The Psychobiology of Behavioral Development

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Preface

Research in behavioral development, specifically the contributions of physiological and experiential factors acting alone and in concert, has been carried out for many years. Given the breadth of the subject matter, it is no wonder that the questions posed about the forces that shape the development of behavior and the experimental methodologies established to answer them have been extraordinarily diverse. Despite such diversity, or perhaps because of it, a formal research specialty known as *developmental psychobiology* has emerged. I call it a formal specialty because it is represented by a research society, The International Society for Developmental Psychobiology, and the journal *Developmental Psychobiology*. Furthermore, departments of psychology on occasion advertise specifically for developmental psychobiologists.

The purpose of this endeavor is to provide developmental psychobiology with a textbook, one appropriate for both undergraduate and graduate students. Undergraduates will best profit from the book if they already have completed an introductory psychology course. It also would be helpful if they have taken a course with some emphasis on conditioning and learning. Graduate students with a background in psychology should have little difficulty with the material.

A colleague once remarked that psychology courses are defined by whatever the instructors wish to teach. In other words, the discipline is so broad that instructors have great latitude in selecting topics for coverage. Therefore they essentially define the subject matter of the specialty areas in question. The same is true for writers of textbooks, who also must select a rather small subset of topics. Regarding this book, I have tried to choose for consideration those topics regarding the psychobiology of development that have received enduring attention: embryonic behavior, early stimulation, and the influence of hormones, to name a few. The reader, however, might be struck by one notable omission—the relation of genes to behavioral development—a topic that obviously must not be excluded from the education of future developmental psychobiologists. I chose to omit the subject because it requires the mastery of so much background information about genetics it cannot be adequately considered in a chapter or two. The interested reader should consult one of the excellent specialty textbooks, such as Plomin, DeFries, and McClearn's *Behavioral Genetics: A Primer.*

As will become readily apparent, close attention has been paid to the older literature as well as to data of a recent vintage. I used this approach for two reasons. First, as historians tell us, the present is more clearly understood by examining the past, a point that is certainly true for science. The questions investigators ask and the way in which they attempt to answer them do not spring de novo from their fertile imaginations but are in large measure a product of what has come before. By considering the early literature the reader is able to place current research in perspective, thereby fostering a better understanding of it and allowing one to make informed predictions about future research directions.

There is another reason for paying such close attention to early research; much of it is outstanding and remains current. This point serves to demonstrate that research should not be dismissed merely because it was performed prior to the advent of high-powered technology; electron microscopy, radioimmunoassays, computer science, and so forth. Much of those data were collected by observation. A prime example is the 1885 study of Wilhelm Preyer, who meticulously monitored the reactions of chick embryos of differing ages to various forms of stimulation. Advances in our knowledge about the development of behavior have been and continue to be made by careful observation of behavior.

ACKNOWLEDGMENTS

There are many individuals to whom I am indebted for inspiring this book and providing valuable assistance in its preparation. I am indebted to the undergraduate and graduate students who have taken my course in developmental psychobiology over the past 20 years and asked those seemingly simple questions that, after periods of numbing silence, I realized I could not answer. I thank them also for informing me that, my lectures notwithstanding, they would have greatly benefited from a textbook. Thanks also are extended to some anonymous reviewers, to former graduate student Scott Graham, and especially to my colleague Richard Lore, all of whom helped with insightful comments on less developed versions of the manuscript.

September 1991 R. G.
New Brunswick, N.J.

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Origin and Function of Embryonic Behavior

The organism is inexplicable without environment. Every characteristic of it has some relation to environmental factors. And particularly the organism as a whole, i.e., the unity and order, the physiological differences, relations and harmonies between its parts, are entirely meaningless except in relation to an external world.

C. M. Child, 1924

"I am born." So begins the chronicle of David Copperfield's development. Like Dickens, most psychologists, at least until recently, also began their study of behavioral development with the neonate, thereby discounting the potential import of activities and events that occur during the embryonic period. Even embryologists, whose attention by definition is focused on prenatal or prehatching processes, have been concerned principally with the development of structure. Because most viewed behavior as a by-product of structural development, they seldom considered the possibility that embryonic activity might influence the very structures they were examining.

