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Time of birth and daily activity mediated by feeding rhythms in the pregnant rat

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Summary. The temporal relationship between time of birth and daily physical activity has been studied in rats submitted to different feeding rhythms. Animals, put under 14 h of light and 10 h of darkness (lights on from 6 to 20 h), were isolated at mating (day 1 of gestation) and assigned from day 8 to one of five groups. Group C was fed *ad libitum*, and groups 2PF, 9PF, 14PF and 21PF had food available for three hours per day from 2, 9, 14 and 21 h, respectively. In groups 9PF and 14PF, births were clustered in one single period during the night between days 22 and 23 of gestation. In groups C, 2PF and 21PF, births were distributed into two periods, during the afternoon of day 22 before darkness and after dawn of day 23. The birth rates of these groups were 55.3, 74.2 and 27.6 %, respectively, on day 22 and 44.7, 25.8 and 72.4 % on day 23. No births occurred during the times that food was available ; they were noted in all groups at times when the animals were least active according to records kept throughout gestation. Thus, restricting food availability to periods of normal inactivity (groups 9PF and 14PF vs group C) led to a major shift in the time of delivery as well as to a distortion of the normal activity patterns. These results confirm that feeding rhythms are potent entrainers of birth time in rats and that they interact with the light regime. Pregnant rats seem to be organized so that birth either precedes the main daily physical activity or follows it, depending upon the environmental conditions.

Introduction.

The time of birth is photodependent in rats. When caged alone and fed at will they show two main periods of delivery ; the relative number of births during these periods and the respective times they occur on each of the last two days of gestation characterize the photodependent effect (Lincoln and Porter, 1976 ; Bosc, 1981). Between these periods, few or no parturitions occur ; this interval coincides with the dark phase of the photoperiod (Bosc, 1981).

Other environmental cues, such as an imposed feeding rhythm, may affect birth distribution in this nocturnal species (Bosc and Nicolle, 1985). When food and water are given only during the early light phase of a standard light regime, most deliveries occur during the night between the usual last two days of pregnancy. This periodic presentation of food and water at a given daily time also entrains a feeding rhythm (Obled *et al.*, 1977 ; Morimoto *et al.*, 1979 ; Miyabo *et*

al., 1980) which differs from that of animals fed *ad libitum*, since the latter usually eat during the nocturnal period (Besch, 1970 ; Obled *et al.*, 1975, 1977).

The difference in birth time between rats fed at will and those with an imposed feeding rhythm has suggested the existence of an obligatory shift between two types of activity : labor on one hand, and feeding or related activities on the other (Bosc and Nicolle, 1985). The aim of the present study was to test this assumption. Time of birth and daily activity were recorded in rats submitted to a standard photoperiod and fed, according to the experimental group, during the resting or active period of the light-dark cycle.

Material and methods.

Rats from strain 03 of our colony (Wistar origin) were used. They were kept in constant temperature rooms ($20^{\circ}\text{C} \pm 1$) under a standard light regime of 14 h of light and 10 h of darkness (14L/10D) with lights on from 6 to 20 h. At 70-90 days of age, the females were caged with a male and mating was assessed by the presence of spermatozoa in vaginal smears (day 1 of pregnancy). Mated females were then isolated (one/box) and allocated to one of five experimental groups. One pregnancy was allowed per female. During the experimental period they received a commercial food (U.A.R. Paris), and water, available at will, was renewed twice a week ; the litter in the boxes was not changed at any time during pregnancy.

Food was given *ad libitum* to the control group (C) ; in the other four groups it was available for only three hours per day from day 8 of gestation. Depending on the group, food was available at the following times : 2 to 5 h (group 2PF), 9 h to noon (group 9PF), 14 to 17 h (group 14PF) and 21 h to midnight (group 21PF). In order to facilitate food distribution during darkness (groups 21PF and 2PF), half of the rats were put under an inversed standard photoperiod with lights on from 17 h 45 to 7 h 45. The transition from the normal to the inversed photoperiod was achieved progressively over four days, 5-6 weeks before the males were introduced. About one-half of the animals of the control group were submitted to this inverted light regime ; as their birth distribution was similar to that under the original light regime, the data of the two subgroups were pooled for analysis. Analysis was carried out after the data had been reconverted into the actual times of the colony.

