

Chance and Chunks in the Ontogeny of Fetal Behavior

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In the course of communicating the findings of our fetal research to scientific and lay audiences alike, the subject that invariably elicits the most comment is the image of a living fetus. Relationships and patterns of significance may pique the intellect, but a visual image evokes wonder. The advent of noninvasive technology that permits visualization of human fetuses and improvements in surgical and experimental procedures for viewing nonhuman fetuses has created unprecedented access for observing fetuses *in vivo*. It is the thesis of this essay that, in addition to inspiring awe and curiosity, much stands to be learned from the observational study of fetal behavior.

Early observations by behavioral embryologists (e.g., Coghill, 1929; Windle, 1944) engendered much discussion of general principles in the process of prenatal behavioral development. But the conceptual dichotomies created by these early workers, such as the distinction between integration and differentiation in behavioral development, proved to be simplistic and intellectually sterile. Observational study of fetuses was virtually nonexistent between 1940 and 1970.

Overlapping this period of stasis was the discovery of DNA, the mechanisms regulating embryological development, the existence of teratogens, the diversity and complexity of neurochemistry, the processes of maternal-fetal physiology, and a host of other phenomena fundamental to fetal development. Perhaps because these new fields offered such promise, and perhaps because earlier workers had claimed to have seen all there was to see in the behavior of fetuses, the observation of fetal behavior remained an historical curiosity until the widespread use of automatic recording devices (see Robertson, this volume) and ultrasonographic imaging (see Birnholz, this volume). As the chapters in this volume attest, the obser-

vational study of prenatal behavior is once again a thriving, rapidly growing field.

LEVELS OF BEHAVIORAL DESCRIPTION

'Behavior' is a shorthand word that is used to refer to overt expressions of the functioning of a complex system of neurons and muscles. Some investigators have argued that inferences drawn from observation of behavior are inadequate as a basis for firm conclusions about the presence or absence of underlying neural or motor organization. What is needed, they claim, is a more reductionist investigation of organization at the neurophysiological level. This emphasis is proper if one is primarily interested in neural mechanisms. And it is certainly true that neuroethological approaches have and will continue to offer valuable perspectives on problems of behavioral control. But emphasizing neurophysiological questions and methods in explicit preference to observation of overt behavior obscures the broad objective of understanding the development and organization of behavior.

There is a more basic difficulty with abandoning behavioral study for the allure of neurophysiological objectivity. The obverse face of this question may be referred to as the "degrees of freedom problem." Behavior consists, at the neurophysiological level of description, of stimulation or inhibition of activity in individual motor units. The human body, to select a representative animal at nonrandom, comprises nearly 800 muscles distributed among over 100 flexible joints. The description of a behavioral event at the level of muscles and joints therefore could require specification of an expression consisting of roughly 10^3 terms, each of which could vary continuously within a range of values and change from moment to moment. It was recognition of the problem of degrees of freedom that led Weiss (1941) and others (e.g., Dawkins, 1976; Kugler et al., 1982; Fentress, 1983) to argue that the neuromotor system must be organized in a hierarchy of levels. Since Weiss presented his six-level scheme of neural organization many neural structures that function at hierarchical levels above that of the individual motor unit have been identified. But high-level neural correlates typically have been discovered not through naive neurological exploration, but confirmed after their existence was inferred from overt behavioral data.

The reverse face of the same problem is the technology of measurement. Ideally, a pattern of motor behavior could be uniquely specified by measuring the degree of muscle contraction in all motor units involved in the pattern. But even if a limited pattern of behavior (one involving only a handful of motor units) formed the focus of study, the current technical

reality of recording simultaneously from multiple muscles is that the overall form of a behavioral event cannot be reconstructed from neurophysiological data. The degree of muscle contraction must be inferred from the strength of the EMG signal, which also varies as a function of electrode placement, characteristics of individual muscles, physical/mechanical context, etc. Quantitatively relating many different EMG signals therefore is too imprecise to permit specification of, say, the relative position of two limbs during their trajectory through space. The study of behavior will continue to be as important to the understanding of neurobiology as the study of the nervous system is to the understanding of behavior.

THE BASIS OF BEHAVIORAL DEVELOPMENT

Because behavior does not have a physical existence separate from neurons and muscles, it is possible that behavioral development can be explained solely by reference to cellular and tissue-level events in the neuromotor system. One can construct a functioning machine without any understanding of its functions, for example, if provided with a sufficiently detailed blueprint for attaching nuts, bolts, cams, cogs, etc. By this view, behavioral development is merely a visible manifestation of an architectural plan that is configured in neural and muscular maturation (see Smotherman & Robinson, this volume).

If, however, functioning of the neuromotor system as a whole plays any role in directing the course of development of the system, and therefore of behavior, then adequate developmental explanations must entail reference to higher levels of organization than cell-to-cell interaction (see Hofer, this volume). When function is involved in determining the development of structure, the system may be said to exhibit properties of self-organization.

The degree to which behavior exhibits self-organization during early development remains an open question. If early behavioral patterning merely reflects intrinsic organizational events within the nervous system, then descriptions of development at a behavioral level ultimately may be unnecessary. If, on the other hand, behavior exhibits self-organization during ontogeny, analysis at the behavioral level is mandatory. It is reference to the involvement of such higher levels of organization that we intend when we advocate observational analysis.

