Human Behavioral Development and Genetics

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Behavioral development during childhood is examined in relation to recent concepts and data from evolutionary theory and developmental genetics. The epigenetic framework of Waddington is proposed as a powerful tool for analyzing the progressions in behavior, particularly for recognizing that development involves coordinated pathways of change over time. Many of these pathways appear to depend upon the activity of timed gene-action systems that switch off and on according to a predetermined plan. Behavioral development thus gives expression to the dynamics of pre-programmed change; and in this perspective, behavioral discontinuities may be as strongly rooted in the epigenetic ground plan as the continuities are. The present paper aims to pull together some common themes from different areas that bear on the central issues of behavioral development—the neural foundations, the time course followed, the interplay of maturation and experience, the extent of preorganization furnished by the genetic program, and the adaptive significance of such behaviors in an evolutionary perspective. The final section touches on some hypotheses drawn from developmental neurobiology and developmental genetics that may enrich the analyses of human behavioral development.

Key words: Behavioral development, Evolution, Neurobiology, Developmental genetics, Twins

INTRODUCTION

The topic of this paper is at once an inquiry into the distinctive behavioral programs that characterize all members of Homo sapiens, and at the same time an inquiry into the variations that mark each specimen as unique. If there is a basic species prototype on which each member is modeled, it is also true that variations on the main theme are equally important attributes. Each specimen thus represents a rough casting from the species mold, as shaped by the long course of evolution, but with substantial sculpting added by the genetic diversity among species members. Both aspects are ultimately rooted in the genetic core of the population—the species main effect and the dispersion of individual differences—and it is to these principal factors that the present paper is addressed.

Recent advances in evolutionary theory and developmental genetics have revitalized a fresh interest in the intrinsic determinants of behavior. The distinctive behavioral attributes of Homo sapiens must have been shaped by natural selection as surely as the

physical characters were and must be as strongly rooted in the evolutionary history of the species [25]. Indeed, Waddington [48] has argued that behavior is the driving force in evolution, and in this sense the behavioral repertoire of man is at least as distinctive and as genetically rooted as the physical morphology.

Mayr [51,52] remarks on the genetic basis of certain characteristic behaviors in each species, and how these distinguishing behaviors may help identify which species or subgroup a particular animal belongs to. He concludes that in their genetic basis as well as in their phylogenetic history, such behavioral characters are completely equivalent to morphological characters that are distinctive to each subgroup. Mayr further notes the striking and persistent individual differences in behavior which often seem to be genetic in origin.

Evolutionary theory has made several fundamental contributions to the analysis of human behavior. First, it has brought to bear questions of adaptive significance in infant behavior, and the extent to which such behaviors are intrinsic in the sense of being preprimed and readily evoked under most conditions. Second, it has focused on certain of these behaviors as facilitating the bond with the caretaker, upon whom the infant is massively dependent for survival.

Third, it has brought to bear the techniques of ethology, with its emphasis on detailed observation of emergent behaviors in the natural habitat, as a means of assaying the patterning and adaptive significance of early behavior [53–55]. Finally, it has highlighted the central issue of development as an ongoing, dynamic process by which a single zygote ultimately becomes transformed into a multibillion-cell organism of extraordinary differentiation and detail. Insofar as these manifold growth processes are initiated and regulated by programs in the genetic code, the resultant behaviors must be guided by the same processes.

From this perspective, the powerful concepts from embryology and developmental genetics may furnish a stimulating framework for the analysis of human behavioral development. In particular, this framework keeps attention focused on development as a continuous dynamic process, with episodes of differentiation and growth being switched on and off in accordance with the detailed instructions in the genetic program.

We might suggest that the principles of developmental regulation applicable to biological structures also apply equally to emergent behaviors. Caspari, after surveying the wealth of evidence for gene-controlled regulatory processes that guide cell differentiation, then concluded: "If the general properties of developmental systems are applied to the development of behavioral characters, it does not appear as if any additional principles have to be involved" [7: p 9].

WADDINGTON ON DEVELOPMENT

Few workers have contributed as much to the understanding of developmental processes as the distinguished embryologist C.H. Waddington [45–48]. His concepts have been profitably employed by several investigators in the area of behavior genetics and child development, notably Gottesman [17], McClearn [27], Scarr-Salapatek [37], Bateson [1], and particularly, Fishbein [12].

Waddington himself describes the ideas from embryology as potentially useful analogies for model building in developmental psychology, and he remarks on two important features:

Note first that any concept applicable to development must be one which involves progressive change as time passes; thus we are thinking not of a constellation of processes which just persists, but of a pathway of development.
The characteristic of the pathways of development . . . is that the course they pursue is resistant to modification. If we act . . . to divert it from its normal course, we find that it tends, after the initial fluctuation, to get back to the trajectory along which it had begun to travel [47: pp 19–20].