Observations were done as previously described (Bosc and Nicolle, 1980). The rats were checked every two hours on days 22 and 23 of gestation, and their births were therefore plotted at two-hour intervals, the onset of expulsion being the time of delivery. Birth distributions were then compared using the Kolmogoroff-Smirnof test (Siegel, 1956) or as to the interval between birth and a given reference point such as last dawn or last feeding ; the latter was chosen according to observed birth distribution (variance analysis ; Vessereau, 1960). The homogeneity of the five groups was assessed on the basis of litter size, still-birth rate and birth weight of live pups (Vessereau, 1960). The weight gain of the dams between days 8 and 20 of gestation and fertility was also taken into account in each group.

In the present experiment, the individual activity of additional rats was monitored throughout gestation (two recording sessions per group; each group treated as previously described). The oscillations produced by each animal were recorded on a polygraph (6.9 mm/min) (Rapidgraph RP2, Enertec Schlumberger, France) by a transducer (capteur SIAC-VHAT 64BL, Paris) in each box, fixed on a floating floor and forming a whole with the cover. The activity corresponding to total motor activity was monitored 15 min/30 min. The two 15-min periods were considered as representative of hourly activity and were analysed in two ways. First, the main periods of activity were visualized individually for a whole gestation. The hours during which the rats were active for at least 25 % of the time were determined and represented by a dark horizontal bar for each 24-hour period, each day also being represented by a line underneath the bar. Second, the total activity time per hour and per rat was taken into account at three 24-hour periods, at definite stages of pregnancy, *i.e.* from noon on days 6, 14 and 20 of pregnancy. To test homogeneity per group and per stage of gestation, the Spearman rank coefficient (Siegel, 1956) was used. The total hourly activity time of a group was also used to study homogeneity at the three stages of gestation or to compare the five groups at one stage.

Results.

The rats fed at will (group C or control group) had a biphasic birth distribution: 55.3 % of the deliveries occurred on the afternoon of day 22 of gestation and 44.7 % on the morning of day 23 (figs. 1a, 1b). The rats fed at the beginning or end of the dark part of the light/dark cycle (groups 21PF and 2PF, respectively) also showed two birth periods which started at the same times as observed in group C, but the relative number of rats delivering during each of these periods depended on the feeding rhythm ($P < 0.01$). Thus, 74.2 % of the births occurred on day 22 in group 2PF, whereas 72.4 % of them were observed on day 23 in group 21PF (fig. 1a). Groups 21PF and 2PF differed from group C in this respect ($P < 0.05$ or < 0.01). In these three groups (C, 21PF and 2PF), the absence of deliveries between the two birth periods corresponded to night, and this phenomenon was more marked in groups 21PF and 2PF than in group C (fig. 1a). The rats fed during the first or second part of the light phase (groups 9PF and 14PF, respectively) had a single birth period located during the last night of gestation. Their birth distributions were similar ($P > 0.05$) but differed from the other three groups (C, 2PF and 21PF; $P < 0.01$ or < 0.001).

As delivery occurred at definite periods, it was possible to estimate the interval between onset of expulsion and a given reference point (table 1). When dawn (or lights on) was taken as the reference point for the births on day 22 of gestation, this interval differed in rats fed during the light phase (groups 9PF and 14PF) from that of rats fed during the dark phase (groups 2PF and 21PF) (18 h 30 and 19 h 20 vs 8 h and 8 h 30, respectively; $P < 0.01$). When the beginning of the last feeding was taken as the reference point, the interval between feeding and parturition on day 22 or 23 was different in rats fed during the light phase (group

9PF vs group 14PF ; 15 h 30 vs 11 h 20 ; $P < 0.01$) and in those fed during the night (group 2PF vs 21PF ; $P < 0.01$; 12 h 30 vs 17 h on day 22, 9 h vs 12 h on day 23).