The observational study of behavioral development need not consist of qualitative behavioral commentary, such as was characteristic during the heyday of behavioral embryology (1920–1940). Rather, behavioral analysis has come to be considerably more sophisticated. Quantitative techniques

borrowed from theoretical mathematics, cybernetics, physics, economics, linguistics and many other disciplines have had a profound impact in certain areas of psychology, ethology and behavioral ecology (Colgan, 1978; Sackett, 1978; Martin & Bateson, 1986). The advantage presented by these analytic techniques is that they apply specific organizational models to the complexity of behavioral output. Sometimes these approaches confirm subjective impressions of behavioral organization that is not perceptible to an observer and is not obtainable from measurement of low-level elements of the neuromotor system. The sections that follow briefly introduce how some of these observational approaches have been applied to the study of behavior before birth and, further, how they can yield fresh insights into the self-organization of behavior during early development.

PRENATAL DEVELOPMENT OF MOTOR COORDINATION

Behavioral scientists who are accustomed to working with mature subjects may tend to assume that motor behavior must involve some degree of coordination. However, subjective notions of random motility in the fetus call this assumption into question. Most of the early students of fetal behavior, and many investigators since, concluded that fetal behavior was lacking in coordination. But coordination is an inherently quantitative concept, encompassing synchronized motor activity at levels ranging from contraction of fibers within a muscle to finely tuned movements involving the entire body, that requires quantitative techniques for its characterization and explication.

When examining behavioral events that are not perfectly coordinated—a situation that applies especially to the prenatal development of behavior—it is necessary to have a standard to which observed performances can be compared. One strategy for providing a suitable standard is to compare the frequencies or rates of different behavioral performances within the same individual. This method has been effectively used by Provine (1980) in characterizing the development of interlimb coordination in chick embryos (*Gallus domesticus*). Chick embryos ranging in age from 7–19 days of incubation were observed through a small opening in the egg and individual movements of left and right wings and legs scored as independent movement events. Because the timing of each movement was preserved, it was possible to calculate the percentage of time that two limbs moved concurrently. From day 7 until about day 14, movements involving a wing and the ipsilateral leg occurred about as often as movements comprising right and left wings. After this time, wing-wing movements increased

sharply in frequency as wing-leg synchrony diminished. This quantitative demonstration of emergent coordination between wings thus depends upon explicit comparison to a standard presumed to lack coordination (wing-leg synchrony).

The issue of interlimb coordination in mammalian fetuses has been addressed by Bekoff and Lau (1980) in a study of rats (*Rattus norvegicus*) on embryonic day 20, the penultimate day of gestation. Observation consisted of filming fetuses that had been externalized from the uterus into a warm saline bath following preparation of the mother by mid-spinal transection. Analysis was restricted to focal events involving synchronous forelimb or hindlimb activity. Filmed records were examined frame-by-frame to quantify the timing of individual stroke cycles of limb movements. The degree of coordination was assessed by comparing the duration and phase of each stroke cycle by limbs within the same girdle (shoulder or pelvic). A peak in the phase values near 0.5, and complete absence of values at 0 and 1.0, indicated that limb movements in the pelvic girdle were performed in alternation. The timing of these strokes was comparable to that exhibited during swimming by postnatal rats (Bekoff & Trainer, 1979). Alternation was also evident to a reduced degree in forelimb-forelimb strokes, providing a clear demonstration of interlimb coordination as early as one day before birth. It is important to recognize that these findings, like those reported by Provine, are predicated upon a measurement of motor patterning with reference to an implicitly random process (phase values distributed uniformly between 0 and 1.0).

Although Bekoff and Lau (1980) confirmed that some of the motor activity of fetuses exhibits coordination, they concurred with earlier observers that “the vast majority of movement observed was of the type described . . . as ‘random’ and lacking coordination.” Randomness is a recurrent theme in qualitative descriptions of fetal behavior (Angulo y Gonzalez, 1932; Windle, 1944; Narayanan et al., 1971; Hamburger, 1973), yet the issue of randomness has rarely been subjected to empirical scrutiny. In our own program of research on the behavioral biology of the rat fetus, we have sought to make concepts of behavioral randomness explicit and operational (Metz, 1974). Stochastic models have been extensively employed to characterize emergent behavioral organization and to probe the age-dependent and environmental influences that contribute to the prenatal development of behavior (Smotherman & Robinson, 1986a; Robinson & Smotherman, 1987).

In this research, pregnant rats are prepared with a reversible spinal anesthetic and placed in a temperature-regulated bath containing a physiological saline solution. Individual fetuses are then directly observed through the transparent uterine wall or after delivery into the bath with

or without intact embryonic membranes. Care is always taken to maintain placental attachment to the uterus and undisturbed umbilical blood circulation. These procedures provide healthy fetuses as subjects for behavioral observation for one hour or more (Smotherman et al., 1986), although typical observation sessions last 30 min or less. Fetuses observed under these conditions exhibit a diverse repertoire of motor behavior that expands from the onset of motility (about day 16 of gestation) through term (day 21.5; Smotherman & Robinson, 1986a). The fact that these measures of fetal behavior are not artifacts of the conditions of observation has been confirmed by endoscopic visualization of fetuses in vivo (Smotherman & Robinson, 1986b). Using these observational procedures, we have found that some of the spontaneous movements of rat fetuses can indeed be characterized as random. However, within a few days of the onset of motility, fetal behavior begins to exhibit nonrandom organization in temporal pattern and spatial form.

