

The Louisville Twin Study: Developmental Synchronies in Behavior

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WILSON, RONALD S. *The Louisville Twin Study: Developmental Synchronies in Behavior*. CHILD DEVELOPMENT, 1983, 54, 298–316. The Louisville Twin Study includes nearly 500 pairs of twins and their siblings who have participated in a longitudinal study of mental development, beginning in infancy and extending to adolescence. The results show that individual differences in intelligence progressively stabilized by school age, and each child followed a distinctive pattern of spurts and lags in mental development. Monozygotic twins became increasingly concordant over ages and matched each other closely for developmental trends. By contrast, dizygotic twins regressed to an intermediate level of concordance, comparable with that found for siblings and parent-offspring sets. A comprehensive home assessment was performed to identify the home/family variables that contributed to mental development. The overall results pointed to a strong developmental thrust in the growth of intelligence, which was principally guided by an intrinsic genetic ground plan. Qualitative features of home and family did, however, add significantly to prediction of offspring IQ. The results are interpreted in the context of Waddington's developmental model, and some recent advances in neurobiology and genetics are surveyed for their implications for developmental behavior genetics.

"It is most important to appreciate that the influence of genes is not manifested only at conception or at birth or at any other single time in the individual's life history. Developmental processes are subject to continuing genetic influence, and different genes are effective at different times" (McClearn, 1970, p. 61). "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'" (Waddington, 1971, p. 19).

In capsule form, these two quotations express the essence of developmental behavior genetics. As a specialty, it focuses on the emergence and development of behavioral processes, and it inquires into the role played by genetic factors in promoting behavioral development. The operative concepts are drawn from evolutionary theory and developmental genetics, which keep attention focused on development as a continuous dynamic process.

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It explicitly acknowledges that phases of neural differentiation and growth may be switched on and off in accordance with instructions in the genetic program and suggests that there are functional parallels at the behavioral level. Developmental processes thus give expression to the dynamics of pre-programmed change, constantly incorporating new episodes of growth into the preexisting phenotype and being selectively attuned to certain dimensions of environmental input.

Twins and Development

If physical growth is taken as a model, the study of developmental processes in twins furnishes a powerful resource for examining the role of gene-action systems in guiding the course of growth. While there is a steady and rapid progression from birth onward, the growth rate is not entirely uniform for a given child; rather, it moves in episodes of acceleration and lag. The timing of the growth spurts follows a distinctive pattern for each child, and consequently a child who may be smaller than average at one age may

then enter a phase of rapid growth and ultimately catch up with or surpass his peers at a later age.

The effect of such individualized patterns of growth is that many children may change in relative size from one age to the next; and in this sense it may appear that the underlying developmental processes are erratic rather than coherent. But if there is an underlying ground plan, a chronogenetic pattern, then the distinctive developmental gradients should unfold in synchrony for twins sharing the same genetic makeup. Episodes of acceleration and lag in growth would then occur in parallel for both twins and would presumably represent the activity of timed gene-action systems, which switch on and off according to a predetermined plan (Wilson, 1981b).

Turning to the area of behavioral development, how might these individualized pathways be revealed? The most extensive data have been collected in the area of mental development, and Bayley (1955, pp. 813–814) gave a clear description of how such distinctive developmental gradients might be shown: “[In] individual growth curves, there may be plateaus, periods of no growth, and occasionally actual decrements. There may be rapid forging ahead. Each child appears to develop at a rate that is unique for him.”

The problem of confirming these individualized pathways in mental development as a systematic effect has been complicated by the problem of measurement error when assessing young children. If there are age-to-age discontinuities, do they reflect measurement error and/or transient environmental influences, or are they an expression of genuine asynchronies that may have a biological basis? In recent years such discontinuities have been used to challenge the validity of infant tests and to dismiss the possibility of any intrinsic determinants of mental development.

But as Manning notes (1976, p. 338), “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,” that is, the changes in behavior measured over successive ages. This observation suggests that some behavioral discontinuities may be plausibly related to the time ordering of

developmental processes in the genetic program.

From this perspective, a longitudinal research program with infant twins offers a powerful resource to study the determinants of behavioral development. Monozygotic (MZ) twins provide the rare natural experiment with humans in which two zygotes share exactly the same genotype and are raised in the same family environment.

Dizygotic (DZ) twins, by contrast, share a variable number of genes in common (50% on the average), proportionally the same as any other pair of siblings from the same family. However, dizygotic twins have further shared the homogeneous experiences of being born and raised as twins, which should enhance their similarity in comparison to siblings. If the collective influences of gene action and prenatal and postnatal environment dictate the course of mental development, then the contributions of the various factors may be estimated from comparison of monozygotic twins with dizygotic twins and nontwin siblings.

Assessment of Mental Development

Method

The Louisville Twin Study was initiated more than 25 years ago (Falkner, 1957), and the backbone of the program is the large number of young twins who have made regular visits to the study for testing. At present, there are 494 pairs of twins active in the longitudinal study, ranging in age from 3 months to 15 years. Recruitment has been an ongoing process, with 25–35 pairs added each year since 1963.

The twins have been recruited from the Board of Health records of twin births in the metropolitan Louisville area, and a special effort has been made to make the sample as representative as possible. In terms of socioeconomic status, 27% of the twin families are ranked in the lowest two deciles of the occupational rating scale (Reiss, 1961); 11% are in the highest two deciles. The other families are distributed in roughly equal proportions among the six intermediate deciles (8.8%–11.8%). Attrition has been minimal because of intensive efforts to follow up on families that move frequently and to maintain their cooperation.

