Behavioral embryology

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Introduction

William James speculated that infants are born into a "blooming, buzzing confusion," which stemmed from the long, dark sleep within the womb devoid of experience. Although this passive view of the neonate has remained influential for nearly a century, a conceptual revolution has occurred more recently in developmental psychology. This new view sees the newborn as an active participant in its own behavioral development. One reason for the dramatic change in perspective is that investigators have become more proficient at asking questions. Rather than evaluating infants in terms of adult perceptual or behavioral abilities, research programs have addressed neonatal behavior and cognition by adapting experimental procedures to abilities that are relevant to the infant. This research strategy has yielded important demonstrations of behavioral competence in infants within days after birth.

Appreciation of neonatal behavioral competence raises a fundamental question: what is the source of these behavioral abilities? It is possible that the competencies of the newborn arise abruptly, preformed in the maturation of the nervous system in utero. Alternatively, the abilities of the newborn may be foreshadowed by an extended period of *behavioral* development, which includes the expression of organized movement and sensory experience before birth (Smotherman & Robinson, 1996). It is to the prenatal period that researchers have turned to seek answers to this dilemma, which has brought developmental psychology into contact with the field of embryology.

The embryo as foundation

Embryology literally is the study of embryos. An embryo is an immature animal that develops within the egg or womb, comprising the span from fertilization to hatching or birth. A prevalent view of the relationship between embryonic development and life after birth is expressed by the analogy of a house. A completed house comprises many rooms with different purposes, just as a mature body comprises many functional systems. But the different rooms cannot be used, the house cannot even be built, without first laying down a solid foundation to support later construction. Embryonic development is also a period of foundation building, in which neural sub-strates are constructed that later will permit the elaboration of more complex networks for governing behavior.

A presumption of the foundation analogy is that prenatal development is biology, and psychology begins after birth. This depiction may be accurate only during early embryogenesis, in which the basic structural organization of the organism is created. Interactions between cells and tissues, governed by a complex network of membrane-bound proteins, growth factors, extracellular chemical signals, and many other products of gene activity, are responsible for creating the raw materials from which the nervous system will be constructed. For the developmental psychologist interested in the prenatal roots of behavior, a more relevant beginning may be the inception of motility, when activity within the central nervous system results in active movement by the embryo. All vertebrate species show spontaneous movement before birth. But the relationship between embryonic activity and later behavior has been the subject of considerable debate.

Behavior as a factor in prenatal development

Teratology provides perhaps the most dramatic evidence that prenatal events can have an impact on postnatal behavior. A teratogen is any substance that can be transmitted to the fetus in utero to alter prenatal development. Alcohol is probably the best-known example of a teratogen. Chronic abuse of alcohol can lead to Fetal Alcohol Syndrome (FAS), which involves a collection of dysmorphologies including facial abnormalities and lung hypoplasia. Lesser exposure can produce more subtle behavioral effects such as irritability, hyperactivity, poor attention, decreased motor coordination, and cognitive deficits in language acquisition, problem solving, and learning. Many other substances, including pesticides, heavy metals, and drugs of abuse, have joined the list of recognized teratogenic agents.

Less widely appreciated are the teratogen-like effects that result from a simple absence of embryonic motor activity (Moessinger, 1983). Fetuses that experience a period of akinesia (loss of movement through drug exposure or myopathy) exhibit a suite of morphological effects, including microstomia (small mouth), retarded lung development, skin and facial abnormalities, immobilized joints and altered bone growth, short umbilical cord, and long-term movement disabilities (Fig. 1). Fetal Akinesia Deformation Sequence is a stark demonstration that fetal movement is an important contributor to prenatal morphological and behavioral development.

Early behavioral embryologists disagreed over whether embryonic movements were the result of endogenous neural activity, or reflexive responses to indeterminate environmental stimuli. This controversy was resolved through the work of Viktor Hamburger and colleagues, who demonstrated that chick embryos continued to produce spontaneous activity in the central nervous system after the ventral spinal cord was surgically isolated from the brain and from incoming sensory information. Spontaneous neural activity now is recognized to play a crucial role in guiding neuromotor development. Activity in motoneurons and their associated muscle fibers is necessary for normal processes of cell death, synapse elimination, and re-structuring of neuronal connectivity within the motor system. Moreover, the amount of activity appears to be less important than the pattern; bursts of electrical stimulation are more effective in promoting selective elimination of synapses than a steady rate of stimulation.

