

Endocrine regulation of periparturient behaviour in pigs

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Pigs begin behavioural preparations for birth about 1–2 days before parturition. Prepartum sows wander to select a suitable site and then construct a maternal nest. The signal that initiates this behavioural cascade probably results from fetal maturation but is unknown. However, endogenous $\text{PGF}_{2\alpha}$ appears to be involved early on in an endocrine pathway that projects to the brain and can generate most of the prepartum behavioural components. This period of intense activity is followed by a quiescent phase of lying in the nest for some hours before fetal ejection occurs. Feedback from a completed nest or abdominal discomfort may both contribute to the end of nest building. In the postpartum phase, sows have to deal with the apparently conflicting drives of remaining passive to reduce accidental or deliberate damage to piglets, while at the same time responding actively to their needs. In commercial environments, animals frequently fail in this task. Although environmental influences on piglet survival have received much experimental attention, the genetic, social and endocrine drives that control sow behaviour after parturition remain poorly understood and their clarification is a major challenge for the future.

Introduction

Behavioural changes associated with birth consist of much more than the process of fetal expulsion alone. For the purposes of this review the onset of periparturient behaviour is defined as the first observable prepartum behavioural change and the end as the establishment of stable neonatal–maternal relationships with the onset of regular nursing.

Variations in maternal behaviour result from the product of genetic background, individual previous experience and immediate environmental feedback impinging upon innate drives. Although modern domestic sows are many generations removed from their wild boar ancestors, innate periparturient behaviours appear to be similar (Špinková *et al.*, 2000). As the sequence of behaviours seen during birth are not observed at other times and their timing is crucial for reproductive success, it seems likely that signals from mature fetuses or placentae are likely to trigger these behavioural changes. Such signals could be relayed from the uterus to the brain by afferent nerve stimulation via ascending spinal pathways or through the bloodstream and across the blood–brain barrier via areas of ‘leakiness’ such as the

circumventricular organs (McKinley *et al.*, 1998) or by specific carrier systems. The initiation of the physiological and endocrine events that lead to parturition in sheep has been traced to fetal pituitary adrenocorticotrophic hormone (ACTH) secretion (for review see Challis and Lye, 1994). However, there is no clear evidence that a similar system operates in pigs (Randall *et al.*, 1990). This is an example of an argument (Naaktgeboren, 1979) that multiparous animals (for example, pigs, rabbits, carnivores and rodents) and usually uniparous animals (for example ungulates) should be considered in two broadly separate categories in most aspects of their periparturient physiology.

With the advent of intensive husbandry systems, the environment in which commercial pigs give birth is frequently very different from that of their wild ancestors. Concern over the extent to which intensification prevents or alters normal behaviour patterns, potentially causing maternal stress, has been the subject of much recent research. However, this review will concentrate on describing parturient behaviours unhindered by potentially impoverished environments, and what is known of their endocrine regulation, in an attempt to place these applied studies in context.

The prepartum period

Normal behaviour

Preparatory behaviours for birth in domestic sows with space to roam through different environments and terrain in large semi-natural enclosures have been described in a series of reports (for example, Jensen, 1986; Jensen *et al.*, 1987, 1991, 1993). The first observable changes in behaviour occur about 48 h before giving birth, when animals become restless before a period of concentrated walking, interpreted as nest-site seeking and selection behaviour. During this time, either as an indirect consequence of increased locomotion or as a result of deliberate action, animals tend to leave the herd home range. They may walk several kilometres and build one or more 'mock nests' before final nest-site selection and construction. The nest is built by first digging a hollow in the ground using the snout and raking movements with the front hooves. A mixture of vegetation is gathered from nearby and arranged within the hollow using the snout and hooves to form a nest with a deep bed. This sequence of behaviours may continue for more than a day, declining 3–7 h before birth of the first piglet. In preparation for this phase, sows characteristically push their bodies into the nest using a lowered, turned head and forelegs before lying recumbent on their sides. Nest building does not normally occur after this time (Petersen *et al.*, 1990), although some repairs and improvements after parturition have been observed (Jensen *et al.*, 1987). Nest quality is an important determinant of the timing of the end of nest building, as sows with access to fewer types of material continued to build, in some cases into the postpartum period (Damm *et al.*, 2000).

Motivation to change behaviour in the prepartum period may initially be the result of 'internal factors' such as endocrine change, with 'external factors' such as environmental feedback becoming increasingly important as nest-building progresses (Jensen *et al.*, 1993).

