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Basic neuroendocrine events before puberty in cattle, sheep and pigs

J. Pelletier, S. Carrez-Camous* and J. C. Thiery

*I.N.R.A., Physiologie de la Reproduction, 37380 Nouzilly, and *I.N.R.A., Elevage des Porcs, 78350 Jouy en Josas, France*

Summary. Neuroendocrine events before puberty are compared in male and female cattle, sheep and pigs. The patterns of secretion of gonadotrophin, the age-related LH responses to castration or LH-RH administration and the effects of prolonged steroid treatment give information about the maturity of the hypothalamic–pituitary axis. It appears that in all three species the mechanisms involved in the expression of puberty are progressive rather than abrupt events. Some original contributions reported here, such as age-related changes in plasma levels and pulses of LH in the gilt, and the variations in pituitary cytosol receptors to 5α-dihydrotestosterone and oestradiol-17β in the male lamb support this contention. Finally, this brief review of the neuroendocrine events known to occur before puberty in three domestic mammals underlines numerous missing links in our understanding of the prepubertal processes.

Introduction

In a recent review, Ramaley (1979) summarized the numerous theories concerning puberty drawing mainly on data relating to rodents. These are at variance with the gonadostat hypothesis expounded by Ramirez & McCann (1963) and it seems that no single mechanism can explain the changes leading to puberty. There is less information on domestic species, although numerous studies are now being conducted, and it is of interest therefore to review briefly our current knowledge of the neuroendocrine events which take place between birth and puberty in these species.

Neuroendocrine changes before puberty

Cattle

Sexual development is well documented for the male calf. Three phases can be distinguished from measurements of plasma luteinizing hormone (LH): (i) a phase of increasing LH during the first weeks after birth, (ii) a period from 2 to 5 months after birth when the mean LH level is high but with large individual week-to-week fluctuations, and (iii) a return to the early post-natal situation (Lacroix, Garnier & Pelletier, 1977; Rawlings, Fletcher, Henricks & Hill, 1978). This pattern of LH release has been established from studies with Charolais and Angus × Hereford bull calves, and has also been observed for Friesian, Hereford, Limousin and Maine-Anjou breeds (A. Lacroix, F. Mennissier & J. Pelletier, unpublished data). It is further supported by the studies of Rawlings, Hafs & Swanson (1972) and Mori, Masaki, Wakabayashi, Endo & Hosoda

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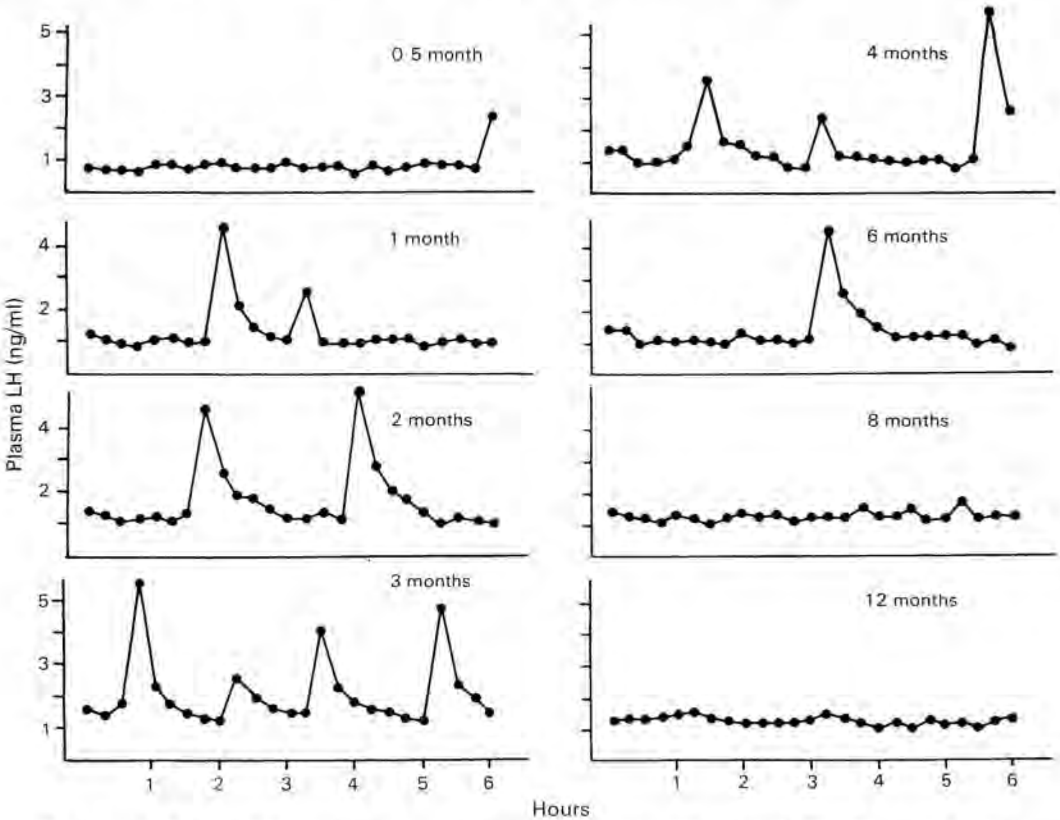
(1974). The mean LH concentration established from weekly or even monthly bleeding reflects the occurrence of LH pulses. The number of these pulses determined from monthly sequential bleedings reaches 3/6 h at 3–4 months of age (Text-fig. 1) and declines to a mean of $\leqslant 1/6$ h after 6 months (Lacroix & Pelletier, 1979a; McCarthy, Convey & Hafs, 1979).



