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DEVELOPMENT REACTION TO ENVIRONMENT**

Every organism, including man, lives under the influence of not one, but two environments. The one more generally recognized is that which surrounds it, hence is external. However, each organism also has an internal environment set up by its internal organs, their function and the secretions, hormones, enzymes, etc., which they produce.

Every organism, from the simplest to the most complex, responds to the external environment, largely by neuromuscular activity. This response constitutes its visible or overt behavior. However, the responses made to the internal environment, which constitute the invisible or covert behavior of the organism, have a profound effect in modifying overt behavior, and vice versa. Hence, the over-all response exhibited by an organism is a resultant of the interaction of the responses to both environments and varies greatly in its specific nature, depending on a variety of factors set up by its immediate needs and capacities.

Whatever the nature of the response may be, it is a reaction, involving activation and inhibition, of the whole organism capable of functioning, not of any specific part alone. This is obvious in the normal adult. In the developing organism it is not so generally recognized, but is, nevertheless, equally true. Because the various organs, including the nervous system and the muscles, develop in a seriatim manner, they do not all reach a functional state at the same time. Consequently, the behavior of an embryo or fetus is constantly changing as new neural connections, both within and without the central nervous system, and new organs attain a functional state. It is to the earlier aspects of this changing pattern that this communication is directed.

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Many in previous centuries have written down their observations of embryonic movements in many animal forms,[16, 18, 20, 48] but these were more or less casual observations. It is only within the last 50 years that any real attempt has been made to study carefully the sequence of development of the neuromuscular apparatus in relation to behavior. The work of Coghill, summarized in his book,[13] which was not only the first but the most complete physiological and morphological study of any form to the present, established the nature of the development of the amphibian, Amblystoma. In essence, his conclusions indicate that, when response to the external environment begins (specifically to exteroceptive stimulation with a fine hair), all of the embryo capable of neuromuscular function participates in the reaction. As the neuromuscular mechanism continues to develop, which it does in a cervico-caudal direction, the response pattern expands caudally.

Because of the involvement of all of the functional neuromuscular mechanism in this expanding response, Coghill termed this type of reaction a "total pattern," i.e., a participation of the whole organism capable of functioning in such an activity. As he states,[12] "The behavior of this animal [Amblystoma] begins as a total reaction, and continues as such until after locomotion is established" (p. 125). Later, when still further neural development makes them possible, specific reflexes appear. These Coghill termed "partial patterns" and regarded them as being "individuated" from the total pattern, though the latter always remains dominant.

The early work of Swenson (unpublished) and all of Angulo's observations[3-5] (both of them students of Coghill's at Kansas who went with him to the Wistar Institute) convinced Coghill that the basic principle of the developmental sequence of behavior established for Amblystoma held also for the rat and probably was of universal application to all vertebrates, including man. His 1929 paper,[14] setting forth this belief for the human embryo, was not too well received. However, this application of the basic principle derived from Amblystoma to man was no purely theoretical extrapolation, as was assumed by some. It was based, not only on the then incomplete work on the rat, to which reference has already been made, but also on data derived from publications of Erbkam,[15] Zuntz,[62] Strassmann,[46] Yanase,[60] Krabbe,[33] Bolaffio and Artom,[10] and M. Minkowski.[36-39] Unfortunately for Coghill's purposes, only the papers by Minkowski have any validity as far as the recorded observations are concerned. Many of the others contain only cursory observations and all of the others were carried out under conditions so abnormal as to render the results suspect.

Most students in the field have accepted Coghill's conclusions for Amblystoma, even when, with varying degrees of dissent, they have objected to the application of his basic principle to other vertebrates and, especially, to man. This is the more interesting as it is well known that the development of the neural tube and of the musculature is identical in principle in all vertebrates. Consequently, one might expect, a priori, that functional development might also follow a common principle. However, two basically different schools of thought arose, one following Coghill's principles, one diametrically opposed to them. In addition, several minor variations of less importance have arisen.

