

LETTER TO THE EDITOR

Fetal Behavior in Developmental Psychobiology

To the Editor:

Prenatal behavior has long held allure and mystery, to some extent due its relative inaccessibility. Surgically implanted sensors, endoscopy, and ultrasound-based imaging techniques have provided important glimpses of fetal movements and responses (Birnholz, 1988; Bradley & Mistretta, 1975; Smotherman & Robinson, 1986a). The most detailed and definitive data on prenatal behavior come, however, from studies of the mammalian fetus externalized from the mother's body with intact umbilical connections (Carmichael & Smith, 1939; Kodama & Sekiguchi, 1982; Narayanan, Fox, & Hamburger, 1971; Smotherman & Robinson, 1987). Developmental psychobiology has been a particularly fertile area for the emergence and growth of research programs in fetal behavior.

The increasing breadth and intensity of prenatal research may create, for some observers, a kind of disordered panoply of results. But we see coherence, not confusion. We recognize three broad themes among fetal behavior investigations. We shall define these themes (with references to specific studies, but without attempting an exhaustive review), and then consider their place in the field of developmental psychobiology and beyond. From this perspective there emerges a picture of progress and promise: Fetal behavior retains its role as antecedent raw material for the subsequent growth and differentiation of behavioral repertoire. At the same time, fetal behavior

serves as a well from which we can draw for answers to basic questions of organization, function, and multileveled integration central to behavioral science.

Assembly of behavior. Traditionally, behavioral embryologists have been concerned with the origins and the subsequent steps by which behavior is formed or assembled. Are early movements autogenous and spontaneous in origin (e.g., Preyer, 1885), or are they responses to stimulation (e.g., Hamburger, Wenger, & Oppenheim, 1966)? Concerning developmental changes, they debated whether a complex behavior emerges by differentiation from an amorphous, total pattern (e.g., Coghill, 1929) or, alternatively, if it is constructed by sequential integration of separate elements (e.g., Windle, 1944).

The embryologists' classical formulations present wonderfully clear polarities. Perhaps this explains the impressive longevity of their questions. The answers, it turns out, are more varied and complicated than the questions. Not surprisingly, the forms of early behavior, like bodies themselves, differ across species (see, e.g., Provine, 1986).

Legacies of the embryologists' original questions remain discernible amidst modern inquiries, which are aimed more at identifying specific characteristics of early behavioral change than at universal principles of operation. Investigators such as Bekoff and Lau (1980) maintain tradition when they employ frame-by-frame analysis to describe organizational dimensions of fetal rat behavior, such as

Reprint requests should be sent to Dr. Jeffrey R. Alberts, Department of Psychology, Indiana University, Bloomington, IN 47405, U.S.A.

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synchronous activity of the limbs. Kinematic methods applied to questions of proximate influences such as the mechanical effects of the amniotic sac on temporal microstructure of fetal limb movements (Ronca, Kamm, Thelen, & Alberts, 1994), express similar foundations of inquiry.

Smotherman and Robinson have explored principles of early behavioral assembly with a variety of stochastic models applied to the interlimb patterns of the fetal rat (Robinson & Smotherman, 1987; Smotherman & Robinson, 1986b). Robertson (1988) has also examined temporal features of fetal behavioral organization, via analyses which focus on organized patterns of relatively short, ultradian rhythms of fetal activity.

One way or another, much of the contemporary scene can be related methodologically or conceptually to initial questions posed by behavioral embryologists. Thematically, this tradition is devoted to examining the organizational principles that describe behavior as it is first expressed and as it changes sequentially during pre- and early postnatal life.

Recognizing the determinative roles of *function* in the assembly of behavior has been a breakthrough for developmental analysis. The fetus' sensory and motor activities are not just elements to be elaborated and to be interconnected. They are also driving and shaping forces of the assembly of brain, body, and behavior. Gottlieb (e.g., 1976, 1978) has been a beacon on this aspect of developmental analysis; neuroscientists have also carried the torch (e.g., Purves, 1994).