During the 1980s, however, embryonic behavior became the focus of increasing attention. We now recognize that consideration of such behavior is central to an understanding of development—that activity of the embryo[1] is a critical element in ontogenesis. It has become clear that behavioral development does not only proceed in a structure → function direction but that behavior itself contributes to the structural development of the nervous system (function → structure). Moreover, we now understand that various aspects of postnatal/posthatching behavior have their origins in the interaction between the embryo and particular types of environmental stimulation. Hofer (1988) was indeed correct when he remarked that prenatal behavior is one of the sculptors of the organism.

A number of factors have contributed to the attention being paid to embryonic behavior. One is the development of noninvasive ultrasonic imaging techniques that permit monitoring of human fetal behavior repeatedly and over rel-

[1]The distinction between *embryo* and *fetus* is not well defined. For example, according to *Webster's Ninth Collegiate Dictionary*, an embryo becomes a fetus after "attaining the basic structural plan of its kind." Regardless of what that actually means, the timing of the transition from embryo to fetus is species-dependent. Therefore for the sake of simplicity and consistency, the term *embryo* is used throughout the text.

atively long periods of time. Before these techniques were available, data were gathered from aborted fetuses whose viability, because of the immediate onset of asphyxia, was questionable. Also, the emergence of new techniques in various subfields of neuroscience, e.g., neuroendocrinology, enables researchers to address questions central to important theoretical issues in behavioral development. Finally, concern with the consequences to the newborn of embryonic exposure to drugs and other substances has proved highly influential.

This chapter considers factors that influence the initiation and maintenance of embryonic behavior, the modifiability of embryonic behavior, and the relation of such activity to postnatal behavior. Early research, in addition to providing much of the basic information (which remains current) yielded a surprising amount of theory (as well as a surprising amount of vitriol among investigators with opposing theoretical viewpoints). Some of those theories are mentioned here for historical reasons and because they provide a useful framework within which to examine the data.

EMBRYONIC MOTILITY AND SPONTANEOUS NEURONAL DISCHARGE

Modern research on the study of embryonic behavior had its origins in 1885 with the publication of W. Preyer's *Specielle Physiologie des Embryo.* Among other findings, Preyer reported that the chick embryo begins to display movement several days prior to the time a reaction can be evoked by a tactile stimulus. A similar result was reported later for another species, the toadfish (Tracy, 1926). The first movement of the toadfish—bending the trunk in the anterior region—also occurred before movement could be evoked by tactile stimulation. Tracy referred to this behavior as "spontaneous" and suggested that it is caused by changes in blood chemistry, such as accumulation of carbon dioxide. Only later does the embryo begin to respond to sensory stimulation, the initial modality being tactile. Later still, the organism responds to light, vibration, and acid (pain).

In fact, through the work of several researchers it was found that differences exist among species with regard to whether a sensory system becomes functional during the embryonic period. Receptor complexes generally become morphologically mature in the embryos of species with long gestation periods. Also, the more mature the motor system at birth or hatching, the more likely it is that particular sensory systems, especially vision, will possess the capacity to function during the embryonic period (Gottlieb, 1971; Bradley & Mistretta, 1975).

Preyer's and Tracy's results indicated that the initiation of embryonic motility is not caused by the development of reflex mechanisms. Rather, it is generated endogenously by spontaneous discharges of motor neurons, i.e., by the automatic firing of nerves that arise in the spinal cord and innervate muscle tissue. In other words, early movement is a product of the neuromotor system and thus is solely a consequence of the development of that system. This early account of the genesis of embryonic motility probably did little to pique the interest of psychologists, as it discounted the role of stimulation. In the parlance of psychologists, that means that the environment is of little or no consequence. Because it generally was regarded that neuromotor development follows a preset course, early behavior was viewed as being *predetermined*.

The notion that embryonic motility is caused by the spontaneous discharge of motor neurons received additional support from early neuroanatomical experimentation. The neuronal circuitry that mediates reflex activity of the chick embryo is completed *subsequent* to about day 6 of the 21-day incubation period (Visitini & Levi-Montalcini, 1939; Windle & Orr, 1934), well after movement is first observed.

