BEHAVIOURAL ASPECTS OF PARTURITION

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ABSTRACT

The author describes several types of parturient behaviour in mammals. The dislocking of parturient behaviour seems to be established by endocrine changes, which also play a role in the initiation of labour and lactation. Psychogenic uterine inertia is described in several species. It is an adaptation to dangerous situations and is mediated by an extra output of epinephrine. Parturient behaviour is well adapted to the biological demand for survival of the species.

INTRODUCTION

Parturition is a highly complicated process, regulated by many factors. The regulation of normal delivery is only possible if a well balanced equilibrium between morphological, mechanical, physiological, endocrinological and behavioural parameters of both the mother and the fetus can be established. In spite of the huge amount of literature covering details of these aspects of parturition, we are still far away from understanding the complexity of interaction between the several factors. This is even more difficult since there exist very important differences between several animal species. Observations, made on laboratory animals therefore may not always lead to extrapolations which also hold for agricultural animals or for the human. For example in sheep the onset of parturition seems to be controlled primarily by the fetal hypophysis (Liggins, 1969), whereas in the human and the rat this is not true (Honnebier, 1974). Maternal behaviour in several species is also induced by different factors. The ewe only accepts its lamb if she has been able to lick it immediately after birth, but the bitch and many other carnivores, easily accept their own whelps if they are given to the mother some hours or even more than one day after birth. They often accept foster whelps without serious difficulties, even if they belong to another species (Naaktgeboren and Ridder, 1975). Thus parturition in every species has its particular phenomena. Comparative
research concerning parturition has to describe these differences and to search for characteristics which are common to more or even all mammalian species. Those aspects of parturition which do not differ between species certainly are of basic importance and perhaps may be regarded as phylogenetical old features, whereas the interspecific variation have to be regarded as younger adaptations to the environment and the way of living of certain species. For understanding the meaning and the importance of both the variations and the common features it is necessary to regard them in the light of their biological value, i.e. their contribution to the survival of the species. Even the best balanced delivery would be of no biological value if the behavioural aspects were not functioning properly. Lacking or underdeveloped maternal behaviour leads to neonatal death, thus destructing the effect of pregnancy and parturition. It is for this reason important to know that the regulation of parturient behaviour is among other factors effected by the endocrine changes, which also influence the uterine activity, the cervical dilatation and the lactation, whereas environmental factors may influence the animal's behaviour and by this even the course of labour (Naaktgeboren and Bontekoe, 1976). In this chapter several aspects of parturient behaviour will be described and discussed in the light of their biological relevance. A more detailed description of animal parturition as well as plenty of references are given by Naaktgeboren and Slijper (1970).

MULTIPAROUS AND UNIPAROUS MAMMALS

The animal's behaviour at parturition displays a large variety, which corresponds with the type of animal. From a comparative-obstetrical point of view the mammals can be divided in two groups namely the multiparous and the uniparous mammals. This division does not correspond with the systematic classification in orders and families, since there are many mammalian orders to which representatives of both groups belong. The multiparous mammals give birth to quite a large litter (3-5, up to over 15 in some domestic animals) and the uniparous mammals as a rule only deliver one young (occasionally twins), although in some species twins are more frequent than single births. In most multiparous mammals the newborn young are not yet fully developed. They are blind and deaf in most species and quite often they have no hair, whereas in other species they have nesthair, which must be moulted before leaving the nest. The head is comparatively large, the neck and the legs are short. At birth the legs use to be folded against the body. These young have to be born in a well adapted nest. If not they have no chance to survive. The pig also belongs to this group, but the piglets are well developed at birth and are immediately able to walk and to react to their environment. The multiparous mammals further include most rodents, the rabbit, most insectivores, and the carnivora fissipedia. The uniparous mammals constitute a much more
heterogenous group. Their young sometimes are extremely well developed and immediately follow the mother by walking (most ungulates) or swimming (cetaceans) or they clamp themselves to the mother's body (primates, chiroptera). In some species the young are less developed and are born in a nest. The body-proportions at birth are very different, depending on the species and corresponding to this fact, also the mechanism of birth differs. In fact parturition mechanisms differ extremely. In many mammals the young has to pass a firm pelvic girdle (rabbit, rat, ungulates), but in other species the pelvic girdle is enlarged by softening of the tissue of the symphysis pelvis (cavia carnivora pinnipedia), whereas it is also possible that the pelvic girdle is opened and remains declosed (talpa, chiropters) and last but not least there are mammals without a pelvic girdle, even in embryonic stages (cetaceans). The presentation at birth may differ from around 96% head presentation (horse) to between 90 and 100% of tail presentations (cetaceans), whereas in pinnipedia and most multiparous mammals head- and breech presentations occur more or less in the same frequency. Birth may occur in a nest, in the sea, in a tree, on the shore, in a burrow, between members of the herd or in solitude. Because the parturient behaviour is adapted to anatomical and ecological features of the species it is well understandable, that many differences occur, both among uniparous and multiparous mammals.