The major hypothesis opposing Coghill's principles, although originally put forward by Swenson[47, 48] in his later papers, has been fostered largely by Windle and his students.[58] This group has postulated, especially for mammals and man, that behavior develops by the appearance of a 'simple' reflex, usually in the head or upper extremity, then of another which is integrated with the first, of a third and so on. In other words, the individual 'simple' reflexes are the building blocks which, secondarily integrated, form behavior.

The concept of the 'simple' reflex undoubtedly comes from Sherrington,[44] who used the term as "probably a purely abstract conception" but found it a "convenient, if not a probable, fiction." When integration occurs is a matter quite aside from the probably fictitious nature of simple reflexes. On this score, Coghill[12] had no doubts as to Amblystoma. There integration is always primary, never secondary. Integration must occur before a reflex becomes elicitable. Each alteration in response pattern is preceded by the development of the specific neural connections needed for its execution and their integration with existing neural mechanisms. Then only can the new addition become functional. This is also the generally accepted view of most neurologists[57] for nervous system integration in all vertebrates.

A number of investigators have concluded from their studies that the basic principle of 'total pattern—partial pattern' set forth by Coghill holds good in at least some species in nearly all of the vertebrate classes. Among these are Tracy,[50] on Opsanus, Coghill, himself, for Opsanus and Fundulus,* Youngstrom[61] on Rana, Acris, and Pseudacris, Wang and Lu[56] on Rana and Bufo, Tuge[51] on Terrapene, Smith and Daniel[45] on Caretta, Tuge[52, 53] on pigeons, Kuo[34, 35] on the chick, Angulo[3, 4, 5] on the rat, Pankratz[40] on the rabbit, Barcroft and Barron[7, 8] and Barron[9] on sheep, and the Pittsburgh studies[21-32] on man.

It is important to emphasize that it is the basic principle of Coghill's concept of 'total pattern—partial pattern' that these investigators agree upon as having a wide application. Each form studied has its own minor variations, even in the early stages. As the embryos of the different classes

* See Herrick,[19] pp. 96-97, 94-96, and 264-267 for a posthumous account of Coghill's work on these forms.

grow older, more marked variations occur, until major differences become evident. These are the characteristics of the species being studied, for variations exist even in the same family. Of course, as the organism under the study rises in the phylogenetic scale, the more specialized it becomes and the greater is the change in its behavioral capacities. It should also be noted that there are very minor differences even in the same species, hence the emphasis on the basic principle.

When Coghill first suggested the universal application of his Amblystoma pattern of behavior, there was relatively little evidence, confirmatory or otherwise, upon which to base his idea insofar as man was concerned. Although it had long been this writer's desire to study such living human fetuses as might become available from time to time, it was not until the autumn of 1932 that it became possible to do so. When it did become possible to make such observations, it seemed advisable, *inter alia,* to check on Coghill's hypothesis regarding man's earliest developmental activity sequence.

Nearly 28 years and more than 150 cases later, the sequential pattern of the different stages forming the fetal components of human overt behavior is beginning to assume a recognizable form, although much still remains to be done. From the evidence now available, it would appear that, as human overt behavior develops, a number of different major categories of activity are manifested. The first two to appear consist of exteroceptively elicitable reflexes and proprioceptive reflexes resulting from muscle stretch and other appropriate stimuli. A third early type of movements to be exhibited are of the kind generally denominated as spontaneous. Voluntary movements, almost certainly not found in fetal life, are the last to appear and eventually constitute the major part of the motor activity of the adult. Each major type of activity, with the possible exception of proprioceptive movements, passes through a distinctive development of its own. However, almost none of the essential elements of any of these categories of activity is ever lost. Rather, the earlier forms of activity are gradually incorporated, with a new orientation, into the overt behavior pattern characteristic of any particular age of the organism. It is true, however, that the earlier types of activity usually assume less important roles as later types take over.

The exteroceptive reflex category of activity begins at about 7½ weeks of menstrual age.* At the moment, it is not possible to state definitely when proprioceptive activity begins. It almost certainly begins as soon as the exteroceptive reflex type.[30, 58] So-called spontaneous movements begin very

* All age references given will be to the menstrual age of the human fetus.

shortly after the exteroceptive reflexes, by 9½ weeks, if not before, but do not assume any great importance until the 18th week or later. These constitute the overt behavior of the fetus and neonate. As noted, voluntary activity almost certainly does not make its appearance until later in infancy.