FIRST ORDER MODEL OF MOVEMENT SYNCHRONY

Many fetal investigators have noted that fetuses occasionally move several parts of the body at the same moment, a performance that seems to deny randomness and imply coordination. Simultaneous events may occur by coincidence, however. A null hypothesis of movement synchrony therefore assumes that simultaneous motion of two or more body regions (e.g., foreleg and rearleg) results from the chance association of independent, simple movements. Calculation of an expected frequency of chance association provides an alternative to comparing the incidence of synchronous movements to a different behavioral standard (as in the study of wing-wing coordination described above). This approach has been adopted in an explicit test of a stochastic model of movement synchrony in the rat fetus (Smotherman & Robinson, 1986a).

To apply this first order model, the overall probability (P) of simple movement events (acts involving just one body region, such as head, foreleg or trunk) is calculated for each subject fetus by dividing the total number of fetal movements by the number of 1-s intervals during the observation session in which fetal activity potentially could be scored. From basic probability theory, multiplying this simple probability by itself yields the probability of two independent movements occurring during the same interval (P^2). More generally, P^i gives the probability of co-occurrence of i independent events. Thus, the sum of P^i over the number of simple categories, multiplied by the number of intervals during an

observation session, generates a predicted frequency of synchronous movements.

Predictions generated by the first order model accord well with the actual occurrence of motor synchrony on days 16 and 17 of gestation (Figure 1). Subsequent to day 17, however, synchronous movements become more abundant than can be accounted for by chance association. Just prior to parturition (day 21), comparison with model predictions

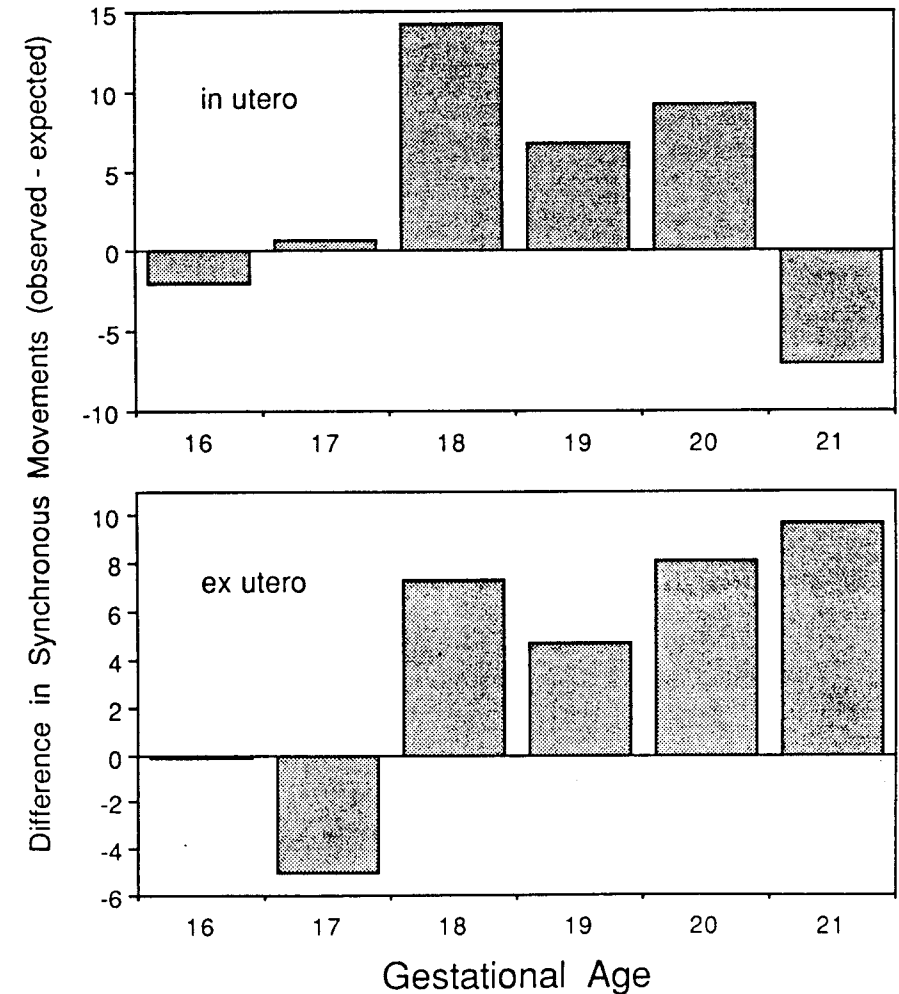


Figure 1. Discrepancy between frequencies of synchronous movement and predictions generated by the first order model of synchrony. Data are plotted as a function of gestational age for each of two micro-environments of observation (in utero and ex utero).

reveals that synchronous movements are in fact less common than should occur by random association when fetuses remain within the uterus during observation. However, when fetuses are delivered from the uterus into a warm saline bath prior to observation, taking care to preserve the integrity of umbilical blood circulation, no such reduction in synchronous movement on day 21 is apparent. We have interpreted this effect as evidence of the behavioral effects of physical restraint imposed by diminished free space within the uterus near term. The clear implication of these results is that the behavior of the rat fetus exhibits subtle organization that emerges over the last four days of gestation and exhibits sensitivity to changes that occur within the intrauterine environment (Smotherman & Robinson, 1988).