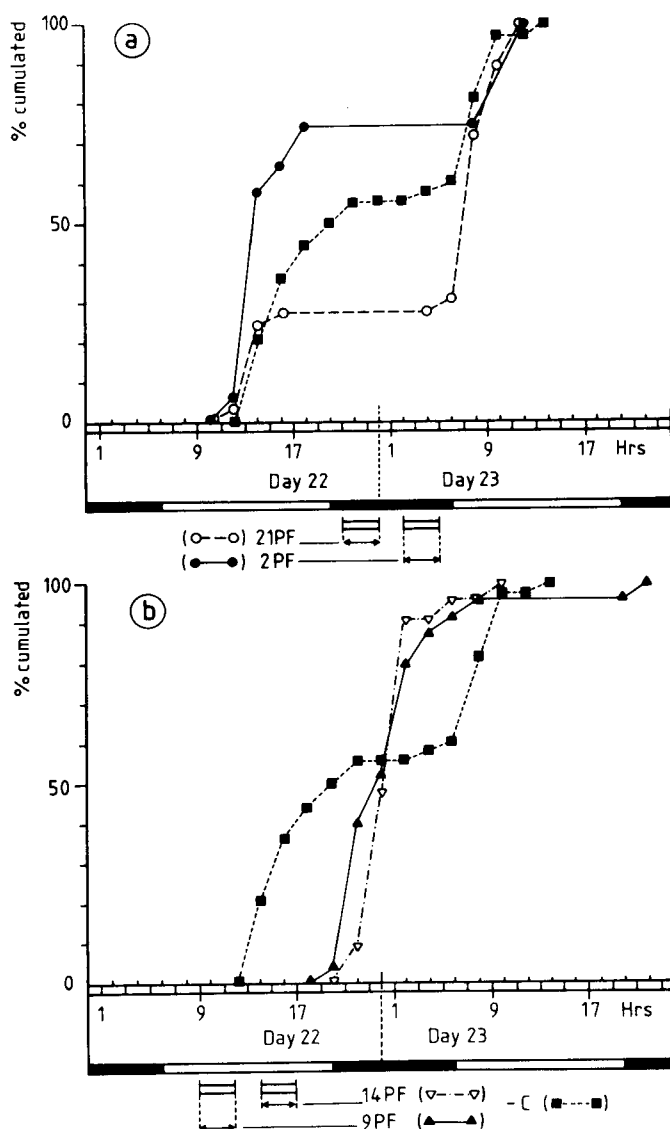


FIG. 1. — Birth distribution on days 22 and 23 of gestation in rats under the standard photoperiod and fed « *ad libitum* » (group C) or fed 3 hrs daily from day 8 of gestation (other groups) : Part a : group C ($n = 38$) and groups 2PF ($n = 31$) and 21PF ($n = 29$) which had food available from 2 or 21 hr respectively. Part b : group C (repetition) and groups 9PF ($n = 25$) and 14PF ($n = 23$) which had food available from 9 or 14 hr respectively. The LD cycle and the respective times of food availability are indicated at the bottom of each panel.

TABLE 1

Interval (h, min) between onset of expulsion and dawn (I) or beginning of last feeding (II) preceding birth at days 22 and 23 of gestation.

Group	Day 22				Day 23			
	(n)	I	II	(sd)	(n)	I	II	(sd)
C	(21)	10.45	—	(2.40)	(17)	2.40	—	(2.05)
2PF	(23)	8.30	12.30	(1.40)	(8)	5.00	9.00	(1.00)
9PF	(24)	18.30	15.30	(3.00)	—			
14PF	(23)	19.20	11.20	(2.30)	—			
21PF	(8)	8.00	17.00	(1.00)	(21)	3.00	12.00	(1.30)

Group C : rats fed at will ; groups 2PF, 9PF, 14PF and 21PF : from day 8 of gestation, food was available for three hours daily from 2, 9, 14 and 21 h, respectively.

Litter size and birth weight varied together with the length of gestation. It was difficult to take into account these three parameters for a statistical analysis according to birth time. Nevertheless, the five groups were homogeneous for litter size, number of dams with still-born and still-birth rate ($P > 0.05$) (table 2). Fertility was the same in the five groups ($P > 0.05$), but in group 14PF it was less than in the other four groups (table 2). The relative weight gain of dams between days 8 and 20 of gestation varied according to the group ($P < 0.01$) ; it was higher in group C than in the other four groups ($P < 0.01$) and less in group 14PF than in groups 2PF, 9PF and 21PF ($P < 0.01$) (table 2). In fact, 52.2 % of the rats in group 14PF presented a weight loss, whereas only a limited number of dams in the other groups lost weight : 0 % in group C, 3.2, 16.0 and 17.9 % in groups 2PF, 9PF and 21PF, respectively. Therefore, it appears that the regime in which food was offered during the second half of the light phase was the most disturbing.

TABLE 2

Characteristics of the five experimental groups.