These general concepts led Waddington to more detailed ones such as chreods or stabilized pathways of development, of canalization and buffering to protect against disruptive influences, of sensitive periods in which development is most readily accomplished, and of time-linked gene-action systems that are switched on and off in sequential order. Developmental processes thus give expression to the dynamics of preprogrammed change, constantly incorporating new episodes of growth into the preexisting phenotype, and being selectively attuned to certain dimensions of environmental input.

This paper presents a highly selective review of several topic areas which seem to offer fruitful concepts and analogies for analyzing human behavioral development. No attempt is made to itemize all relevant studies from behavior genetics which display concordance among twins or family members for various categories of behavior. Excellent reviews may be found in McClearn [27,56], Lindzey et al [57], Broadhurst, Fulker, and Wilcock [58], Scarr-Salapatek [37,59], DeFries and Plomin [60], Willerman [61] and Henderson [62].

Rather, the aim is to pull together some common themes from different areas which seem to bear on the central issues of behavioral development—the neural foundations, the time course followed, the interplay of maturation and experience, the extent of preorganization furnished by the genetic program, and the adaptive significance of such behaviors in an evolutionary perspective. We shall consider first several integrative papers that touch on these themes, then turn to more specific analyses within each topic area.

FISHBEIN ON EVOLUTION AND CHILD DEVELOPMENT

Fishbein [12] has written a stimulating book in which he traces the progressive increments of brain structure that have evolved for Homo sapiens, and how these newly evolved structures of the neocortex only gradually become functional during childhood. One recurrent theme concerns the different rates of maturation for these structures and their effect upon the specific behavioral capabilities supported by these structures.

Fishbein provides an illustration by showing that, while language and other motor skills are correlated on a species-wide basis, there may be considerable asynchrony for a given child—that is, language development may be delayed while other motor skills are not, or vice versa. Bateson [1] has remarked on the same phenomenon and also noted that early or late development is rarely significant for the ultimate level attained. These data suggest different gradients of maturation for particular capabilities which may be partially out of phase, but which have no necessary influence on the level attained at maturity. It is a theme that will reappear in several contexts.

Fishbein [12] has also provided a comprehensive translation of Waddington's concepts [46] into the area of developmental psychology, and he proposes that behavioral development is guided by epigenetic processes that have been mapped out by evolution in the

genetic blueprint. Development proceeds towards certain targets or end-states—guided by an intrinsic template, so to speak—and it maintains this directional focus by means of canalization. Fishbein defines canalization as follows:

> Canalization involves a set of genetic processes which insure that development will proceed in normal ways, that the phenotypic targets will be attained despite the presence of minor abnormal genetic or environmental conditions. Canalization processes operate at each point in development to correct minor deflections from the sought-for phenotypic targets [12: p 7].

Canalization means that certain patterns of behavior are easily, almost inevitably, acquired by all species members under the normal circumstances of life. Such behaviors come with a high degree of preorganization and priming laid down in the brain structure by evolution, and they are actuated in straightforward fashion except in the most extreme circumstances. In this sense, canalization underwrites the species-specific behavioral programs that push each member along a common developmental pathway. However, canalization also preserves the dispersion of individual differences by buffering the zygote against early insult and reorienting each infant along its unique developmental pathway if once deflected.

BATESON ON SELF-STABILIZING DEVELOPMENTAL PATHWAYS

Bateson [1] gives a thoughtful interpretation of Waddington's epigenetic model as it pertains to the capacity of a developing system to correct itself after some disruption. He illustrates with a model for weight regulation and recovery after early deficit, and he relates this self-correcting process to a similar concept from systems analysis, whereby the same final state may be reached by convergence via different routes.

Bateson then considers whether there may be two or more alternative systems controlling the development of a particular behavior pattern. Clearly, redundant developmental systems would be highly adaptive, with the added systems helping to protect against failure or to cope with a changed environment. Such redundant systems would provide a degree of plasticity in the face of different environmental conditions, and the actual behavior patterns would be guided by control systems that match actual input values with some intrinsic end-state values. This is also the essence of the canalization concept, whereby development is impelled along a particular pathway with constant self-correcting adjustments until some targeted end-state is reached.

It might be noted that these concepts touch on some fundamental questions related to gene activity—for example, what furnishes the signal that a particular developmental mission is accomplished and that the differentiating processes can stop rather than running on unchecked? The whole concept of targeted end-states, or intrinsic templates to be matched, implies that developmental processes are self-limiting and are constantly involved in a match-to-model process with the inherent growth equation.

