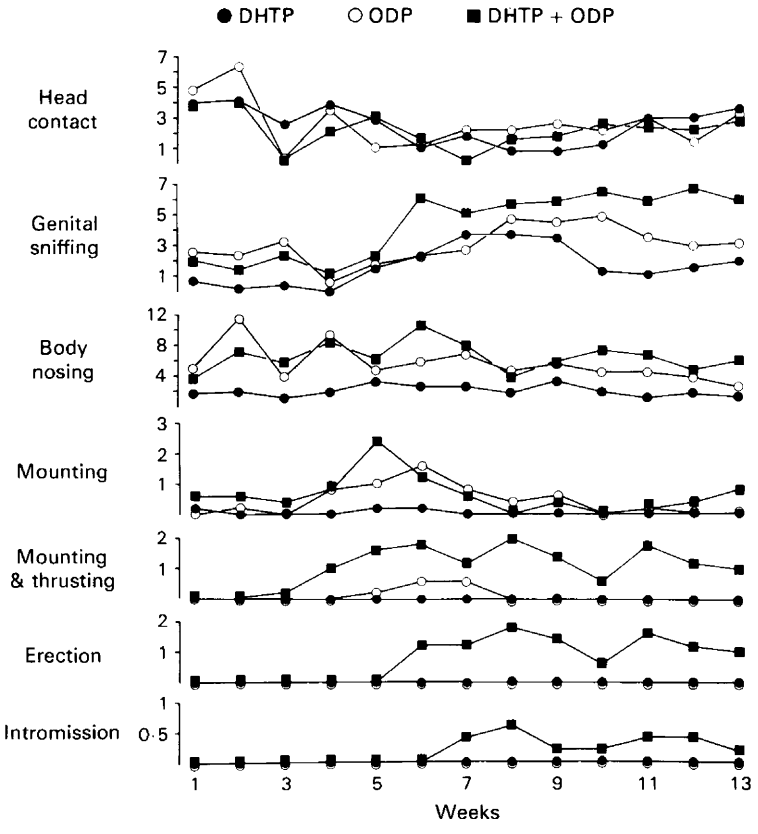
at a similar level in the three groups. The frequency of genital sniffing increased in pigs in Group C in the 6th week and remained elevated for the rest of the experimental period. Body nosing in pigs in Group A occurred at a consistently lower frequency than in the other two groups.

The mean mount frequency reached a maximum in the 5th week in pigs in Group C and a smaller peak was apparent in animals in Group B in Week 6 (Text-fig. 2). However, in Group C pigs mounting declined and mounting with thrusting took its place, but in Group B pigs mounting with thrusting declined first. In pigs in Group C erections were first seen in the 6th week of testing and intromissions in the 7th week.

Exposure of the castrated pigs to a mature boar resulted in mixed behavioural responses. Only one pig from each of Groups B and C exhibited a lordosis response. The majority of pigs in Group C attempted to mount each other but none of these animals stood to be mounted. Copious amounts of saliva were produced only by pigs in Group B and the largest pig in this group made aggressive moves towards the boar. The pigs in Group A showed no particular responses to the boar. Treatment with 'Boarmate' did not facilitate any behavioural responses.

Body weight and genitalia

Final body weights were just over 70 kg, and analysis of variance showed that there were no significant differences due to treatments; therefore, all organ weights and dimensions are expressed as actual rather than relative weights.



Text-fig. 2. Frequency of behavioural responses in groups of prepubertally castrated boars (5 animals per group) treated with 5α-dihydrotestosterone propionate (DHTP, Group A), oestradiol dipropionate (ODP, Group B) and DHTP + ODP (Group C), expressed as the mean number of events recorded each week during the 13-week test period.

As shown in Table 1, penis length and weight were the same in pigs in Groups A and C and significantly greater than in animals in Group B. The ischio- and bulbocavernosus muscles were significantly smaller in pigs in Group B than in the animals in the other two groups. The weight of these muscles was about 70% greater in Group A than in Group B animals and ~185% greater in Group C than in Group B.

Table 1. Mean ± s.e.m. penis length and organ weights in boars castrated prepubertally and receiving 5α-dihydrotestosterone propionate (Group A), oestradiol dipropionate (Group B) and both steroids (Group C)

Group	Penis length (cm)	Organ weights (g)		
		Penis	Ischiocavernosus muscle	Bulbocavernosus muscle
A	42·40 ± 1·03[a]	28·86 ± 1·81[a]	34·57 ± 4·38[a]	35·70 ± 1·13[a]
B	35·80 ± 0·64[b]	18·40 ± 0·96[b]	19·48 ± 1·88[c]	21·80 ± 1·62[d]
C	42·30 ± 0·77[a]	27·98 ± 0·48[a]	56·92 ± 2·45[b]	59·12 ± 4·28[b]

* *Analysis of variance:* a × b, b × c, b × d, $P < 0{\cdot}001$; a × c, $P < 0{\cdot}01$; a × d, $P < 0{\cdot}05$.

