Differentiation of sexual behaviour in pigs

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Summary. Behaviour in pigs is sexually dimorphic as early as 1 month of age; mounting of penmates is observed more frequently for males than for females. This mounting reaches its highest frequency during the 2nd month of life and then declines to a low frequency in prepubertal pigs. During the prepubertal period (3–5 months of age), bipotentiality of sexual behaviour is apparent in boars because they will not only mount oestrous females but they are also receptive to mounts by older, mature boars. If males are castrated during neonatal development (first 2 months of life) and treated acutely with oestrogen during adulthood, they display sexual behaviour that is characteristic of females; i.e. show a selective preference to remain near mature boars in a choice test, are receptive to mounts by mature boars, and have a short latency to receptivity after contact with a mature boar. Males that are castrated at 6 months of age or later, or males that are castrated neonatally and treated chronically with oestrogen or testosterone during the prepubertal period, display significantly less female behaviour after acute oestrogen treatment than do males castrated neonatally. Additionally, exposure of females to elevated testosterone during early fetal development results in no detectable changes in oestrous behaviour as adults. These observations support the hypothesis that defeminization of sexual behaviour in boars occurs as a result of elevated testicular steroids during pubertal development. The limited data available on masculine sexual behaviour in pigs indicate an activational role for gonadal steroids with little evidence for true masculinization *per se*. After prolonged testosterone treatment of mature females or males that are castrated before puberty, considerable courtship and mounting behaviours are exhibited by these individuals when placed with oestrous females. Studies have not evaluated differential sensitivity of such animals to dosage or duration of testosterone treatment. Differentiation of sexual behaviour in boars therefore involves primarily a loss of sensitivity to display female-typical behaviours. Presently, pigs differ from other mammals that have been investigated because sexual differentiation of reproductive behaviour occurs during pubertal development and not during gestation.

Keywords: pig; masculinization; defeminization; receptivity; proceptivity

Introduction

Sexual behaviour in adult pigs differs between females and males due to the additive effects of two general actions of gonadal steroids, namely, their organizational and activational actions. Differentiation of sexual behaviour is the consequence of organizational (or morphogenic) changes within the brain produced by androgens and/or oestrogens (De Vries *et al.*, 1984; Gorski, 1985). Current understanding of sexual differentiation originated with studies on morphological development of the urogenital system, but these concepts are now extended to sex differences in pattern of gonadotrophin secretion, sexual behaviours, non-reproductive behaviours, etc. (Feder, 1981; Jost & Magre, 1984; Adkins-Regan, 1988). In mammalian species, genetic sex is determined at conception,

but development of the masculine phenotype is dependent upon responses to testicular secretions during discrete, sensitive periods of development. These sensitive periods generally occur during late gestation and early postnatal development in species with short gestations and prenatally in species with longer gestations (Goy & McEwen, 1980); however, as explained later, pigs are an exception in that significant differentiation of sexual behaviour occurs during pubertal development. The second way that gonadal steroids affect dimorphic behaviour is through their activation of behavioural processes that exist within an animal. Expression of the behaviour is dependent upon the presence or recent presence of the gonadal steroid, defined as concurrent facilitation by Feder (1981). Organizational changes that are caused by gonadal steroids are irreversible (permanent) in contrast to reversible, activational actions on sexual behaviour.

The capacity of mammalian brains is regarded as inherently female or undifferentiated, and sexual differentiation involves the action of testicular androgens which are transported to the brains of males and aromatized to oestrogens (Naftolin & MacLusky, 1984). Extensive data exist that implicate oestrogen as the final active steroid in brain differentiation, but for certain behaviours, testosterone itself appears to be directly involved in behavioural differentiation (Baum & Tobet, 1988). The earlier assumption that brains of females remain neutral throughout early development is probably not entirely justified as recent evidence with female rats indicates that females must be exposed to low amounts of oestrogen early in life for feminine sexual behaviour to develop fully (Döhler *et al.*, 1984). Extensive investigation of this concept has not been conducted with other species.