Text-fig. 1. Plasma LH concentrations in one representative Charolais bull calf sampled every 15 min for 6 h at various stages of sexual development (adapted from Lacroix & Pelletier, 1979a).

In contrast relatively little is known concerning prepubertal changes in follicle-stimulating hormone (FSH). One report suggests that it does not vary throughout the first year of life (Karg *et al.*, 1976) whilst another study of prepubertal bulls suggests that it is secreted in pulses synchronized with those of LH (Schams, Gombe, Schallenberger, Reinhardt & Claus, 1978). Probably, the relatively constant levels of FSH conceal important changes in the feed-back exerted by steroids and/or inhibin-like testicular proteins (see below).

Prolactin, in contrast to LH and FSH, appears to be related to photoperiodic changes (Schams & Reinhardt, 1974; Bourne & Tucker, 1975) but not to age and puberty (Lacroix, Ravault & Pelletier, 1977). Presumably, prolactin is not essential for genital tract development although it may act on specific features such as the appearance of testicular LH receptors (Bex & Bartke, 1977). Such effects may not require a change in the level of prolactin *per se* because this hormone is probably released in amounts which are always excessive in this regard.

Testosterone is the main secretory steroid of the testes in bull calves although at all ages substantial amounts of androstenedione (about 0·2 ng/ml) are also secreted (Bedair & Thibier, 1979; McCarthy *et al.*, 1979). There is general agreement concerning the changes in plasma testosterone; concentrations are low during the first months of life and increase between 6 and 12 months of age (Rawlings *et al.*, 1972; Secchiari, Martorana, Pellegrini & Luisi, 1976; Lacroix *et al.*, 1977; Lunstra, Ford & Echternkamp, 1978). Before 4 months of age, LH pulses are not followed by a release of testosterone (Lacroix & Pelletier, 1979a). In older animals, significant amounts of testosterone are secreted following each LH pulse; a phenomenon thought to be related to the increase in testicular weight which takes place in Charolais bull calves between 3 and 4 months of age (Attal & Courot, 1963). Initially, the testosterone response to LH is low and irregular (Rawlings *et al.*, 1978) but it increases in magnitude with age. The interval between peaks of LH and testosterone is 61 min in British Friesian bull calves at 11 months of age (Schams *et al.*, 1978). An important consequence of the increase in plasma testosterone is the augmentation of the negative feed-back effect exerted on the hypothalamus and pituitary gland; and this causes a decrease in the number of LH pulses observed after 5 months of age.

