

Cyclic Motor Activity in the Fetal Rat (*Rattus norvegicus*)

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Rat fetuses were observed on Day 20 of gestation using a technique that permits direct observation of fetal behavior. The resulting time series was analyzed to assess cyclic organization in fetal movement. Fetal activity did not occur randomly but showed significant cyclic variation with a mean frequency of 0.61 cycle/min. This finding agrees with studies of human fetuses, which also exhibit short-period cyclicality in motor activity.

Cyclic activity is ubiquitous in postnatal life, cutting across both phyletic and ontogenetic bounds. Behavioral rhythms vary from long-period seasonal and circadian cycles to short-period cycles measured in seconds or minutes (Aschoff, 1981). Cyclic motor activity in immature vertebrates with a cycle time of a few minutes has been documented early in the embryonic period and appears to be autonomous (nonreflexive) and neurogenic (Corner, 1977; Hamburger, 1963; Repert, 1984). Rhythmicity has been used as a behavioral indicator of the development of supraspinal control and proprio-spinal integration in the immature motor system (Oppenheim, 1975).

The behavior of human fetuses has been studied with the aid of external monitoring technology, such as tocodynamometry and real-time ultrasonography (deVries, Visser, & Precht, 1982, 1985; Sorokin, Pillay, Dierker, Hertz, & Rosen, 1981). Long-period (30-60 min) activity cycles have been documented during the last trimester of gestation (Dierker, Pillay, Sorokin, & Rosen, 1982; Nijhuis, Precht, Martin, & Bots, 1982; Sterman & Hoppenbrouwers, 1971). The increasing association of cyclic motor activity with periodic changes in respiration, heart rate, and eye movements in the last month of gestation has been viewed as a milestone in central nervous system development, which is manifested as coherent behavioral states in the newborn (Nijhuis et al., 1982). Using strain gauges on the mother's abdomen, short-period (1-5 min) activity cycles in human fetuses also have been documented during the second half of gestation (Robertson, 1985; Robertson, Dierker, Sorokin, & Rosen, 1982) and have been shown to persist in the newborn (Robertson, 1987).

Studies of fetal behavior in rodents have employed different techniques for measuring motor activity. Surgical procedures permitting direct observation of fetuses have provided detailed information on the occurrence of specific patterns of fetal movement and thus have deemphasized gross activity (Naray-

anan, Fox, & Hamburger, 1971; Smotherman, Richards, & Robinson, 1984). Recent observations have provided evidence of temporally organized behavior in the rat fetus, although this behavior has not been studied for its precise cyclic characteristics. During the last 4-5 days of gestation, fetal movements tend to occur in bouts or clusters of activity separated by relatively longer intervals with fewer movements (Smotherman & Robinson, 1986). Synchronous movements of two or more body regions (e.g., limbs, head, or trunk) also increase in absolute and relative abundance during late gestation (Robinson & Smotherman, 1987; Smotherman & Robinson, 1986). The appearance of temporal patterning and synchronized movement has been interpreted as evidence for the emergence of supraspinal organization of fetal behavior (Smotherman & Robinson, 1988).

Comparison of different species is an important tool for investigating prenatal behavioral development. The primary aim of the present study was to investigate the temporal organization of spontaneous behavior of rat fetuses by combining methods of direct observation developed for the rat (Smotherman et al., 1984) and analytic techniques originally applied to the human (Robertson, 1985). In spite of dramatic species differences in body size, gestation length, and relative maturity at birth, among others, this report documents that rat and human fetuses exhibit short-period activity cycles with similar characteristics.

Method

Subjects

Subject fetuses were the offspring of female Sprague-Dawley rats (Simonsen Laboratories, Gilroy, California) bred to Long-Evans males. Vaginal smears were taken daily to identify the day of conception (first detectable sperm = Day 0 of gestation). Females were housed in groups of three in polycarbonate cages (32.7 × 37.8 × 9.5 cm) until Day 20 of gestation, when they were rehoused individually. Females remained in a temperature- and humidity-controlled colony room on a 12/12-hr light cycle (lights on at 0700 hr). Food and water were provided ad lib to females throughout gestation. Adult and fetal rats were maintained in accordance with guidelines for animal care established by the National Institutes of Health, the International Society for Developmental Psychobiology, and the Animal Behavior Society.

William P. Smotherman is supported by National Institutes of Health Grant HD 16102 and Research Career Development Award HD 00719. Steven S. Robertson is supported by National Institutes of Health Grant HD 11089.