From 7½ weeks to about 9½ weeks, the progressive development of the reflexes is dependent upon the level of development of both the nervous and muscular systems. Thereafter, the changes depend almost entirely upon the developmental level of the nervous system alone, as practically all muscles necessary for movements have appeared by that time. Just as little or nothing of the activity patterns is ever lost, so little or nothing of the underlying nervous mechanisms that makes them possible disappears. On the contrary as the fetus develops, the neural mechanisms previously present become incorporated into the expanding mechanism of the late fetus, the infant, and the adult.

At 7½ weeks, the typical reflex is elicitable on stimulation with a fine hair in the sensitive area located about the mouth and the alae of the nose. This is the region supplied by the maxillary and mandibular divisions of the trigeminal nerve. The sensitive region at this age is, however, much more restricted than is the case later. No other region of the fetal integument is reflexogenous to light stimulation at this age. However, both at this age and for a brief period before it, as well as thereafter, movements may be secured by direct mechanical stimulation (pressure or pricking) of the musculature or by its electrical stimulation. Such activity, of course, is not reflex.

At 7½ weeks, the typical reflex in response to stimulation with a fine hair in the reflexogenous area is a lateral flexion of the neck away from the side stimulated. By 8 weeks, the area exhibiting predominantly contralateral flexion has begun to expand caudally to include the uppermost trunk and shoulder muscles, the latter feebly. By 8½ weeks, the entire trunk enters into the chiefly contralateral flexion, both brachia extend markedly at the shoulders, and the pelvis shows some rotation. These activities become more complete by 9½ weeks. During this period, all movements of the upper and lower extremities are brought about by their girdle muscles and are exhibited only in conjunction with trunk movements. Neither upper nor lower extremities are capable of independent movement until later.

During the two-week period from 7½ to 9½ weeks, the reflexogenous area of integument supplied by the maxillary-mandibular divisions of the trigeminal has expanded slightly. By 10 to 10½ weeks, the upper eyelid has become sensitive to light stimulation, but until 10½ weeks no other area of integument over the entire body is reflexogenous. At 9½ weeks, local reflexes appear in the face area, at 10½ weeks in the upper extremity, at 11 weeks* in the lower extremity, and at 13 weeks in the trunk.

The responses of the human fetus between their first appearance at about 7½ weeks and the beginning of local face reflexes at 9½ weeks constitute a total pattern in Coghill's sense. From the beginning they involve all of the neuromuscular mechanism capable of functioning reflexly in the entire organism. At their appearance they are highly localized in the neck region, but as new neural and nerve-muscle connections are established they expand caudally. As these new connections within and without the nervous system develop, they are primarily integrated with those already existing. Specific local reflexes begin to appear or, to use Coghill's terminology, partial patterns begin to be individuated from the total pattern at 9½ weeks and continue to be elicitable in a caudal direction. By 14 to 14½ weeks, or earlier in some individuals, the total pattern has largely been replaced by specific local reflexes (the partial patterns of Coghill), but the total pattern never entirely disappears.

At about 15 to 16 weeks, the fetus seems to become relatively inert. Certain reflexes, as those in response to stimulation of the palm and sole, may be elicited until stopped by hypoxia, but many others become very difficult to evoke. Curiously, though this same phenomenon was noted by Barcroft and Barron[7,8] in the sheep fetus, it has not been mentioned by those who studied other mammals. This sluggishness of response persists until about 18 to 20 weeks, though a vestige of it remains until ages at which the fetus may be resuscitated. However, lack of oxygen does not appear to be the primary cause of the sluggishness observed.

The fetus may be temporarily resuscitated at about 22 weeks or a little earlier. When resuscitated, the fetus becomes very active. From this time on until birth, the great difficulty in studying reflex responses is to distinguish between movements evoked by the stimulus applied and activities of the so-called spontaneous category that might have appeared in any case. From 22 weeks to birth, spontaneous activity becomes the chief type of movement exhibited.