SECOND ORDER MODEL OF MOVEMENT SYNCHRONY

The first order model is sufficient to explain the simultaneous movement of several body regions from the onset of fetal motility (day 16) through day 17 of gestation. The relative abundance of synchronous movements on and after day 18, however, must be addressed by a more detailed model. A second order model has been developed to determine whether some aspects of the synchronous behavior of fetal rats after day 17 continues to be shaped by random processes (Robinson & Smotherman, 1987). Unlike the first order model, which generates the predicted total frequency of synchronous movement from the observed total frequency of fetal movement, the second order model is not dependent upon the rate of fetal activity. Instead, it focuses on the eight most common categories of synchronous movement and predicts the frequency of each category from (a) the total frequency of all synchronous movements and (b) the probability of occurrence of each category of simple movement. The second order model thus generates predictions about how behavior will be distributed among specific categories of synchronous movement. Predictions involve calculation of the probability (P_i) that a given synchronous movement includes motion of body region i . For example, the synchronous movement event foreleg-rearleg-head includes movements in three distinct body regions. P_i and its complement (which indicates the probability that a given movement does not comprise body region i) are calculated for each body region. From these probabilities, the likelihood of a movement involving regions i and j , but no other (P_{ij}), is computed as the product of P_i , P_j , and the complements of the probabilities of all other regions.

The second order model is broadly predictive of the occurrence of the focal categories of fetal movement over days 17–21 of gestation. (Because synchronous movements are almost nonexistent on day 16, the model is inapplicable at this age.) However, several categories of synchronous movement occur more frequently than can be accounted for by a simple random process (Figure 2). Noteworthy among these are the movement combinations: foreleg-rearleg, foreleg-head, and head-mouth. Other categories, such as head-rearleg, occur less often than chance association would predict. These particular linkages are intriguing because they constitute components of action patterns that assume importance during the early postnatal period. Interlimb synchrony (foreleg-rearleg) is, of course, fundamental to the development of quadrupedal locomotion, including crawling and walking. But another pattern of locomotion—punting—predominates during the first few days of postnatal life when altricial offspring are unable to support their body weight (Altman & Sudarshan, 1975).

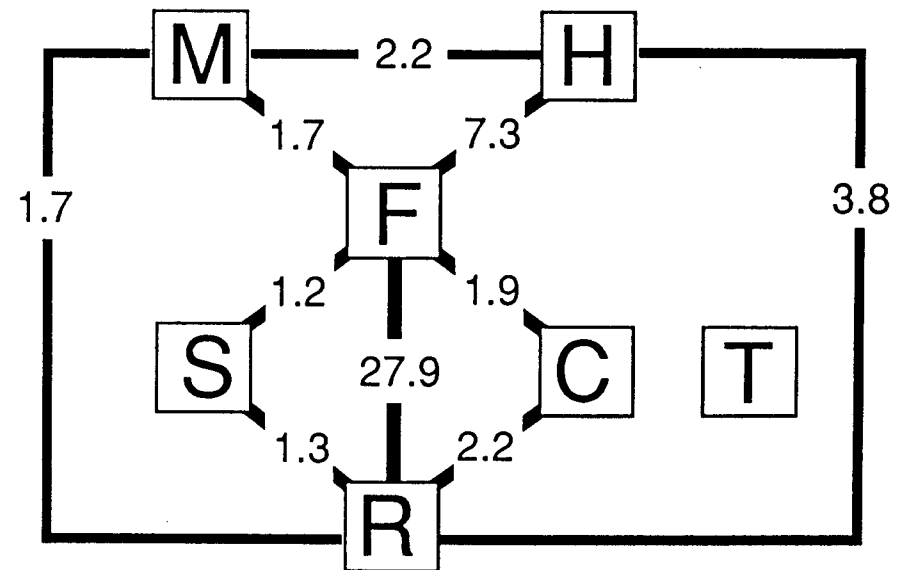


Figure 2. Diagram depicting linkage relationships between pairs of body regions on day 21 of gestation, with fetuses observed *ex utero*: M (mouth), H (head), F (foreleg), S (dorsal trunk stretch), C (ventral or lateral trunk curl), T (thoracic twitch), R (rearleg). Each line connects two regions that moved synchronously with a mean frequency exceeding 1.0 movements per 10 min. Numbers superimposed on lines show actual mean frequencies of synchronous occurrence.

Punting involves spreading the rearlegs, supporting the anterior half of the body with the head, and sweeping one foreleg laterally. The result of these coordinated movements is to pivot the pup around an anchor point provided by the rearlegs. With punting alone, neonatal rat pups are able to orient and move toward preferred objects (such as the nipple) and to maintain their position in a huddle with littermates within the nest (Alberts & Cramer, 1988). Yet if any of the three principal elements of punting were to drop out of the pattern (anchoring by the rearlegs, support by the head, propulsion by a foreleg), the whole pattern would lose its locomotor effect.