Early capabilities. Another research theme involves revelation of unrecognized and in many cases, unsuspected sensory and motor capacities of the fetus. It has now been revealed that fetal rats: (a) produce motoric sequences that resemble grooming by older rats, (b) make tongue and mouth movements associated with feeding, (c) and can emit movements characteristic of the "stretch response" to milk letdown seen postnatally in pups, as well as (d) orally grasp an artificial nipple (see Fentress & McLeod, 1986, Robinson, Hoelzel, Cooke, Umphress, Murrish, & Smotherman, 1992; Smotherman & Robinson, 1987).

Sensory and perceptual function are behaviorally relevant capabilities that have been found in fetuses. Onset of function in a sensory

system is one level of capability, but the rule that onset of function precedes functional maturation (cf. Alberts, 1984; Gottlieb 1973) indicates the need for careful evaluation of development following onset of function. Depending on species and gestational stage, fetal sensory and perceptual capabilities can be rather astonishing. The fetus is clearly able to detect stimuli normally available within the intrauterine environment (Ronca & Alberts, 1994; Fifer & Moon, 1988). Rat chemosensory and human auditory function are among the most impressive phenomena that have emerged from empirical contests of fetal capability in the sensory-perceptual domain (Decasper & Fifer, 1980; Teicher & Blass, 1976).

The ability of a fetus to respond with patterns of autonomic reaction resembling the orienting response to novel stimuli (Lecanuet, Granier-Deferre, Cohen, LeHouezec, & Busnell, 1986; Ronca & Alberts, 1990; Smotherman, Robinson, Ronca, Alberts, & Hepper, 1991), and to learn, for example, by showing habituation (Vince, Armitage, Walser, & Reader, 1982), or some form of associative learning such as classically conditioned responses (Smotherman, 1982), were other stunning revelations about fetal life. The well-known studies of Spelt (1948) on classically conditioned responses in prenatal humans to vibrotactile cues presaged several experiments with rats in which prenatal conditioning was revealed during postnatal tests (Chotro, Cordoba, & Molina, 1988; Pedersen & Blass, 1982; Stickrod, Kimble, & Smotherman, 1982).

Learning, by traditional psychological conceptualizations, is a means of characterizing how "experience" shapes behavior. There are, in addition, other ways in which fetal experience has been treated as a significant capacity. Gottlieb (1970), for example, detailed a variety of behaviorally relevant roles of prenatal experience that do not conform to traditional conceptualizations of learning. These effects are dependent on functional capacities in sensory-perceptual inputs as well as organized responses to the stimulation. The importance of activity-dependent processes echoes in another dimension of development organization.

Adaptation. In many spheres of behavioral research, increased attention has been given to ecological context and to the func-

tional significance of behavior in relation to environment. Fetal behavior in the uterine environment has been recognized in terms of adaptive specializations to a distinct context (Alberts & Cramer, 1988; Smotherman & Robinson, 1988). Developmentally, this type of analysis is especially interesting because the fetus faces not only the adaptive challenge of life within the uterus, but it must also be prepared for the transitional event of birth as well as rapid adaptation to life outside the uterus (Ronca & Alberts, 1995).

Numerous perspectives have been applied to functional analyses of fetal behavior. A classic example from the avian literature is Drachman and Sokolov's (1966) observation that chick embryos immobilized for relatively brief periods (24–48 hr) develop rigid leg joints, implying that a functional role of embryonic movements is to maintain normal joint development. Whereas others might focus on central control of leg movements or on their circadian rhythms, the focus here was on functional consequences. It has also been suggested that some of the mammalian fetus' movements can serve to disentangle the umbilical cord (Smotherman & Robinson, 1988). Presumably, these movements would be triggered by a relevant cue, such as impaired blood flow or by hypoxia.