Sheep

Endocrine events. A similarity between the patterns of LH release after birth in sheep and cattle is evident when one compares the three stages described above with the data of Cotta, Terqui, Pelletier & Courot (1975), Foster *et al.* (1978) or Wilson & Lapwood (1979). In addition, the relationship between the pulsatile secretion of LH and testosterone release observed in the male lamb by Foster *et al.* (1978) is similar to that reported for the male calf (see above, Lacroix & Pelletier, 1979a). However, these events appear to be independent of the season, which is at variance with what has been found in the adult (Cotta *et al.*, 1975; Illius, Haynes, Purvis & Lamming, 1976). The slight difference in the timing of the LH increase after birth observed between studies probably has a genetic basis and seems to be related to the prolificacy of the breed. For example, from samples taken over 6-h periods it has been found that the maximum LH pulse frequency is observed in Romanov rams at 6 weeks, in Préalpes du Sud rams at 8 weeks and in the Ile-de-France breed at 10–11 weeks of age (M. R. Blanc, M. Courot, J. Pelletier & J. Thimonier, unpublished data). These figures parallel the ovulation rate of the adult females which are 2·9, 2·0 and 1·2 respectively. As in bovine species, the decrease in the number of LH pulses observed thereafter is highly correlated with an increase in testosterone secretion. This suggests a negative feed-back effect on the mechanism of pulse generations although a change in the maturity of the hypothalamus remains a plausible explanation.

In the ewe lamb, LH secretion is low for several weeks after birth (Foster, Lemons, Jaffe & Niswender, 1975; Tassel, Chamley & Kennedy, 1978), although pulses of LH are observed during the first 2 weeks of life (Foster *et al.*, 1978). The number of LH pulses then increases, as in the male, but differ in that the marked pulsatility of LH secretion extends over a longer period of time, up to 25–30 weeks. Thereafter, an increase in the amplitude of the pulses occurs which is characteristic of puberty (Foster *et al.*, 1978). This increase in pulsatility could be the result of a decrease in the sensitivity of hypothalamic–pituitary axis to oestradiol of which Foster & Ryan (1979) have provided elegant demonstrations. In comparison to LH, plasma FSH does not exhibit major variations throughout puberty in either sex although an increase shortly after birth is frequently noticed (Foster, 1974; Lee *et al.*, 1976a; Blanc & Terqui, 1976; Fitzgerald & Butler, 1978).

Plasma levels of prolactin are relatively low during infancy compared to the adult and appear to be related to the photoperiod soon after birth (Ravault & Courot, 1975; Ravault, 1976; Wilson & Lapwood, 1979). However, a very intriguing peak of prolactin has been observed in Ile-de-France lambs 12 weeks after birth by Ravault & Courot (1975) and Ravault (1976) and was noted in Romney lambs by Wilson & Lapwood (1979). When plasma prolactin levels were depressed by bromocriptine between 10 and 21 weeks of age, neither plasma LH and testosterone nor the establishment of spermatogenesis were modified, but there was a decrease in the weight of the seminal vesicles and their fructose content was also reduced (Ravault, Courot, Garnier, Pelletier & Terqui, 1977).

Studies of receptors. An aspect which may be of significance in age-related changes in hormone feed-back is the influence of the number of steroid receptors in the hypothalamus and pituitary gland. Testosterone and oestradiol-17β receptors have been identified both in male and female calves as early as 1–2 weeks of age (Armstrong, Villée & Villée, 1977). The extremely low levels of oestradiol receptors (16 and 32 fmol/mg protein for the male and female, respectively) are perhaps related to age (see below). However, the difference between sexes must be regarded with caution because the comparisons were made between pools of cytosols, thus masking between-animal variance. Having established the validity of the technique of steroid receptor measurement in the pituitary of adult rams (Thieulant & Pelletier, 1979) a study of the cytosol receptors for 5α-dihydrotestosterone (DHT) and oestradiol-17β in the anterior pituitary gland of Préalpes du Sud rams was carried out (Table 1). The ages chosen for this experiment extend from 20 to 80 days, and cover the period of infancy up to the initial stage of rapid testicular growth (mean testis weight 0·85 g at 20 days: 7·1 g at 80 days). Pituitary gland concentration and total content of both DHT and oestradiol-17β receptors tend to increase between 20 and 80 days of age. Values at 80 days were however only 50–75% of the adult level. If one excludes the high value found for oestradiol receptor concentrations at 60 days of age, for which no convincing explanation can be given, it appears that during the time period studied no abrupt change occurs in DHT or oestradiol receptors in the pituitary gland. An interesting point is the significant relationship ($r = 0{\cdot}97$; $P < 0{\cdot}05$) between the testicular size and the number of both receptor types in 80-day-old lambs. Association constants (overall means $4{\cdot}88 \times 10^9$ and $3{\cdot}66 \times 10^9\ \text{M}^{-1}$ for DHT and oestradiol-17β, respectively) did not differ with age.