Steroid-dependent glands

As shown in Table 2, the weights of the seminal vesicles were lowest in pigs in Group B, significantly greater in those in Group A and larger still in animals in Group C. Similar effects were seen with regard to the bulbourethral glands, with a larger weight increase occurring in Group C than in Groups A or B. In contrast, the weights of the prostate and muscular urethra were increased in Group B compared with those in Group A, but there was no further stimulation in Group C. The weights of the seminal vesicles, bulbourethral glands and prostate in pigs in Groups A and C were due in part to the volume of the secretions produced by the active secretory tissue, as confirmed by histology. On the other hand, the weights of the accessory sex organs in pigs in Group B were due primarily to the extensive development of fibromuscular tissue. The length of the muscular urethra was greatest in Group C pigs whereas the diameter was largest in Group B animals; this was primarily due to thickening of the wall of the urethra rather than its surrounding muscle.

Table 2. Mean ± s.e.m. organ (mean single glands) weights and length and diameter of the muscular urethra in boars castrated prepubertally and receiving 5α-dihydrotestosterone propionate (Group A), oestradiol dipropionate (Group B) or both steroids (Group C)

	Organ weights (g)				Muscular urethra	
Group	Seminal vesicle	Prostate	Bulbo-urethral	Muscular urethra	Length (cm)	Diameter (cm)
A	$45{\cdot}80 \pm 6{\cdot}59^{a}$	$3{\cdot}05 \pm 0{\cdot}36^{d}$	$24{\cdot}26 \pm 1{\cdot}73^{a}$	$29{\cdot}70 \pm 1{\cdot}91^{a}$	$14{\cdot}80 \pm 0{\cdot}41^{a}$	$2{\cdot}20 \pm 0{\cdot}13^{e}$
B	$5{\cdot}95 \pm 0{\cdot}22^{b}$	$6{\cdot}44 \pm 0{\cdot}65^{a}$	$13{\cdot}59 \pm 5{\cdot}42^{a}$	$50{\cdot}32 \pm 3{\cdot}10^{b}$	$15{\cdot}70 \pm 0{\cdot}12^{e}$	$2{\cdot}98 \pm 0{\cdot}02^{d}$
C	$116{\cdot}00 \pm 5{\cdot}51^{c}$	$6{\cdot}48 \pm 0{\cdot}83^{a}$	$63{\cdot}14 \pm 4{\cdot}39^{b}$	$47{\cdot}04 \pm 1{\cdot}64^{b}$	$16{\cdot}66 \pm 0{\cdot}19^{b}$	$2{\cdot}56 \pm 0{\cdot}10^{a}$

Analysis of variance: a × b, a × c, b × c, d × e, $P < 0{\cdot}001$; a × d, $P < 0{\cdot}01$; a × e, b × e, $P < 0{\cdot}05$.

The concentration of zinc (mean ± s.e.m.) in the seminal vesicles was 3·56 ± 0·06 μg/g in Group A pigs and 3·53 ± 0·36 μg/g in Group C pigs. These levels were higher ($P < 0{\cdot}01$) than those in Group B animals (1·18 ± 0·09 μg/g).

The submaxillary salivary glands weighed between 16 and 17 g and the differences between the treatment groups were not significant. The percentage area (mean ± s.e.m.) occupied by the serous cells in histological sections of the submaxillary glands was 32·4 ± 3·76 in Group A and 38·0 ± 5·55 in Group B pigs. However, the area of serous cells in pigs in Group C was 51·7 ± 4·90 and this was greater ($P < 0{\cdot}05$) than in Group A pigs.

The length of the mammary teats (mean ± s.e.m.) in pigs in Group B (2·20 ± 0·19 cm) was significantly greater ($P < 0{\cdot}001$) than in pigs in Group A (1·00 ± 0·08 cm) or Group C (0·99 ± 0·07 cm).

Discussion

The results indicate that oestradiol was more effective in inducing sexual behaviour in prepubertally castrated boars when administered together with 5α-dihydrotestosterone than when given alone. In contrast, 5α-dihydrotestosterone was behaviourally ineffective, although it had marked stimulatory effects on the genitalia.