Group	C	2PF	9PF	14PF	21PF
Dams (n)	38	31	25	23	29
Litter-size (m)	10.1	10.0	9.1	9.9	10.8
% of dams with still-born pups	15.8	25.8	20.0	26.1	17.2
% of still births	1.8	5.1	2.6	2.6	4.1
Birth Weight (gr) of live pups	6.0	5.3	5.6	5.4	5.2
Fertility (%)	67.9	75.6	65.8	57.5	70.7
Relative weight gain (*)	0.266	0.105	0.080	0.005	0.070

(*) Relative weight gain of dams between days 8 and 20 of gestation =

$$\frac{\text{Wt.d.20} - \text{Wt.d.8}}{\text{Wt.d.8}}$$

The general motor activity of the five groups was monitored throughout gestation. Figures 2 and 3 show the main periods of activity from day 4 (13 h) to the end of gestation in 6 different rats. The control animals (figs. 2a, 3a), fed at will, were mostly active during darkness, whatever the day of gestation. Those fed at the beginning or end of the dark phase (groups 21PF, fig. 2b and group 2PF, fig. 2c) remained active during darkness, but from the beginning of periodic food presentation (day 8 of gestation) and as gestation progressed, their main activity

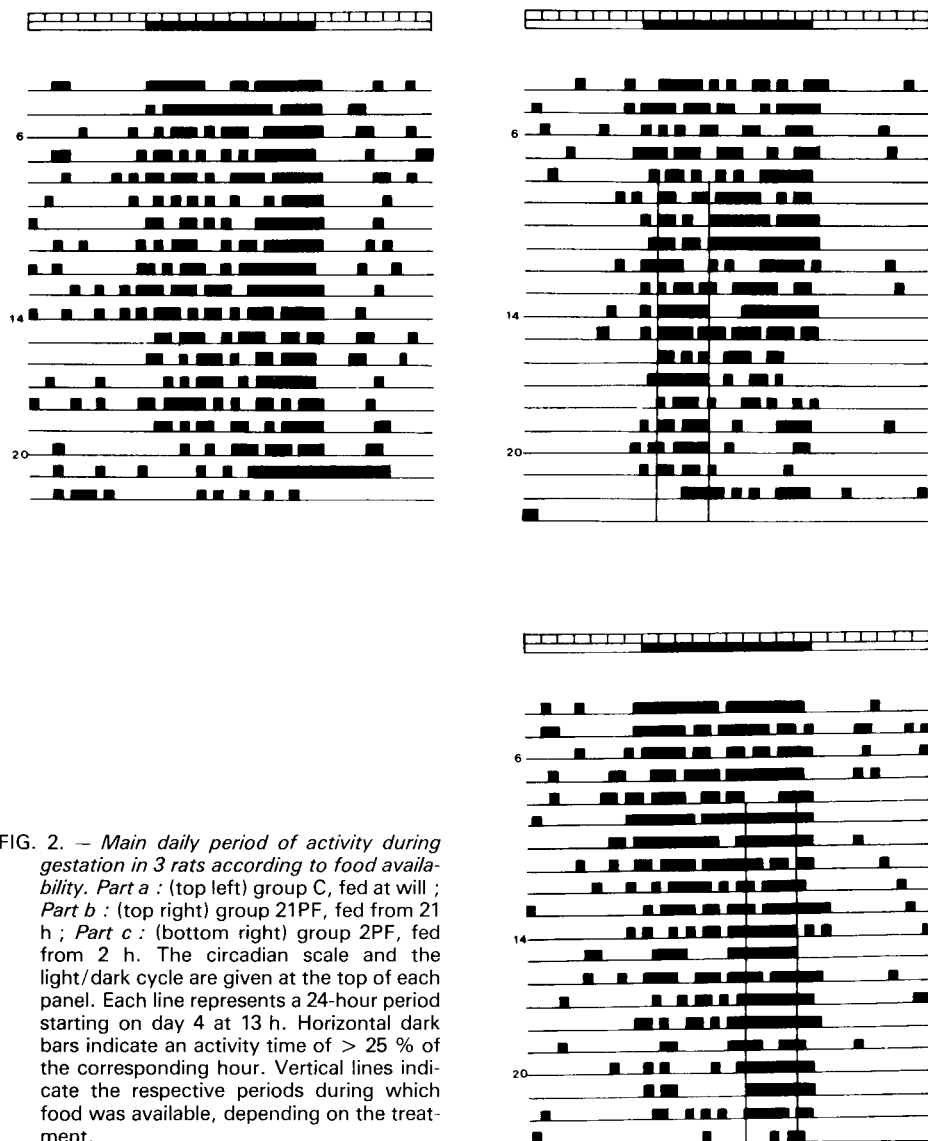


FIG. 2. — *Main daily period of activity during gestation in 3 rats according to food availability. Part a :* (top left) group C, fed at will ; *Part b :* (top right) group 21PF, fed from 21 h ; *Part c :* (bottom right) group 2PF, fed from 2 h. The circadian scale and the light/dark cycle are given at the top of each panel. Each line represents a 24-hour period starting on day 4 at 13 h. Horizontal dark bars indicate an activity time of > 25 % of the corresponding hour. Vertical lines indicate the respective periods during which food was available, depending on the treatment.