A study of hypothalamic receptors may reveal other age-related changes in sensitivity to steroids.

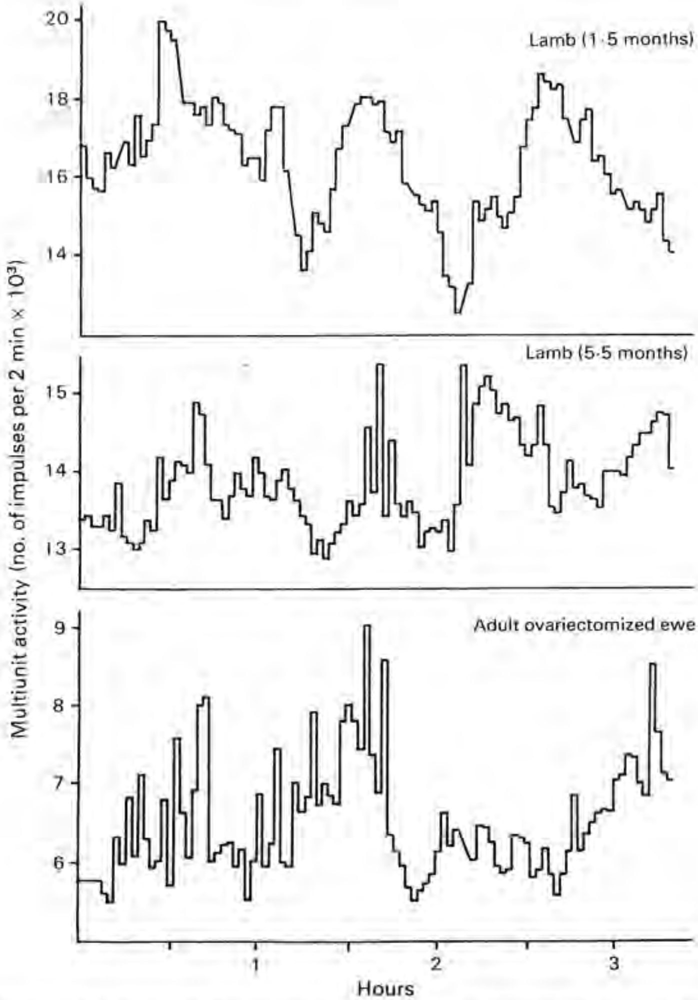
Table 1. Anterior pituitary cytosol, 5α-dihydrotestosterone and oestradiol-17β receptors in immature male lambs

Age (days)	Anterior pituitary wt (mg)	5α-Dihydrotestosterone Conc. (fmol/mg protein)	5α-Dihydrotestosterone Content (fmol)	Oestradiol-17β Conc. (fmol/mg protein)	Oestradiol-17β Content (fmol)
20	136 ± 6·0[a]	6·7 ± 0·95[a]	39·8 ± 5·67[a]	62·0 ± 7·28[a]	374 ± 48·1[a]
40	227 ± 26·8[b]	6·9 ± 0·58[a]	54·7 ± 6·06[ab]	108·5 ± 4·68[b]	1078 ± 240·0[b]
60	251 ± 45·0[b]	7·2 ± 0·97[ab]	60·5 ± 9·99[ab]	197·2 ± 23·2[c]	1497 ± 406·2[b]
80	249 ± 44·5[b]	9·2 ± 0·67[b]	110·1 ± 22·49[b]	109·2 ± 6·63[b]	1283 ± 250·2[b]

Values are mean ± s.e.m. for 4 lambs/age, castrated under local anaesthesia 24 h before slaughter to desaturate occupied sites.

Groups in each column with different superscripts are significantly different ($P < 0{\cdot}05$) (Student's paired *t* test).