Although activity-dependent processes such as selective pruning in the nervous system mark the embryo as an active participant in its own development, embryonic movements seem far removed from behavioral abilities traditionally studied by developmental psychologists. Indeed, classic studies of fetal motility stressed how embryonic movements appeared random, purposeless, and lacking in coordination. However, more careful analyses of chick embryos observed in ovo and rodent fetuses in utero have demonstrated a remarkable degree of organization underlying embryonic movement. Chick embryos show patterns of muscle activity and leg movement that are highly similar during spontaneous motor activity, hatching behavior, and post-hatching locomotion (Bekoff, 1992; see Fig. 2). The spontaneous movements of mammalian fetuses express organization in multiple dimensions, including temporal rhythmicity, movement synchrony, organization of active and quiet sleep, and motor coordination during species-typical action patterns that are related to postnatal grooming, suckling, and locomotor behavior (Robinson & Smotherman, 1992). Given the wealth of recent discoveries about fetal behavioral organization, the historical depiction of the fetus as a passive object during prenatal development is no longer defensible.

Figure 1. Photographs of term rat fetuses after normal gestation (left) and akinesia induced by curare during the last three days of gestation (right). The curarized fetus exhibits thin, tight skin, immobilized joints, and underdeveloped hindlimbs, and retains the flexed head position characteristic of a younger fetus. From A. C. Moessinger, 1983. Fetal akinesia deformation sequence: an animal model. *Pediatrics*, 72, 857–863.

The principle of induction

Late in the 19th century, Hans Spemann was among a handful of experimental embryologists who formulated the principle of induction as a mechanism of embryological change. Induction is a form of interaction in which the presence of one cell type causes a second cell type to undergo change. The concept is well illustrated by interactions that occur during the process of gastrulation (Fig. 3). As cells of the blastula invaginate, an intermediate layer of cells (mesoderm) migrates beneath the outermost layer of cells (ectoderm). The migration of the underlying mesoderm layer provides an inductive trigger to the overlying ectoderm, causing it to thicken, lengthen and roll up into the neural tube, which is the