Endocrine regulation

Although a great deal is now known about how pig plasma concentrations of substances relevant to parturition vary over time, we are still a long way from understanding how these variations translate, if at all, into the molecular and neuronal events that drive behavioural change. However, plasma concentrations of many reproductive hormones are in a rapid state of change in the prepartum period, when behavioural change occurs (see Fig. 1) and some

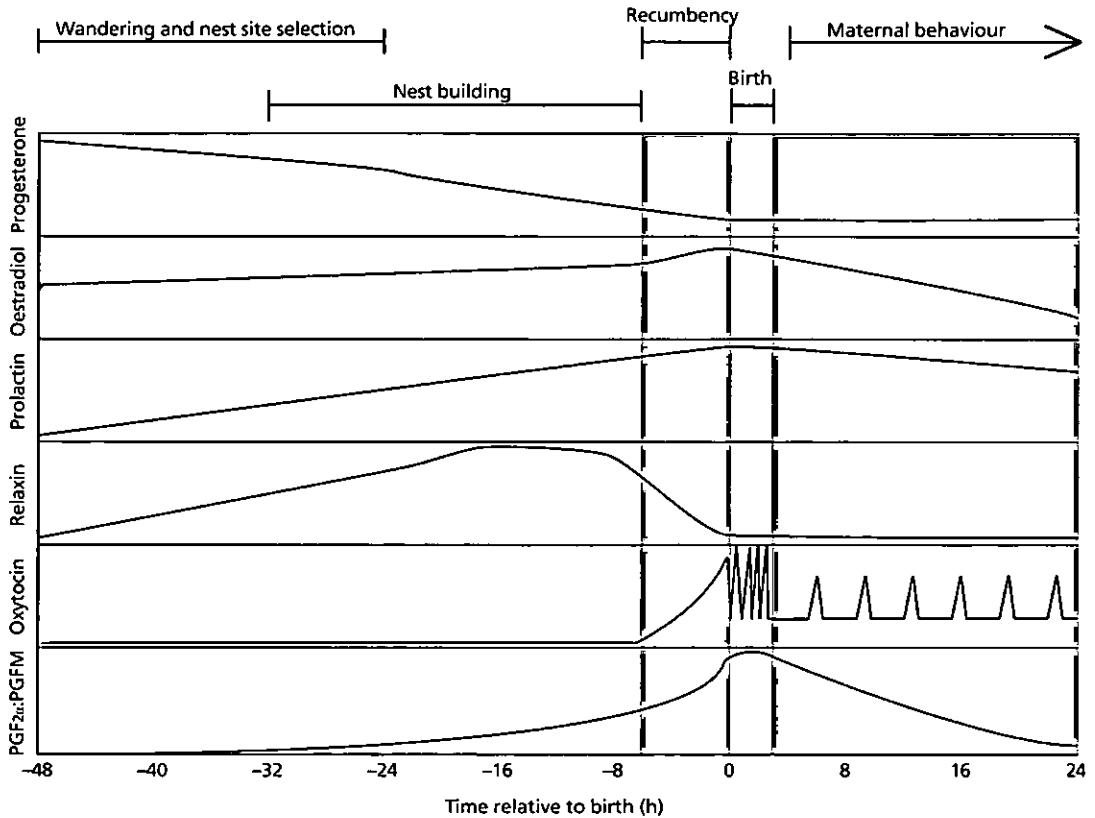


Fig. 1. Trends in plasma concentrations of key hormones about the time of parturition in pigs and their relationship to behavioural change. No scaling of absolute values is given. Sources of data include: Ellendorff *et al.* (1979); Taverne *et al.* (1982); Watts *et al.* (1988); King and Wathes (1989); Whitely *et al.* (1990); Meunier-Salaün *et al.* (1991); Castrén *et al.* (1993a,b); Gilbert *et al.* (1994); and Gilbert (1999).

experiments have been performed in which alteration in plasma hormone content has led to behavioural change. Of these, the main known causal relationship between the endocrine system and nest building is the strong evidence that endogenous $\text{PGF}_{2\alpha}$ initiates and mediates these behaviours (see Fig. 2).