NORMAL PARTURIENT BEHAVIOUR

In the multiparous mammals the first sign of the onset of parturition is nestbuilding. The start of nestbuilding usually is found one to two days before giving birth. The nest is built from dry grass and leaves in many rodent species or from twigs in swine. The domestic pig uses straw (if available). Wild carnivores often dig a hole in which they deliver the whelps. The rabbit gives birth in a chamber of the burrow which is inhabited by several individuals. Does with a low status in the rank order often leave the common burrow and dig a special hole. The birth chamber then is furnished by dry leaves and grasses and after that has been done the doe plucks loose fur from her coat. She plucks while sitting outside the burrow and carries the plucked wool into the nest. Domestic rabbits who have to deliver in a cage where digging is impossible nevertheless display digging behaviour before actual nestbuilding. During many hours they scratch on the floor of the cage. The sow also displays nestbuilding behaviour in a cage and restlessness: she scratches the cage and tries to bite in the walls of the cage. Nestbuilding behaviour seems to be an inevitable part of parturient behaviour, which even occurs if the construction of a specific nest is impossible. In spite of many generations reared in domestication this behaviour has not changed. It certainly belongs to the genetic characteristics of the species. However the moment of display seems to be dislocked by endocrine factors. Rabbits
Fig. 1 Synchronous changes in plasma progesterone, oestrone (E1) and oestradiol-17β (E2) concentrations (upper part) and parameters of uterine electrical activity (lower part) during late pregnancy and parturition in sow nr. XIII. Steroid data before parturition represent mean values of 13 samples taken at 15 minutes intervals. During parturition data of single samples are presented. The total duration of electrical activity (seconds/hr) and the number of distinct phases of electrical activity per hour are given for electrode number 1, which relative position is indicated by the diagram. During the 12 hours preceding the expulsion of the piglets no significant changes in sex-steroid levels occur. The increase of uterine activity starts about six hours after the onset of nest building behaviour. (Compare the contributions of Ellendorf (1979) and of Taverne (1979) in these proceedings).