periods were concentrated around and during the respective times that food was available. When food was given at the beginning or end of the light phase (group 9PF, fig. 3c and group 14PF, fig. 3b), the rats were also active during its presentation (from day 8); daily spurts of activity were evident from about mid-gestation but, in general, the rats became progressively less active during the night. All monitored rats gave birth at the times noted for their respective groups (figs. 1a, 1b), times which occurred before or after the respective main, daily

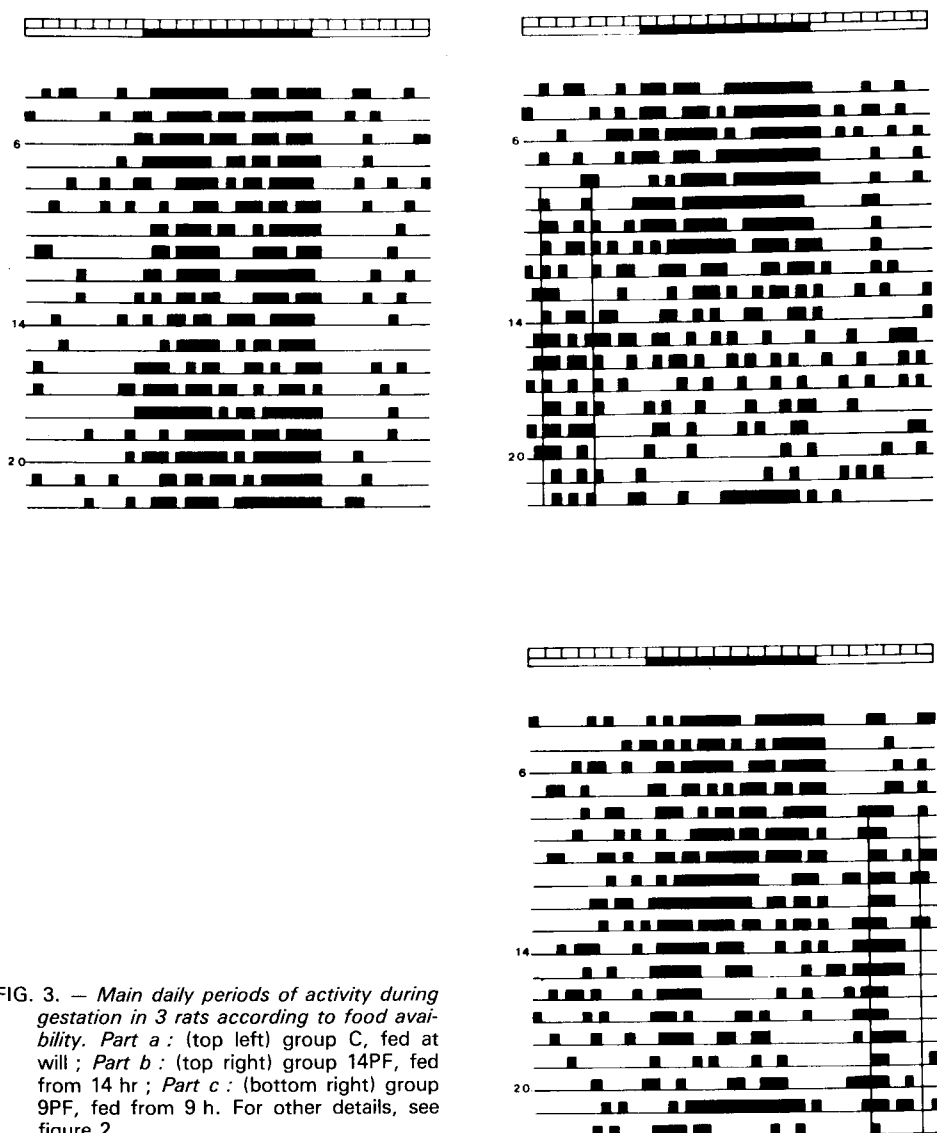


FIG. 3. — Main daily periods of activity during gestation in 3 rats according to food availability. Part a: (top left) group C, fed at will; Part b: (top right) group 14PF, fed from 14 hr; Part c: (bottom right) group 9PF, fed from 9 h. For other details, see figure 2.