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Surgical Preparation

Pregnant females were surgically prepared to eliminate sensation from the lower body, thereby enabling direct observation of fetuses in utero without the use of general anesthesia, which suppresses fetal activity (Smotherman et al., 1984). Under ether anesthesia, each female received an injection of 20 μ l 100% ethyl alcohol into the spinal cord between the first and second lumbar vertebrae (chemomyelotomy). The resultant spinal anesthesia immobilized the hindquarters of the female throughout the period of fetal observation. Each prepared female was restrained in a Plexiglas holding apparatus, its uterus exteriorized through a midline laparotomy, and its uterus and hindquarters immersed in the temperature-controlled ($37.5 \text{ }^\circ\text{C} \pm 0.5 \text{ }^\circ\text{C}$) saline bath. The mother and fetuses were allowed to recover from the ether anesthesia and acclimate to the water bath for 20 min before behavioral observations began. These methods, which have been extensively used in previous studies of rat fetuses, provide environmental conditions that maximize fetal vitality.

Preparation of the Fetal Microenvironment

After the prepared female was placed in the bath, a single subject fetus was selected for behavioral observation from the ovarian end of one of the uterine horns. Ovarian fetuses were selected as subjects to control for intrauterine variation in development and to technically facilitate observation. Following the 20-min acclimation to the bath, the subject fetus was delivered out of the uterus and out of its amniotic sac into the saline bath, with the umbilical connection to the placenta and placental-uterine attachment intact. The condition of all but one of the fetuses was unremarkable, as evidenced by normal pink coloration and intact placental attachment at the end of the observation. The one fetus that experienced partial placental separation during the observation (DCIL) was excluded from the behavioral analysis. (Although this fetus was active, it performed only 27% as many movements as the other 19 fetuses and showed no evidence of temporal patterning of activity.) The 19 fetuses observed in this study included both males and females; we have found no evidence that fetal sex influences spontaneous activity in rats (Smotherman & Robinson, 1986).

Behavioral Observation

The behavior of each fetal subject was recorded during a 30-min observation period, conducted between 1300–1700 hr. To facilitate visual observation, subject fetuses were illuminated with cool white light from a fiber optic lamp. Each instance of fetal movement, including movements of foreleg, rearleg, head, mouth, curl (a flexion of the trunk), stretch (an extension of the trunk), or twitch (a spasm in the thorax) was noted by an observer and entered into a real-time event recorder. The sum of these movements over a given interval was taken as a measure of fetal activity. Previous use of this protocol has been shown to have high reliability (interrater reliabilities $> .90$) while preserving a continuous temporal record of fetal behavior during the observation period (Smotherman & Robinson, 1985, 1986). After the data were collected, the female and fetuses were humanely sacrificed.

Analysis of Cyclic Patterns

The data from each fetus were quantified by counting the total number of movements recorded in successive 5-s intervals. The resulting time series (Figure 2) were then analyzed in two stages using methods previously developed to detect and quantify cyclic variation in human fetal and newborn movement (Robertson, 1982, 1985). Separate analyses of cyclic patterning in different categories of move-

ment were not conducted owing to the relative infrequency of events in these categories.

In the first stage, each time series was analyzed to determine whether the fluctuations in the number of movements over successive 5-s intervals were random. Using a procedure suggested by Jenkins and Watts (1968), the total movement variance was first partitioned into independent components in the frequency domain with Fourier analysis. The cumulative variance distribution derived from this analysis was then compared to the expected distribution of random data (white noise), in which all frequency components contribute equally to the variance, using a Kolmogorov-Smirnov test (Siegel, 1956).

If the fluctuations in the movement of a given fetus were nonrandom, the time series was spectral analyzed to identify specific cyclic patterns. In this second stage, the movement spectrum was computed by taking the Fourier transform of the autocorrelation function with the use of an algorithm written by Jenkins and Watts (1968). A Tukey lag window, $w(u) = 1/2 [1 + \cos(\pi u/M)]$, where u is the lag and M is the truncation point of the autocorrelation function, was used to balance the bias and variance of the spectral estimates (Jenkins & Watts, 1968). The bandwidth of the corresponding spectral window was 0.32 cycle/min. Computed this way, the movement spectrum is an estimate of the normalized spectral density function (power spectrum divided by total variance) and provides statistically stable estimates of the relative strength of periodic fluctuations occurring at different frequencies. The area under the movement spectrum between two frequencies is the proportion of variance accounted for by frequencies in that band. Linear trends in the data (which accounted for between 0% and 4.3% of the movement variance) were removed before the movement spectra were computed. A peak in a movement spectrum was considered to reflect the presence of significant cyclic organization if it exceeded the 99% confidence limits of the spectral estimates of random data.