Ages at testing.—The twins are tested initially at 3 months of age, and they make

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subsequent visits every 3 months during the first year, every 6 months during the second and third years, and annually thereafter to age 9 years. A final follow-up test is scheduled at age 15 years. The ongoing nature of recruitment means that many twins have not completed 15 full years in the program, but nearly two-thirds of the sample have test data covering at least 6 consecutive years.

Tests of mental development.—The tests employed in this program have been selected from the best standardized and most carefully constructed psychometric tests available. In this regard, some new and revised tests for preschool children have become available within the past 15 years which represent major advances in assessment. Bayley's lifetime work in mental development culminated in the Bayley Scales of Infant Development (1969), and it was the first well-standardized instrument for infant appraisal. The Stanford-Binet Form L-M was restandardized on a fresh sample in 1972 (Terman & Merrill, 1973), and these new norms corrected for many of the deficiencies in the original 1937 standardization sample.

The Wechsler Preschool and Primary Scale of Intelligence (WPPSI) was published in 1967 (Wechsler, 1967), and it represented a well-standardized downward extension of the Wechsler Intelligence Scale for Children. The McCarthy Scales of Children's Abilities (McCarthy, 1972) were recently published, and while the scales differed somewhat in focus from the Binet and WPPSI—particularly by avoiding any reference to IQ—nevertheless they sampled domains of cognitive abilities that were collectively metricized by a general cognitive index. Finally, the revised version of the Wechsler Intelligence Scale for Children (WISC-R) was released in 1974, and it updated the norms, items, and scoring of the WISC to contemporary standards (Wechsler, 1974).

The importance of such standardized psychometric instruments can hardly be overestimated. They furnish a means of appraising mental development during a period of rapid growth, as well as a means of obtaining a reliable assessment of individual differences. Children are compared with a representative sample of their age peers, and their relative placement (whether advanced or delayed) is expressed in a standard-score format that remains constant across ages and tests. Episodes of acceleration and lag now become interpretable as genuine phenomena, not simply as by-products of measurement error.

These crucial features of standardization and scoring have never been available in previous tests, and in a literal sense the recent tests may be classified as benchmarks of mental measurement. When employed with a longitudinal twin sample from birth into the school years, the tests yield a detailed picture of each twin's mental development from infancy onward and a measure of concordance among co-twins.

Tests and ages.—The Bayley Mental Scale has been administered at 3, 6, 9, 12, 18, and 24 months of age; the Stanford-Binet at 30 and 36 months; the WPPSI at 4, 5, and 6 years; and the WISC or WISC-R at 7, 8, 9, and 15 years. Recently the McCarthy test has been substituted for the WPPSI at 4 years because it gives a broader sample of the child's behavior at this age. Each test converts the raw scores into age-adjusted standard scores with a mean of 100 and SD of 16 (15 for the WPPSI and WISC).

At each visit, the twins were tested by separate examiners, who also alternated between the twins over successive visits. The test procedures were rehearsed intensively to assure comparability among examiners, and the test scoring was verified by a third examiner before the scores were recorded.

Zygosity determination.—Zygosity was established for same-sex pairs by blood typing on 22 or more red cell antigens (Wilson, 1980). If the results were concordant for all antiserum tests, the twins were classified as monozygotic; if the results were discordant for any test, dizygotic. For technical reasons, the blood typing was deferred until the twins were 3 years old, so the infant tests were completed before zygosity was established. Opposite-sex twins were classified as dizygotic on the basis of the sex difference.

Results

Since these twins have been tested repeatedly during infancy and childhood, the basic data may be illustrated by plotting the mental development curves for several pairs. These pairs were selected to illustrate the different trends that may be found and the degree of congruence within each pair in matching the trend. The curves are presented in Figure 1.

The monozygotic twins shown in Figures 1A, 1C, and 1D display quite different trends in mental development, but there is a high degree of congruence within each pair. Note especially the upward trend for the twins in Figure 1A and how it contrasts with the