Two classifications of sexual behaviour are used in discussions of differentiation—masculinization and defeminization. Masculinization is acquisition or enhancement of male-typical behaviours, whereas defeminization is reduction or loss of female-typical behaviours. Such changes may not be total losses or acquisitions of specific behaviours; rather, differentiation may alter sensitivity of behavioural traits to activation by a given steroid, i.e. a change in frequency. The time during development when differentiation occurs varies with each trait of interest. Originally, it was proposed that a single, discrete period of exposure to steroid hormones caused differentiation of each specific behaviour, but evidence is accumulating that consecutive periods of exposure are more effective (Weisz & Ward, 1980; Baum & Tobet, 1988). In rats, testosterone administered both pre- and post-natally masculinizes and defeminizes sexual behaviours more effectively than does testosterone at either time alone (Ward, 1969; Hoepfner & Ward, 1988). Thus, within a species the sensitive period for differentiation is not a narrowly restricted time, but rather a more prolonged process.

With pigs, the numbers of studies into differentiation of sexual behaviour are limited; most relate to defeminization, and masculinization has not been evaluated adequately. The purpose of this review is to summarize what is known about the development of sexual behaviour in pigs and to identify those areas that require additional investigation.

Changes in reproductive steroids during prenatal and postnatal development

Because gonadal steroids play a pivotal role in sexual differentiation, review of their changes throughout development (Colenbrander *et al.*, 1982a) helps to identify potential sensitive periods when neural modifications could be expected. In domestic pigs, gonads of both sexes are similar at 24 days of gestation, but by 26 days testes are morphologically distinct from ovaries. Testosterone secretion in male fetuses *in vivo* or by fetal testes *in vitro* is elevated at 35 days of gestation; after Day 40, the penis and scrotum are easily identified and serum testosterone concentrations decline in male fetuses but remain greater than those in female fetuses. Differentiation of sexual behaviour would be expected to occur after 40 days of gestation if the rodent and sheep differentiation model is extrapolated to pig because defeminization of sexual behaviour in these two species occurs shortly after the external genitalia in males are fully developed.

Further interest in endocrine differences between the two sexes during late fetal development again relates to the model that has emerged from studies with rodents. In rats, defeminization of sexual behaviour occurs shortly after the appearance of immunoreactive luteinizing hormone-releasing hormone (LHRH) in neurones and nerve terminals of the median eminence (Mess *et al.*, 1983; Nemeskeri *et al.*, 1983). These developmental changes occur during the second half of gestation in fetal pigs. By 60 days of gestation, LHRH immunoreactive fibres reach the median eminence and differentiated hypophysial–portal capillary loops are observed by 70 days (Danchin & Dubois, 1982). After 70 days of gestation, luteinizing hormone (LH) release in response to LHRH treatment or to hypothalamic stimulation increases progressively with fetal age (Colenbrander *et al.*, 1982b; Bruhn *et al.*, 1983). Placentae of pregnant sows synthesize and secrete considerable quantities of oestrogen, but no differences are observed between male and female fetuses during the second half of gestation in fetal blood concentrations of oestrone sulphate, total unconjugated oestrogen (which is predominantly oestrone) or oestradiol (Knight *et al.*, 1977; Ford & Christenson, 1986; Ponzilius *et al.*, 1986). The high concentrations of oestrogens during development of the hypothalamic–pituitary axis are in apparent opposition with a role for oestrogen in sexual differentiation. Pig α-fetoprotein has not been reported to bind oestrogen with high affinity and its concentrations decrease after 60 days of gestation (Stone, 1981). The circulating oestrogen is apparently biologically active because the vulva and teats of newborn piglets are often enlarged. It therefore appears that any sexually dimorphic changes that occur during the second half of gestation would be caused by higher testosterone concentrations in male fetuses and not related to fetal blood oestrogen concentrations.