Further, these targeted end-states are not "known" in any teleological sense. They must reflect evolved mechanisms that terminate the ongoing process via the same material agents that also initiated the process. An adequate explanation must encompass all three features—the dynamics of growth itself, with its extraordinary differentiation of form and function; the capability to preserve the prescribed developmental pathways in the face of deflecting agents; and the precise termination of developmental episodes as each

subroutine of the developmental program is accomplished. Some speculative hypotheses from developmental genetics and neurobiology will be briefly considered at a later point.

GOTTESMAN ON DEVELOPMENTAL GENETICS AND CHILD DEVELOPMENT

Gottesman [17] provided a stimulating paper which, in his words: ". . . has as one of its main objectives the communication of my conviction that we must start now to build a bridge between developmental genetics and ontogenetic psychology" (p 55). Gottesman reviews the recent work in developmental genetics concerning the switching on and off of gene-action systems, and he then illustrates how these concepts can enrich the interpretation of individual growth curves. The differences in timing of rapid growth spurts brings to the forefront questions about the differential switching on and off of maturational processes and stages.

Gottesman also notes that only a small portion of the genotype is active at any given time, a feature that in itself contributes to time-linked phases of development and thus may generate different developmental trajectories even for closely related zygotes. The dispersion of individual differences is further emphasized by Gottesman for the concepts of canalization and buffering against deviant conditions: some behavior patterns are canalized species-wide, but with significant individual variations in the strength of canalization and resistance to deflection.

MANNING ON GENES AND BEHAVIORAL DEVELOPMENT

Manning [26] moves a step further in relating individual differences in development to the effects of genes. He states the central question as follows: "How is behavioural potential encoded in genetic terms and expressed in the course of development?" (p 327). He adds that there must be a strategy to behavioral development, and different sets of genes may be operating at different times.

Manning (p 338) then makes a trenchant observation: ". . . we must also look for genetic discontinuities in the course of development. Such discontinuities could indicate the existence of distinct sets of genes becoming activated that would in turn have a bearing on the units problem" [i.e., the changes in behavior measured over successive ages]. This particular observation has direct bearing on several current theories that emphasize discontinuities in behavioral development [eg, 63–65], and it suggests that some discontinuities may be plausibly related to the time-ordering of developmental processes in the genetic program.

The point may be illustrated by mental development data obtained for a large sample of monozygotic and dizygotic twins. The twins were tested from 3 months to 6 years of age, and several representative curves are shown in the Figure (from Wilson [49]).