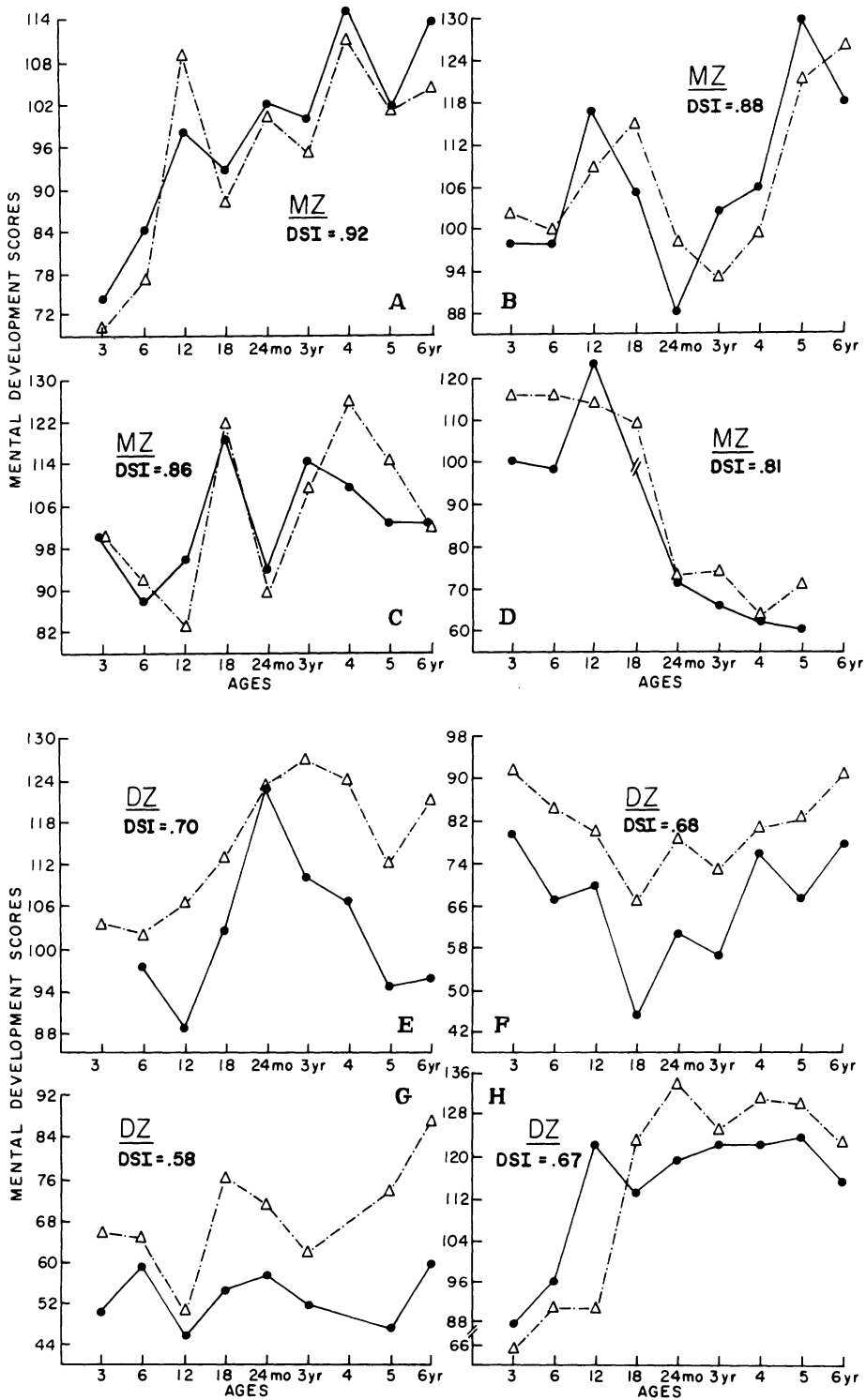


FIG. 1.—Trends in mental development during early childhood for four MZ pairs and four DZ pairs (from Wilson, 1978).

downward trend in Figure 1D. It appears that the inner programming can dictate trends in either direction, and the degree of advancement or lag in the early months has little bearing on the ultimate level reached by school age.

The dizygotic twins in Figures 1E and 1F show a greater divergence in trend during childhood, although the main directional shifts are much the same. The pair in 1H exemplifies those dizygotic twins that maintained quite similar trends after the first year, perhaps reflecting a high degree of genetic overlap and common experience.

Each pair's concordance for developmental trend can be expressed by a developmental synchronies index, which reflects the goodness-of-fit between the two curves. It was computed in a manner analogous to the within-pair correlation for the full sample;¹ as shown for the pairs in Figure 1, the values ranged from .58 to .92. Thus, while the developmental trends may have generated sharp peaks and troughs over ages, the MZ pairs in particular displayed a synchronized pattern of change.

When the full sample was considered, the basic question was whether monozygotic twins as a group were more concordant for mental development than dizygotic twins. As a prologue to this analysis, however, the continuity in mental development from infancy onward was appraised for the entire sample.

The curves in Figure 1 showed that there was considerable change in scores from age to age for some infants, and it appeared to be more pronounced at the earlier ages. On a samplewide basis, the extent of this discontinuity would be revealed by the intercorrelations between test scores at various ages. The correlations were computed for the entire sample and are presented in Table 1.

The results show that the intercorrelations were quite modest in the first year, even for tests given only 3 months apart. But with increasing age, the predictive power steadily increased and the ordering of individual differences progressively stabilized, reaching $r = .90$ between ages 8 and 9. Each child

appeared to move at his or her own distinctive tempo, with age-linked episodes of acceleration and lag, until finally reaching a level that remained relatively stable.

The progressive stabilization of mental measurements can be best visualized by plotting predictor curves that show the percent of variance accounted for by each test. For example, the 3-month scores have been correlated with every subsequent test to age 9 years; and when these correlations are expressed as percentage of variance accounted for, the bottom curve in Figure 2 is obtained. Similarly, when the 6-month scores are correlated with every subsequent age and then expressed as percentage of variance accounted for, the second curve is obtained, and so on for each successive age treated as a predictor. The family of curves is shown in Figure 2, slightly smoothed for clarity of display.

The tests through 12 months gave a relatively low-order prediction of later scores, accounting for less than 15% of the variance from 3 years onward. The measures of precocity or lag in the first year were only distantly related to the measures of intelligence in the early school years.

But between 12 months and 3 years there was a major gain in predictive power,

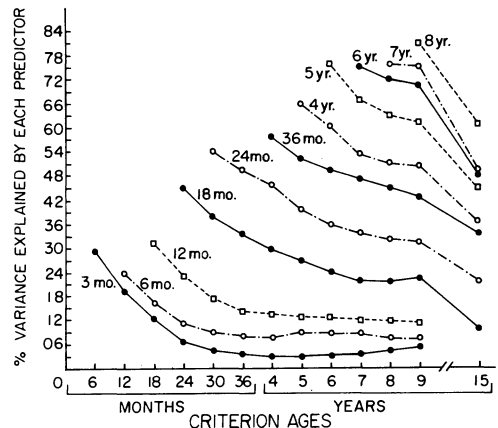


FIG. 2.—Predictor curves for mental tests: Percentage of variance accounted for at each age by prior tests.