After birth, testicular secretion of testosterone and oestrogens is elevated during the first month of life and, during this period, negative feedback control of LH secretion by steroids is diminished in males; secretion of LH is high and castration fails to cause an additional increase (Colenbrander *et al.*, 1982a; Ford, 1983a; Ponzilius *et al.*, 1986). Furthermore, exogenous steroids are not highly effective at decreasing LH secretion in neonatal males, but the hypothalamic–pituitary axis of male pigs then undergoes some type of maturation after 1 month of life such that regulation of LH secretion becomes under the greater control of testicular steroids. After the neonatal period of elevated activity, secretion of testicular steroids decreases and remains low until the onset of pubertal development at approximately 3 months of age (Colenbrander *et al.*, 1982a; Allrich *et al.*, 1982; Ford, 1983a). In females, blood oestradiol concentrations are low from birth until the week before first ovulation (Lutz *et al.*, 1984). Collectively, exposure of the developing brains of pigs differs greatly between the two sexes. Males experience elevated testosterone secretion around Day 35 of gestation, during the 1st month of life, and during and after pubertal development. Presently, these first two periods of androgen exposure have not been identified as having any effects on sexual differentiation of behaviour.

Juvenile and prepubertal behaviours

Behaviour in pigs is sexually dimorphic by 1 month of age. Mounting activity is observed more frequently in males than in females (Fig. 1) and this activity is at its greatest by 2 months (Berry & Signoret, 1984). When males are castrated at birth, their mounting activity is reduced at 1–2 months of age and is comparable to that observed in females, but when castration is delayed until 30 days of age, mounting activity develops to the frequency observed in intact males. Most of this juvenile mounting behaviour in males, therefore, results from activational actions of testicular secretions, and once activated, continues for 1 month in the absence of testes.

Social play, defined as pushing, butting, biting or mounting that persists for at least 5 sec, is also observed more frequently in 2-month-old males than in females (Table 1), and each sex interacts more with members of its own sex than with individuals of the opposite sex (Dobao *et al.*, 1984/85). It has been suggested that such juvenile behaviours are a means to develop functional skills that are required in adulthood (Fagen, 1981); however, boars deprived of these behaviours by being
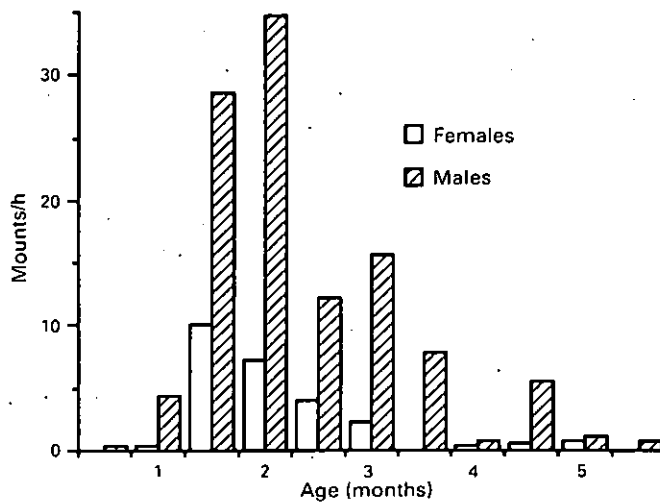
Fig. 1. Mounting behaviour in young male and female pigs. (After Berry & Signoret, 1984.)

individually reared from 3 to 12 weeks had normal adult, sexual behaviour except for a minor reduction in one aspect of courtship behaviour (Hemsworth & Beilharz, 1979). These latter observations leave one to question the developmental value of juvenile mounting behaviour in male pigs. Similarly, mounting was observed in infant lambs of both sexes, and rearing males individually during infancy had no influence on their adult sexual behaviour (Orgeur & Signoret, 1984).

Table 1. Social play in 2-month-old pigs†

Sex of subject	No. of play encounters observed	% with females	% with males
Female	115	71·3	28·7
Male	349	14·9	85·1

†Pigs (24 of each sex) were observed from 50 to 68 days of age. Social play was pushing, butting, biting or mounting behaviours between 2 animals that persisted for at least 5 sec. (After Dobao *et al.*, 1984/85).