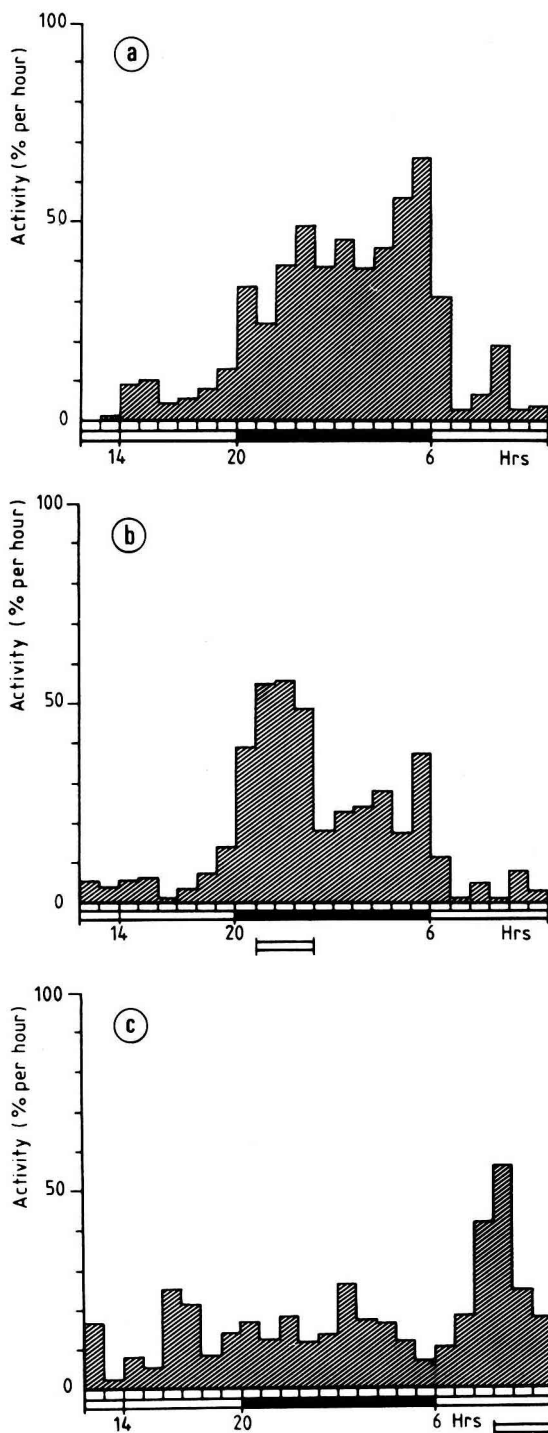


FIG. 4. — Mean distribution of physical activity (in % per hour) over a 24-hour period at the end of gestation from noon on day 20. Part a : (top) group C (n = 6) feeding *ad libitum* ; Part b : (middle) group 21PF (n = 4) feeding between 21 and 24 hrs ; Part c : (bottom) group 9PF (n = 6) feeding between 9 and 12 hrs. The circadian scale, the LD cycle and time of food availability in rats fed 3 hrs daily (from day 8 of gestation) are indicated at the bottom of each panel.

periods of activity. These results were confirmed when all activity times per hour and per group were taken into account at the three selected stages of pregnancy. They are illustrated in only three groups in figure 4 (group C : part a ; group 21PF : part b ; group 9PF : part c) over a 24-hour period, beginning from noon on day 20, at the end of gestation. In all groups, there was a decrease in the total amount of daily activity from day 6/7 to day 20/21 of gestation, and this decrease was apparently more pronounced in rats fed periodically than in the controls (table 3). According to the values of the Spearman rank coefficients, the activity patterns of control rats or those fed during darkness (groups 2PF and 21PF) were more homogeneous (table 3). This was not the case of rats fed during the light phase (groups 9PF and 14PF) ; the daily activity pattern of these animals was disturbed the most (table 3), even if they were more active at food presentation than at all other times of the day (figs. 3c, 3b or fig. 4c).

TABLE 3

Mean activity time (min/rat) and Spearman rank coefficients (r) computed per 24-hour period at three stages of pregnancy.