Interestingly, within 24 hours after birth, movements involving all three components (the triplet foreleg-rearleg-head) occur more often than any other category of synchronous movement. This triplet is even more in evidence if pups are mechanically supported to reduce postural, gravitational and substrate constraints on movement. The most parsimonious explanation for the postnatal appearance of this pattern is the establishment of a linkage relationship between the doublets foreleg-rearleg and foreleg-head, which predominate fetal activity late in gestation. Punting thus appears to be one example of a postnatal pattern of behavior that emerges from a hierarchy of linkage relationships established in utero.

ASYNCHRONOUS TEMPORAL PATTERNING

Synchrony is but one aspect of the temporal organization of behavior. Postnatal behavior characteristically entails fluctuations in levels of activity on multiple time scales. One aspect of temporal patterning is cyclic activity, which can be manifest on the level of circadian rhythms (see Reppert & Weaver, this volume) or cycles of much shorter periods (see Robertson, this volume). Goal-directed behavior typically exhibits non-cyclic temporal patterning as well. Events occur in bouts and higher level clusters of bouts. The existence of bouts is often invoked as a subjective appraisal from observation, but is subject to definition by more rigorous quantitative analysis. Chief among these is analysis of the length of time intervals between successive behavioral events.

If the occurrence of a particular event is independent of the time of occurrence of events that preceded it, then the cumulative distribution of inter-event interval lengths will be described by a log survivor (negative exponential) function (Fagen & Young, 1978). When such a distribution is plotted on a semilogarithmic graph, with the ordinate displaying the log of the number of intervals of length greater than t , the data fall along a straight line (Figure 3). Behavioral data that are well described by a

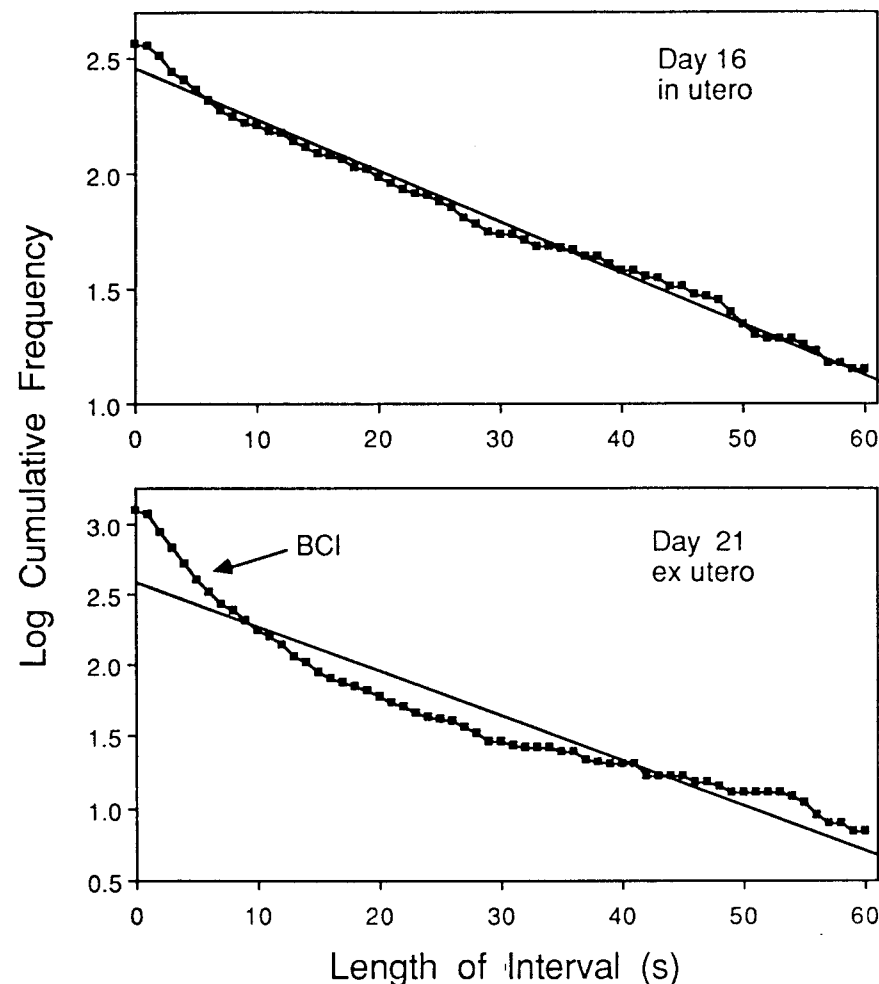


Figure 3. Representative log survivor curves of intervals between successive fetal movements on days 16 (in utero) and 21 (ex utero). Points are superimposed on the best-fitting negative exponential function as determined by a recursive algorithm. The objectively determined bout criterion interval is indicated on the graph for day 21 fetuses.

log survivor function can be considered as point events with a constant probability of occurrence in a given time interval.

We have employed log survivor analysis of interval length to determine whether asynchronous temporal patterning is evident in the activity of rat fetuses (Smotherman & Robinson, 1986a). In general, fetuses on day 16

of gestation exhibit movements that are temporally independent of one another. At later ages, short inter-event intervals (0–5 s) become more common than can be explained by random production of movements in time. Deviation from the log survivor model is most pronounced on day 21, when the number of short intervals exceeds predictions by more than 150%.