As boars mature during the prepubertal period (3–5 months), they will mount oestrous females and also are receptive to mounts by older, mature boars (Signoret *et al.*, 1989). Both of these behaviours result from activation by gonadal steroids because their frequency is reduced greatly in castrated males. The rationale for boars to possess this bipotentiality for sexual behaviour during this stage of development is not clear. A question that requires further investigation is whether young boars that allow older boars to mount them are sexually receptive in the same sense as an oestrous female or is this immobilization a submissive reaction towards a more dominant male? The latter seems likely because Signoret *et al.* (1989) indicated that most of the evaluations for receptivity began with antagonistic interactions between the prepubertal boars and the mature boar.

Defeminization of sexual behaviour

The most apparent behaviour in oestrous females is sexual receptivity which is characterized by a rigid stance, arched back and erect ears (Signoret *et al.*, 1975). An immobile posture similar to this

was observed in adult male pigs that were castrated neonatally and treated after 7 months of age with oestrogen (Diehl *et al.*, 1972). This indicated that male pigs may not have undergone defeminization of receptive behaviour and led to a series of studies to determine the degree of similarity between females and males in their responses to acute oestrogen treatment.

An early study determined that neonatally castrated males were similar to females in their sensitivity to oestrogen (Ford, 1982). As dosage of oestrogen increased, the proportion that displayed receptivity in the presence of a mature boar increased for ovariectomized females and males castrated at 2 weeks of age (Fig. 2). Receptivity in males castrated at 8 months of age was low and the proportion responding to oestrogen did not increase over the dosage range that was evaluated. In addition, the number of consecutive evaluations in which receptivity was observed increased with dosage of oestrogen and was similar in ovariectomized females and neonatally castrated males (Ford, 1982; Berry & Signoret, 1984). Moreover, latency from contact with a mature boar until receptivity is observed was similar in females and neonatally castrated males (Berry & Signoret, 1984; Table 2). All of these observations indicate that receptivity in neonatally castrated males and ovariectomized females is similar; therefore, differentiation of neural processes that control sexual receptivity has not occurred in these males.
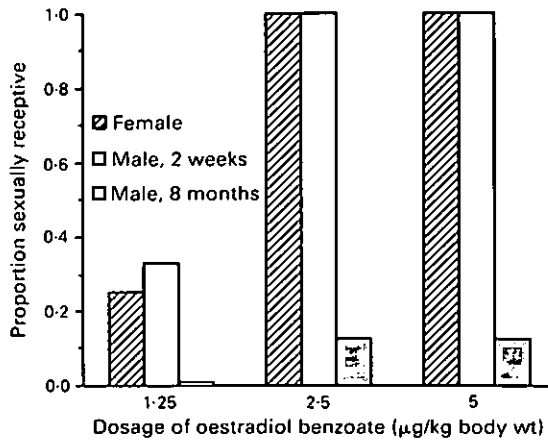

Fig. 2. The influence of sex, age at castration of males and dosage of oestrogen on sexual receptivity in pigs. Percentage of animals that displayed the immobilization response was determined in the presence of a mature boar. Age at gonadectomy was 8 months for females and 2 weeks or 8 months for males. (After Ford, 1982.)

To determine when defeminization of receptivity occurred, males were castrated at different ages from birth to 8 months of age. The proportion that displayed sexual receptivity after acute oestrogen treatment decreased as age at castration increased (Ford, 1982; Berry & Signoret, 1984; Ford & Christenson, 1987). The observed decreases were gradual, and there was variation among the three studies as to which age group gave the first significant decline in receptivity. A reduction in the duration of receptivity occurred in males castrated between 2 and 4 months, and decreases in the proportion that became receptive were observed in males castrated between 4 and 6 months. Further support for defeminization of receptivity during pubertal development was obtained from studies in which neonatally castrated males were given prolonged treatment with testosterone (treatment from 3 to 6 months) or oestradiol (treatment from 3 to 5·5 months). When these males were evaluated at an older age, receptivity after a single treatment with oestrogen was reduced (Ford & Christenson, 1987; Adkins-Regan *et al.*, 1989). Moreover, this effectiveness of testosterone in males castrated at birth establishes that the neonatal increase in testicular steroids is not essential for testosterone to defeminize receptivity during pubertal development; however, the possibility that neonatal steroids may increase the sensitivity to pubertal steroids cannot be excluded. An