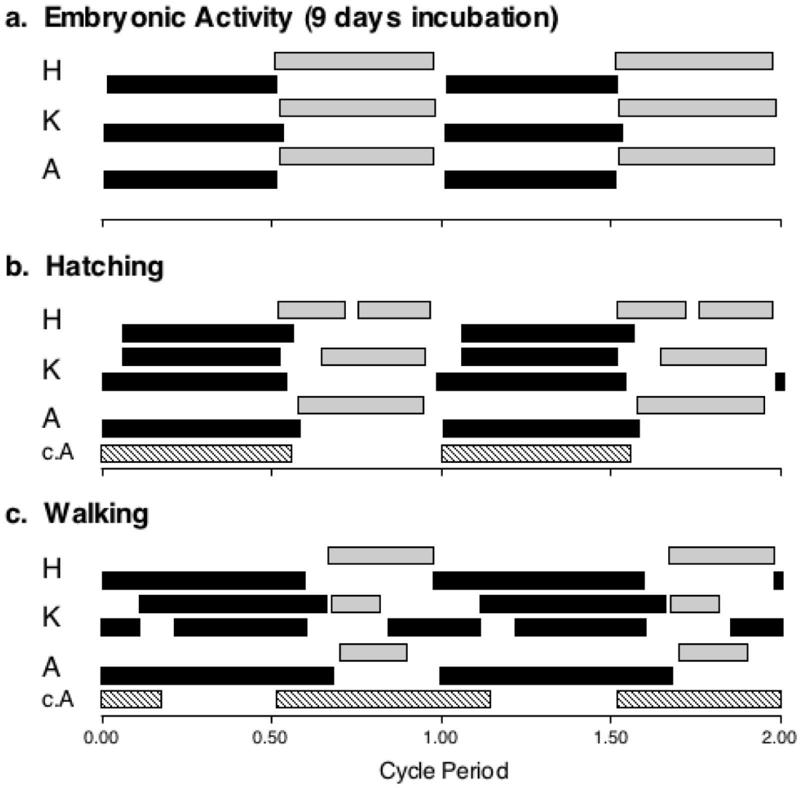

Figure 2. Similar patterns of chick leg muscle coordination during spontaneous embryonic movement, hatching behavior, and postnatal walking. Bar graphs depict normalized bursts of EMG activity for muscles of the right hip (H), knee (K), and ankle (A); extensor muscles are indicated by black bars and flexors by gray. Hatched bars show activity of the contralateral ankle extensor as a measure of interlimb coordination during hatching and walking. Redrawn from A. C. Bekoff, 1992. Neuroethological approaches to the study of motor development in chicks: achievements and challenges. *Journal of Neurobiology*, 23, 1486–1505.

earliest rudiment of the brain and spinal cord. In embryological terms, the neural tube forms as a consequence of the inductive influence of mesoderm on ectoderm.

The most relevant aspect of the concept of Induction for developmental psychology is the flexible definition of what constitutes environment. Psychologists may be inclined to see a clear delineation between the organism and its environment: everything under the skin is organism; everything else is environment. But to embryologists, environment denotes a relationship. The extracellular matrix can be environment to individual cells, one tissue can be environment to another, and the dispersed products of cellular biosynthesis can be environment to other tissues. The concept of induction necessitates that environment be defined relative to the thing that changes.

A flexible definition of environment helps to clarify the multilevel, interactive process of development. This is especially important in studies of prenatal development, where the contribution of environment often is assumed to be minimal. For example, considerable attention has been devoted to determining what environmental stimuli may be available to the fetus in utero. Stimuli in some modalities, such as light, are effectively excluded by the barriers that surround the fetus: the mother's abdomen, the uterus, the chorion and amnion that envelop the fetus, and the amniotic fluid filling the space within these membranes (Fig. 4, left). But sound and mechanical vibration can be transmitted through these barriers, and chemical stimuli, including constituents of maternal diet, can cross the placenta to enter amniotic fluid. Human and animal experiments have confirmed that fetuses can detect and respond to environmental stimulation in these modalities.

The world outside the mother's skin is not the only relevant source of environmental influence for the fetus (Fig. 4, left). In mammals, the mother also serves as a critical component of the fetal environment. The fetus' needs for nutrition, oxygen, and waste removal are met by the mother through the placenta. Chemical signals, including hormones, can be transmitted across the placenta to provide communication between mother and fetus. Although the fetus possesses an independent neural substrate for generating 24-hour rhythms in its activity (in the suprachiasmatic nucleus of the hypothalamus), the rhythm is synchronized to the circadian pattern of the mother by chemicals that cross the placenta. Sounds produced by the mother, such as voice, or physical forces that result from changes in posture or maternal exercise also can be detected by the fetus. These are but a few examples that illustrate the complexity of environmental influences that derive from the maternal-fetal relationship.

Self-stimulation by the embryo

The embryo also can influence its own environment. Avian embryos typically begin to vocalize several days before hatching. In some species, the rate of vocalization is a reliable indicator of egg temperature, which provides feedback for the mother to regulate incubation. Embryonic vocalizations also can influence auditory development. Newly hatched ducklings exhibit a bias to approach the source of maternal calls, whether it is produced by the mother duck or a mechanical speaker. Experimental dissection of this bias has revealed that prenatal auditory experience is both sufficient and necessary for the auditory preference to develop. The embryo's *own* vocalizations provide the necessary auditory experience to create a post-hatching bias; ducklings that are experimentally de-vocalized and isolated from acoustic stimuli fail to express a preference for the maternal call.