$\text{PGF}_{2\alpha}$ and nest building behaviour. Peripheral injection of luteolytic doses of $\text{PGF}_{2\alpha}$ to late pregnant sows rapidly induced behaviours very similar to nest building, whereas a synthetic analogue of $\text{PGF}_{2\alpha}$ cloprostenol, had a minimal behavioural effect (Widowski *et al.*, 1990). Remarkably, $\text{PGF}_{2\alpha}$ has also been shown to induce nest building behaviours in postpartum (Blackshaw, 1983), pseudopregnant (Boulton *et al.*, 1997a) and cyclic (Blackshaw, 1983; Burne *et al.*, 2000a) sows. Behavioural elements that have been recorded include increased locomotion and isolation in outdoor enclosures, comparable to prepartum wandering (Gilbert *et al.*, 2000a), snout rooting and front leg pawing at the ground, and carrying and arranging straw (Burne *et al.*, 2000a,b). These induced behaviours appear to be dependent on environment (outdoors, strawed pen or farrowing crate), but are separate from the nest building associated with temperature regulation (Burne *et al.*, 2001). This is an important distinction as thermoregulatory motivators can also generate nest building, particularly in

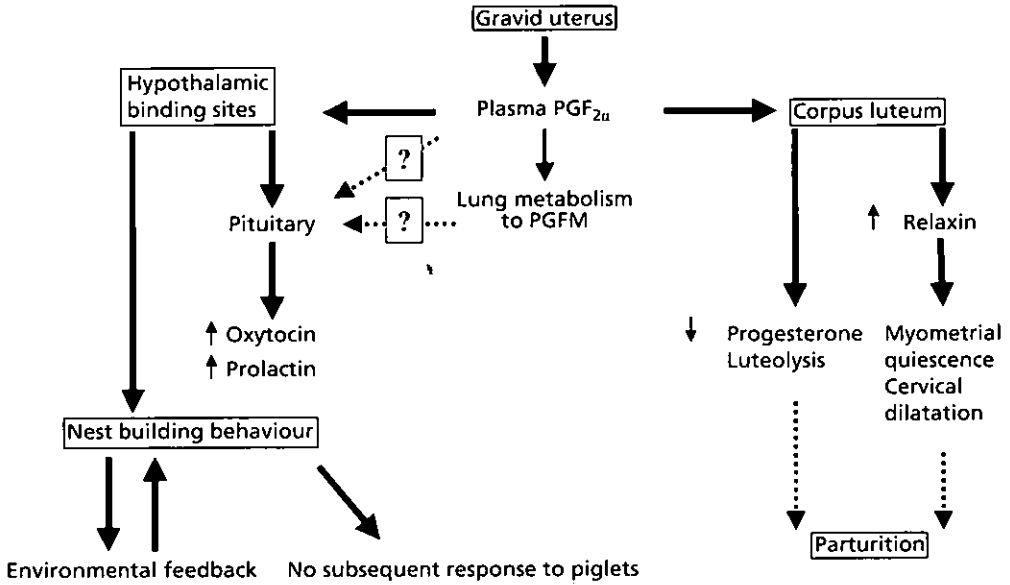


Fig. 2. Schematic representation of proposed regulation of parturient behaviour in pigs by endogenous $\text{PGF}_{2\alpha}$. Although $\text{PGF}_{2\alpha}$ is able to bring about all of the changes shown, it remains unclear whether it is the primary endogenous regulator in all cases. PGFM: 13,14 dihydro-15-keto- $\text{PGF}_{2\alpha}$.

rodent species (Bhatia *et al.*, 1995). Recently, Burne *et al.* (2000c) suggested that the development of $\text{PGF}_{2\alpha}$ -induced nest building is dependent upon age and appears at about the time of puberty.