Table 2. Proportion of pigs receptive and latency to receptivity on Days 3
and 4 after treatment with oestradiol benzoate†

Sex of pig	Evaluation at 11 months		Evaluation at 13·5 months	
	Day 3	Day 4	Day 3	Day 4
Female (gonadectomy at 8 months)				
Proportion	10/12	10/12	12/12	12/12
Latency (sec)	26 ± 12‡	10 ± 3	28 ± 9	17 ± 9
Male (gonadectomy at birth)				
Proportion	6/10	8/10	10/10	10/10
Latency (sec)	8 ± 2	8 ± 1	28 ± 10	7 ± 1
Male (gonadectomy at 8 months)				
Proportion	0/12	3/12	ND	ND
Latency (sec)	—	65 ± 30		

†Pigs were penned individually and treated with oestradiol benzoate (2·5 µg/kg body wt at 11 months and 5 µg/kg at 13·5 months). Pigs were moved from their pens to a second room and placed in an evaluation pen that was located between 2 pens that housed mature boars. Back pressure was applied intermittently for 4 min, after which pigs that were not receptive were placed in direct contact with a mature boar for 2 additional min. Latency was time from entry into the evaluation pen until receptivity was observed. (J. J. Ford, unpublished data).
‡Mean ± s.e.m. of those that were receptive; ND = not determined.

additional observation is that ovariectomized females implanted with oestradiol from 3 to 5·5 months of age also showed some reduction in receptivity after acute oestrogen treatment at 6·5 months (Adkins-Regan *et al.*, 1989). These latter observations are potentially confounded with antagonistic behaviour due to the high incidence of fighting by these females with the boar used to detect receptivity.

A second component of oestrous behaviour in female pigs, which is observed in neonatally castrated males after acute oestrogen treatment, is proceptivity (solicitation of mature boars) (Ford, 1983b; Adkins-Regan *et al.*, 1989). After oestrogen treatment, the time spent in close proximity to a mature boar was greater for neonatally castrated males than for males castrated during pubertal development (Fig. 3). From these studies, it was concluded that defeminization of proceptivity occurs sooner in development than does defeminization of receptivity. These two studies differ in that neonatally castrated males showed proceptivity similar to that of ovariectomized females in one, but in the other males were less proceptive than females. Differences between the studies that require further evaluation are age at castration (birth and 3 weeks) and the influence of chronological age on proceptive behaviour. Proceptivity was evaluated at 6·5–8 months of age by Adkins-Regan *et al.* (1989) and after 12 months by Ford (1983b). Because prenatal exposure to androgens delays sexual maturity in female monkeys and pigs (Ford & Christenson, 1987; Goy *et al.*, 1988), it seems possible that neonatally castrated pigs may undergo physiological maturity more slowly than females due to their exposure to endogenous androgens during gestation. Presently, definitive data are not available on proceptivity in female pigs throughout pubertal development.