Study of neuronal activity. Electrophysiological studies could provide a valuable approach with which to evaluate the role of the brain in endocrine events before puberty. Multiunit activity recorded between the median eminence and the optic chiasma has been shown to be related to the pulsatile release of LH in adult ovariectomized ewes (Thiery, Pelletier & Signoret, 1979). Multiunit activity was recorded in these same areas of anaesthetized male lambs at 1·5 and 5·5 months of age when the numbers of LH pulses were respectively high and low. The mean LH levels were drastically reduced as compared to those in unanaesthetized animals of the same age. Consequently, regular pulses of LH could not be detected. However, the electrophysiological characteristics of these areas did not differ with age and were also comparable to those previously described for the adult female (Text-fig. 2) (J. Pelletier, J. C. Thiery & F. Przekop, unpublished data). When cumulated every 2 min over a period of several hours, the multiunit activity showed periodic variations. The length of the periods between maximum variations in amplitude were 53·5 ± 9·8, 43·6 ± 1·9 and 55·0 ± 2·8 min (mean ± s.e.m.) for lambs aged 1·5

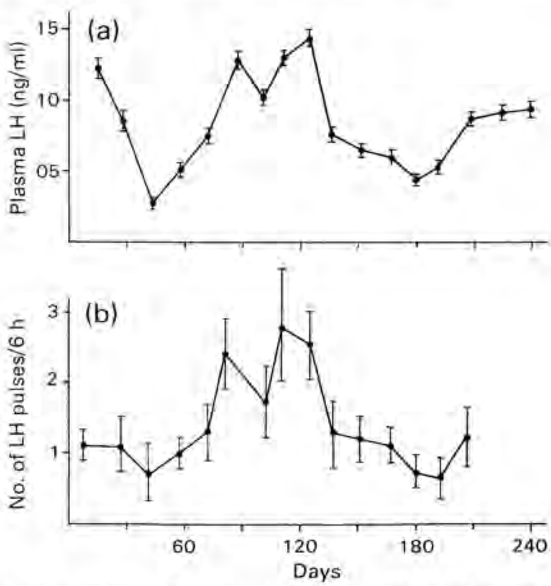


Text-fig. 2. Multi-unit activity of the retrochiasmatic area and anterior median eminence in two lambs, 1·5 and 5·5 months old, and in one ovariectomized ewe. Note the occurrence of rhythmic changes in the firing rate of the recorded neuronal elements (number of impulses per 2 min), at 40- to 60-min intervals in the lambs as well as in the ewe.

and 5·5 months, and adult ovariectomized females, respectively. Thus, under acute experimental conditions the infradian period of multiunit activity in lambs does not show any age-related change and is similar to that observed in adult ovariectomized females. The extension of this technique to conscious animals may allow an analysis of brain activity during the pulsatile release of LH.

Pigs

Florcruz & Lapwood (1978) have used a longitudinal approach to describe the profile of plasma LH in the prepubertal period of boars. This follows the pattern described for cattle and sheep, having a temporary period of high levels between 100 and 160 days of age. However, this pattern was not found by Colenbrander, Kruip, Dieleman & Wensing (1977). They observed elevated levels of both LH and testosterone in the 1- or 2-week-old piglet, but a constant low level of LH was found over 4 weeks of age (Colenbrander, de Jong & Wensing, 1978). The high levels of LH and testosterone found in cross-bred Dutch Landrace × Yorkshire boars at 1–2 weeks of age were not recorded by Elsaesser, Ellendorff, Pomerantz, Parvizi & Smidt (1976) in the miniature pig, which exhibits high progesterone values (2–3 ng/ml) during the first weeks after birth. Although there is a clear indication that testosterone levels increase progressively with age (Meusy-Dessolle, 1975; Colenbrander *et al.*, 1978) multiphasic increases have also been reported (Florcruz & Lapwood, 1978). There is less information concerning prepubertal endocrine changes in the gilt. Plasma LH is said to decrease in the miniature pig soon after birth (Elsaesser, Parvizi & Ellendorff, 1978) and to exhibit a pulsatile pattern of secretion when the gilts are 9–10 weeks of age (Foxcroft, Pomerantz & Nalbandov, 1975). At more than 100 days of age, plasma LH has been shown to increase from 0·9 to 3·3 ng/ml at about 210 days of age (Ntunde, Hacker & King, 1979). To clarify the situation, a longitudinal study of LH in Large White gilts, covering the period from 2 weeks of age until puberty, is presented below. Mean plasma levels of LH and the number of LH pulses (considered as increases greater than 1 ng/ml) are presented in Text-fig. 3. After a steep decrease in plasma LH during the first month of life, the level increases to a maximum between 82 and 125 days of age. Plasma LH levels then decrease between 125 and 180 days, and increase again just before puberty. The number of the pulses determines the overall LH concentration (Text-fig. 3, lower panel). In particular, the number of pulses during the 82–125-day period is significantly higher than in the previous and the subsequent periods ($P < 0{\cdot}001$). However, there is a discrepancy between the mean LH level and the number of pulses at 2 weeks of age. At this time the pulses are few but are of a larger magnitude and long duration. These high LH levels found in young gilts agree with comparable data observed after birth in the boar (Colenbrander *et al.*, 1978). By comparison, the almost complete absence of data concerning FSH, LH-RH or prolactin before puberty is striking.