The curves show that many individual twins made substantial changes in their test scores from age to age—a graphic illustration of behavioral discontinuities, and a reflection of age-linked spurts and lags in mental development for each twin. But in the case of monozygotic twins, these spurts and lags were synchronized over age, and to a significantly greater degree than for dizygotic twins [49]. These synchronies in the course of mental development suggested that the underlying processes were guided by timed gene-
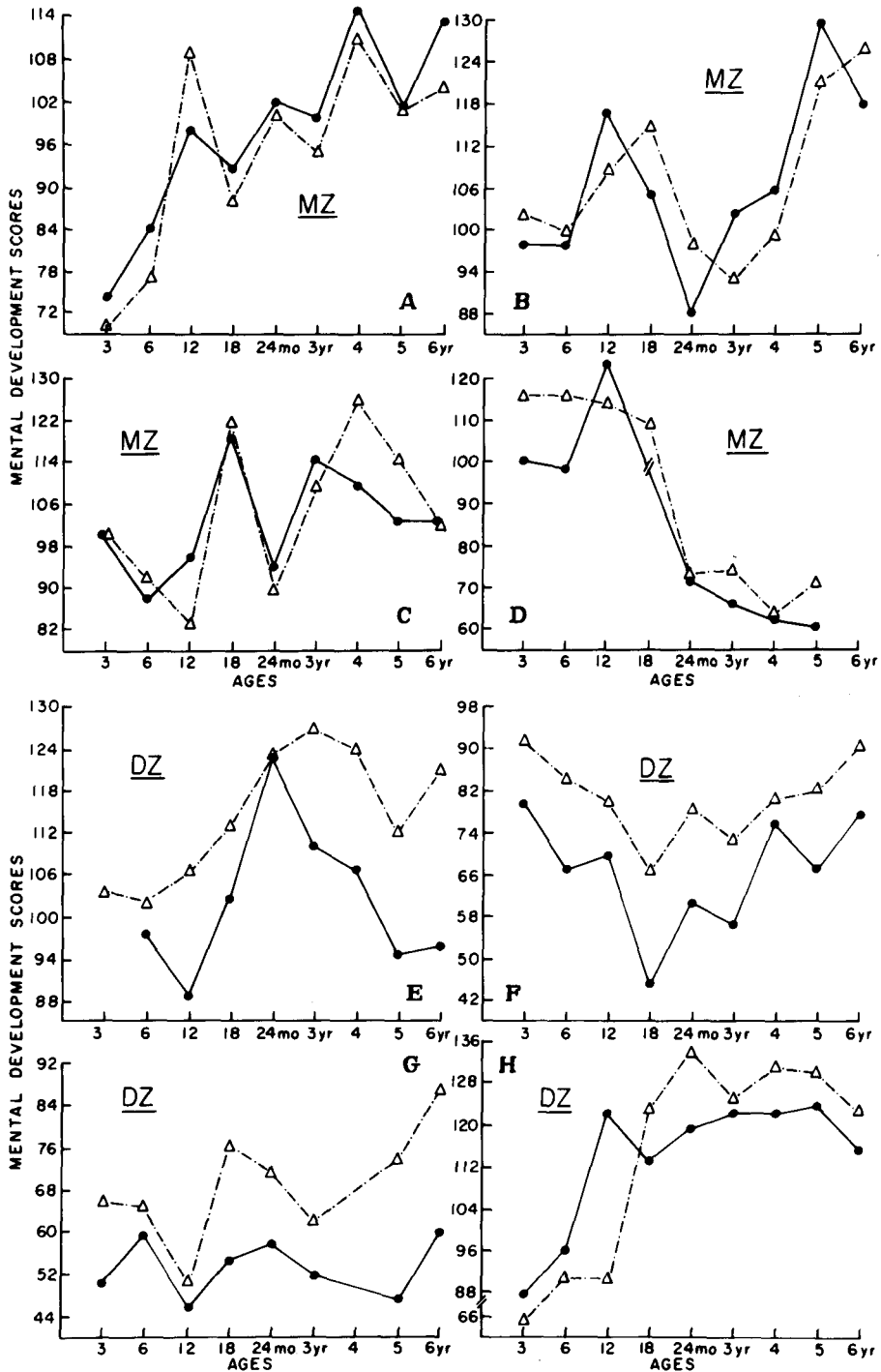
Figure. Illustrative mental development curves for monozygotic (MZ) and dizygotic (DZ) twins. From Wilson [49].

action systems, which became activated in sequential fashion and which followed a parallel course for two zygotes sharing the same genotype. The behavioral discontinuity, therefore, had its roots in time-ordered developmental processes originating in the genotype.

FREEDMAN ON HUMAN INFANCY

We turn now to studies that focus upon the adaptive significance and survival value of infant behavior. Freedman [13] builds upon the same background of evolution and natural selection as the previous studies, but he gives special emphasis to the characteristic behaviors of the human infant and what adaptive function these behaviors serve. In fact, adaptive significance is the principal theme in Freedman's analysis, and it is at the core of his interpretation of infant smiling and attachment. Freedman concludes [13: p 45]: "Some of the capabilities of the newborn . . . are clearly adaptive from the infant's viewpoint in the sense that they strengthen the social bonds and elicit caretaking on the part of the parent."

The newborn's capabilities extend beyond these socially facilitative behaviors, however. After reviewing the data on perceptual constancies as demonstrated in infants, Freedman remarks:

> Given the basic adaptive value of the perceptual constancies, is it possible that they have to be relearned in each lifetime? Evolutionary logic yields a negative answer and it seems that learning proceeds easiest in directions determined by phylogenetic evolution; that is, evolution has dug the major channels through which the river of experience runs. Said another way, natural selection frequently yields differential thresholds for learning rather than full-blown species-specific behaviors [13: p 28].

Freedman furnishes several notable illustrations of canalization in infant development and the powerful self-directing tendencies of these developmental pathways. He further notes the striking individual differences among infants in strength of attachment and response to separation, a point that is also confirmed by Sroufe and Waters [66] and by Mineka and Suomi [67].

SUPER ON CROSS-CULTURAL DEVELOPMENT

If the various features of infant behavior are an end-product of evolutionary adaptations, and if these are uniformly represented among all populations of infants, then it is of interest to see how strongly the communalities are represented across cultures. Super [40] has just completed such a survey, which in the number of titles cited (over 500) gives an indication of how prolific such studies have become.