While prenatal behavior can serve immediate, proximate functions, we (Ronca & Alberts, 1995) have suggested that the fetus' intrauterine experiences of the mother's behavior and physiology are important for adaptive reorganizations required in the transition from fetus to newborn. Rat pups that were delivered without experiencing uterine contractions failed to initiate continuous postnatal respiration. Exposure to simulated uterine contractions was sufficient to induce normal onset and development of pulmonary respiration in surgically delivered pups (Ronca & Alberts, 1995).

New integration and synthesis? Connections are forming among the thematic domains. We applaud this trend, for it portends new and promising integrative efforts. Neuroscience methods, in particular, seem to be one avenue carrying researchers across boundaries that have separated the different thematic traditions. For example, manipulations of the central opioid system affect fetal activity, speci-

fic "precocial" behavior systems, as well as learning (Robinson, Arnold, Spear, & Smotherman, 1993; Robinson, Moody, Spear, & Smotherman, 1993). Thus, such methods serve all three of our themes, and integrate concepts and questions that have been separate in the past. Such potential for multileveled integration is also suggested by other neuroscience methods, such as the use of markers for neural activity. The use of deoxyglucose autoradiography to reveal patterns of neural activity in the fetal superchiasmatic nucleus (Reppert & Schwartz, 1986) relates to the assembly theme, the precocity of circadian rhythms in fetal rats contributes to capability, and studies of maternal–fetal interactions of behavioral and physiological rhythms relate to adaptation.

Structure–function relations have a long and important history in behavioral embryology. For some researchers, prenatal preparations offer a "simple system" because fetal brain is often relatively rudimentary, sensory pathways appear streamlined, and behavioral repertoire is limited. Nevertheless, with increasing awareness of the fetus' behavioral capabilities, there will be insight into the minimally sufficient elements for integrated behavioral expression, as well as the potential for understanding how behavioral repertoire unfolds during the differentiation of the body and brain. While such approaches offer some promise, we also anticipate increasing use of principles such as systemogenesis (Anokhin, 1964), to define functional systems in fetal behavior and to integrate these into a coherent adaptive, even evolutionary perspective.

Studies of fetal experience, especially when experience is broadly defined as a form of intrinsic stimulation, also promise integrative advances. Many of the physiological pathways of the adaptations that are critical for surviving the birth transition have been nicely delineated (Lagercrantz & Slotkin, 1986), but the factors initiating the fetus' state shift were unknown. Fetal experience has been invoked as a triggering or modulating event for the developmental transition of birth (Alberts & Ronca, 1993; Ronca & Alberts, 1995). Other forms of fetal experience, including learning, are actively under investigation as aspects of preparation for postnatal life. Learned associations involving intrauterine cues that help the

newborn orient to parental stimuli and organize suckling behavior (Pederson & Blass, 1982; Abel, Ronca & Alberts, 1995) exemplify this area of integrative analysis.

Gottlieb and others have sensitized us to the important, bidirectional interplay between structural development and functional status in the domain of brain and behavior (cf Gottlieb, 1971, 1976). These important constructs are central to each of the themes reviewed here. Moreover, the processes that are illuminated by this epigenetic perspective, which seem particularly clear during fetal development, are valuable for those interested in toxicological and teratological studies of development (Gottlieb, 1978). Aberrant phenotypes reflect detours in typical development process. The interpretation and remediation of prenatal insult depends on a full, integrated science of fetal ontogenesis.

We chose not to address a variety of more applied, biomedical issues that are also pertinent to the topic of fetal behavior. The themes that we have discussed are ripe for further integration. They can inform each other and should yield a complex, yet cogent picture of behavior as both cause and consequence in development. Although the mystery is shrinking, fetal behavior remains alluring, and promises many fundamental contributions to our science in the coming years.

Jeffrey R. Alberts
April E. Ronca
Department of Psychology
Indiana University
Bloomington, IN 47405
phone: (812) 855-3309
fax: (812) 855-4691

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