For each movement spectrum that contained a significant peak, three parameters were calculated in order to quantify important properties of the corresponding movement cycle: (a) The frequency of the spectral peak at its maximum was used to measure the rate of the cyclic fluctuations in the movement. The 5-s sampling interval resulted in a maximum detectable frequency of 6.0 cycles/min. (b) The maximum spectral density of the peak was used as a measure of the relative strength of the dominant motor activity cycle. (c) The width of the peak at its half-maximum point was used to measure the dispersion of movement variance in the region around the dominant cycle. If a local maximum or second peak occurred before the half-maximum point, a straight line extrapolation from the peak through the adjacent minimum was used, and if the spectral density did not reach half maximum before zero frequency, the width was taken to be twice the measurable half width.

In addition to these three parameters of the movement spectrum, the proportion of the movement variance that could be attributed to cyclic fluctuations between 0.18 and 1.02 cycles/min (the primary band) was determined for each fetus by calculating the area under the movement spectrum between these frequencies. In previous studies of cyclic motor activity in the human fetus and newborn (Robertson, 1982, 1985, 1987; Robertson & Dierker, 1986; Robertson et al., 1982), this frequency band included almost all of the dominant motor activity cycles.

Results and Discussion

Overall Activity of Fetuses

All of the fetal subjects exhibited spontaneous activity throughout the 30-min period of observation. Fetuses performed 521.5 ± 45.9 movements ($M \pm SE$), for an average

rate of 17.4 movements/min. This compares to the 13.8 movements/min reported in a previous study of Day 20 rat fetuses observed outside the amniotic sac over a period of 10 min (Smotherman & Robinson, 1986). Fetuses were equally active at the beginning and end of the observation session: An average of 17.6 ± 2.7 fetal movements were recorded during the first minute of the observation session, and on average of 17.2 ± 2.6 movements were recorded during the last minute. On a more detailed level, the distribution of fetal movements among the seven individual categories that contribute to overall activity (Figure 1) was comparable to earlier reports, which involved briefer observation sessions (Smotherman & Robinson, 1986). The consistency of these behavioral measures indicates that fetuses can be externalized into the saline bath and observed for periods up to 30 min without an effect on the quality or quantity of fetal behavior.

Cyclic Organization of Fetal Activity

Analysis of the individual movement time series from the 19 subjects provided substantial evidence that cyclic motor activity is present in the rat fetus near the end of gestation. For 18 fetuses, the cumulative variance distributions derived from the Fourier analysis of the movement time series departed significantly from that of white noise ($p < .001$, except for $p = .37$ in CB1L), which indicates that the fluctuations in movement were not random. Spectral analysis of the movement from the 18 fetuses in which the fluctuations were nonrandom revealed a dominant motor activity cycle with a frequency of 0.12 to 1.37 cycles/min in all but one fetus (DA1R), which was indicated by the presence of a peak in the movement spectrum exceeding the 99% confidence limits of a white noise process (Figures 2 and 3). A single peak dominated the movement spectra from 9 fetuses, whereas the remaining 8 contained smaller but significant secondary peaks as well. In 5 of the 8 subjects with a secondary peak, the fluctuations in movement corresponding to the weaker secondary peak were slower than the dominant cycle in motor activity; in the remaining 3 subjects they were faster.

Comparison of Rat and Human Fetuses

Table 1 contains the mean frequency, magnitude, and width of the spectral peak corresponding to the dominant

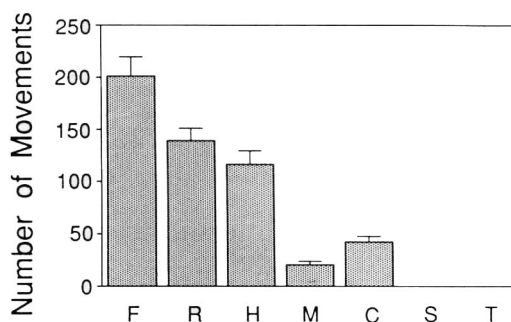


Figure 1. Mean number ($\pm SE$) of fetal movements per 30 min in seven behavioral categories: F (Foreleg), R (Rearleg), H (Head), M (Mouth), C (Curl), S (Stretch), and T (Twitch).