¹ The developmental synchronies index is derived from the variance components that jointly express the degree of concordance for overall score profile, taking into account both the elevation and the patterning of the scores. The variance components are drawn from a repeated-measures analysis of variance for twins (Wilson, 1979), but instead of averaging over pairs, the disparities in score profile are computed and held separately for each pair. These deviation scores are then processed through the equation for within-pair (intraclass) correlations, and the resultant figure expresses the developmental synchronies index for each pair. The closer this figure comes to 1.00, the smaller the disparity and the closer the fit in the curves (e.g., Figure 1A).

TABLE 1
INTERCORRELATIONS BETWEEN MENTAL TEST SCORES, AGES 3 MONTHS TO 15 YEARS

	MONTHS									YEARS						MEDIAN N FOR R's
	3	6	9	12	18	24	30	36	4	5	6	7	8	9	15	
3 months....54	.48	.44	.36	.26	.25	.16	.13	.22	.20	.24	.18	.30	N.A.	297
6 months....56	.49	.41	.29	.34	.29	.19	.31	.32	.32	.25	.31	N.A.	352
9 months....60	.46	.36	.40	.36	.27	.32	.29	.22	.21	.20	N.A.	314
12 months....56	.48	.42	.40	.31	.38	.36	.32	.32	.33	N.A.	365
18 months....67	.62	.60	.54	.54	.49	.47	.47	.48	.31	410
24 months....70	.74	.68	.63	.61	.54	.58	.56	.47	419
30 months....78	.71	.66	.66	.60	.59	.56	.55	333
36 months....76	.72	.73	.68	.67	.65	.58	424
4 years....80	.79	.72	.72	.71	.60	365
5 years....87	.81	.79	.79	.67	343
6 years....86	.84	.84	.69	336
7 years....87	.87	.69	315
8 years....90	.78	301
9 years....80	242
15 years....	172
\bar{X}	89.5	91.7	92.0	89.2	90.3	90.8	86.9	89.4	90.3	96.1	100.1	95.8	99.2	100.1	100.4	
SD.....	15.8	15.1	16.8	16.6	16.3	16.2	14.5	16.4	15.2	15.2	14.2	13.4	13.7	13.8	13.2	

NOTE.—Median N for \bar{X} 's was 570.

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to the point that the 3-year scores accounted for nearly 44% of the variance in scores at 9 years. As argued elsewhere, a major transformation in mental functions has begun to take place during the second year, during which the principal attributes of intelligence gradually assume prominence (Wilson, 1977, 1978). As this transformation takes place, the ordering of individual differences is considerably reorganized; then each child becomes more securely positioned in the distribution of intelligence-test scores.

Some changes still occur into adolescence, and the final ordering may not be definitely settled until adulthood. But as each child tracks his or her developmental gradient toward adulthood, the fluctuations around the targeted end point are progressively diminished.

Concordance in mental development.—With these results in focus, we turn to the measures of concordance for monozygotic and dizygotic twins. The intraclass correlations were computed for the twin pairs at each age, and the results are shown in Table 2.

In the first year, the concordance values were essentially comparable for MZ and DZ twins, but beginning at 18 months there was significantly greater concordance for MZ pairs. The MZ correlations reached $R_{MZ} = .82$ at 18 months and remained consistently in the mid-.80s thereafter, ultimately reaching $R_{MZ} = .88$ at 15 years.

The MZ correlations exceeded the age-

to-age correlations throughout the preschool years, so that each twin was a better predictor of the co-twin's score than of his or her own score at the following age. In fact, if MZ twins were treated as replicates in a test-theory sense and used to estimate the reliability of the true score for the pair, the true-score correlations approached the reliability of the test (Table 2).

By contrast, the DZ correlations reached a high point at 36 months, then progressively declined to an intermediate level by school age, ultimately reaching $R_{DZ} = .54$ at 15 years. As individual differences in intelligence progressively stabilized, the concordance within DZ pairs regressed to a level roughly consonant with the proportion of shared genes. This divergence occurred in the face of continuing exposure to the same home environment, so there was a limited extent to which such common influences could compress the differences in DZ pairs. Furthermore, the differences were equally evident in same-sex and opposite-sex DZ pairs (Wilson, 1981a).

The trends were even more sharply drawn by a comparison of within-pair variances, which depend on the distribution of score differences within pairs. The MZ score differences were substantially smaller, $p < .001$, than the DZ differences at most ages after the first year (Table 2), and the range of MZ differences also narrowed over age. From 6 years onward, the DZ within-pair variances were larger than the MZ variances

TABLE 2
WITHIN-PAIR CORRELATIONS FOR MONOZYGOTIC AND DIZYGOTIC TWIN PAIRS

AGE	CORRELATIONS		MZ TRUE SCORE R	N PAIRS (MZ-DZ)	F RATIO (DZ _{wi} /MZ _{wi})
	MZ	DZ			
3 months.....	.66	.67	.79	72-90	1.5
6 months.....	.75	.72	.86	81-101	1.7*
9 months.....	.67	.51	.80	73-84	2.0*
12 months.....	.68	.63	.81	89-92	1.6
18 months.....	.82*	.65	.90	92-113	2.4**
24 months.....	.81	.73	.90	88-115	1.6*
30 months.....	.85**	.65	.92	72-93	2.6**
36 months.....	.88*	.79	.94	104-125	2.0**
4 years.....	.83*	.71	.90	105-120	1.9**
5 years.....	.85**	.66	.92	129-138	2.4**
6 years.....	.86**	.59	.93	139-141	4.0**
7 years.....	.84**	.59	.91	116-119	3.1**
8 years.....	.83*	.66	.91	146-138	2.8**
9 years.....	.83*	.65	.91	85-86	3.2**
15 years.....	.88**	.54	.94	78-64	3.0**

NOTE.—MZ correlations at 7, 8, and 9 years slightly attenuated by reduced SDs for IQ scores (about 12.4); if range-corrected, $R_{MZ} = .86$ at each age.