Text-fig. 3. Mean ± s.e.m. plasma LH concentrations and number of LH pulses in 8 Large White gilts according to age.

In summary, bovine, ovine and porcine species exhibit very similar LH patterns before puberty. There is a transient, high number of LH pulses at a time when the feed-back effect of steroids are ineffective or low. The decrease in the number of LH pulses observed thereafter is presumably due to the increasing level of steroid, although a change in hypothalamic and pituitary gland sensitivity cannot be completely excluded. The differences observed after birth between pigs, on the one hand, and sheep and cattle on the other may be artefactual because birth does not occur at an equivalent physiological stage in each species. Thus the decrease in plasma LH in the young piglet born at a relatively immature stage may correspond to a similar phenomenon which occurs towards the end of fetal life in sheep and cattle (Foster, Cook & Nalbandov, 1972; Challis *et al.*, 1974; see also Levasseur, 1979).

Experimental approach to the maturation of the hypothalamic–pituitary axis

The maturity of the hypothalamus and pituitary gland has been tested in several ways in the three species considered here. The sensitivity to LH-RH in the early post-natal period may be considered as a direct test for the response of the pituitary gland to the hypothalamic hormone alone, but later, when testosterone release follows the increase in plasma LH, the response of the pituitary gland becomes modulated by the steroid. On the other hand, the classical procedures of castration and steroid injections help to define whether the changes in the responses of the hypothalamus or the pituitary gland can be interpreted as differences in maturity.

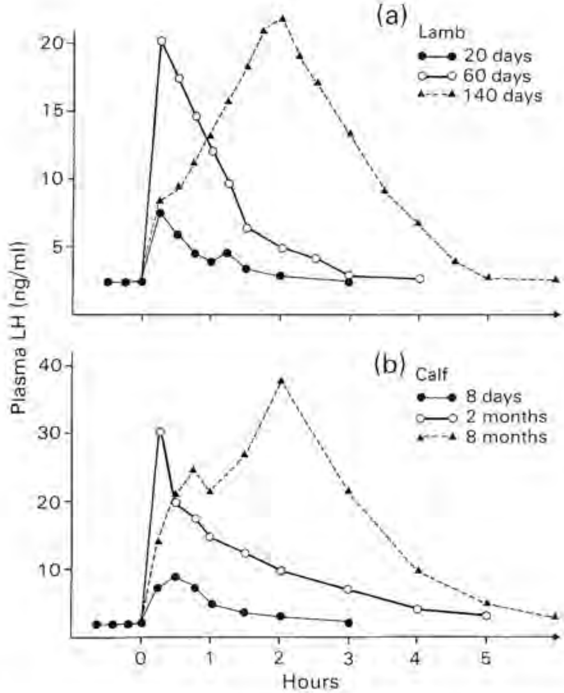
Effect of LH-RH treatment on LH and FSH release in relation to age before puberty

In cattle (Kesler & Garverick, 1977; Bass, McNeilly & Moreton, 1979; Lacroix & Pelletier, 1979b) and sheep (Galloway & Pelletier, 1974; Lee *et al.*, 1976b) the magnitude of the LH response to LH-RH injections increases during the first weeks following birth. Thereafter, there is disagreement. In bull calves, the response has been found to continue to increase to a maximum at puberty (Lacroix & Pelletier, 1979b) whilst in another study a decrease at 7 months of age was found (Chantaraprateep & Thibier, 1979). However, in the latter study the dose of LH-RH was kept constant (250 μg) whilst the body weight of animals increased greatly between 3 and 13 months of age.