with premature labours do not build a nest and do not pluck wool. Sometimes they pluck after delivery, but in most cases the young by that time have died already. Pseudopregnant rabbits do pluck wool, although they do not deliver (Zarrow et. al. 1961, Carter et. al. 1971). In the sow the onset of nestbuilding behaviour more or less coincides with the drop of peripheral progesterone levels and the increase of prolactin, which occurs almost at the same time (Taverne et. al., 1979). Apparently nestbuilding behaviour is sensitive to the change in the
hormone levels in an earlier stage than the myometrium (Fig. 1). This explains that the nest is ready or almost ready at the time of onset of labour contractions. The bitch and the female cat often try to find a quiet place in the house and quite often they find this under furniture or in a human bed. Some bitches however dig a large hole as wolves do. Many bitches ask attention from the human, who normally cares them. This is in accordance with the wolf's behaviour (the dog's ancestor) since the male wolf stays with the labouring wolf bitch. The human has to take over the role of the partner (Naaktgeboren and Ridder, 1975).
The uniparous mammals mostly do not make a nest. They deliver inside the group or herd in which they live. The members of the group usually show great interest in the process (pinnipedia) and from several species it is known that they surround the animal in labour as a protecting ring (for example elephants) or that other animals assist at delivery (apes) or the newborn to reach the surface of the sea (dolphins). But there are also species where the highly pregnant female leaves the group some 1 or 2 days before delivery in order to give birth in absolute solitude (cervus elaphus). It may be concluded that in all mammalian species the labouring female tries to find a place of security - in a burrow or a nest, in the group or in solitude as it fits in the characteristic behaviour of the species - before actual birthgiving occurs. This behaviour, common to all mammals, certainly is deeply rooted and as we will see later disturbance of this behaviour may cause delay of parturition and inhibition of the labour-contractions.
Actual delivery of the young may begin quite unexpected in many animals. As a matter of fact the dilatation phase is, apart from nestbuilding activity, hardly to recognize. The onset of the expulsion phase is much easier to observe, since it is characterized by the occurrence of straining-movements. After cervical dilatation is completed reflex straining commences. This can easily be observed from the outside, whereas in the dilatation phase the uterine contractions usually cannot be observed without special recording-techniques. The straining movements occur during the uterine contractions. At the same time the frequency and the intensity of the uterine contractions increase (Naaktgeboren et. al., 1975). In most mammals straining occurs in the same body position as defecation. The multiparous mammals usually frequently lick the genital outlet, thus removing expelled mucous, blood and fetal fluids. Some uniparous mammals display the same behaviour but in many uniparous species the female is not able to reach the vulva by licking. Many monkeys explore the vagina manually. As soon as the fetal membranes appear in the vulva they are torn by biting (rodents) or licking (dog, cat) or they rupture spontaneously (most ungulates). The young is expelled by one single straining-movement (rabbit) or by several straining-movements (most multiparous mammals), whereas in the majority of uniparous mammals the expulsion is completed after quite a lot of straining-movements. At the end of the expulsion phase straining also occurs between uterine contractions. In many species, both uniparous and multiparous, we have observed that the labouring female displays
a special way of superficial and high-frequent breathing (Naaktgeboren and Slijper, 1970). In many ungulates one can observe that the female shows signs of discomfort ("labour-face") or utters voices, which we cannot explain in another way, then assuming that the animal feels pain. This assumption is supported by our observations, made in several species in which we recorded uterine activity. It is quite common that a female displays the described behaviour or suddenly rises after the uterine contraction has already begun. Since we made this type of observations in rabbits, dogs, sheep and sows, we believe that it is allowed to conclude that just like in the human female, also in many other mammals the stronger labour contractions are painful. However many labouring animals behave very quiescent. Many ungulates lay down, rise again and lay down a.s.o., whereas many multiparous animals turn around in the nest or burrow. However, it is an exception if a female displays a hysteric behaviour, although this has been described from sea-elephants (Mirounga) and from primiparous cats (Naaktgeboren and Slijper, 1970).

Almost every animal-mother licks the young as soon as it is born. This is not the case in tylopods (camels, vicugna) where the young is covered by a well developed epitrichium nor in aquatic mammals. Licking the young has a cleaning function and it stimulates breathing activity and circulation. In the ruminants it is of vital importance for the establishment of the mother-child bond. Experimental research in sheep and goats has shown that olfactoric stimuli from the fetal fluids induce this licking behaviour. However, only around the moment of parturition the ewe or she-goat is sensitive to these smells. If licking is prevented the newborn will not be accepted by its mother, but if another ewe is able to lick a foster lamb she will adopt it, provided she is shortly before or after her own delivery (Rheingold, 1963). The behavioural reaction is evoked by the smell of the fetal fluids (Klompfer and Gamble, 1966) and seems to be dependent on hormonal factors, corresponding with the onset of parturition. It may be assumed that this also holds for the placentophagy, since this behaviour is also common in herbivorous mammals. Some species even eat meat or dead birds, which they normally would disgust (Kurt, 1963). The umbilical cord either ruptures spontaneously at a preformed rupture spot (horse, ruminants, whales) or at a non-specific spot (hippopotamus, swine). In most multiparous mammals the mother bites the cord. This is also the case in many non-ungulate uniparous mammals such as monkeys and chiroptera. However, here it has been reported that on occasions that the newborn falls down, if it does not grasp the mother's coat immediately, its fall is prohibited by the umbilical cord (Kolb, 1966).