Research of a more recent vintage was presented by Hamburger and his associates who, in an elegant series of experiments, provide strong support for the notion that embryonic movement can be initiated and maintained by the spinal cord independent of stimulation. These researchers began by carefully monitoring the behavior of the chick embryo (Hamburger, 1963; Hamburger & Balaban, 1963). Their observations were summarized as follows:

> [W]e have characterized the motility of the chick embryo, up to 17 days, as random movements that are performed periodically, activity phases alternating with inactivity phases. All parts of the embryo which are capable of motility at a given stage participate during the activity phase; however, the movements of the different parts are not related to each other. For instance, the two wings do not move together in a coordinated manner as in flight, nor do the two legs move in an alternating pattern as in walking. Yet, both wings and legs may perform flexions and extensions simultaneously. Head movements, beak clapping and opening or closing of the beak and of the lower eyelid may all occur independently or as part of a total body movement. (Hamburger & Oppenheim, 1967, p. 171)

The duration of the activity phases increases with advancing age of the embryo (see Figure 1.1).

Hamburger and his associates (1965) then asked if motility could be elicited by the spinal cord itself. A section of the cervical portion of the cord was surgically removed in 2-day-old chick embryos, thereby severing the spinal cord from the brain. Any movement of the embryo thus would necessarily be produced by efferent or motor neurons that exit the cord and innervate muscle. As shown in Figure 1.2, although overall activity was reduced (by about 20%), the spinally transected embryos did exhibit motility in an age-related pattern similar to that of the intact preparations. These findings are in agreement with the electrophysiological work of Provine (1972), who recorded electrical activity directly from the spinal cord. Bursts of electrical activity, which are taken as indicative of complex bioelectrical events, were seen as early as day 5 of incubation. Moreover, the electrical bursts appeared coincident with body movement (Ripley & Provine, 1972) (see Figure 1.3). O'Donovan and Landmiesser (1987) reported a similar result by recording electrical activity in the ventral root of the isolated cord. Moreover, it appears that it is the initial portion of the electrical burst that actually triggers muscle activity (Landmiesser & O'Donovan, 1984). Lastly, Provine and Rogers (1977), whose findings are in close agreement with those of Ham-

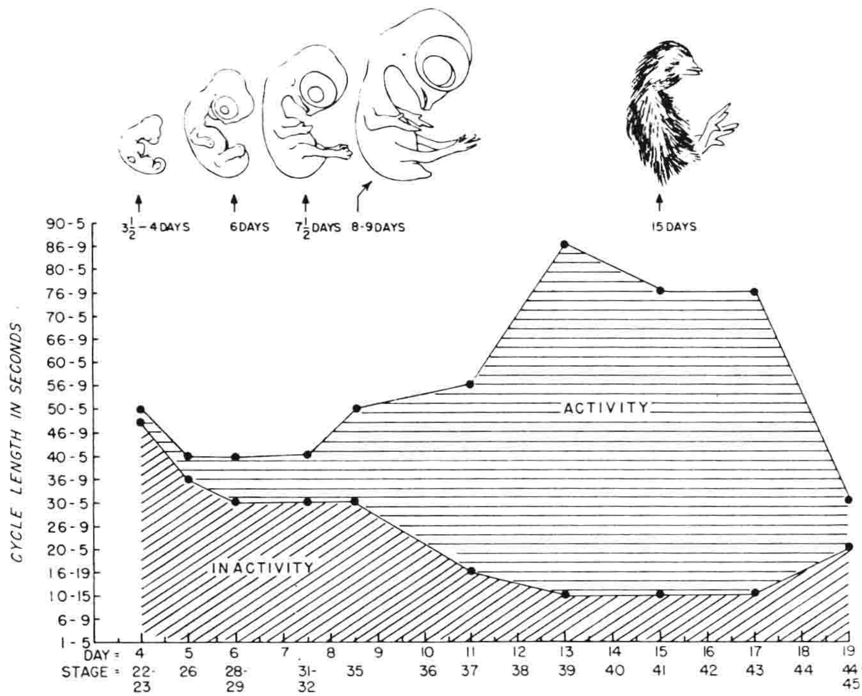

Figure 1.1 Mean duration of activity and inactivity phases and of length of cycle at different stages of development of the chick embryo. (From Hamburger et al., "Periodic motility of normal and spinal chick embryos between 8 and 17 days of incubation." *Journal of Experimental Zoology, 159,* 1–13. © 1965 by Wiley-Liss, a division of John Wiley and Sons. Reprinted by permission.)

burger, reported similar patterns of electrical activity from the spinal cords of intact embryos and those whose brains were severed from the cord.