$\text{PGF}_{2\alpha}$ can be synthesized by the uterine endometrium (Uzumcu *et al.*, 1998) and may be released by the placenta in preparturient animals (Silver *et al.*, 1979), although the stimulation of release is not understood. Studies in other species support the idea that feto-placental synthesis of prostaglandins occurs in late pregnancy (Mitchell *et al.*, 1995). Plasma secretion of $\text{PGF}_{2\alpha}$ in the prepartum period has been measured (Watts *et al.*, 1988; Whately *et al.*, 1990) through assay of the major metabolite 13,14-dihydro-15-keto- $\text{PGF}_{2\alpha}$ (PGFM). Metabolism of $\text{PGF}_{2\alpha}$ to PGFM in the lungs of pigs is only 80% efficient, whereas in a non-nest-building species, sheep, this figure approaches 100% (Davis *et al.*, 1979). Therefore, it is likely that some peripherally secreted $\text{PGF}_{2\alpha}$ could access the brains of pigs. However, no study so far has convincingly demonstrated an increase in circulating concentrations of $\text{PGF}_{2\alpha}$ or PGFM coincident with the nest-building phase. Insufficient sampling frequencies plus the use of a metabolite assay may have contributed to this deficiency. In addition, prostaglandin synthesis in the brain may be occurring that is not measurable by peripheral sampling. However, there is clearly a sharp increase in PGFM immediately before parturition, after nest building has finished and during the behaviourally quiescent, recumbent phase (Fig. 1). This presents the hypothesis with a problem. Behaviours that are readily inducible with exogenous $\text{PGF}_{2\alpha}$ are not observed at the time when endogenous PGFM concentrations are at their peak. This paradox is a good example of the danger inherent in trying to understand endocrine control of behaviour from the standpoint of plasma concentrations alone, without related data on receptor kinetics and signalling events. Unfortunately, information of this latter type is very scarce for pigs (especially in the central nervous system). However, if the $\text{PGF}_{2\alpha}$ -induced nest-building hypothesis is correct, the continuing increase in plasma prostaglandin

concentrations during the recumbent phase requires either alterations in the sensitivity of central behavioural receptor systems to $\text{PGF}_{2\alpha}$ or other systems acting to override the stimulatory effect of $\text{PGF}_{2\alpha}$ on nest-building. Increasing prepartum peripheral oxytocin concentrations (Gilbert, 1999) correlates with the end of nest building in pigs (Castrén *et al.*, 1993a), together with the associated increase in intensity of uterine concentrations and abdominal discomfort (Naaktgeboren, 1979; Taverne *et al.*, 1979). Whether recumbency and behavioural quiescence are a simple function of a response to abdominal discomfort or specific effects produced directly by an altered endocrine state is unclear, but the former option seems plausible. However, central neuronal activation has been observed after prepartum increases in peripheral oxytocin concentrations (Antonijevic *et al.*, 1995) and central oxytocin is an important mediator of postpartum behaviour in rodents (see below).

Receptors to $\text{PGF}_{2\alpha}$ are synthesized in pig hypothalamic nuclei (Burne, 2000). Cells in similar areas are activated by peripheral $\text{PGF}_{2\alpha}$ treatment (Walton *et al.*, 2001). This is a possible site of action for the initiation of prepartum behavioural change. Although it is uncertain which cell type possesses $\text{PGF}_{2\alpha}$ receptors, glial cells express $\text{PGF}_{2\alpha}$ mRNA in rats (Kitanaka *et al.*, 1996) and brain microvessels possess these receptors in pigs (Chemtob *et al.*, 1996). In rats, local $\text{PGF}_{2\alpha}$ infusion altered the firing rate of neurones in the supraoptic nucleus (Setiadji *et al.*, 1998). However, no information is available on $\text{PGF}_{2\alpha}$ modulation of neuronal activity in pigs and the downstream central mechanisms that result in behavioural changes are unknown.

In addition to altering behaviour, $\text{PGF}_{2\alpha}$ also generates rapid increases in plasma concentrations of prolactin and oxytocin (Boulton *et al.*, 1997b). Plasma concentrations of progesterone increase acutely, followed by a longer-term decrease associated with luteolysis (Boulton *et al.*, 1997b). It is possible that these induced increases may account for some of the reported correlative data between these hormones and nest building behaviours. For example, the preparturient increase in plasma prolactin concentrations may be responsible for the initiation of nest building, as these events occur at similar times (Castrén *et al.*, 1993a). However, these data do not imply causality and Boulton *et al.* (1998) showed that profound reduction of peripheral prolactin concentrations with bromocriptine failed to prevent $\text{PGF}_{2\alpha}$ -induced nest-building behaviours. It is possible that central mechanisms that generate nest building also produce downstream prolactin secretion. Similarly, the duration of straw gathering behaviour has been positively correlated with plasma progesterone concentrations (Castrén *et al.*, 1993a), but neither the sex steroid ratio (Boulton *et al.*, 1997b) nor oestradiol supplementation (Burne *et al.*, 1999) affected $\text{PGF}_{2\alpha}$ -induced nest-building behaviour. However, endocrine control of nest building appears to be species-specific, as both prolactin and variations in the ratio of circulating oestrogen:progesterone affect digging, straw-carrying and hair-pulling (to line a nest) behaviours in late pregnant rabbits (Gonzalez-Mariscal *et al.*, 1996).