He remarks that each cultural niche does seem to have some bearing on the rate at which certain capabilities develop, but perhaps the strongest theme is the species-wide regularity in the way stations of development. While there is no aspect of human development unaffected by culture, the hallmark of cognitive abilities is perhaps the least malleable by our cultural variety. As with motor skills, there is a fine patterning in the timing of universal developments [40: p 160].

PIAGET ON COGNITIVE DEVELOPMENT

Super's reference to the species-wide regularities in cognitive development may be co-ordinated with the Piagetian conception of successive stages unfolding in invariant order and building upon the experiences of the preceding stages. Piaget's theory [32] touches on the fundamental operations and transformations accomplished by all human infants, and indeed his detailed microanalysis of cognitive functioning may be regarded as the basic itinerary for the species.

Since some of Piaget's interpreters in this country, notably J. McV. Hunt [20,21], have given very heavy emphasis to the role of cumulative experience in initiating the progressions in cognitive development, it is instructive to consider Piaget's own statements about the foundations of cognitive processes. The issue is addressed principally in *Biology and Knowledge* [33]. Piaget opens by remarking that knowledge does not imply making a mere copy of reality, but rather of transforming the input in accordance with the basic programming of the brain, and in accordance with prior experiences and actions. He adds:

> It goes without saying that these regulatory mechanisms, in knowledge at all levels, raise the problem of their relationship with organic regulations. The central problem with which this book will have to deal is, therefore, that of the relationships between cognitive and organic regulations at all levels [33: p 12].

Piaget then draws specifically from Waddington for developmental concepts applicable to growth of intelligence. He employs the term chreods (or necessary routes) to describe how an embryo becomes progressively differentiated into a complex organism, then concludes:

> It is impossible to take note of such a picture without immediately thinking of the far-reaching analogies it has with the development of schemata or ideas in the intelligence. . . . Briefly, intellectual growth contains its own rhythm and its "chreods" just as physical growth does. The epigenetic process which is the basis of intellectual operations is rather closely comparable to embryological epigenesis. . . . [33: pp 21–23].

Piaget's further application of epigenetic concepts to the growth of intelligence is detailed and extensive, and he draws at length on many recent works in developmental biology, population genetics, and evolutionary theory. It is perhaps time to acknowledge this fundamental framework within which Piaget's theory has been formulated, and to recognize that the premise of genetic regulation of cognitive development is not the anathema for Piaget that it is for some who cite him frequently.*

A balanced discussion of Piaget's theory from a psychobiological perspective may be found in Kohen-Raz [68], and this volume also provides coverage of other topics and theorists that attend to the biological foundations of cognitive development. The conclusion seems inescapable that the integrative power of the brain is the end product of developmental processes that have been endlessly sharpened and refined by evolution, and that are played out according to a unique chronogenetic schedule for each specimen.

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*A recent paper by Kitchener [23] also examines the concept of epigenesis and whether it might be applicable to behavioral development. After an extended discussion of organic epigenesis as being relatively impervious to environmental fluctuations, Kitchener then argues that the concept cannot apply to behavioral development, since everyone agrees that environmental factors play a powerful role in human behavior. This conclusion, however, seems to rely mainly upon implied consensus and personal conviction, and it does not furnish a persuasive reason for excluding the concept of epigenesis from developmental psychology.

THOMAS AND CHESS ON TEMPERAMENT

Perhaps no aspect of infant behavior is more obvious to parent or professional than the earliest patterns of irritability and reactivity in the neonate. They seem to reflect intrinsic response characteristics, and they exert a marked influence on the developing infant-caretaker relationship [3,24].

A detailed and provocative body of research on temperament has been conducted by Thomas and Chess and their colleagues at the New York Longitudinal Study [42,43]. The focus of the program was upon behavioral differences found among infants in the early months of life, and how these differences influenced later development. For many infants, individualized patterns of reactivity were evident at this early stage, and certain behavioral clusters were observed that seemed to reflect different styles of temperament—easy, difficult, and slow to warm up.

In considering the origins of temperament, Thomas and Chess [43] surveyed the evidence for genetic influences and concluded that they played an appreciable but by no means exclusive role. Environmental influences might accentuate, modify, or even change temperamental traits over time.

Carey [5] in his recent review reached essentially the same conclusion, and he called particular attention to the problem of assessing the consistency in temperament for a given infant (a matter also discussed by Rutter [36] and Thomas and Chess [43]). The general expectation is that if temperament is rooted in constitutional/genetic variables, there must be some continuity in its expression over the developmental history of the child.