Collectively, there is compelling evidence that defeminization of sexual behaviour is associated with pubertal development in male pigs. This conclusion is substantiated by the lack of defeminization in females that are exposed to exogenous testosterone prenatally (Ford & Christenson, 1987). These females had marked virilization of the external genitalia but most had normal oestrous cycles and displayed receptivity after ovariectomy and acute oestrogen treatment. Somewhat contrary to this are the observations that duration of receptivity was shorter for female pigs that were located *in utero* between 2 males than for females located between 2 females (Rohde Parfet *et al.*, 1988). This effect of in-utero position was subtle as it was not apparent in the first two oestrous periods; during
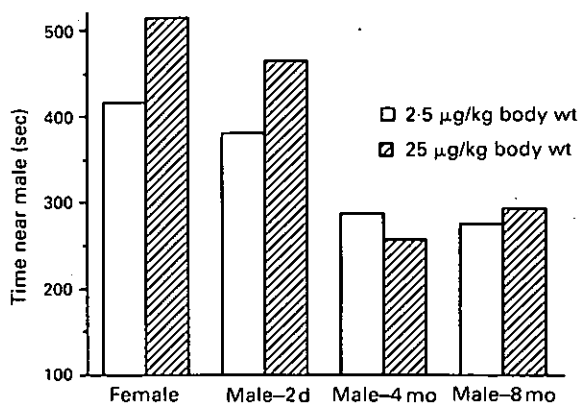
Fig. 3. The influence of sex and age at castration of males on sexual proceptivity in pigs. Amount of time that pigs spent near a mature male was determined during 5-min evaluations on Days 3 and 4 after oestrogen treatment. Male-2 d = males castrated within 48 h of birth; Male-4 mo = males castrated at 4 months of age; Male-8 mo = males castrated at 8 months of age. Two separate studies were conducted with the same animals. In the first, dosage of oestradiol benzoate was 2·5 µg/kg body weight and, in the second, dosage was increased to 25 µg/kg body weight. (After Ford, 1983b.)

the third oestrus after puberty, it was most pronounced when receptivity was evaluated in the absence of a mature boar. A mechanism for this reduction in receptivity is not obvious. The situation in mice is different because adult behaviours of females that were located between 2 males *in utero* are decidedly less feminine and more masculine than those of females that were located between 2 females, and steroid hormones are implicated as the causative agents for such effects (vom Saal, 1989).

The primary sensitive periods for differentiation of proceptivity and receptivity coincide with early pubertal development in boars. This is later than observed in other species investigated to date; however, the nervous system is now regarded as more amenable to modification during later life and is not as rigid in its development as once thought (Arnold & Breedlove, 1985). Pigs also differ from cattle and sheep in sexual dimorphism of body weight. Steers and wethers are larger and leaner than their female counterparts, but in pigs, females are leaner than castrated males (Kay & Houseman, 1975; Fuller, 1981). It is concluded that sexual differentiation of growth processes occurs prenatally in cattle and sheep, but predicted that in pigs this may not occur until pubertal development (Ford & Klindt, 1989). If gonadectomy of both sexes were conducted near puberty, male pigs may then grow faster and continue to have leaner carcasses than females. If this is the case, sexual differentiation of growth in all three of these species would occur in association with defeminization of sexual behaviour.

Masculinization of sexual behaviour

At the present time, masculinization of sexual behaviour is not apparent from data that are available. When mature females are given prolonged testosterone treatment, they develop precopulatory and mounting behaviours which are similar to those observed in males (Scheffrahm *et al.*, 1981; J. J. Ford & D. Levis, unpublished observations). These testosterone-treated females display vigorous side-nudging behaviour towards oestrous females, mount, remain mounted for prolonged periods of time and, on frequent occasions, show pelvic thrusts. From these observations, one could conclude that male pigs do not undergo significant degrees of masculinization during development because male-typical behaviours can be activated in females by extended periods of exposure to testosterone. Such a conclusion would be premature without comparative data from castrated

males to determine whether males are more sensitive to testosterone and show sexual behaviour more rapidly or at a lower dosage of testosterone than females. For example, ewes that are given prolonged testosterone treatment display considerable amounts of masculine sexual behaviour when placed with oestrous ewes (D'Occhio & Ford, 1988); however, testosterone-treated ewes are not as sexually active as rams (Fabre, 1977) and ewes exposed to testosterone *in utero* exhibit greater courtship behaviour and mounting activity after oestrogen or testosterone treatment during adulthood than control ewes (Clarke & Scaramuzzi, 1978; Clarke, 1978/79). Therefore, it is apparent that ewes have the potential to exhibit masculine sexual behaviour after appropriate stimulation with steroid hormones, but their responsiveness is greater if they are exposed to testosterone prenatally during a sensitive period of development. It is therefore considered that masculinization of sexual behaviour occurred prenatally in these androgenized ewes. Until comparable studies are conducted with pigs, we cannot estimate the relative contributions of differentiation and activation towards masculine sexual behaviour in these animals.