The work of Hamburger and others, though demonstrating that embryonic motility can be generated by the discharge of spinal neurons, did not address the issue of stimulation. Perhaps motility is the result of spinal reflexes, i.e., sensory (afferent) input into the cord that triggers output to muscle fibers. Although it was not the purpose of the studies reviewed here to stimulate the embryo, it is possible that such stimulation either was given inadvertently or was produced by the embryo itself. Hamburger, Wenger, and Oppenheim (1966) asked specifically if stimulation is necessary for the display of embryonic motility. To that end, the thoracic portions of the spinal cords of 2-day-old embryos were removed so sensory input originating from the legs could be eliminated. Leg motility was then assessed in 8.5-, 11-, 13-, 15-, and 17-day-old embryos. Except for the 17-day-old embryos, the percent of leg motility during a 15-minute test period was the same for experimental and intact preparations (17-day-old experimental embryos showed a deficit). There is, then, direct support for the notion that sensory input is not required for embryonic motility.

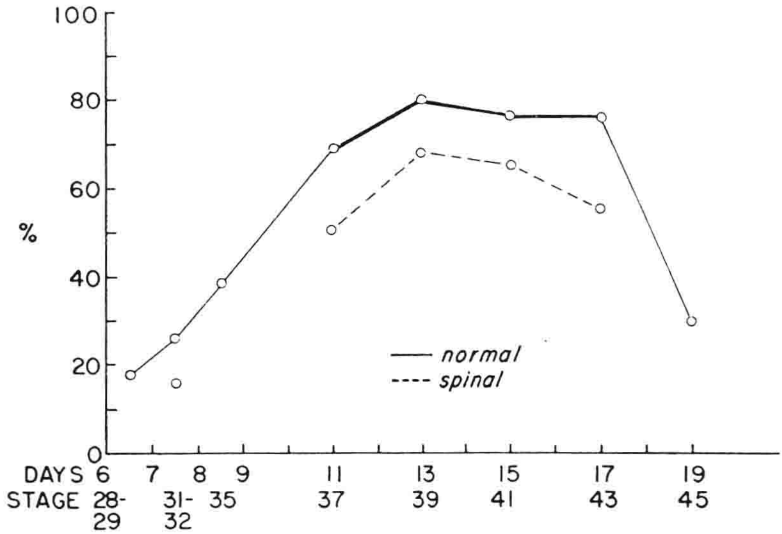

Figure 1.2 Mean percent of time spent in activity during 15-minute observation periods for normal and spinally transected chick embryos. (From Hamburger et al., "Periodic motility of normal and spinal chick embryos between 8 and 17 days of incubation." *Journal of Experimental Zoology, 159,* 1–13. © 1965 by Wiley-Liss, a division of John Wiley and Sons. Reprinted by permission.)

The early findings that embryonic movement occurs prior to the time embryos respond to the application of stimulation and the work of Hamburger, Provine, and others lend strong support to the notion that embryonic motility can be initiated by spontaneous discharge of the neuromotor system. Is it the case, however, that stimulation is really without influence? Whereas Hamburger et al. (1966) demonstrated that surgically prepared embryos can exhibit motility in the absence of afferent input, perhaps under *normal* conditions embryos do respond to exteroceptive stimulation. As we will see, other data show that embryos are indeed responsive to such stimulation. In other words, although embryos possess the *capacity* to respond spontaneously, they may not normally do so.