The existence of bout structure in the behavior of fetuses on days 17–21 has been confirmed through the use of an objective method for identifying a bout criterion interval. Successive events separated by an interval less than the bout criterion are defined as belonging to the same bout. The bout criterion is often determined subjectively by estimating the point on the log survivor curve where the slope changes most abruptly (Fagen & Young, 1978). But the bout criterion can be determined objectively through the application of a recursive algorithm (Machlis, 1977). The algorithm consists of six steps: (a) The bout criterion interval is initially set at 0 s. (b) The cumulative distribution of all intervals exceeding the bout criterion is tabulated. (c) A best-fitting log survivor function is determined through successive approximations to a negative exponential distribution; (d) the observed distribution is statistically compared to the exponential distribution with a nonparametric goodness-of-fit test. (e) If the null hypothesis cannot be rejected, then the procedure ends and the current bout criterion interval is adopted. (f) If the observed distribution is found to significantly differ from the theoretical distribution, then the bout criterion is incremented by one and steps (b) through (f) repeated.

Machlis (1977) developed this procedure for the temporal analysis of bout structure in the pecking behavior of chicks. She found not only that pecks tend to occur within objective bouts, but that bouts occur in higher units of clustering, which she termed superbouts. Other investigators have found that, in different applications, an objective bout criterion is problematic to determine (Slater & Lester, 1982). These facts argue that the procedure is robust in identifying bouts when bout structure exists and breaks down when the temporal organization of behavior is not well described by the concept of events clustering in bouts. When this procedure is applied to the activity of rat fetuses, an objective bout criterion is not apparent on day 16, but can be determined within the narrow range of 2–5 s in all comparisons conducted between days 17 and 21 of gestation. Although the deviation from a random temporal distribution is more pronounced later in gestation (especially on day 21), the bout criterion interval remains consistently less than 6 s. This finding may be interpreted as particularly strong evidence that fetal activity is randomly distributed on day 16 but exhibits an increasing tendency to cluster in bouts on day 17 and thereafter.

SEQUENTIAL BEHAVIORAL STRUCTURE

Postnatal behavior, and goal-directed behavior in particular, is often organized in functional sequences. Much can be inferred of underlying mechanisms controlling behavior from sequential analysis (Hailman & Sustare, 1973; Fentress & McLeod, 1986). Most analyses have assumed a Markov model in dealing with sequential relationships (Fagen & Young, 1978; Bakeman & Gottman, 1987). A Markov process exists when a system can express any of a finite number of discrete states, but knowledge of the immediately preceding state completely determines the next state to occur. More useful for biologists, a Markov chain broadens the concept of Markov process to allow for a stochastic, rather than deterministic, relationship between successive states.

To apply a Markov sequential model to behavior, the frequency of all possible ordered pairs of behavioral events is tallied in a transition matrix. Obviously, the size of this table increases as the square of the number of behavioral categories, so careful thought should be devoted to the manner in which the stream of behavior is parsed into discrete, operationally defined categories (see Fentress & McLeod, this volume). The pattern of transitions between categories can be expressed as joint probabilities (i.e., the probability of the sequence of event *i* followed by event *j*) or, which is often more informative, as contingent probabilities (the probability, given the immediate occurrence of event *i*, that event *j* will occur next).

Several methods are available for interpreting the information in a transition matrix (Bakeman & Gottman, 1987). It is possible to determine the statistical significance of individual transitions between focal categories of behavior or to test whether the distribution of transitions in the entire table deviates from a stochastic model of independence. The most common model for generating expected frequencies of transition is that used in the familiar Chi-square test: row and column totals are used to calculate the expected frequency in each cell of the matrix. When applied to a matrix of two-event transitions for rat fetuses, the observed sequential pattern is nearly exactly described by a stochastic model on day 16 of gestation. On days 17 through 21, however, observed patterns of sequential transition differ greatly from the random model.

The developmental change in sequential structure implied by this analysis can be more precisely described through the mathematics of formal information theory (Shannon & Weaver, 1949). The logic of using information measures to interpret sequential data is well discussed by Hailman (1977). Briefly, information theory provides a quantitative means for expressing the total amount of uncertainty or entropy in a closed

system. H_0 , the maximum entropy of a system, is defined solely in terms of the number of states a system can occupy; in behavioral analysis $H_0 = \log_2 N$, where N is the number of discrete behavioral categories. Entropy is expressed in bits per event, representing the number of dichotomous guesses required on average to specify an event or sequence of events. The entropy of a real system will equal H_0 when all categories of behavior exhibit the same probability of occurrence. If simple event probabilities (P_i) are not equal, then the overall entropy of the system will be described by the more general expression:

$$H_1 = \sum_{i=1}^N P_i(-\log_2 P_i)$$

Similarly, the entropy of the system described at the level of transitions between pairs of events (H_2) is calculated as the weighted average of the entropies for each row of the matrix. When the observed frequencies in a transition matrix are completely described by row and column totals (meaning that all events are sequentially independent), $H_1 = H_2$.