After the young has been expelled the third phase of labour, the afterbirth-phase begins in the uniparous mammals. Sometimes the mother removes the placenta by pulling manually at the umbilical cord (monkeys), but in most species the afterbirth is expelled after some time by uterine contractions. Quite often the
mother starts to eat the membranes before the complete afterbirth is expelled (sheep, deer). In the multiparous mammals young and placentae more or less alternate. Almost all mammals eat the afterbirth. Placentaphagy does not occur in the horse, in the giraffa and the elephant, nor in aquatic mammals. The common occurrence of this behaviour suggests that it is of great value for the species. Since it has been shown that the old assumption that placentaphagy would stimulate milk secretion is not right (Naaktgeboren and Slijper, 1970) the only importance of this behaviour can be seen in a protection of the newborn. In species delivering in a nest, it is understandable that cleaning the nest is of vital importance. In other species (ruminants) the smell of an afterbirth could easily indicate the spot, where a young has been born, to predators. Those mammals who have not to fear predators or who deliver in an aquatic environment, where the afterbirth is removed by water, do not eat the placenta. These species do not need doing this for protection of the newborn. It is interesting that jackals wait for the afterbirth of zebras delivering in the plain fields. The newborn foal can so rapidly stand and walk quickly that the waiting jackals do not constitute a danger. Sometimes a labouring zebra-mare is surrounded by several jackals (Klingel and Klingel, 1956). Near the islands where many pinnipeds use to deliver in colonies large troupes of gulls are specialized on feeding with the afterbirths during the birth season (Naaktgeboren and Slijper, 1970). The hypothesis that placentaphagy-behaviour primarily serves to increase the survival chances of the newborn fits well with the fact that it is common to almost all orders of mammals, which indicates 1. that it probably is a phylogenetically old type of behaviour and 2. that it might have been so important, that as a rule it could not be abandoned during evolution, even not in herbivorous species.

DANGER AND THE COURSE OF PARTURIATION

The female mammal is well adapted to her task to give birth. Only if she survives and if the newborn survive(s) the reproductive process is of biological value. It has often been suggested, that the labouring animal is in high risk, since she should be an easy prey to predators. However, remarks like this are the result of philosophy, more than of observation. First of all we have to state that the delivery most often takes place at the time that the animal has it's resting time e.a. day-active animals such as the horse most often deliver at night, whereas night-active animals usually deliver during day-time (golden hamster) (Naaktgeboren and Slijper, 1970). As we have seen all mammals choose a place where they are as safe as possible. This already diminishes the risk of being seized by predators. In many species it has been observed that anxiety may prolong parturition. Severe fright suppresses the labour activity, thus enabling the animal to flee and to deliver after the danger has disappeared (Naaktgeboren and Bontekoe, 1976). The mare is a wellknown example. Even the presence of a
Fig. 2 A Normal uterine activity (sec./12 min.) in a control ewe (ewe 24) and in a ewe, disturbed during parturition (ewe 2). Description in text.
I Ewe 2 connected to cable of recording apparatus. II Observer enters pen of ewe 2. III Birth of lamb (this spot is the same for ewe 24 and ewe 2). IV Start of recording of post partum uterine activity in ewe 2.