EMBRYONIC MOTILITY AND SENSORY STIMULATION

Stimulation and Assessment of Nervous System Development

Initially, researchers stimulated an embryo to assess nervous system development rather than to examine the relation between the embryo and its prenatal milieu. Stimulation was thought not to influence the course of development; behavioral development was viewed even by those interested in reactivity to

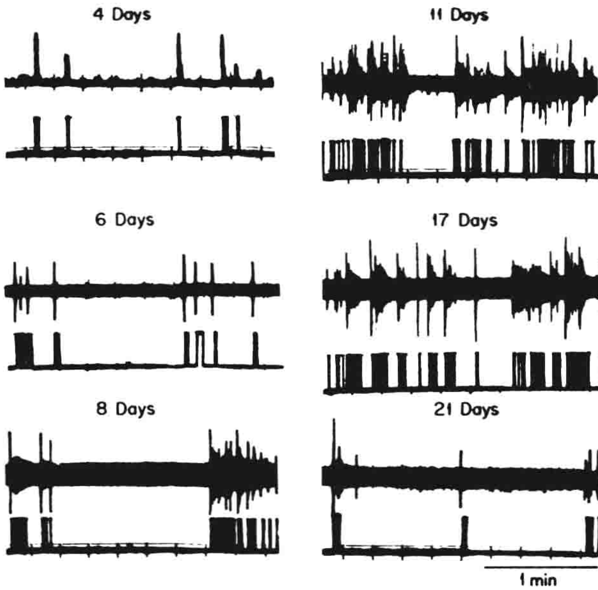

Figure 1.3 Comparison of cord burst discharges (upper traces) with visually observed body movements (lower traces) on days 4 to 21. The 4-day cord activity was integrated to emphasize the low-amplitude activity. Cord discharges were made from the lumbosacral region, except at 4 days, when the brachial cord was monitored. (From Ripley and Provine, "Neural correlates of embryonic motility in the chick." *Brain Research, 45,* 127–34. © 1972 by Elsevier Science Publishers. Reprinted by permission.)

stimulation as an inevitable and invariant outcome of nervous system maturation. Those examining embryonic responsiveness to stimulation also recognized that motility can occur in the absence of overt stimulation.

The neuroanatomist G. E. Coghill, whose work first appeared in 1902, was a pioneer in the study of embryonic development because of his carefully performed empirical research and his views concerning the development of embryonic motility (e.g., Hooker, 1936; Oppenheim, 1978). The salamander embryo served as the subject for most of his investigations. Correlations were drawn between the extent to which tactile stimulation (from a human hair) elicited movements and the level of nervous system development. Responsiveness to the stimulus initially appears near the snout because, according to Coghill, it is in the head region, that connections are first established between motor neurons and muscle tissue. The head typically is moved away from, and occasionally toward, the source of the stimulation (Coghill, 1929). Later, responses can be evoked from other areas, spreading in a rostrocaudal direction following the sequential development of neuronal innervation of muscle. Once again, behavioral development was seen as following a course determined by nervous system maturation.

Coghill also reported that the initial movements of individual structures, e.g., gills, hindlimbs, and forelimbs, are undifferentiated, resulting from the overall movement of the embryo's trunk. In other words, the motility of individual structures is part of a larger response involving motility of the trunk. It is only later that the embryo is capable of performing discrete, independent movements of individual structures. Coghill called the process of going from undifferentiated to differentiated activity *individuation*. In his words, "Behavior develops from the beginning through the progressive expansion of a perfectly integrated total pattern and the individuation within it of partial patterns which acquire various degrees of discreteness" (Coghill, 1929, p. 38). At the time, this approach was considered revolutionary because it had been widely held that overall patterns of behavior resulted from the summation of discrete, simple reflexes.

Coghill's use of the term *pattern* with reference to behavior was reminiscent of the then popular Gestalt movement, which emphasized overall patterns of central neural activity in its quest to understand perceptual processes. Lest anyone confuse Coghill's interpretation of behavioral development with that of Gestalt theorists and perhaps place the subject of embryonic behavior within the intellectual domain of psychology, Hooker (1936) stated the following:

> In a way, I think it possibly unfortunate that Coghill has used the term "pattern." The existence of patterns is denied by many and is rather generally associated with the principles of Gestalt psychology. It is true that the emergence of individual reflexes from a total response, as described by Coghill for Amblystome, has been gathered to the Gestalt bosom. However, I wish to emphasize that the total response, from which individual reflexes emerge, was forced upon Coghill by his functional-morphological findings, and was not evolved to give aid and comfort to the Gestalt point of view. (p. 581)