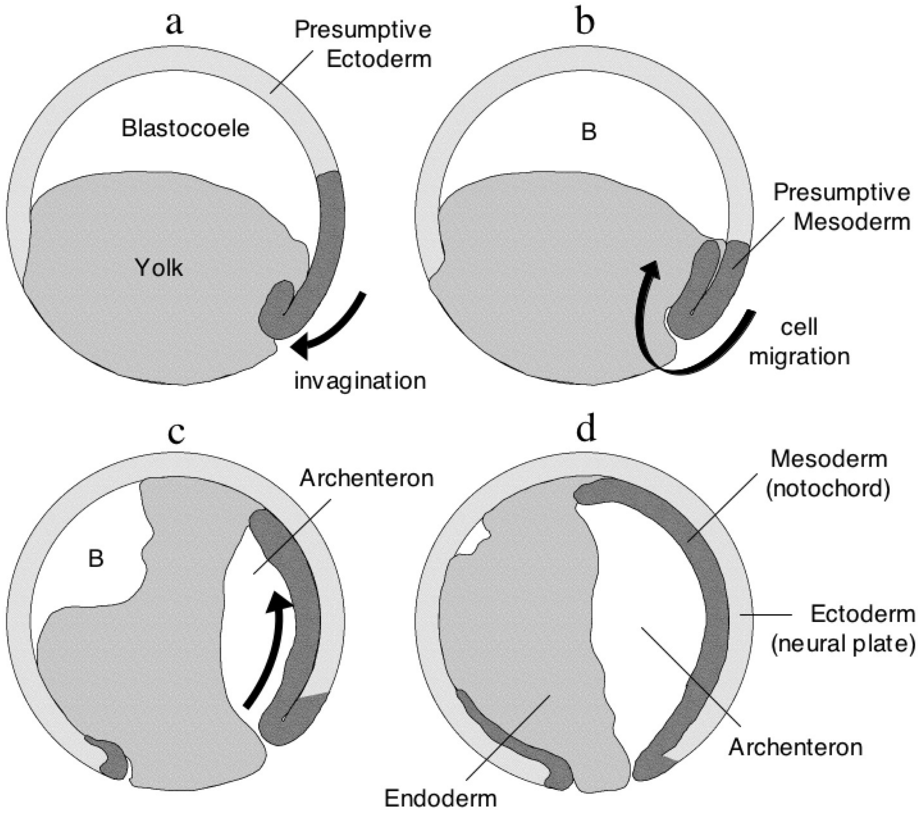

Figure 3. Diagram of midsagittal sections of frog embryos during gastrulation. The developmental sequence depicts: (a) early invagination of presumptive mesoderm cells in the late blastula stage, (b) migration of cells into the hollow blastocoele (B), (c) formation of the primitive gut or archenteron, and (d) disappearance of the blastocoele and formation of the three primary germ layers (ectoderm, mesoderm, endoderm) of the gastrula.

Mammalian fetuses may benefit from self-stimulation in a chemical modality. The fetus is surrounded by amniotic fluid (AF), which is derived partly from chemical constituents of maternal blood, and partly from chemicals produced in the placenta, umbilical cord, embryonic membranes, or the skin, lungs, and kidneys of the fetus. AF provides a fluid space in which fetal movements can occur. The presence of membranes and fluid around the fetus can serve as a kind of scaffolding, facilitating some aspects of early motor coordination. Too little fluid (oligohydramnios), however, results in movement restriction and its deleterious consequences. AF is swallowed and breathed by the fetus, and thereby contributes to the development of the mouth, gastrointestinal tract, and lungs. In addition to its physical properties, AF contains a complex assortment of phospholipids, carbohydrates, and proteins, including hormones that can influence the sexual development of neighboring fetuses in the womb.

Fetuses show distinctive behavioral responses upon oral exposure to AF (Korthank & Robinson, 1998), which triggers changes in fetal motor activity and responsiveness to sensory stimuli (Fig. 4, right). During parturition, the pregnant rat distributes AF on her own ventrum, and the odor of AF helps newborn rats to locate the nipple for the first time. Pups prefer the odor of AF and odor cues introduced into AF before birth. Such exposure learning can produce olfactory memories that are retained after birth to influence orientation and ingestive behavior of newborn, juvenile, and adult rats. Thus, it is evident that AF, which is produced largely by the fetus, can contribute in important ways to perinatal behavioral development. In these ways, the fetus helps to construct its own environment within the womb.