But a variety of normal phenomena may confound efforts to demonstrate stability of temperament, not the least of which are varying rates of maturation of the underlying CNS structures and of age-linked behavioral competencies that may markedly alter the mode of expression for a given temperamental style. The problem (and the challenge) is one of determining when dissimilar behaviors over time reflect the same characteristic style, recognizing that the behavioral criteria must necessarily be age-specific, and therefore the criteria must coordinate with each other as homologies rather than exact replicas.

It is worth noting that there are now several longitudinal twin studies in progress that are examining the patterning and concordance of temperament variables for infant twins [69–72]. Aside from addressing the issues of continuity/discontinuity over ages, these studies may reveal whether the apparent changes in temperament occur in parallel for both members of a twin pair. The earlier quote by Manning [26] might be recalled here, since it relates to possible genetic discontinuities in behavior. Perhaps the discontinuities in temperament may also reveal an underlying patterning or synchrony for monozygotic twins, as was true for mental development.

MATURATION AND BEHAVIOR

The theme of maturation has been revived in several of the preceding papers after a period of virtual exclusion from developmental psychology, and it may be instructive to reconsider some of the earlier findings. Two of the classic twin studies contributed to the area—Gesell and Thompson's study [15] of twins raised in a nursing home from 2 weeks to 18 months of age; and McGraw's longer study [28], continuing until the twins were 6 years old. In both studies one twin was given special training and the other was not, being left simply to its own devices for self-initiated activity. The effects of special training were transient at best, particularly in relation to the standard species-typical activities such as grasping, crawling, creeping, and walking. McGraw [28] remarked that

the major aspects of these phyletic activities had become determined during phylogeny to such an extent as to be resistant to alteration. She noted some greater effects of specialized training on more complex activities such as swimming, skating, and riding a tricycle, although the interpretation was clouded somewhat when the twins were later diagnosed as fraternal rather than identical.

Gesell's twins were clearly identical and thus provided a co-twin control for assessing the net benefits of special training, and the contrasting role of maturation in promoting behavioral competencies without special training. Gesell noted that there was a high degree of similarity in the twins' development, and the differences were of a small nature, even in the area of emotional behavior. He concluded [15: p 114]: "These findings point consistently to the preponderant importance of maturational factors in the determination of infant behavior pattern . . . . Although function enters into the growth, training does not transcend maturation."

Munn and Carmichael on Maturation

Aside from these two case studies of twins, the behavioral development of children and its correlation with maturational status has been broadly surveyed in Munn [30,31] and Carmichael [6]. Both of these sources are useful for their very detailed coverage of the behaviors that may be studied in the human infant and for illustrating the nominal effects of special training or exercise in accelerating these behaviors. Munn's conclusions basically echo those of McGraw and Gesell, but he adds one of particular interest, namely that the efficacy of training or special exercise is directly proportional to the degree of maturation of the underlying mechanisms.

This latter point is significant not only for coordinating behavioral development with the steady advance in maturation of brain structures, but also for identifying a crucial dimension of individual differences. The differences in maturation rate have a profound influence on the degree of advancement or lag for individual children, and indeed there may be an uneven rate of progression within the same child for different behavioral capabilities [11].

THE BRAIN AND BEHAVIORAL DEVELOPMENT

Since the brain is the ultimate structure underwriting human behavioral development, it is instructive to consider the present evidence for the extraordinary precision and detail by which the various regions of the brain become progressively interconnected and rendered functional. Sperry, a premier contributor in this area, provided an eloquent overview and interpretation of his work [38,39], and then offered his conclusion that the growth of neural circuits is principally guided by indigenous chemical processes.

> The complicated nerve fiber circuits of the brain grow, assemble, and organize themselves through the use of intricate chemical codes under genetic control. The outgrowing fibers in the developing brain are guided by a kind of probing chemical touch system that leads them along exact pathways . . . [until they] connect with certain other neurons, often far distant, that have appropriate molecular labels [39: 30–32].

Exactly how this precise wiring is coded in the DNA and then executed remains an unsolved problem [19]. There is no doubt, however, that the brain becomes wired in an extremely precise manner during development, and an excellent survey of how these connections become established and organized may be found in Cowan [9].

Equivalently precise wiring for the autonomic nervous system has been reported [73], with central neurons extending to highly specific peripheral sites; and it now appears that, in infant mammals, central pathways within the brain can be regenerated and accurately reconnected even after damage [22]. The authors reported that when the pyramidal tract axons were cut in infant hamsters, there was a massive regrowth of the severed axons to their appropriate terminal sites in the medulla and spinal cord. The results were interpreted as suggesting that CNS axons damaged early in life might regenerate in a functionally useful way.