Prepubertal and pubertal male and female pigs display a dose-related response to LH-RH, but this is usually low (<5 ng/ml) in adult pigs compared to that observed in cattle and sheep (Chakraborty, Reeves, Arimura & Schally, 1973; Pomerantz, Ellendorff, Elsaesser, König & Smidt, 1974; Foxcroft *et al.*, 1975). A more systematic study is required to ascertain whether the LH response after LH-RH treatment varies according to age in both sexes.

The change in the magnitude of the response corresponds to a modification in the time of LH release. The peak LH value after LH-RH tends to occur later with increasing age, e.g. when the testis weight increases in the lamb (Courot, 1962; Galloway & Pelletier, 1974), or when testosterone increases are seen following LH stimulation, i.e. between the 4th and 6th month of age (Lacroix & Pelletier, 1979b). This delay in the LH peak, which has been related to the presence of testosterone in the adult ram (Galloway & Pelletier, 1975), can be considered as an indication of a new relationship between the gonads and the hypothalamic–pituitary axis which does not imply *per se* a shift in the sensitivity of the feed-back mechanism to the steroid (Text-fig. 4).

The FSH response after LH-RH administration is said to be negligible in intact bull calves (Bass *et al.*, 1979), low and variable in young male lambs (Lee *et al.*, 1976b), or present but of a lower magnitude than the LH response in the prepubertal gilt (Vandalem, Bodart, Pirens, Closset & Hennen, 1979). The LH and FSH releases after LH-RH administration are increased in castrated prepubertal (4–6 months) calves (Lacroix & Pelletier, 1979b; Bass *et al.*, 1979) but a more prominent LH response is observed when castrated male calves are subjected to a short period of testosterone propionate treatment before the injection of LH-RH (Lacroix & Pelletier, 1979b). After such treatment there is an increase in the time to the peak LH level in addition to the increased magnitude of the LH release. This may be attributed to a direct effect of testosterone on LH release.



Text-fig. 4. Age-related release of LH following an LH-RH injection (0 h) in (a) a male lamb and (b) a male calf. Data from Galloway & Pelletier (1974) and Lacroix & Pelletier (1979b).

Effect of castration and steroid replacement

The bovine pituitary gland does not respond to castration performed at birth with an immediate increase in LH release but shows a delayed response at 4 weeks of age (Bass, Peterson, Payne & Jarnet, 1977). Later, at 4 months of age, the removal of testicular steroids induces a significant LH increase on the second day after surgery (Lacroix & Pelletier, 1979b) while at 5 months of age the LH increase is apparent within 7–8 h of castration (McCarthy & Swanson, 1976). A comparable situation is observed in male and female lambs. The increase in plasma LH is delayed by 1 week or more when gonadectomy is performed at birth or at 2 weeks of age (Foster *et al.*, 1972; Foster, Jaffe & Niswender, 1975). Over 4 weeks of age, the LH response to castration is faster (Crim & Geschwind, 1972). Similarly, there is no change in plasma LH for a few days after gonadectomy in male or female pigs at 1 week of age, but the level steadily rises in castrated pigs compared to boars after a delay of 3 weeks (Colenbrander *et al.*, 1977; Ford & Schanbacher, 1977; Elsaesser *et al.*, 1978).

Experiments with neonatal castration have generally led to the conclusion that steroid feedback was present soon after birth. However, the delay in the LH increase after surgery appears considerably longer in such animals than when castration is done in older animals. This suggests that the feedback is weak in the period shortly after birth. The concomitant low plasma LH levels and the weak feedback observed in the early post-natal period suggest the presence of an inhibitor other than steroids, possibly factors within the central nervous system as postulated by Levasseur (1977). The weak post-natal feedback of steroids could be responsible for the progressive increase in plasma LH registered after birth in the three species mentioned here.