Conclusions

Prenatal self-stimulation, whether through movement, sound, or the chemical milieu, is instructive as a model for the bidirectional and interactive processes that characterize embryonic development. A relational definition of environment, including self-stimulation, can help to clarify the multiple determinants of behavior and neural development before birth. Indeed, understanding the complex ways that experience can contribute to early development represents one of the major challenges facing developmental neuroscience.

Little of the motor activity of embryos can be characterized as explicit practice, nor can most of the

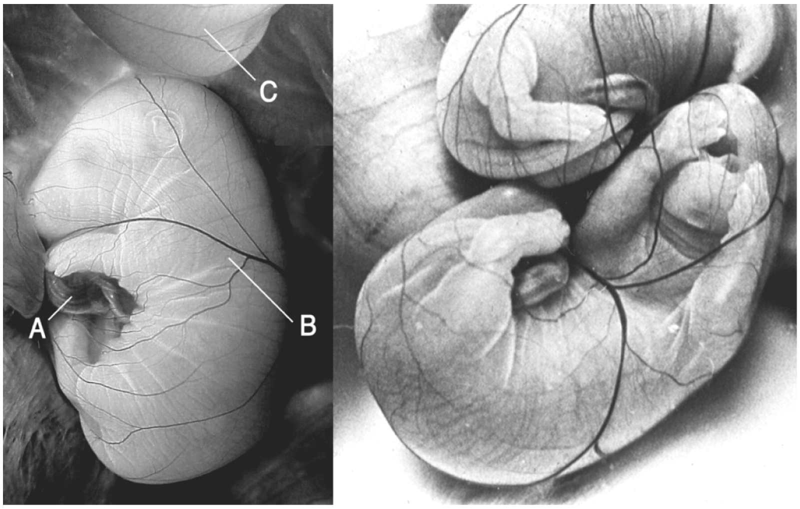

Figure 4. Rat fetuses photographed in vivo two days before birth (day 20). At left, key features of the fetal environment are indicated: (A) umbilical cord, which restricts the range of fetal movement but grows in response to tension produced by motility; (B) chorion and amnion, membranes that contain amniotic fluid and constrain fetal movements; (C) an adjacent sibling, which is a source of physical stimulation and may produce hormones that can affect development of other fetuses. Fetal movements are further constrained by the uterus; non-labor contractions of the uterine myometrium compress the fetus, which stimulates endocrine activity and promotes certain aspects of brain development. At right, a fetus responds to amniotic fluid with mouthing, swallowing, and forelimb treadling. Oral exposure to amniotic fluid alters sensory responsiveness and the organization of fetal movements, and can influence postnatal olfactory behavior.

sensory features of the intrauterine environment be thought of as providing specific experience with contingencies relevant for postnatal behavior. Rather, the challenge for developmental researchers is to explain how general motor or sensory experience in utero may help to build neural systems that govern coordinated action and sensorimotor integration after birth.

Similarly, the advent of molecular technology in modern embryology has fostered the search for genetic causes of developmental change. But much remains to be discovered about how embryonic activity and sensory experience serve to regulate gene expression or the modification of gene products in the developing embryo. In these ways, concepts and research methods that originally were developed within the respective disciplines of developmental psychology and embryology will continue to be useful in deciphering the tangle of cause and effect in prenatal behavioral ontogeny.

See also:
The concept of development: historical perspectives; Understanding ontogenetic development: debates about the nature of the epigenetic process; Neuromaturational theories; Ethological theories; Learning theories; Cross-species comparisons; Conceptions and misconceptions about embryonic development; Normal and abnormal prenatal development; The status of the human newborn; Perceptual development; Motor development; Development of learning and memory; Brain and behavioral development (I): sub-cortical; Locomotion; Sleep and wakefulness; Developmental genetics; Ethology; Viktor Hamburger; Wilhelm T. Preyer

Further reading

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