Relaxin. The timing of the endogenous prepartum relaxin surge is not fully understood. Some experiments have shown that corpora lutea of pregnancy produce a relaxin surge 112–114 days after mating even in the absence of a gravid uterus (for example see Felder *et al.*, 1988). This raises the intriguing idea of an 'internal clock' in the ovary or central nervous system that measures the duration of gestation independently of uterine signals and initiates endocrine events leading to parturition. Although $\text{PGF}_{2\alpha}$ stimulates relaxin secretion (Sherwood *et al.*, 1979; King and Wathes, 1989) and prepartum plasma concentrations of relaxin appear to be closely related in time to nest-building behaviour (Fig. 1), relationships between the prepartum relaxin surge and behaviour have not been tested systematically. In

rodents, relaxin can affect neuronal activity in the hypothalamus through binding to receptors in areas of blood-brain barrier weakness (Heine *et al.*, 1997; McKinley *et al.*, 1998). Summerlee *et al.* (1998) proposed that in rats a central relaxin system controlling the timing of birth exists discretely from the peripheral system regulating uterine motility and cervical softening, but the only report of centrally applied relaxin affecting behaviour relates to drinking (Summerlee and Robertson, 1995).

In addition to central effects, relaxin has important functions in the late pregnant uterus, preventing inappropriate early myometrial contractions and inducing cervical softening (Bagnall *et al.*, 1993). The co-ordination of cervical softening, prevention of inappropriate early uterine contraction and parturition behaviour by a single system is an attractive hypothesis, as the events clearly need to be co-ordinated in time. It is possible that relaxin may act to counteract the uterotonic influences of PGF_{2α} during nest building, with the end of the relaxin surge allowing myometrial activity to increase, which would in turn adjust behaviour away from nest building towards recumbency and expulsive effort.

Fetal delivery

Notwithstanding effects on nest-building behaviour, prostaglandins also appear to be required for parturition to occur (Nara and First, 1981). This effect is probably due to a peripheral action of PGF_{2α} on the corpora lutea of pregnancy to remove luteal support to the pregnancy, as has been shown clearly in PGF_{2α} receptor knockout mice (Sugimoto *et al.*, 1997). Indeed, PGF_{2α} analogues are frequently used commercially to induce parturition and various combinations of PGF_{2α} and oxytocin have been tested experimentally (for review see Gilbert, 1999).

Piglets are nearly always born with sows lying in lateral recumbency and fetal expulsion through the birth canal is accompanied by visible and powerful contractions of the external abdominal musculature (Randall, 1972). The rate at which piglets are expelled is variable. Mean duration of second stage labour has been reported as 2.5 h with a range of 0.5–10.5 h, and mean piglet interval as 16.0 min with a range (per litter) of 4.2–48.4 min with animals in a variety of commercial environments (Randall, 1972). Data sets from semi-natural environments are much smaller, but report somewhat slower (Petersen *et al.*, 1990) or similar (Jensen, 1986) birth rates. Although nest building is discontinued during parturition, some postural changes occur. Typically, sows stand, inspect piglets and lie down again (Petersen *et al.*, 1990). This behaviour has been studied more systematically in more intensive conditions (Edwards and Furniss, 1988) and appears to be observed more frequently after birth of the first piglet compared with later littermates. Similarly, Jarvis *et al.* (1999) showed that maternal responsiveness to piglets was high at the onset of farrowing, decreased over the following 4 h and was restored by the following day.

Endocrine regulation

The physiology underlying the initiation of powerful uterine contractions at birth has been described elsewhere (for example see Ellendorff *et al.*, 1979; Taverne *et al.*, 1982; Silver *et al.*, 1983). The powerful and visible contractions of the external abdominal muscles that accompany delivery have been described as the 'fetal ejection reflex' in rats, which requires intact pelvic nerves and may be initiated by cervical dilatation (Higuchi *et al.*, 1987). Once the cervix is open, fetal expulsion is achieved by a combination of uterine smooth muscle and abdominal striated muscle contractions. Much of the increase in uterine smooth muscle activity may be attributable to an increase in circulating oxytocin secretion, which begins to

increase above baseline values at about 7 h before birth (Gilbert, 1999). However, oxytocin gene knockout mice were able to give birth normally (Nishimori *et al.*, 1996), indicating that other uterotonic agents (Challis and Lye, 1994) are able to compensate for a lack of oxytocin, and implying considerable flexibility and redundancy in the system (Russell and Leng, 1998).