The so-called spontaneous category of fetal activity makes its appearance by 9½, possibly, though very rarely, by 8½ weeks of age. At the time of its first appearance, it plays a very minor role. This role increases with the age of the fetus, assuming some importance by 18 weeks and becoming the dominant type of activity in later fetal life, as already noted. When it first appears, reflex activity is in the phase of neck-trunk total pattern move-

* In earlier publications, this date was given as a few days earlier. A careful recheck of all protocols and motion picture records has proved the earlier age to be in error.

ments. The spontaneous activity exhibited at this age consists of short bursts of side-to-side repetitions of the same kind of movements elicitable reflexly. In general, spontaneous activity seems to lag slightly behind reflex capacity in the appearance of the different types of movement.

Much has been presented[19, 54, 55] on spontaneous activity with little illumination as to its precise nature and cause or causes. Some observers, like the writer[28] in earlier communications, have believed some spontaneous movements to be reflexes in response to unrecognized exteroceptive stimuli. In the Pittsburgh collection of motion pictures of living human fetuses is one of an 8½ weeks' case (#116) which responded to each of two widely separated stimulations with a fine hair in the side-to-side manner characteristic of spontaneous activity. This is the only case in which a known stimulus, in so young a fetus, has been seen in the Pittsburgh studies to cause such activity. However, at 9½ weeks and later, the handling during extraction of a fetus has frequently brought on the spontaneous type of movement. This is probably also elicited by the stimulus of handling. In the human fetus, contrary to the author's findings in the rat fetus (unpublished), spontaneous movements are of relatively short duration until 20 to 22 weeks, when some resuscitation may be possible.

Paton[41, 42] and Wintrebert,[59] among others, have demonstrated an intermittent rhythmic automatism of the trunk musculature in selachians. Such movements are clearly indicated by Wintrebert to be myogenic in character. Paton, however, believed the similar movements he observed were due to the presence of nerve-impulse-transmitting intercellular bridges, shown by Harrison[17] not to exist. Wintrebert[59] thought these early myogenic activities—they precede reflex movements—might aid the respiration of the embryo. Tracy[49] is of the opinion that the earliest movements of the toadfish, Opsanus tau, are caused by internal stimulation by the accumulation of CO_2. There is clear evidence from a number of sources that such O_2-CO_2 imbalance may cause muscle contractions in fishes prior to the onset of reflex activity. Angulo[2] refers to "endogenous stimulation by metabolites," meaning CO_2, as a cause of spontaneous movements in albino rat fetuses. Graham Brown[16] pointed out that progression in adult decerebrate cats may still occur rhythmically after deafferenting the hind limbs. He believed that the efferent neurons acted in such cases as "half centers," stimulated from within by CO_2. They could also be activated by balanced alternate stimulation and inhibition from cephalic levels of the nervous system.

Weiss[57] has demonstrated that, under experimental conditions, the central nervous system may give rise to spontaneous activity through automatically released rhythmic bursts of impulses to muscle tissue. Such discharges have been found in the respiratory center,[1,11] where CO_2 is the stimulus. However, automaticity may be an inherent property of the central nervous system without such stimuli.

Certainly, spontaneous activity is nonvoluntary in character, whatever its actual cause may be. At this time, it appears likely that there is no one cause, but that a variety of causations produce the movements termed spontaneous. Hence, it may be that spontaneous movements are, in some cases, responses to the external environment, in others to the internal environment, or even to both, or possibly to neither. In the last case, they may be truly automatic.[67]

Under normal circumstances, the mammalian fetus *in utero* has a quite constant external environment. There is, of course, no method of determining whether the very early types of activity occur in this constant external environment, before the so-called 'quickening.' However, there is no question of the capacity for response to environment, even at 7½ weeks in man.

It might be pointed out that many activities of postnatal infants, which seem to be voluntary, are in fact reflex. Here, also, some are responses to the external environment (as to visual or auditory stimuli, for example), or to stimuli from within (as hunger, internal pain, etc.).

In the development of both fetal and neonatal activity, it is noteworthy that the two environments, external and internal, play an all-important role. Initially, the external environment appears to be the more significant, although even at fairly early ages internal environmental factors may affect the pattern of activity. There seems little doubt that, as the age of the fetus increases, the role of the internal environment assumes more importance.

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