The long-standing observation of greater recovery of function among the young after CNS injury [18] now appears to have a possible foundation in the regeneration of neural connections, and this in turn raises the fundamental question of how specific cells become committed to a certain fate, and how they retain the capability to duplicate again a previously executed pattern of growth.*

MATURATION AND CNS FUNCTIONING

In addition to the precise wiring accomplished in the central nervous system, the orderly progression of functions is intimately connected to the maturation of these neural structures. Goldman [16] has recently surveyed a large number of studies with reference to the maturation of the nervous system and its effect upon behavior. She notes that there is a strong interdependence of structure and function, even at the cellular level, and many cells do not attain fully mature status and become functional until long after they originate. She adds that the gradient of maturation is not necessarily synchronized for neurons of different types, nor for similar neurons located in different regions of the brain.

Goldman then turns to studies showing that certain cortical regions responsible for delayed-reaction responses and complex perceptual tasks only slowly mature, and that in some animals this process of maturation may extend over a period of 2 years or more. With humans, of course, the period is even further extended [8]. Other reviewed studies on visual deprivation and on cortical lesions inflicted at various ages all testify to intrinsic regenerative processes that affect the extent of deficit and degree of recovery.

Goldman's review [16] is very thorough and detailed, and her summary is worth quoting.

> Development is by definition a sequential process. One function of a stepwise maturational progression may be to regulate the order and impact of internal and external stimuli and experience on the developmental process itself. Thus . . . the maturational status of the organism provides a filter through which only a subset [of stimuli] can be effective at particular times [16: pp 70–71].

This review suggests a revised view of maturation that is closely coordinated with definable properties of the nervous system at every level from the cell upward. The

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*The regeneration of neural connections is only one of several remarkable findings now emerging from developmental neurobiology. It has become apparent that many more neural cells are generated than ultimately survive, and these cells are eliminated by tightly programmed phases of cell death [9]. Further, there is a proliferation of synaptic connections for each neuron during early development, but the surplus connections are progressively eliminated until only a single neural connection remains [35]. A concise but wide-ranging summary of recent developments in this field may be found in Purves [74], and it illustrates the far-reaching effects of programmed biological events on the wiring of the brain and its regulation of behavior.

functioning of the brain is dependent not just on the formation of cells or influx of experience—it is dependent on the maturation of these structures, which involves growth in cell size, myelination of fibers, proliferation of dendrites, and the exponential gain in connections among cells and fibers [16,41].

Further, maturational processes are subject to wide and pervasive individual differences; and even within a given child, the time course of development across behavioral systems may be partially disjunctive and out of phase. These phenomena suggest a foundation in timed gene-action systems that furnish a detailed timetable of emergent capabilities, fixed in broad outline by the basic species program, but idiosyncratic in detail for the individual.

CONCEPTS FROM DEVELOPMENTAL GENETICS

This final section will touch briefly on some recent advances in developmental genetics that seem to hold promise for a fuller understanding of the mechanisms underlying behavioral development. The focus is upon gene action at the cellular level and its role in promoting the differentiation by which a cell becomes committed to a particular function and then matures according to a set schedule.

Since all cells start with the same genetic material, it seems apparent that only a limited portion of the gene complex is activated within each cell, and this in turn is dictated by the timing of certain key regulatory events. Related clusters of cells then construct the integrated components of the central nervous system, and these several components interconnect and become functional in accordance with intrinsic maturational schedules. The developmental progressions in behavior therefore represent the end-product of an extraordinary collection of timed gene-action systems that have their origin at the cellular level, and that in aggregate dictate the rates of growth and maturation for the interlocking neural systems that underwrite behavior.

How is the commitment of each cell to a particular function determined? Present evidence suggests that, in each cell, only the small subset of genes needed to guide that cell's special behavior are activated, and the remaining genes are inhibited or repressed [10]. At a prescribed point in the developmental process, the target genes are activated that shape the cell into a particular form, and all other genes thereafter remain repressed.

Prior to the point of differentiation, the cell is virtually equipotential—it can be shifted to an alternate outcome if transposed to another site—but once differentiation has taken place, the cell is committed to a particular fate, and the repressed genes lose their effectiveness.

While there is some disagreement about whether these genes are irreversibly repressed or not [eg, 4], the major conclusion seems clear: As development proceeds, the developmental potential of each cell (ie, its ability to differentiate into a number of different phenotypes) is markedly restricted. Thus, a large portion of cells from developmentally advanced tissues have restricted potential, and the percentage of cells that retain unlimited potential progressively declines as development proceeds [4].