Oxytocin secretion during parturition is under inhibitory regulation by central endogenous opioids (Leng and Russell, 1989), which are responsible for inhibiting parturition in stressful circumstances (Lawrence *et al.*, 1992). However, as parturition is likely to be inherently both stressful and painful, opioid systems may also be involved normally in regulating oxytocin secretion to time parturition (Gilbert *et al.*, 2000b), help space births (Jarvis *et al.*, 2000) and, through separate spinal systems, attenuate pain perception (Jarvis *et al.*, 1997).

Cervical dilatation and maternal behaviour. In sheep, recognition of individual lambs and selective bonding occur rapidly after birth and are triggered by mechanical cues from the fetus passing down the birth canal modulating hypothalamic relays, involving centrally released oxytocin with progesterone and oestrogen priming (Kendrick and Keverne, 1991). In pigs, individual recognition of piglets by sows is not observed reliably at day 1 after parturition, but develops by day 7 after parturition (Horrell and Hodgson, 1992; Maletínská *et al.*, 2000). Although vagino-cervical dilatation at birth increases peripheral oxytocin secretion in pigs (Gilbert *et al.*, 1997), there is no evidence that this process contributes to maternal behaviour.

Oxytocin secretion and nursing behaviour. During parturition, oxytocin secretion is increased above pre-term values with pulsatile release superimposed (Castrén *et al.*, 1993b): additional pulses associated with fetal ejection are measurable as increases in intra-mammary pressure (Gilbert *et al.*, 1994). This may aid the release of colostrum, which can be expressed continually during birth. Newborn piglets are highly precocious and often vocal. Having cleared the fetal membranes from around their heads, piglets normally rise rapidly (within 2 min of birth) and begin to nuzzle their dam, seeking a nipple (Randall, 1972). The discrete milk ejection reflexes characterized by maternal behavioural (Algers *et al.*, 1990; Jensen *et al.*, 1991), endocrine (Ellendorff *et al.*, 1982) and neuronal (Jiang and Wakerley, 1995) changes that develop as lactation progresses are not behaviourally apparent immediately after parturition (Herskin *et al.*, 1999). This apparently minimal maternal constraint to suckling may help neonates, as teats may initially be hard to find or regain once lost, due to sibling competition, so a continuous letdown maximizes the chance of an early meal (for review see Fraser *et al.*, 1995).

The postpartum period

Normal maternal behaviour

Normal pig maternal behaviour is rather different in the 24 h after birth compared with later periods during lactation (Jensen *et al.*, 1991) and is characterized by high nest occupancy (Stangel and Jensen, 1991). In the immediate postpartum period, removal of placental membranes and licking of individual piglets by sows does not normally occur. Furthermore, in contrast to species such as the rat (Bridges, 1990), carrying of offspring in the mouth and retrieval to the nest is not observed. Duration of maternal lateral lying in the first day after parturition is high (Meunier-Salaün *et al.*, 1991; Cronin and Smith, 1992). Newborn piglets may be weak (Fraser, 1990) and are often located at or near the udder on the day after birth

(Cronin and Smith, 1992), such that relatively minor postural changes by the mother (such as rolling over) can endanger piglets (Weary *et al.*, 1996), with a greater likelihood of accidental damage or death to piglets than later on in lactation (Marchant *et al.*, 2001). Newborn piglets are relatively small ($\approx 0.5\%$ of maternal weight) but highly precocious and will fight for access to teats. They normally establish a stable teat order and dominance hierarchy within a few days, thereby minimizing further antagonistic interactions (Fraser *et al.*, 1995).

Throughout this period of maternal behaviour there is a conflict between the sow investing in her own wellbeing and that of her piglets. The inability of some sows to adapt sufficiently to perform adequately the tasks associated with maternal care is shown by the existence of 'death-prone litters' (Fraser, 1990; Fraser *et al.*, 1995), in which too many deaths occur for the overall frequency of mortality to conform to a Poisson distribution (Fraser, 1990). Large litter size, maternal disease or low milk yield may account for some death-prone litters, but many are the result of poor maternal care. In sows with an equivalent metabolic status and similar husbandry systems (such as housing and temperature regulation), there is still large variation in maternal behaviour (van der Steen *et al.*, 1988; Fraser, 1990), which must be caused by either genetic predisposition or the consequences of an individual's previous experience. An example of selective breeding producing effects on maternal behaviour has recently been published (McPhee *et al.*, 2001). The effects of earlier maternal experience (Jarvis *et al.*, 2001) and other physical and social experiences also appear to influence the subsequent maternal behaviour of pigs (for example, Varley and Stedman, 1993; Beattie *et al.*, 1995). For example, sows that are dominant during pregnancy are more active immediately before farrowing and allow their piglets to suckle more freely than do lower ranking sows. In contrast, low ranking sows are more restless in the early phase after farrowing and can show stereotyped and redirected behaviour patterns (Csemmely and Nicosia, 1991).