		C	2PF	9PF	14PF	21PF	Total (groups)
Rats : (n)		6	3	6	5	4	
Day 6/7	Time r	448 0.67**	429 0.77**	446 0.54**	443 0.49*	368 0.49*	431 0.76**
Day 14/15	Time r	356 0.59**	308 0.61**	404 0.35**	350 0.13	378 0.64**	364 0.32
Day 20/21	Time r	337 0.66**	232 0.37	251 0.18	235 0.30	253 0.59**	267 0.05
Total (days)	Time r	380 0.82**	323 0.56**	367 0.20	342 0.07	333 0.80**	353 —

r = * p < 0.05 ; ** p < 0.01

Day 6/7 before, day 14/15 and 20/21 after the beginning (day 8) of periodic food presentation in groups 2PF, 9PF, 14PF and 21 PF.

Group C : feeding *ad libitum* throughout gestation.

Intra-group and inter-group rank coefficients r were also estimated.

Discussion.

The results of this experiment confirm that feeding rhythms are potent modulators of birth time in rats. These rhythms act by an interaction with the photoperiod, as observed previously in other conditions (Bosc and Nicolle, 1985). The two types of activity, *i.e.* delivery or end of labor and feeding or related behaviour, occurred at different times of the day, indicating that the endogenous clock of the pregnant rats was regulated in such a way that either labor had to precede

feeding or its associated activity, or follow it, depending on the environmental conditions. These results provide an insight into the endogenous organization in rats which leads to birth in this species.

The interaction between the photoperiod and the feeding rhythm is illustrated by the variation in the interval between the onset of expulsion and a given reference point, chosen in regard to an exogenous signal (here, last dawn or last feeding) (table 1). The feeding procedures had different effects according to the time of food presentation. For example, in the two groups of rats fed during the light phase (groups 9PF and 14PF), the first-half of birth was delayed and the other half advanced as compared to rats fed *ad libitum* (group C, fig. 1b). The difference in the interval between feeding and birth raises a question concerning the putative variations in the duration of labor or in the time at which birth is initiated. It is not known if the mean duration of labor in rats is subject to circadian variation, as described in humans (Malek *et al.*, 1962 ; Breart and Rumeau-Rouquette, 1979) ; however, it is unlikely. The still-birth rate, which increases with the duration of expulsion (Bosc and Nicolle, 1979), was low in all groups (table 2) and thus provides an indirect argument for this statement. In contrast, it is known in this species that the interval (about 25 h) between the necessary decline in blood progesterone concentration and the onset of birth remains constant under photoperiodic conditions which have been studied (Bartholomeusz *et al.*, 1976 ; Nicholas and Hartmann, 1981 ; Puri and Garfield, 1982 ; Sherwood *et al.*, 1983). It is also worth noting that, in this species, the increase of EMG activity of the uterus starts 20 to 24 h before the first fetus is expelled (Legrand and Maltier, 1981 ; Germain *et al.*, 1985). This suggests that, in our conditions, the time of luteolysis and the beginning of labor may occur at different times of the day, depending on the phase relationships of the two exogenous entrainers.

The obligatory shift between delivery and feeding is illustrated by the following facts. The feeding procedure adopted in this experiment generated a main circadian period of activity at the time of food availability (figs. 2, 3, 4) and resulted in definite and characteristic birth distributions (fig. 1). From the records of activity and from the birth distribution curves, it can be seen that births occurred during the least active period of the day and never during the feeding periods. The control rats fed at will and normally active during darkness (figs. 2, 3, 4) delivered before or after the night between days 22 and 23 of gestation (fig. 1). Feeding the rats during the afternoon (group 14PF) or the morning (group 9PF), times at which they would have given birth if fed *ad libitum*, caused parturition to occur between these times (fig. 1b). At least, *ad libitum* rats preferentially ate their food at the beginning and end of the nocturnal period (Obled *et al.*, 1975) ; feeding the rats at one of these times (group 21PF or 2PF) resulted in two periods of birth, as for the controls, but changed the birth rate of each period (fig. 1).