One intriguing speculation that the above conclusion suggests is a model for the greater recovery potential following CNS insult in younger organisms, whereby a larger number of cells might retain unlimited developmental potential and would subsequently be recruited to help restore a compromised function. As Goldman [16] has observed, the developing nervous system has a quantitatively greater capacity for reorganization than the mature nervous system; and both clinical and experimental data on brain injury and recovery of function seem to be emphatic on the same point [18:especially Chapter 9].

Perhaps there are distinctive gradients in the retention of developmental potential among the various cell clusters of the brain, and the recuperative potential of each cluster declines as the cells become differentiated and fixed into a specific state. A speculation might be that the evolutionarily more recent brain structures, and those that are slower to mature, are the ones with a higher retention of developmental potential in the cell cluster. It may also be that the strongly directional and self-correcting processes involved in canalization are ultimately dependent upon the retained potential of aggregate cell clusters to proceed towards their targeted end-states. Once a cell cluster has been given its direction by the target genes, the cluster moves persistently in that direction until the differentiating processes have run their course.

COMPARTMENTS OF DEVELOPMENT

How does the commitment of individual cells to a particular fate ultimately produce a highly differentiated organism? A detailed and lucid description of how gene-regulated developmental processes serve to construct the organism on a piece-by-piece basis has been published by Garcia-Bellido et al [14]. They note initially that the blueprint for accurate development is encoded in the DNA; then they remark that organisms seem to be made up of different but fundamentally homologous compartments.

The authors describe experiments in which each segment of an insect seems to result from the activity of a few founder cells that determine the actual structure to be formed, and then accomplish this by creating daughter cells that carry genetic information about where to locate and how to form. These cloned cells have a precisely defined destiny in the sense of contributing only to their home compartment, and they become marked by a distinctive genetic address that is subsequently passed along to their progeny.

> In summary, we suggest that each piece of the insect—a compartment made by a particular group of cells—is specified by a genetic address, in effect a binary zip code representing the decisions of key regulatory genes. The final binary code in an adult cell contains the history of the decisions made by the cell's ancestors [14: pp 107–108].

The authors then consider whether the same model might be applicable to higher organisms, and they close with the following query: "Do insects, mice and man all develop according to a similar genetic strategy, expressed in compartments?" (p 110). Acknowledging the rhetorical nature of the query, the implied answer would seem to be in the affirmative.

These studies bear witness to the extraordinary precision and detail of gene activity in regulating the course of development. Perhaps the above question might be paraphrased in the following terms: Is behavioral development guided by a genetic strategy analogous to that for biologic development? The answer would also seem to be yes, both at the species level and in the realm of individual differences. If, as Carmichael [6] says, behavior is structure in action, then it can hardly be divorced from the profound developmental processes by which the structures are formed.

The end-product—the phenotypic behavior of the human, cradle to grave—is distilled from the constant interplay of genetic material and the environmental surroundings. But the message, the conserved microfilm of evolution's choices, is preserved in the genotype, and it is progressively actualized throughout the life span. Perhaps an appreciation of this fact can help anchor the concepts in developmental psychology and lead to a more comprehensive model for assaying the determinants of behavior.

IMPLICATIONS FOR RESEARCH STRATEGY

What strategy for studying behavioral development would seem most appropriate from this standpoint? Clearly, if each child's development is characterized by distinctive episodes of spurt and lag—if, indeed, the steady progression of behavioral capabilities in any domain is subject to individual variations—then it would require detailed longitudinal data to document the collective pathways of development. Waddington's remark is worth recalling here, to the effect that a developmental process is one that involves progressive change as time passes, not one that simply persists. The phasing and scope of these progressive changes only become evident via repeated measurements on the same individual over time.

This strategy also puts a high premium on reliable data, so that the continuities and discontinuities in behavioral development may be confidently treated as genuine phenomena, and not as by-products of measurement error. It is a particular burden in early childhood, since standardized behavioral assessments are more the exception than the rule, but it is an absolute core requirement if we are to fully comprehend the progressions in development. Given the state of the art in behavioral assessment, a multimethod approach would be the preferred vehicle for securing a stable composite measure on each child.

Finally, if the continuities and discontinuities in behavior are to be examined for potential genetic influence, then the use of infant twins may be recommended as a vital first step. To the extent that monozygotic twins display synchronized pathways of development in significantly greater degree than dizygotic twins or sibling pairs, the role of genetic factors may be affirmed. In fact, the relative contribution of genetic and environmental factors to the pathways of development may be articulated by examining the patterns of convergence and divergence among matched pairs of infants. Ultimately, it is from such comparisons that the behavioral trajectories will be brought into coordination with the underlying foundation processes.

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