Underprivileged piglets may eventually die as a result of overlying, hypothermia or intercurrent disease. However, excessive maternal activity for whatever reason is likely to contribute to accidental damage to offspring. Indeed, Jarvis *et al.* (1999) suggested that optimum maternal behaviour in the first day after parturition is characterized by passivity, unresponsiveness to piglets and lateral lying, allowing both a reduced risk of crushing and maximum access to teats. However, it is also clear that later in lactation, as maternal-piglet relationships develop, responsiveness to piglet distress calls plays an important part in reducing crush injuries (Wechsler and Hegglin, 1997).

Aggressive infanticide

In addition to accidental injury, deliberate maternal aggression of sows towards offspring has been described in large surveys of commercial piggeries with incidences of 8% (Knap and Merks, 1987) and 7–12% (van der Steen *et al.*, 1988) of sows giving birth, a significant heritability and prevalence in primiparous sows (gilts). The behaviour is characterized by sows killing some or all of their offspring by biting them to death. Most piglets are killed within day 1 after parturition. Although animals that are predisposed to aggressive infanticide do not show obvious warning signs before farrowing, recent evidence suggests that variations in posture in the day before birth might be useful as behavioural predictors (Appleyard *et al.*, 2000), and animals that show maternal aggression appear to be less aggressive to pen-mate sows during pregnancy (McLean *et al.*, 1998).

Whether this phenotype is part of a continuum of poor maternal behaviour related to a failure in maternal passivity (Jarvis *et al.*, 1999) or an entirely separate event is unknown. Carcasses may be consumed but are often discarded, so hunger is unlikely to be the cause.

Whether this aggressive behaviour is limited to a sow's own offspring, or would be directed to any piglets or other foreign objects, has not been tested. This would be useful information as it might show whether the sow's aggression is a response to a general increase in reactivity or fearfulness or is a specific rejection of her own piglets.

Endocrine regulation

Most studies on maternal behaviour support regulation by neuro–endocrine systems that originate in and are co-ordinated by hypothalamic nuclei, particularly the medial-pre-optic area, paraventricular nucleus, supraoptic nucleus and associated projections. These brain areas are responsive to the changes in ovarian and uterine hormone secretion that occur in late pregnancy. Much of this evidence is derived from studies in laboratory rodents (for example see Bridges *et al.*, 1999) but some studies have also been performed in pigs.

Sex steroids. In rats, increased circulating concentrations of oestrogens with progesterone promote maternal behaviour in virgin rats exposed to newborn pups (for review see Bridges, 1990), whereas in mice, marginal progesterone concentrations during pregnancy increased maternal rejection of pups (Wang *et al.*, 1995). Although similar studies have not been performed in pigs, sedative treatment of sows for maternal aggression was associated with high prepartum oestrogen:progesterone ratios and high postpartum plasma oestradiol concentrations (McLean *et al.*, 1998). Both oestrogen receptor α and β are found in the brain in rodents, with high concentrations of both subtypes again located in the hypothalamus (Laflamme *et al.*, 1998). Progesterone receptors are found in rat hypothalamus, preoptic area, hippocampus and frontal cortex, with hypothalamic expression of the B-isoform being sensitive to reproductive status (GuerraAraiza *et al.*, 2000). Both genomic and non-genomic effects of progesterone on central neurotransmitters relevant to reproductive behaviour have been reported (Schumacher *et al.*, 1999). Many neurones that contain either oestrogen or progesterone receptors are neuroendocrine in type, as they have been shown to project to the median eminence (Goldsmith *et al.*, 1997).