* $p \leq .01$ for $R_{MZ} > R_{DZ}$, or DZ within-pair variance > MZ within-pair variance.

** $p \leq .001$ for $R_{MZ} > R_{DZ}$, or DZ within-pair variance > MZ within-pair variance.

by a factor of 3:1, indicative of the markedly smaller score dispersion within MZ pairs. In fact, the median difference score for MZ twins was 4 points during this period; the DZ median difference score was 8 points.

Concordance for developmental trends.—The correlations at each age are informative, but to capture the essence of synchronized developmental trends an analysis was needed of the entire score vector over ages. The analysis employed a repeated-measures analysis of variance specifically adapted for twin data (Wilson, 1979), and it appraised the concordance for both elevation and patterning of the scores, jointly considered. The resultant correlation for this score vector expressed the degree of concordance for developmental trend among MZ and DZ twins.

In setting up the analysis, the test ages were grouped into five separate periods so that any shift in patterns of concordance would be evident. The first period included the tests given at 3, 6, 9, and 12 months, when prematurity effects might be pronounced; the second period included the tests at 12, 18, 24, and 36 months, which covered the previously noted transition phase in cognitive functions; and the third period included the tests from 3 through 6 years of age, where individual differences had become more stabilized and zygosity effects were more sharply drawn. The fourth period covered the transition into school (6, 7, and 8 years), and the final period represented the bridge from childhood to adolescence (8 and 15 years).² The results are shown in Table 3.

Beginning in the second period, MZ twins were significantly more concordant for the trends in mental development than DZ twins; from that point onward, over 80% of the variance in the mental growth curves for MZ twins was accounted for by concordance within pairs. The estimated true-score reliability for these developmental pathways remained near 0.90 throughout, which suggested that each pathway was guided by a powerful inner template.

Dizygotic twins also displayed correlated trends that, while significantly lower than the MZ trends, nevertheless remained in the mid-.60s until the final period. At that point, the dispersion in developmental trend reached $R_{DZ} = .50$. Just as the scores at each age became less concordant for DZ twins, so also did the divergence in developmental trend. For the moment, we defer the question of how DZ twins could become less alike over age and turn to another source of data—the mental test scores for siblings from the same families.

Concordance among siblings and twins.—As an adjunct to the research program with twins, other siblings from the same families have been brought in for testing as a matched control group. While the siblings share the same parental heritage and home environment as the twins, they have been raised as singletons and lack the distinctive prenatal and postnatal experiences that affect twins. Therefore, the contribution of these experiences to the mental development of twins

TABLE 3
TWINS: WITHIN-PAIR CORRELATIONS FOR DEVELOPMENTAL TREND

AGES OF TESTS	TREND R 's		MZ TRUE SCORE R	N PAIRS (MZ-DZ)
	MZ	DZ		
3, 6, 9, and 12 months69	.63	.83	81-84
12, 18, 24, and 36 months80*	.72	.89	66-69
3, 4, 5, and 6 years87**	.65	.93	75-87
6, 7, and 8 years81**	.66	.90	95-85
8 and 15 years82**	.50	.90	76-63

NOTE.—Degrees of freedom for each developmental trend correlation given by $(p - 1)(q)$, where p = number of pairs, and q = number of ages.
* $p < .05$ for $R_{MZ} > R_{DZ}$.
** $p < .001$ for $R_{MZ} > R_{DZ}$.

² Age 9 was omitted in the last two analyses because a number of pairs with otherwise complete data were missing the 9-year tests because of a funding crisis. Since the analysis required complete data at all ages or else the pair was excluded, the sample size would have been considerably reduced if age 9 were included. Other analyses with age 9 included showed virtually the same results for the last two analyses; the MZ trend correlations were somewhat higher but based on a smaller number of pairs. The same considerations applied to the 30-month tests as well.

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may be assessed in relation to this matched control group.

The siblings in this sample were tested on a schedule that yielded age-matched tests for each twin-sibling set. For example, if a pair of 3-year-old twins had a sibling 5 years old, that sibling was given a WPPSI; and when the twins later reached 5 years of age, they were given the same test and compared with the sibling. Age and test matching are crucial procedures for such comparisons to avoid confounding variability from these sources with the actual differences between zygotes.

The intraclass twin-sibling correlations were computed by pairing the sibling first with Twin A, then with Twin B (so designated by alphabetic first name), and averaging the results. In most sets the siblings were born before the twins, and the results are presented in Table 4 for those ages where sufficient sets were available to support the analysis.

The twin-sibling correlations progressed upward into the mid-.50s by 5 years and remained consistently at that level into adolescence, with one mild regression at 8 years. After being markedly lower than the DZ correlations at 3 and 4 years, the twin-sibling correlations were not significantly below the DZ correlations at any subsequent age except 8 years. The degree of similarity among these two-zygote sets gradually converged toward an intermediate value within the same range as DZ twins.