The opposition between birth and the main active periods of the day and/or feeding suggests that the time of birth in rats is regulated by at least two endogenous oscillators related to dawn and dusk. It has already been shown that the nocturnal period of locomotor activity (Pittendrigh and Daan, 1976), or wheel running activity (Edmonds and Adler, 1977), in rodents is controlled by such a mechanism. This is also true of the time of ovulation which is delayed by dusk

light and advanced by dawn light (Sridaran and McCormack, 1979, 1980 ; McCormack and Sontag, 1980). The results observed in the groups fed at the beginning (21PF) or end (2PF) of the night support this interpretation of two oscillators ; these two feeding regimes emphasize the effects of photoperiod (fig. 1a) and therefore the effects of the endogenous events normally related to lights off or to lights on. As for ovulation, lights off had an inhibitory effect on birth (Bosc, 1981) which was reinforced by the presentation of food at that time. By contrast, lights on had a stimulatory influence since the birth period began at dawn on day 23 of gestation in rats fed at will and put under different photoperiods (fig. 1) (Bosc, 1981). The 25-hour latency observed between luteolysis and birth (Bartholomeusz *et al.*, 1976 ; Nicholas and Hartmann, 1981 ; Puri and Garfield, 1982 ; Sherwood *et al.*, 1983) also supports such a mechanism. In this model applied to environmental conditions and birth time in rats, a third component must be included. Two definite periods of birth are often observed, depending on the photoperiod (Bosc, 1981) or the feeding regime (Bosc and Nicolle, 1985) (groups C, 2PF and 21PF in this present experiment). The first period began after midday or noon (colony time) on day 22 of gestation but not necessarily at dawn (fig. 1 ; groups C, 2PF and 21PF). In other words, the interval between the mean time of the two birth periods, when observed, was less than 24 h (here, 16-17 h for group C, 19-21 h for group 2PF and 21PF). This third component is probably influenced by factors limiting variations in the length of gestation. Birth cannot be initiated in a given strain before a certain time, and that time depends to some extent on litter size and/or fetal maturity (Reynolds, 1965 ; Bosc and Nicolle, 1980).

In this experiment, the total activity time decreased as gestation progressed. This was probably due to pregnancy itself but perhaps also to the fact that the rats were isolated at mating. The feeding procedure certainly exerted some effect since the decrease in activity time was more pronounced in rats fed three hours per day than in the controls (table 3). It is interesting also to note that the relative weight gain of the dams during gestation as well as the birth weight of the pups was lower in the groups submitted to periodic food presentation than in those fed *ad libitum* (table 2). The main reason was probably the reduction of dam food intake as observed in non-pregnant females under similar conditions (Krieger, 1974 ; Krieger *et al.*, 1977 ; Morimoto *et al.*, 1979). However, the weight gain of the dams in the three groups fed periodically (2PF, 9PF, 21PF), and which showed different birth distributions (fig. 1), was within the same range (table 2). This indicates that feeding rhythm rather than probable reduced food intake was the main cause for the shifts in the delivery pattern.

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Résumé. *Moment de la naissance et activité journalière chez la ratte. Influence des rythmes alimentaires.*

L'étude des relations temporelles entre le moment de la naissance et l'activité quotidienne a été réalisée sur des rattes soumises selon le lot à différents rythmes alimentaires. Les animaux, placés sous 14 h de lumière et 10 h d'obscurité (lumière de 6 à 20 h) ont été isolés à la saillie (J_1 de la gestation) et répartis à partir de J_8 dans les 5 lots suivants : lot C, nourriture « ad libitum », lots 2PF-9PF-14PF et 21PF nourriture disponible 3h/jour à partir de 2 h-9 h-14 h et 21 h respectivement. Dans les lots 9PF et 14PF, les naissances ont été groupées sur une seule période au cours de la nuit séparant J_{22} et J_{23} . Dans les lots C-2PF et 21PF, les naissances ont été observées au cours de deux périodes ; la 1^{re} au cours de l'après-midi de J_{22} avant la nuit de J_{22} à J_{23} , la 2^e après l'aube de J_{23} ; pour ces trois lots C-2PF et 21PF, les taux de naissance ont été respectivement de 55,3 ; 74,2 et 27,6 % à J_{22} et de 44,7-25,8 et 72,4 % à J_{23} . Les périodes de naissance ne sont jamais observées pendant les heures de disponibilité de l'aliment, elles correspondent aux moments où les animaux présentent l'activité quotidienne la plus faible d'après les enregistrements d'activité effectués en continu. Ainsi limiter la disponibilité des aliments aux périodes habituelles d'inactivité (lots 9PF et 14PF vs lot C) entraîne les modifications les plus importantes des moments de naissance et des distributions de l'activité quotidienne.

Ces résultats confirment que le rythme alimentaire est un entraîneur efficace du moment de la mise-bas chez la ratte et qu'il agit en interaction avec le régime lumineux. Ils montrent que selon les conditions de milieu la mise-bas doit suivre ou précéder le moment de l'activité quotidienne principale.

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