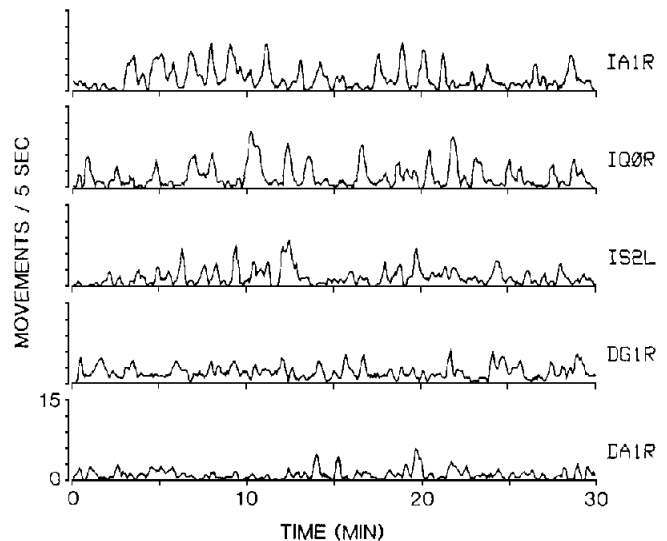


Figure 2. Illustrative time series from 5 fetuses. (To reduce the visual effects of high-frequency variation, the data in these illustrations were smoothed with a three-term moving average filter.)

motor activity cycle in the 17 rat fetuses with statistical evidence of cyclic motor activity, and the percentage of the total movement variance owing to cyclic fluctuations in the primary band in all 19 rat fetuses. Table 1 also contains results obtained from human fetuses studied 1 to 3 times during the last month of gestation (Robertson, 1987), yielding 53 data sets 13–43 min long ($M = 30$, $SE = 1.1$). The results from multiple data sets from a fetus were averaged before computing the group mean. The methods used to detect and digitize

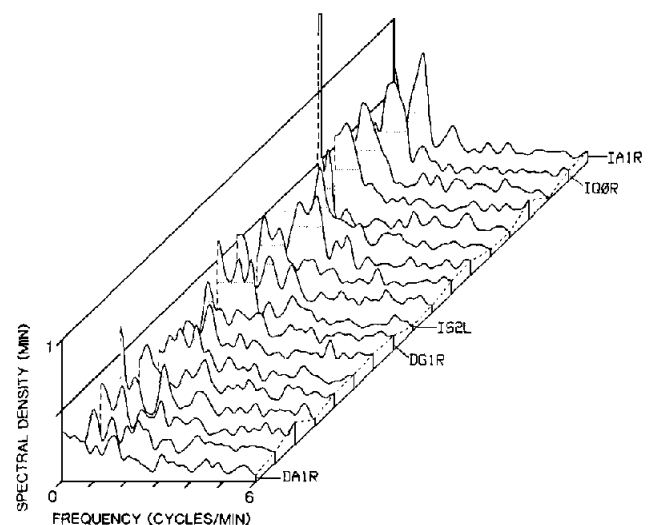


Figure 3. Movement spectrum for each time series in which fluctuations were nonrandom. (The spectra were computed from the raw (unsmoothed) data after removing linear trends and are plotted [front to back] in order of increasing magnitude of the dominant spectral peak. The horizontal lines are the upper 99% confidence limit on the spectral estimates of a white noise process. The subject labels identify the spectra corresponding to the movement time series illustrated in Figure 2.)

Table 1
Parameters of Fetal Movement Spectra

Subject	Frequency (cycle/min)	Magnitude (min)	Width (cycle/min)	Primary band (% variance)
Rat	0.61 ± 0.09	0.54 ± 0.03	0.65 ± 0.05	31.6 ± 2.1
Human	0.42 ± 0.04	0.71 ± 0.04	0.57 ± 0.04	36.9 ± 1.5

Note. Values are $M + SE$. Frequency, magnitude, and width of the dominant peak in the movement spectrum are for those fetuses with statistical evidence of cyclic motor activity (17 rats, 33 humans). The percentage of the total movement variance owing to cyclic fluctuations between 0.18 and 1.02 cycle/min (primary band) is for all fetuses (19 rats, 34 humans). Human data are from fetuses studied within 1 month of birth [Robertson, 1987].

human fetal movement are described in detail in Robertson (1985). Briefly, fetal movement was detected by two strain gauges on the mother's abdomen and was quantified by measuring the duration of movement (excluding breathing movements) to the nearest 0.2 s in successive 5-s intervals, the same sampling interval used for the rat fetuses. The subsequent analysis of the movement time series from the human fetuses were identical to the analysis of the rat data. In particular, the spectral analysis employed the same lag window and truncation point so that the spectral window had the same bandwidth for both species.