A number of subsequent experiments with mammalian embryos supported Coghill's findings with the salamander. Experimentation with the mammalian embryo (except for certain marsupials, e.g., the opposum and kangaroo), however, faces two major problems. One concerns observation. Unlike amphibian embryos, which can be observed directly through the semitransparent gelatinous substance that surrounds them, or avian embryos, which can be easily observed by removing a portion of the shell and coating the underlying membrane with petroleum jelly, mammalian embryos must be removed from the uterus while maintaining the integrity of the placental connection. Relatively mature embryos can be observed through the amniotic membranes, which become taut and transparent during the later stages of gestation. Less mature embryos must also be taken from the amnion. The very act of abruptly removing the embryo from its normal intrauterine environment may itself affect motility. A second problem concerns anesthetizing the mother, which is performed prior to exteriorizing the uterus. Anesthesia must result in blockage of pain and prevention of movement without affecting the embryo. Therefore the administration of an agent such as sodium pentobarbital is unacceptable, as the drug crosses the placenta and anesthetizes the embryo as well as the adult. A number of techniques have been developed to obviate this problem, including occlusion of the carotid artery, transection of the spinal cord, and production of a functional spinal transection by injecting ethyl alcohol or lidocaine and epinephrine into the cord (Smotherman, Richards, & Robinson, 1983; Smotherman, Robinson, & Miller, 1986).

Another early researcher, Angulo Y Gonzalez (1932), turned to the rat embryo. After rendering the adult unconscious by ligating the internal carotid arteries (ether was used only when required as a supplement), the uterus was exposed and the embryos were "shelled out" of the amnionic sacs. The entire preparation was suspended in a temperature-controlled bath of physiological saline, with the adult's head being kept above the level of the solution. The responses of 643 embryos aged 14 to 21 days (gestation period 22 days) to stimulation from a coarse hair were recorded. Observation sessions lasted up to an hour.

The development of rat embryonic activity was strikingly similar to that reported by Coghill for the salamander. The earliest movement, seen at 15.7 days after insemination, was head movement in response to stimulation applied to the snout region. Between days 16.0 and 16.9, movement spread in a caudal direction, involving first the forelimbs, then the rump, and lastly the hindlimbs. During that period the forelimbs moved only in conjunction with trunk movements. Thus a total pattern of behavior, movement of the trunk with accompanying limb activity, was seen. Another total pattern, observed between 17.0 and 17.9 days, consisted of head movement with accompanying opening of the mouth and tongue protrusion. As with the salamander, it was only later that discrete movements developed. Similar results were presented by Narayanan, Fox, and Hamburger (1971). (The problem of anesthetization was dealt with by transecting the pregnant animal's spinal cord at a level that eliminates movement and blocks the receipt of sensory information from the abdominal region but does not prevent respiration.) Responses evoked by tactile stimulation generally begin as a total pattern of motility, and areas of the body that cause movement when stimulated spread over time in a caudal direction (see Figure 1.4).

Human embryos also respond to tactile stimulation. Hooker (1936, 1952) performed a series of experiments with therapeutically aborted embryos. Prior to summarizing the findings, his caveat should be noted: Aborted embryos immediately undergo asphyxiation even when oxygen is provided. "As a result, all conclusions drawn from human fetal activity must be carefully weighed with the effects of asphyxia in mind" (Hooker, 1936, p. 591).

Hooker's findings are summarized in Table 1.1. We see again that tactile stimulation initially elicits a total pattern response and, later, discrete responses. Humphrey (1964), whose results are in general accord with those of Hooker, extended the research by demonstrating a relation between behavior elicited by tactile stimulation and neural development (see Table 1.2).

The data described here supported Coghill's idea that a total pattern of motility precedes discrete activities such as the movement of limbs. Unanimity was not to be reached, however. Windle (1944; Windle & Becker, 1940) argued that the procedures used to study the mammalian embryo produced an artifact that led to spurious data, and that in reality individualized behaviors do predate gen-