These results are further amplified by the correlations in Table 4 for sibling-sibling

pairs. Many families had two siblings in addition to the twins; where possible, both siblings were tested at closely matched ages. Shown in Table 4 are the results for pairs of siblings tested at 5–6 years; a second group of siblings were tested between 8 and 15 years, but under the restriction that the siblings in each pair were age-matched within 2 years.

In both groups the concordance values for sibling pairs were within the same range as the twin-sibling sets and DZ pairs; in fact, the older sibling pairs had virtually the same concordance value as DZ twins at 8 and 9 years. The recurrent theme seemed to be that for any two-zygote pair from the same family—whether DZ twins, a twin matched with a sibling, or two singleton siblings—there was a progressive trend to converge toward some common intermediate value by school age.

Dizygotic twins became less alike, while other two-zygote sets became more alike, during this period, and the ultimate concordance level reached by all two-zygote sets seemed to be powerfully affected by the number of genes shared in common. The unique experiences shared by twins, plus the common experiences shared by all offspring of the same family, played a lessening role in determining the concordance among related offspring.

Trends for infant siblings.—Another source of data is available that bears on the same issue. Whenever a younger sibling was born to one of the participating twin families, that sibling was recruited and tested on exactly the same schedule as the twins. Thus, a sample was created of younger-born siblings whose developmental trends during infancy could be compared with those of the twins. Some illustrative cases are shown in Figure 3.

In Figure 3A, the sibling more closely matched the developmental trend of one twin than did the other co-twin; in Figure 3C, the sibling was markedly different from both twins. Figure 3B was notable for the consistency in phasing of all three developmental trends.

At present, 35 infant siblings have completed at least 3 years in the program, and 19 siblings have completed a full 6 years. The siblings have been coordinated with the twins for an analysis of trend concordance during three age periods, and the results are shown in Table 5.

TABLE 4
WITHIN-SET CORRELATIONS FOR AGE-MATCHED
TWIN AND SIBLING SETS

	Correlation	N Sets
Twin-sibling:		
3 years.....	.38	74
4 years.....	.45	61
5 years.....	.56	88
6 years.....	.54	110
7 years.....	.55	45
8 years.....	.44	126
9 years.....	.53	58
15 years.....	.51	70
Sibling-sibling:		
5-6 years.....	.46	25
8-15 years ^a63	54

NOTE.—Twin-sibling sets significantly less concordant than DZ pairs ($p = .01$) at 3, 4, and 8 years.

^a Sibling pairs age matched within 2 years in this range.

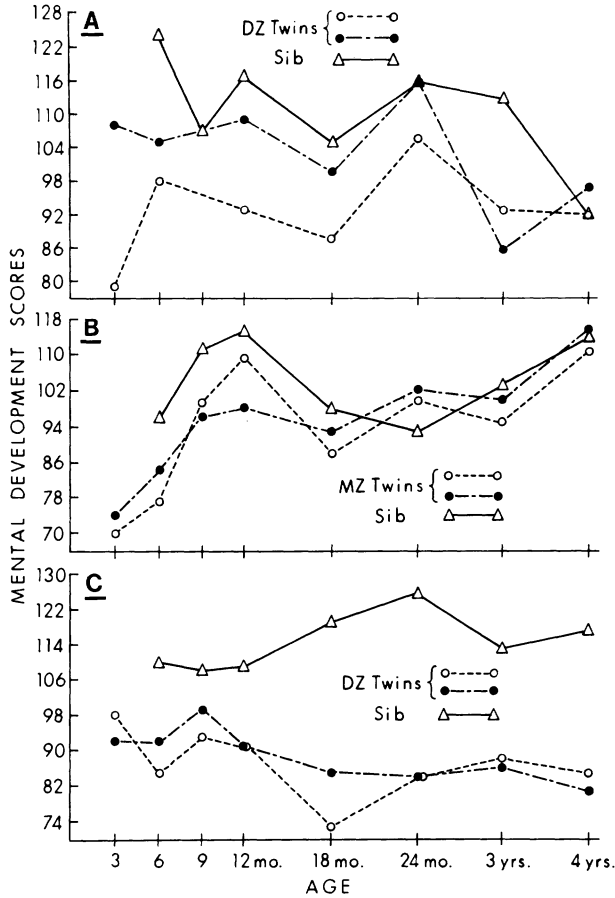


FIG. 3.—Developmental trends for twins and infant siblings (from Wilson, 1978)

TABLE 5
 WITHIN-PAIR CORRELATIONS FOR DEVELOPMENTAL TRENDS OF TWINS AND INFANT SIBLINGS

Ages	Twin-Sibling Trend R	N Sets
3, 6, 9, and 12 months.37	33
12, 18, 24, and 36 months.46	28
3, 4, 5, and 6 years.55	19

In the first year, there was a modest correlation for developmental trend, but in the two succeeding periods the trends became more closely linked. Between 3 and 6 years, the developmental trends for infant siblings followed the same pathways as their previously born twins with nearly the same degree of concordance ($R = .55$) as that obtained for DZ twins ($R = .65$). Related offspring thus appeared to track correlated developmental pathways, and the collective experi-

ences shared by DZ twins did not markedly enhance the curve fit of their developmental gradients in relation to other two-zygote pairs.

Assessment of Home Environment

As an adjunct to the mental testing program, an assessment of the home environment was instituted to give a picture of the conditions in which the twins were raised. The characteristics of the home, and particularly the interaction of the mother with the infant, are reported to have a prominent effect upon the infant's mental development (e.g., Elardo, Bradley, & Caldwell, 1975; White & Watts, 1973).