B Parts of records of ewe 24 (top) and ewe 2 (bottom) about one hour before birth of the lamb. In ewe 2 a complete psychogenic inhibition of uterine activity is established.
human being in the stable is enough to suppress labour activity. The suppression of the course of delivery is established by a decrease or a complete inhibition of myometrial activity (Naaktgeboren and Bontekoe, 1976; Bontekoe et. al, 1977). Here two examples will be discussed in more detail. In the labouring ewe uterine activity reaches peak values by the time the fetus is expelled (Naaktgeboren et. al, 1975). An ewe, used in experiments on uterine motility, was observed to have started to expel the lamb, without being recorded. We decided immediately to start recording uterine activity and observed the uterus to be completely quiescent. The recording technique is described in full detail by Naaktgeboren (1974) and is described briefly in the contribution of Taverne (1979) to these proceedings. After some time uterine activity reappeared, but as soon as an observer had to enter the pen the uterus again became quiescent (fig. 2). Recording now was stopped and the ewe was left alone. The lamb now was born within one hour. After an hour post partum activity was recorded, but remained far below the normal value of the controls. A miniature pig sow had started nestbuilding and had developed normal uterine activity for the first stage of labour. It was necessary however, to remove the animal to another cage. The removal took only a few minutes, but the uterus remained quiescent for almost two successive hours (fig. 3). Disturbance of the labouring female results in suppression of myometrical activity, thus prohibiting the course of labour and the expulsion of the fetus. In nature the animal can flee. This adaptation is of vital biological importance. Naaktgeboren and Bontekoe (1976) have shown that this adaptation occurs in so many species, that it may be regarded as a common feature in mammals.

Fright and anxiety cause an arousal of the organism. This stress situation (Selye, 1956) is caused by an extra output of epinephrine from the adrenals, which is the reaction to stimuli from the environment. Epinephrine influences the heart rate, the bloodpressure and the breathing frequency thus preparing the animal to flee. It also works on the internal organs. Intestine function is inhibited. In the labouring animal uterine activity is decreased by epinephrine. The effects of behavioural stress could be mimicked by exogenous epinephrine (fig. 4) (Bontekoe et. al., 1977). The inhibition of parturition is the immediate effect of stress and seems to be mediated by epinephrine just as the other stress effects. Ledermann et. al. (1978) showed that this is also true in the human female. However the influence of stress on uterine activity is more complex. In the pregnant female stress increases uterine activity. It has been shown by Bontekoe (1979) that the ratio of sexsteroids (progesterone-estrogens) determines whether the uterus reacts by an activation or by an inhibition of its activity. Premature labour and abortion can also be evoked by stress. In the rabbit premature labour induced by the stress of crowding is one of the most effective phenomena regulating population density (Mykytowycz and Fullagar, 1973). Naaktgeboren and Bontekoe (1976) conclude from a vaste material of observations and experiments that both psychogenic abortion or
Part of a record of uterine activity during the dilatation phase in a miniature pig. After the removal of the labouring and nestbuilding animal (arrow) uterine activity shows a sharp decrease. Places of electrodes are shown in the diagram at the top.

B Frequency of contractions (number per 20 min. period). After the removal no contractions occur during one hour.

C Duration of electrical myometrial activity (sec./20 min.). Blood sampling also causes a decrease in uterine activity. Further explanation is given in the text.
Fig. 4 In the post partum ewe uterine activity is suppressed by stress (at arrow the lamb is removed from the mother for a short time). The effect can be mimicked by an exogenous gift of epinephrine.

premature labour and psychogenic uterine inertia during parturition are adaptations which serve the chance of survival of the species in spite of the fact that sometimes the fetus is sacrificed.

CONCLUSION
Parturient behaviour is well adapted to the biological needs of every species in particular. The regulation of parturient behaviour is based on hereditary factors, which are dislocked at the right moment by endocrine changes. The latter are also part of the complex system of regulating the onset of labour and lactation. In this way a well balanced equilibrium between behavioural and physiological aspects of parturition is established. On the other hand environmental stimuli, which are elaborated psychologically are able to change the physiological course of labour. These interactions between physiology and ethology guarantee the greatest possible safety of parturition for the individual mother and child, as well as its effectiveness for the survival of the species.
REFERENCES


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