Similar comments are appropriate for champing and salivation in boars, behaviours that are observed during courtship and aggression. These occur in boars after exposure to saliva of a strange boar (Booth, 1980) and in gonadectomized males and females that have had prolonged treatment with androgens or oestrogens when they come into contact with oestrous females or mature boars (Booth, 1983; Parrott & Booth, 1984; Adkins-Regan *et al.*, 1989). Booth (1983) proposed that oestrogens are involved in sexual differentiation of champing and salivation behaviours in boars, and we interpreted our early observations as supportive of this proposal (D'Occhio & Ford, 1988). However, more recent observations are indicative of an activational role for oestrogen (J. J. Ford, unpublished data). After prolonged exposure to oestrogen, considerable time must pass (months) before acute treatment with oestrogen will not activate champing and salivation in some females.

Submaxillary glands are clearly larger in boars than in females or castrated males and in boars these glands contain greater concentrations of steroidal pheromones (16-androstenes) and a binding protein for these steroids (Booth, 1984). Although exogenous androgens and oestrogens increase salivation in gonadectomized pigs, an increase in size of submaxillary glands after these treatments has not been observed (Booth, 1983; Parrott & Booth, 1984). The 16-androstenes, of which 5α-androst-16-en-3α-ol is the most prominent in boar saliva (Booth, 1980), are signalling pheromones that aid in eliciting receptivity in oestrous females (Melrose *et al.*, 1971; Perry *et al.*, 1980) and they probably promote proceptivity (Signoret, 1974; Pearce & Hughes, 1987). There are receptors for 16-androstenes in the olfactory mucosa of females (Gennings *et al.*, 1977) and 16-androstenes excite specific olfactory bulb neurones of pigs of both sexes (MacLeod *et al.*, 1979). Data are too sparse to evaluate fully how male and female pigs differ in their responses to 16-androstenes and how sexual differentiation and steroidal activation modify such responses.

Prenatal influences on adult, masculine behaviour have been examined in three studies. Oestrogen treatment of pregnant sows at mid-gestation reduced mounting behaviour in their female offspring and copulatory behaviour of their males (Dörner *et al.*, 1977). Feeding the synthetic glucocorticoid, triamcinolone, to pregnant sows during the last week of gestation hastened the onset of mounting and ejaculation in their male offspring (Zavos & Stahly, 1988), and intrauterine position was associated with courtship behaviour during pubertal development (K. Rohde Parfet, W. Lamberson, A. Rieke, F. vom Saal & B. Day, unpublished data). With current understanding of development of sexual behaviour in boars, mechanisms to explain the observations in these studies are not apparent.

Conclusions

In pigs, significant modifications in sexual behaviour occur in association with pubertal development. This is much later than expected on the basis of models of differentiation that have evolved from

studies with rodents and sheep. Defeminization is a major component of sexual differentiation in males, and to date few data are available to assess adequately the impact of masculinization. Males that are castrated shortly after birth show considerable amounts of female sexual behaviour as adults after acute treatment with oestrogen. Such males become receptive in the presence of mature boars, have a short latency to receptivity, and show proceptivity towards mature boars. Activation of these behaviours in neonatally castrated males occurs with the minimum dosage of oestrogen that is effective in ovariectomized females. This late period of development and the definite role of the olfactory system in sexual behaviour identify the pig as an excellent model for studies into mechanisms associated with development and regulation of sexual behaviour.

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