With the tools of information theory, it is possible to describe changes in the overall sequential organization of fetal behavior (Figure 4). The difference in entropy (H_0 through H_2) represents the amount of information

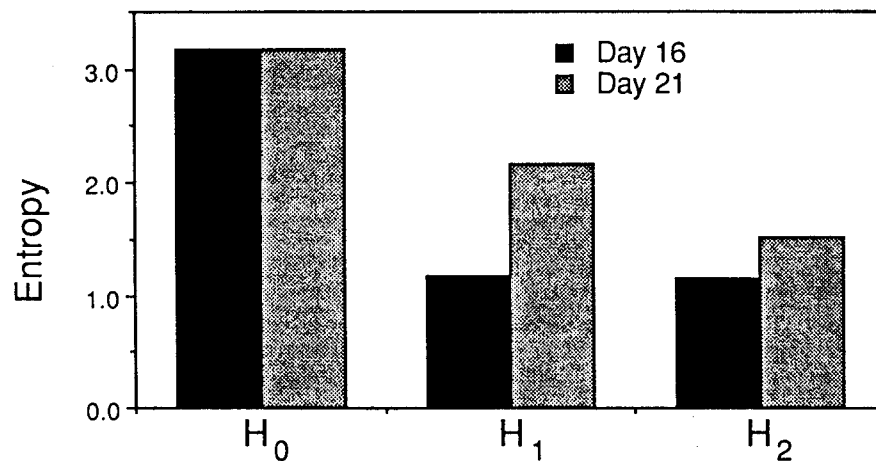


Figure 4. Information gain (bits/event) between progressively more complicated stochastic models of sequential patterning of fetal behavior. Data are presented for fetuses on gestational days 16 (*in utero*) and 21 (*ex utero*).

gained by progressing to successively more complicated levels of description. On day 16 of gestation, the greatest amount of information is gained between H_0 and H_1 ; at this age fetal behavior exhibits low diversity, with a few categories of movement occurring much more frequently than all others, and with almost no sequential structure. Between days 17 and 19, some information is gained between H_1 and H_2 , indicating that sequential organization is beginning to emerge. Closer inspection of patterns of transition suggests that much of this structure is due to self-recursion. In other words, each category of behavior tends to follow itself in a sequence. Another important pattern that occurs at these ages is shared component transition: categories consisting of simple movement events (e.g. foreleg) tend to occur just before or after categories of synchronous movement that comprise the same kind of simple movement (e.g. foreleg and rearleg). This is perhaps not surprising, as the results of the analysis of synchronous movement indicate that specific linkages between simple movements are in the process of crystallizing as discrete categories during this time.

On gestational days 20 and 21, however, much less of the overall sequential structure can be accounted for by shared component transitions. The information gain between H_1 and H_2 is large relative to the information between H_0 and H_1 . This relationship is the defining feature of a semi-Markov process (Hailman, 1977) and is characteristic of most post-natal behavior that has been described by sequential analysis. These findings clearly indicate that by late in gestation fetal behavior exhibits sequential organization. This serial patterning occurs at the same time that discrete categories of synchronous movement can be discerned (Robinson & Smotherman, 1987), bout structure becomes more pronounced, and the behavioral repertoire of the fetus expands in overall diversity (Smotherman & Robinson, 1986a). Extension of this method of sequential analysis to include pairs of events separated by intervening events (lag analysis; Bakeman & Gottman, 1987) and grouping movements into operationally delimited contiguous sets are providing additional evidence that the behavior of fetal rats becomes more contingent upon immediately preceding behavior and begins to exhibit state-like organization prior to birth (Smotherman & Robinson, 1987a).

CHANCE IN PRENATAL BEHAVIORAL DEVELOPMENT

As these analyses of movement synchrony, asynchronous temporal patterning and sequential structure suggest, random processes are likely to be fundamentally important in the early ontogeny of behavior. Before complex behavioral patterns can be expressed, the immature organism

must establish physical and neural connections between the effectors involved in the action. It is possible that the physical wiring of this connectivity may be accomplished passively with respect to behavior. That is, as efferent and afferent neural fibers grow out from the CNS to establish connections with their targets a control network is established. But it is now apparent that there is a considerable overproduction of these fibers and synapses and that much of subsequent neural development consists of the selective attrition of redundant and superfluous connections through neuronal cell death. This sculpting process of neural development is promoted by function of the end organs—muscles and sense organs—and can be suspended if function is interrupted (Oppenheim, 1981; Hofer, this volume).

If behavior participates in shaping the formation of the nervous system that controls it, what is responsible for imposing pattern on behavior before the nervous system is completely formed? This question distorts the reality of embryological development somewhat, because the nervous system is certainly functional at the time of the earliest fetal movements (Hamburger, 1973; Bekoff, 1981) and there is no evidence, in mammals at least, for a preneurogenic period of motility. But it is a question that should be addressed nonetheless, as it relates directly to the problem of self-organization. The informational diversity of patterned behavior, which is now known to exist prenatally (Smotherman & Robinson, 1987b), is not present in the nervous system at the onset of fetal motility. Therefore, behavioral patterning is an emergent phenomenon whose explanation must be sought in the dynamics of a developing system and not as a passive product of anatomical maturation (Oyama, 1985).

A full answer to this question is not available, but it seems necessary that random processes are an important aspect of the self-organization of prenatal behavioral development. Just as there is an overproduction of neurons and synapses during early neural outgrowth, there appears to be an overproduction of certain aspects of behavior during the prenatal and early postnatal period (Marler & Peters, 1982). The initial randomness in movement synchrony, temporal organization and sequential structure that is evident during the first few days of fetal movement (e.g., days 16–17) give way to behavioral organization as successive levels of pattern emerge. It is reasonable to expect that selective attrition of neural structures higher in the hierarchy of control are at the root of this emergent pattern. But without production there would be nothing to select. Random production of seemingly organized activity, such as the chance synchrony of simple movements and random transition between behavioral categories, provides the stuff from which the patterning that is so evident in species-typical action patterns and goal-directed behavior in general is sculpted.

