

## Self-Sensitivity in Fetal Development

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It is an inconvenient truth that the onset of behavior is before birth. In all the mammalian species, for example, behavior begins in utero, hidden within the mother's body. This simple bit of biology has made it difficult to observe or to access fetuses, leaving the beginnings of behavior to the imagination or, even worse, allowing it to be forgotten or ignored. Such truncation of perspective probably helped many to consider behavioral capabilities first seen at birth in a separate, special category termed inborn or "innate."

Gradually, however, behavioral embryologists began to accrue observations of fetal behavior (e.g., Narayanan, Fox, & Hamburger, 1971). They learned how to probe into fetal behavior with questions and methods to obtain rudimentary answers. The early pioneers were joined by some developmental psychobiologists, who brought other traditions to the area (Krasnegor & Lecanuet, 1995; Smotherman & Robinson, 1995).

When studying behavioral embryology in oviparous (egg-laying) species, the living embryo is virtually presented to the investigator, who can cut a window into the eggshell or gain direct access to the embryo within it (e.g., Gottlieb, 1985; Kuo, 1967). With viviparous species, investigators bring the fetus out of the mother's body, carefully preserving the umbilical and placental connections. These dramatic preparations allow researchers to see directly, manipulate directly, and measure more directly, which effectively gave birth to a new field of study.

My comments here are inspired mostly by the impressive and important report by Robinson, Kleven, and Brumley (this issue). This research is a contribution to a continuing literature on rat behavioral embryology and, indeed, to developmental studies in general.

It is helpful to put Robinson et al.'s new study in a broader, historical context. Looking back just a couple of decades, there was a distinctly different character to work in this field. I characterize much of the earlier work as "demonstration studies." When applied to developmental research, demonstration studies often serve to establish the presence of a capability previously unseen at a given age. Such research advances the field when a capability is demonstrated at progressively earlier ages until, perhaps, we follow the capability back in developmental time and into the uterus! Indeed, there have been years when there was palpable excitement in the field of developmental psychobiology when various capabilities—motor control, sensory acuity or discrimination, learning abilities, memory, or homeostatic features—were uncovered at earlier and earlier ages. In fact, the field often seemed to be based on progressive marches backward in developmental time.

The prenatalists' claim to fame became associated with such dramatic demonstrations. This is not to belittle such efforts. These were, and remain, lovely and significant studies. They revealed belief-shattering, even mind-boggling phenomena to those of us trained to see and to understand sequences of age-related milestones of behavioral development as causally linked to age-related milestones of neural development.

Once the fetal rat's behavioral repertoire was identified, researchers used the movements as a measure of sensory responsivity. Fetuses were "asked" if they could detect various stimuli, such as a punctate, tactile probe (Narayanan et al., 1971), or a gustatory cue placed in the mouth (Smotherman, Robinson, Hepper, Ronca, & Alberts, 1991). Again, such studies belong in the realm of demonstrations.

A related approach was to demonstrate that fetuses detect and respond to the in utero stimuli generated by the mother's behavior and physiology, or to outside stimuli that penetrate the mother's body to reach the fetus in utero (Alberts & Ronca, 1996; Ronca & Alberts, 1994; Ronca, Lamkin, & Alberts, 1993). Next, this line of research was extended to demonstrate that the experience of the naturally occurring maternal stimuli facilitated major behavioral milestones, including pulmonary respiration (Ronca, Abel, Ronan, Renner, & Alberts, 2006; Ronca & Alberts, 1995) and suckling (Abel, Ronca, & Alberts, 1998). Here there is a new "bar" to jump over. Success is achieved by demonstrating some "functional significance" of fetal sensory or motor function.