Oxytocin. Central oxytocin appears to be important in mediating maternal behaviour, although this has not been proven in pigs. For example, administration of oxytocin into the cerebrospinal fluid of mice reduced aggressive infanticide (McCarthy, 1990) and similar treatment with an oxytocin antagonist inhibited postpartum maternal behaviour in rats (van Leengoed *et al.*, 1987). However, oxytocin gene knockout mice did not show any gross deficits in maternal care apart from an inability to nurse, which is probably due to peripheral effects (Nishimori *et al.*, 1996). Oxytocin injection into the medial pre-optic area or paraventricular nucleus reduced maternal rejection of lambs in sheep (Kendrick *et al.*, 1992). In our laboratory, we have evidence that gilts displaying aggressive behaviour to offspring also had lowered peripheral oxytocin concentrations at birth (C. L. Gilbert, T. H. J. Burne, J. A. Goode and P. J. E. Murfitt, unpublished; Fig. 3). This could be a clue to causality but it could also simply be that aggressive sows receive less tactile stimulation of the nipples (Algers *et al.*, 1990). Furthermore, endogenous opioid systems may mediate passivity in parturient sows (Jarvis *et al.*, 1999) but generally also reduce oxytocin secretion.

PGF_{2 α} . Despite its effects on prepartum behaviour, peripheral PGF_{2 α} could not be shown to influence responses of female pigs to newborn piglets (Gilbert *et al.*, 2001). Although only a single study of this kind has been performed, this permits the hypothesis that pre- and postpartum mechanisms regulating behaviour may be separate.

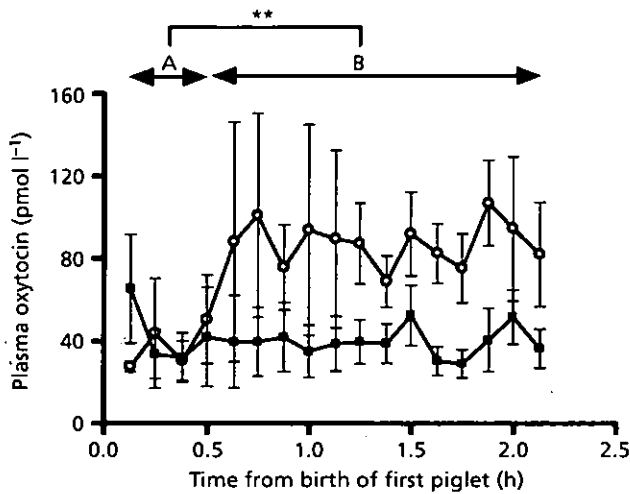


Fig. 3. Plasma oxytocin concentrations in pigs during parturition. Animals were classified as aggressive (■, $n = 4$) if they attacked or bit any of their piglets during the period shown. Non-aggressive controls (○, $n = 4$) gave birth under the same conditions. Data are derived from a large experiment (C. L. Gilbert, T. H. J. Burne, J. A. Goode and P. J. E. Murfitt, unpublished) in which maternal aggression occurred sporadically. All animals had previously received 10 mg $\text{PGF}_{2\alpha}$ to induce parturition. Mean values in period A were subtracted post-hoc from those in period B for each animal separately and compared using a one-way ANOVA. **Indicates significant difference ($P < 0.01$) ($F = 14.5$, $df = 7$).

Prolactin. Studies in rodents have established a clear role for prolactin receptors in maternal behaviour (Lucas *et al.*, 1998). Central receptors (particularly the long form) are located predominantly in the choroid plexus and are also distributed widely in hypothalamic nuclei (Pi and Grattan, 1998).

Conclusion

The active maternal prepartum phase followed by a relatively passive postpartum response to active (but not individually recognized) offspring are features of pig behaviour that, when combined, differ from other domestic or laboratory species and represent a distinctive model for the study of maternal behaviour. Endocrine regulation of prepartum behaviour is becoming more clearly understood, although central relays turning peripheral cues into co-ordinated behavioural output are unknown. Postpartum maternal behaviour has been well described, but what we know of its endocrine control amounts to no more than a few disconnected snippets. Similarities in some aspects of behaviour with other multiparous species allow comparisons of the mechanisms of regulation to be made when information is unavailable in pigs, but these must be treated with caution. An inability to resolve the apparently opposite behavioural requirements of postpartum sows to be generally passive yet responsive to piglet distress may be partly responsible for sows that go on to show inadequate maternal behaviour.

This review has not touched on the large body of work that has examined environmental influences on sow behaviour and endocrinology at birth from the perspective of animal welfare. A thorough understanding of basic mechanisms, once established, will help to place these studies in context and improve the well-being of parturient pigs and their offspring.

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