A maturational event that merits confirmation is the finding that castration between 2 and 13 weeks of age subsequently produces a higher level of LH in the adult than castration performed after testicular growth has occurred (Pelletier, Terqui & Blanc, 1977). It is as if early castration prevents a maturational step which decisively limits LH release, even though castration at a later time is followed by a more rapid increase in LH.

Variations in the plasma levels of FSH in male and female lambs mimic those of LH after castration although the increased secretion does not involve a pulsatile pattern of release (Crim & Geschwind, 1972; Foster *et al.*, 1975). The problem is to decide what is exerting the negative effect upon the hypothalamic–pituitary axis. The steep FSH increase after 5 weeks of age in male lambs made cryptorchid at 2 weeks of age strongly suggests, in the absence of any difference in plasma testosterone levels compared with intact controls, that the inhibin system may also be involved in the feedback mechanisms before puberty (Blanc & Terqui, 1976). This is supported by an experiment involving hemicastrations performed at 1 weeks of age in male lambs (Walton, Evins & Waites, 1978).

The inhibin system could also be involved in the regulation of LH release in the male lamb (Schanbacher & Ford, 1976) and in the adult ram (Blanc *et al.*, 1979); a finding which is generally overlooked when puberty is discussed. The treatment of castrated animals with testosterone depresses plasma LH and FSH to the levels obtaining in intact cattle and sheep (McCarthy & Swanson, 1976; Lacroix & Pelletier, 1979b; Crim & Geschwind, 1972) but, if this demonstrates that testosterone has full potential to inhibit release of the two gonadotrophins, it does not prove that it acts alone under physiological conditions.

Age-related positive feedback effect of oestrogens

An interesting aspect of maturation of the female hypothalamic–pituitary axis is the LH release induced by exogenous oestradiol. As a rule, a positive LH response following the injection or implantation of oestradiol is observed before puberty but not immediately after birth. Thus, oestradiol-17β elicits an LH surge in 5- or 7-month-old heifers but not at 3 months (Swanson & McCarthy, 1978; Staigmiller, Short & Bellows, 1979). Similarly, oestradiol-17β induces LH release at about 5–7 weeks of age in female lambs (Land, Thimonier & Pelletier, 1970; Squires, Scaramuzzi, Caldwell & Inskeep, 1972; Foster & Karsch, 1975) but not before. An oestradiol-induced LH response is also readily observed around 160 days of age in the gilt, although no response is observed at 6 days and a weak response at 60 days (Elsaesser & Foxcroft, 1978; Elsaesser & Parvizi, 1979). The clearest profiles of age-related LH responses to oestradiol are those of Foster & Karsch (1975) who have shown a progressive increase in the magnitude of the LH response as the animals grow older. A lack of LH is unlikely to explain the absence of an early oestradiol-induced LH release, because there is often no LH response to oestradiol at a time when the pulsatile pattern of LH release is well developed. A progressive change in hypothalamic–pituitary sensitivity to oestradiol in the female is the most probable explanation.

Conclusions

It seems that the major lines of approach to the study of puberty are relatively comparable between species, but many aspects require further investigation. Endocrine variations before puberty are now better understood, and the processes before puberty appear to hinge around three major phases of LH secretion which reflects changes in the interactions between brain, pituitary and gonads. One must, however, keep in mind that the origins of these changes are inferred rather than known. Furthermore, many uncertainties remain, particularly concerning the role of FSH, the pattern of secretion of steroids in females and the changes in LH-RH synthesis and release. Some factors relating to puberty and originating from the pineal gland or the gonads (folliculostatin, inhibin) remain to be chemically identified and studied. Thus, the description of the neuroendocrine events involved in puberty is far from complete, but there is no doubt that progress will be significant in this field in years to come. Experimental work to measure changes of hormone feedback within the hypothalamic–pituitary axis is required because results of many studies are inconclusive and there is a need to ascertain whether a shift in sensitivity to steroids does occur. An attractive approach to this problem is the use of gonadectomized animals with implants releasing low but constant quantities of steroid (Foster & Ryan, 1979).

All these studies, however, are based on the idea that prepubertal processes result from an interplay between hormonal events. It will be imperative in the future to define the role played by the brain (Levasseur, 1977). The records of electrical activity in hypothalamus are a first step in this direction. The final understanding of puberty will involve the integration of these different lines of approach.

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