Now consider this article. Robinson et al. (this issue) externalized their fetal subjects from the mother's body and maintained the critical connections. Spinal blockade in the mother was essential, because surgical levels of anesthesia would affect the offspring and this, of course, would interfere with the behavioral investigation. Once externalized into the warm bath, the fetus' hind limbs were connected with a short tether, thus linking the movements of one limb to the other. Movements of one leg engaged the other into a similar movement trajectory. After 30 min of such self-stimulation, the tether was cut and the same fetus was observed

for another half-hour. As the authors describe in detail, both quantitative and qualitative, the fetuses begin to show conjugate leg movements (CLMs). Yes, this is an impressive “demonstration” that CLMs can be learned by rat fetuses as early as Embryonic Day 19 (E19), which had previously been reported for E20 fetuses (Robinson, 2005). Here, however, it is also shown, within the training parameters used by these investigators, that E18 fetuses do not acquire CLMs, but E19s do and there is subsequent shaping over the next two gestational days. Thus, Robinson et al. (this issue) is not just a fine demonstration of an early capability moved earlier; it is also an onset-defining investigation. It is also much more. Here, development means more than pushing earlier the existence of a phenomenon. They are pushing to study ontogenetic process itself.

There are several new and important features to the research presented in this article. Most salient, perhaps, is that this study reveals “development in real time” (cf. Thelen & Smith, 1994). The reforming of hind limb movements here is traced every 5 sec, from the first time one leg is subjected to a dynamic load by the other and is pulled into synchronous motion. Within these tight parameters, nothing is lost. We are seeing behavior develop in the moment! Then comes the big reward.

When the tether is cut and the limb movements of the fetus are unconstrained, they reveal a profound reorganization. We remain in the same framework of real, continuous time. We are not finding some lingering remnants from events long past in the organism’s history, nor are we seeing the emergence of a new function from a previously altered structure. CLMs continue to be expressed (e.g., Figures 2 and 3 in Robinson et al., this issue). This is a head-on view of development, worthy of association with Thelen and Smith’s (1994) characterizations of development viewed “from above” and “from below.”

Another noteworthy feature of the research is that this acquisition of CLM is apparently learning without reward. What is the acquisition process here? It is too early to say, but let’s savor some of the authors’ initial interpretations. First, they review the physics of the interlimb yoking and focus on the “mismatch” produced by one leg dragging the other into action. What might the fetal nervous system do in response to the induced mismatch? Production of conjugate movements is one possibility. There are many imaginable pathways to the achievement of interlimb synchrony (i.e., to learn the CLM). One route, suggested by the authors with reference to a hypothesized, general mechanism (Sporns & Edelman, 1993), is a process of overproduction, shaped by a subsequent selection by elimination of nonadaptive variants. Beautifully, the fetuses in their study displayed an increase in hind limb activity during training. This then, would represent the increased variability in interlimb movements on which selection could be performed. It is appropriate to invoke a dynamic systems perspective here, and the data settle comfortably into this type of framework. The tethering manipulation creates a form of movement perturbation and, as amply shown in Thelen’s studies of early reaching

by human infants (e.g., Thelen & Spencer, 1998), such perturbations are a predicted source of enhanced variability of movement.

Robinson et al. (this issue) recognize the critical role of kinesthetic feedback in any plausible explanation of fetal motor learning. This aspect of the discussion is of paramount importance, for it highlights the role of experience as a driving mechanism of development. The authors point out that E18 fetuses do not alter their behavior when tethered, but E19 fetuses do. Moreover, E20 and E21 fetuses are increasingly responsive to the perturbation. Does this correspond with age-related improvements in the detection and perception (i.e., experience) of their limb movements? The picture of neural development is consistent with such possibilities.

We now know that prenatal experience is a formative, inductive, canalizing, and regulatory mechanism in development. Although hidden from view, dependent on the mother's body for all sustaining physiological processes, and grossly immature, the fetus experiences its world and it experiences itself. This sensitivity of self is part of fetal experience. The details of such experience are likely to be the basis of how the fetus self-organizes and shapes itself into a coherent, adapted, behaving individual. The trajectory of such changes, which we call development, is going to prove dependent on the experience of self and the ability to stimulate oneself. The elegant and detailed analyses in Robinson et al.'s article make an important contribution to this perspective.

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