For all recruited twins, data had been obtained previously from the maternal interviews on both parents' education and the father's occupation, and these data had furnished the basic measures of education and socioeconomic status (SES) for each family. Neither education nor SES directly captured

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the qualitative features of the family environment, however, so a detailed assessment was developed for use during a home visit by a trained social worker.

In the broad outline, the appraisal included the physical characteristics of the home and neighborhood, the social and intellectual atmosphere in the home, the cognitive and temperamental characteristics of the mother, and the opportunities for play and stimulation available to the children.

Method

The home visit protocol was constructed of 200 items based partly on answers to interview questions and partly on direct observations. A complete description of all items in the home interview, plus details of scoring and reliability, may be found in Matheny, Thoben, and Wilson (1982).

In brief, four factor scores were obtained from a factor analysis of the home interview items. The first factor was labeled "adequacy of the home environment," and items loading on this factor represented global judgments about the adequacy of the interpersonal and physical environment for promoting intellectual and social development, plus more specific judgments of play space and qualitative features of the home and furnishings.

Characteristics of the mother were defined by three factors. The first factor was drawn from ratings of the mother's emotional reactivity (e.g., tension, tolerance for frustration, mood, and activity level) and was labeled "maternal temperament." The second factor was represented by ratings of the

mother's intellectual and verbal facility and home management skills and was termed "maternal cognitive." The third factor, termed "maternal social affect," was represented by ratings of the mother's sociability, talkativeness, and interpersonal warmth. These three factors, plus the "adequacy" factor, represented the bulk of the ratings made during the home visit.

The four factor scores were combined with the measures of parental education and socioeconomic status as the composite profile of the home/family environment. These scores were subsequently analyzed for their relationship to offspring mental development during childhood.³

The home assessment program was begun in 1978; 226 families have been visited to date, mostly with twins under 8 years of age. The full report of results may be found in Wilson and Matheny (in press); the major relationships are briefly summarized below. The correlations between the home/family variables and the twins' mental test scores at four marker ages are shown in Table 6.

Results

The relationships were very weak at 6 months, but by 24 months the linkage had strengthened considerably; and from 3 years on, the relationships were highly significant for five of the variables. As the measures of mental development progressively stabilized with age, the relationship to certain key family ratings steadily increased. In particular, measures of parental education and SES, plus ratings of home adequacy and maternal cognitive skills, yielded strong correlations with the twins' 6-year IQ scores.

TABLE 6
CORRELATIONS BETWEEN HOME ASSESSMENT VARIABLES
AND MENTAL TEST SCORES

VARIABLES	AGES AT TESTING			
	6 Months	24 Months	3 Years	6 Years
Father's education.....	.28	.38	.51	.53
Mother's education.....	.19	.33	.49	.50
Socioeconomic status.....	.17	.42	.51	.51
Adequacy of home environment....	.23	.45	.54	.55
Maternal cognitive.....	.24	.40	.41	.52
Maternal temperament.....	.03	.01	.01	-.08
Maternal social affect.....	.10	.23	.35	.25
N cases.....	205	303	321	287

³ Caldwell's Inventory of Home Stimulation (Note 1) and Moos's Family Environment Scale (Note 2) were also completed during the home visit. These results may be found in Wilson and Matheny (in press).

Multiple regression analysis.—With these relationships evident for single variables, the question was what combination of variables would maximize the prediction of mental test scores at each age. Because many of the variables were intercorrelated, a stepwise multiple regression program was employed to identify the variables making independent contributions to the prediction.

The regression analysis was carried out at three criterion ages (6 months, 24 months, and 6 years), and the results are presented in Table 7.

For the 6-month scores, the multiple correlation was quite modest ($R = .28$) and included only father's education as the significant predictor variable. Once it was extracted, no other variable made a significant contribution to the residual variance.

At 24 months, however, the multiple correlation had improved substantially ($R = .56$). The factor score for adequacy of the home environment emerged as the first predictor, and the father's education also made a significant contribution. Finally, maternal temperament entered with a negative weight as a sharpener variable.

Turning to the 6-year analysis, we find that adequacy of the home environment and father's education both appeared as strong contributors; as shown in the last column, both had virtually the same original correlations with 6-year IQ. Three maternal variables then entered as supplementary predictors, and the entire set yielded a multiple $R = .66$. There was clearly a very strong relationship between these measures of home and family and the

intelligence test scores of the offspring at school age.

Since four of the predictors were based on ratings made during the home visit, it would seem to confirm the essential contributions made by positive maternal characteristics and a supportive home atmosphere. The correlations increased over age; in fact, the home/family variables gave a stronger prediction of the child's 6-year test score than did any prior test score for the child through age 24 months (cf. Table 1). The attributes of the home environment did covary in very significant fashion with upward or downward shifts in mental development during childhood.

Minimum set of predictors.—If a home assessment were not feasible, however, is there some minimum set of measures that would show a consistent relationship with mental development? Specifically, would measures of parental education and socioeconomic status serve as significant predictors of offspring intelligence?

Many studies of the family milieu do not include a measure of socioeconomic status because it is regarded as a distal variable that lacks any reference to the experiences generated in the family setting. Similarly, parental education in terms of years completed may seem only distantly related to the opportunities for learning offered in the home.