Comparisons of the rat and human data revealed that cyclic motor activity was weaker in the rat, $t(48) = 2.81$, $p = .007$, and somewhat faster, $t(48) = 2.18$, $p = .034$, although $t(23) = 1.91$, $p = .069$, when corrected for inhomogeneous variances. In rats with statistical evidence of a secondary motor activity cycle ($n = 8$), the dominant cycle was usually faster ($n = 5$). In human fetuses the opposite was true: in 18 of 22 with secondary peaks in the movement spectra, the dominant cycle was slower (Fisher Exact Test, $p = .032$). The dispersion of movement variance in the region around the dominant motor activity cycle (measured by the width of the corresponding spectral peak) was similar in the two species, $t(48) = 1.18$, $p = .242$. Overall, slightly less of the total movement variance in the rat was accounted for by motor activity cycles between 0.18 and 1.02 cycles/min, $t(51) = 2.12$, $p = .039$, the frequency band which contains nearly all of the dominant motor activity cycles in the human fetus and newborn (Robertson, 1985, 1987).

Conclusion

The principal finding of this study is the demonstration that cyclic motor activity is a characteristic of fetal behavior in the rat, the second mammalian species to be investigated to date. The existence of short-period activity cycles is consistent with current evidence of increasing behavioral organization during the last few days of gestation in the rat (Robinson & Smotherman, 1987; Smotherman & Robinson, 1986, 1988). Spontaneous fetal movement is first evident on Day 16 of gestation. Over the next 2 days, activity increases to a maximum (Day 18) and remains at this level until parturition (Day 21). Specific patterns of fetal behavior also exhibit greater organization during this period. The behavioral repertoire increases as new movement patterns appear and exist-

ing patterns differentiate. By Day 20, there exist prenatal antecedents to species-typical action patterns (e.g., the stretch response to milk letdown and facial wiping in response to aversive gustatory stimulation; Smotherman & Robinson, 1987). During the first 2 days of the period of motility, individual movements of different regions of the body are independent and occur randomly with respect to one another. By Day 18, however, synchronous movement of two or more regions occurs more often than can be accounted for by chance association (Smotherman & Robinson, 1986). Specific linkage relations also become apparent (e.g., foreleg-rearleg, head-mouth), which foreshadows coordinated behavioral patterns exhibited by the newborn (Bekoff & Lau, 1980; Robinson & Smotherman, 1987). Cyclic motor activity appears to be another aspect of the manifest behavioral organization expressed by the rat fetus.

One of the issues that have been raised by studies of periodic movement in avian embryos and mammalian fetuses concerns the level at which cyclic activity is controlled. Experiments in which portions of the spinal cord were excised from chick embryos have provided evidence that the highly periodic movements that occur early in incubation are governed by pattern generators in the spinal cord (Hamburger & Balaban, 1963; Provine, 1973). The effects of supraspinal input are not seen before the middle of incubation (Oppenheim, 1975). In humans, cyclic motor activity is evident in both fetuses and newborns, is consistently expressed in all behavioral states, and is quantitatively independent of the total amount of activity (Robertson, 1987). Although the constancy of cyclic fetal movement during late gestation does not preclude the possibility of spinal control, its association with other emerging properties of behavioral organization in the rat (synchrony, linkage, specific action patterns, and behavioral states) and the consistent pattern of state differences in the human suggest that supraspinal influence may also be important.

Ethical considerations and practical limitations restrict the ability to directly test hypotheses concerning the level of control of cyclic motor activity in the human. Because the behavior of fetal rats exhibits cyclic organization, a means is now available for investigating neural mechanisms underlying cyclic motility. The spinal cord of rat fetuses can be surgically transected to isolate portions of the body from supraspinal influence. Transection performed in the midthoracic region of the spinal cord does not disrupt or reduce overall fetal activity but virtually eliminates one aspect of behavioral organization: the occurrence of synchronous movement (Smotherman, 1987). It remains for future research to apply such experimental procedures to prove the neural control of cyclic motor activity.

In view of the differences in fetal development, the degree of similarity between rat and human fetuses in the pattern of cyclic motor activity is striking. Human fetuses experience a much longer period of gestation and are active for a larger portion of total gestation (about 80%) than rats (about 30%). Rats have less body mass, higher basal metabolism, and give birth to multiple offspring that are very altricial at birth. Both species exhibit activity cycles of roughly similar frequency late in gestation. It is presently impossible to determine whether

the similarity in cyclic motor activity of rat and human fetuses is due to chance, evolutionary convergence, or common descent, but it suggests the possibility that cyclic organization of prenatal behavior is a common phenomenon among mammals.

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Received September 13, 1986

Revision received September 12, 1987

Accepted September 13, 1987 ■