In relation to the various indices of courtship behaviour (Signoret, Baldwin, Fraser & Hafez, 1975) that were recorded, it appears that 'head contact' is concerned primarily with individual recognition since this was most frequent at the start of the study and was not differentially affected by the treatments. On the other hand, 'genital sniffing' and 'body nosing', although occurring in pigs treated with 5α-dihydrotestosterone, were enhanced both in terms of the number of animals consistently responding, and in frequency, in animals treated with oestradiol and oestradiol plus 5α-dihydrotestosterone.

Aggressive exchanges took place fairly regularly throughout the experiment. Sometimes fighting was initiated by the male, but more often by the female, particularly when nosing was directed to the head rather than to the genitalia. The occurrence of aggression may have been related to the absence of pheromonal 16-androstene steroids in the saliva of the castrated boars (Booth, 1980). These steroids are primarily of testicular origin (Booth, 1982) and may reduce aggression in social encounters (McGlone, Curtis & Banks, 1981). Although the boars could not produce steroidal pheromones, champing and salivation, which normally serve to distribute these substances (Perry, Patterson, MacFie & Stinson, 1980), were induced by oestradiol; this supports previous findings with oestrone (Booth, 1983). Oestrogen may influence the neural control of salivation and may also have a direct stimulatory effect on the salivary glands. Combined treatment with oestradiol and 5α-dihydrotestosterone resulted in greater serous cell hypertrophy than did treatment with 5α-dihydrotestosterone alone and a similar synergism may take place in the intact boar (Booth *et al.*, 1973).

The earliest that an intact boar is able to mate is around 21 weeks of age (Signoret *et al.*, 1975). In the present study, 5α-dihydrotestosterone combined with oestradiol, and oestradiol alone, induced maximum mounting in the 6th and 7th weeks of the experiment, respectively, i.e. when the pigs were 20 and 21 weeks old. However, whereas most of the pigs receiving 5α-dihydrotestosterone plus oestradiol exhibited full copulation, culminating in ejaculation, in animals treated with oestradiol only, mounting and thrusting declined and erection and intromission never occurred; this confirms earlier work with oestrone (Booth, 1983).

It is apparent from the results that a major effect of 5α-dihydrotestosterone was to increase the size of the penis and its associated musculature and that this latter effect was facilitated by oestradiol. These muscles probably play a role in the control of erection and ejaculation. The physiology of these processes has not been described in detail in the boar but it may be similar to that in the sheep in which erection and ejaculation involve increased penile rigidity due to raised vascular tone, relaxation of the retractor muscle that retains the penis in its sheath, and contraction of the ischio- and bulbocavernosus muscles (May, 1955; Walton, 1960). It follows from this that an oestrogen-treated castrated boar is sexually motivated but, because the penis and associated muscles are underdeveloped, insufficient sensory feedback is available to disinhibit the ejaculatory reflex. Hence, in the absence of sensory stimulation, motivation decays and mounting with thrusting declines, as has been described for the monkey (Herbert, 1973). There is also the possibility of a direct action of 5α-dihydrotestosterone on neurones in the penis and the spinal cord (Hart, 1973).

In tests with a mature boar the majority of the pigs failed to display lordosis in response to back pressure. These results contrast with those of Ford (1982) who found that all prepubertally castrated boars treated with a much smaller dose of oestradiol benzoate showed the immobilization response. Differences between breeds and in experimental protocol may account for the disparity.

The accessory sex glands were larger in pigs treated with 5α-dihydrotestosterone plus oestradiol than in those receiving 5α-dihydrotestosterone alone. This synergism is in keeping with the results of Joshi & Raeside (1973) who found that the volume of ejaculate produced by post-pubertally castrated boars receiving oestrogen plus testosterone was greater than in animals treated only with testosterone. Therefore, the high levels of circulating oestrogens present in the boar (Booth, 1982) may facilitate the production of the large semen volume that is characteristic of this species. The effects of oestradiol alone on the acessory sex glands were similar to those previously described for oestrone (Booth, 1983), i.e. the hypertrophy was primarily due to the development of fibromuscular tissue. The low levels of zinc that were found are consistent with the observation that there was minimal stimulation of secretory tissue. Similarly, the hypertrophy of the mammary teats was apparently due to excess growth of stromal tissue.

The results of this study, and those for post-pubertally castrated boars (Levis & Ford, 1983), favour the view that the libido of the male pig is dependent on oestrogen. The boar is unusual insofar as the testis produces large amounts of oestrogen which could stimulate behaviour directly.

However, the behavioural effectiveness of testosterone in castrates (Joshi & Raeside, 1973) also suggests that central aromatization occurs, although this has yet to be confirmed biochemically. Furthermore, because the behavioural action of oestrogen is fully expressed only in castrates additionally receiving 5α-dihydrotestosterone, it appears that the mating ability of the boar may depend upon an interaction between the behavioural and morphological actions of these two testosterone metabolites.

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