THE CHUNK MODEL OF EARLY BEHAVIORAL DEVELOPMENT

The following verbal model is offered as a working hypothesis of the rules governing the earliest phases of behavioral development. The first movements of the fetus consist of simple elements, comprising one or more motor units acting to produce motion in a single vector. When new elements appear during development their occurrence is spontaneous and random with respect to time, serial relationship and spatial patterning. The chance association of randomly generated simple movements provides afferent feedback that facilitates the selective reinforcement of linkage relationships. In effect, simple motor elements become merged as chunks. As chunks are established, spontaneity is transferred to superior levels of hierarchical control. In this way behavioral organization emerges within chunks, but motor activity continues to be governed by chance at the highest levels of chunking (the incomplete hierarchy). As the depth of linkage increases during development, spontaneity is gradually lost at inferior levels, so non-linked elements and low-level chunks eventually cease to be expressed (although they may not disappear entirely from the repertoire; see Bekoff & Kauer, 1984). In this way, novel patterns of behavior can become established in the repertoire. An example of this process may be seen in interlimb synchronization, in which the linkage of foreleg and rearleg emerges from a background of randomly associated limb movements. As a network of chunks and their constituent elements becomes established, coordinated behavior begins to assume the characteristics of a dynamic system. It is at this time, toward the end of the prenatal period and the beginning of postnatal life, that concepts of synergism can be usefully applied to the control and development of motor behavior (Fentress, 1984; Thelen et al., 1987).

A principal prediction from this working model is the existence of behavioral elements or chunks that exist for a period of time during the early development and later disappear from the repertoire. Such Transient Ontogenetic Behavior (TOB for short) may be viewed as a form of ontogenetic adaptation (Oppenheim 1984). The existence of TOBs is important in early behavioral development in the same way that scaffolding is important in the construction of an arch. The individual blocks of the arch cannot be set in place without supporting structures, but when the arch is complete the support system can be removed. Similarly, TOBs may develop and persist for a brief time to facilitate the elaboration of an organized behavioral network, but disappear after the network is formed. This conception of TOBs as behavioral scaffolding may apply regardless of whether the network is preformed in the sense of a neural plan (analogous to the templates that may be involved in the ontogeny

of bird song; Bottjer & Arnold, 1986) or emergent as a product of self-organization (as in the complex and organized nests that are constructed by uncoordinated activities of social insects; Wilson, 1971).

Is there currently any evidence for the existence of TOBs? Although little effort has been made to date to identify TOBs in prenatal behavioral development, it appears that one important example has been known since the early research of Preyer (1885). Fetal movements are spontaneous. Unambiguous demonstrations exist for avian embryos that such spontaneity is neurogenic and is produced by central pattern generators located within the spinal cord (Provine, 1973; Bekoff, 1981). If neural communication within the spinal cord of mammalian fetuses is interrupted by transection at the cervical or high thoracic level, spontaneous motor activity persists posterior to the site of transection (Smotherman & Robinson, unpublished data). Yet severing the spinal cord in adults produces paralysis. Because local spontaneity of motor activity is an important aspect of fetal behavior, but disappears after higher levels of neural control are established, it may be the best example of transient ontogenetic behavior.

CONCLUDING REMARKS

We hope in this essay to have persuaded the reader that there is a continuing role for the direct observation of behavior in understanding prenatal behavioral development. As Keith Nelson argued over a decade ago (1973), there is a future for the holistic study of behavior. Understanding behavioral development during the prenatal period, like the postnatal period, will continue to demand analysis at a behavioral level. Problems of pattern and process in prenatal behavior are unlikely to be solved in the short term, and may be intrinsically insoluble, if addressed solely from reductionistic perspectives. Prenatal behavior seems to exhibit characteristics of a self-organizing system. In general, this organization takes the form of a transition from randomness to increasing depth of structural relationship.

Application of quantitative concepts, especially those of stochastic models (Metz, 1974) and hierarchical organization (Fentress, 1983), look to be especially useful in revealing empirically consistent rules of prenatal behavioral development. At the least, the testing of stochastic models requires that fetal behavior be observed carefully, recorded accurately and described in quantitative terms, thus providing an objective basis for comparison and description of changes in overall behavioral organization during ontogeny. More importantly, the wider adoption of stochastic

modelling techniques may generate and test hypotheses concerning underlying processes of early behavioral development. Once specific research hypotheses have been generated from observational study, they can be explicitly tested in traditional experimental situations. For example, models of movement synchrony and serial organization can lead to specific predictions about the effects of deafferentation or neural transection experiments. Similarly, the inference of behavioral states from sequential analysis of spontaneous fetal movement suggests that fetuses may respond to stimulation differently as a function of immediately preceding behavior (Smotherman & Robinson, 1987a). Quantitative observation is a research strategy that is independent from but complementary to the neuroethological approach to understanding the prenatal roots of complex behavior.

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Behavior of the Fetus

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