In a large and representative sample, however, these marker variables serve as a useful measure of differences between families. Each measure represents the end product of an enormous amount of life experiences—

TABLE 7
MULTIPLE REGRESSION ANALYSIS OF HOME-VISIT VARIABLES AND MENTAL DEVELOPMENT SCORES

Age, Step, and Variable	Multiple R	Partial R	Initial r with Criterion
6 months:			
Step 1—Father education (no other variable significant)2828
24 months:			
Step 1—Adequacy of home environment4545
Step 2—Father education54	.23	.38
Step 3—Maternal temperament (–)56	–.13	.01
6 years:			
Step 1—Adequacy of home environment5555
Step 2—Father education62	.33	.53
Step 3—Maternal temperament (–)64	–.23	–.08
Step 4—Maternal cognitive65	.15	.52
Step 5—Maternal social affect66	.13	.25
6 years (minimum set of predictors):			
Step 1—Father education5353
Step 2—Mother education58	.23	.50
Step 3—Socioeconomic status59	.17	.51

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the years of schooling completed and the occupation entered as an adult. Parents tend to select mates assortatively on the basis of education ($r = .64$ in this sample); thus the wide variation between individuals becomes translated into variation between families. Indeed, the expectation would be for a strong association between the parent's education and the fostering experiences provided in the home, and this is what was found. For these families, the correlation between parents' education and adequacy of the home environment was $r = .57$.

Therefore, the three variables of father education, mother education, and socioeconomic status were entered into the multiple regression analysis as a minimum set of predictors. Education was measured as number of years of schooling completed (range: 8–22 years), and socioeconomic status was based on the ratings of occupation of head of household (range: 0–99; from Reiss, 1961). The results of the analysis at 6 years are presented at the bottom of Table 7.

Father's education was extracted as the first predictor; notably, mother's education appeared as a significant contributor, although it had not entered previously when the maternal factor scores were included. The SES also entered significantly, after being absent in the prior analyses. By virtue of its high correlation with adequacy of the home environment ($r = .62$), the variance attributable to SES was absorbed whenever the adequacy factor was first extracted in the regression analysis.

From this perspective, the variables in the minimum set yielded a surprisingly strong prediction of offspring IQ scores ($R_{\text{mult}} = .59$). As the measures of offspring intelligence progressively stabilized by school age, the variables of parental education and socioeconomic status played an increasingly larger role in the predictive relationship, ultimately accounting for 80% of the variance explained by all home-visit variables.

Qualitative contributors.—One final question might be considered: After the minimum set of predictors had been partialled out, which of the home/family variables made a significant contribution to the remaining variance in offspring 6-year IQ scores? Insofar as the qualitative features of the family environment reached beyond parental education and SES in influencing mental development, the

significant variables from the home visit should appear in later steps of the regression analysis.

For this analysis, the minimum-set predictors were removed first, then the regression analysis was continued until all remaining significant predictors had been extracted. Four additional variables were extracted: adequacy of the home environment and the three maternal ratings (cognitive, temperament, social affect). These four predictors boosted the multiple R from 0.59 to 0.66 and demonstrated that, when education and socioeconomic status were held constant, the rated aspects of home and mother did improve prediction of offspring IQ scores.

When the home was geared for fostering development and when the mother was intellectually alert, positive in mood, and free of tension and frustration, the children tended to have higher IQ scores than predicted from the minimum set. Conversely, when the opposite characteristics were found, the offspring IQ scores tended to be lower than expected. Clearly, the atmosphere of the family environment augmented the basal relationship between parental capability and offspring IQ, although its effect was perhaps less than implied by other studies that focus exclusively on the qualitative features of the home.

Environment and heritage.—How is the predictive power of the minimum set to be interpreted? One problem in interpreting the studies of environmental influences on mental development is that parents not only create the home environment; they also furnish the biological heritage for their offspring (Scarr & Grajek, 1982). Longstreth, Davis, Carter, Flint, Owen, Rickert, and Taylor (1981) have argued recently for a consideration of inheritance as partially accounting for the correlations between environmental measures and children's IQ. In their study, maternal IQ (which was correlated with measures of the home environment) provided higher correlations with offspring IQ than the environmental measures provided.

From this perspective, most studies of home/family influences are necessarily confounded by the biological linkage between parents and offspring.⁴ The increasing correlations may be a product of cumulative home influences, plus what McClearn (1970) describes as "developmental genetic processes that determine the increasing degree of re-

⁴ Except for adoption studies—see DeFries, Plomin, Vandenberg, and Kuse, 1981; Scarr and Weinberg, 1983.

semblance of offspring and parent on intellectual measures during the first years of life" (p. 68).

We do not have direct measures of intelligence on the parents, but in a large and diverse sample, the years of education completed serve as a useful broad approximation of such measures. As thus identified, the correlations between the parental measures of education and offspring test scores at 6 years ranged from .50 to .53, very close to the expected parent-offspring correlation of .50.

The results further showed that both father's and mother's education contributed significantly to the regression analysis, in spite of the high intercorrelation between them. By way of contrast, the aggregate of other home/family variables, many of which were correlated with parental education, added a relatively smaller proportion of variance to the prediction at 6 years.

We infer from these relations that the principal link between parental intelligence and offspring intelligence is genetic in origin. Although the comprehensive home assessment clearly added to the prediction of mental development, the elementary demographic variables yielded such strong correlations that the attributes of the parents must be transmitted to offspring primarily by mechanisms other than shared family experiences. The impact of these family experiences is dependent on the intrinsic biological foundation of the offspring, and that foundation derives chiefly from the genotype supplied by the parents.

Discussion

The joint relationship among all variables considered thus far and the trends in mental development are summarized in Figure 4. The curves show the progressive change over ages in the correlations for MZ twins, DZ twins, twin-sibling sets, and parent-offspring sets. Also, the steady incremental gain in age-to-age correlations for all subjects in the sample is shown. The curves (except parent-offspring) have been smoothed by employing moving averages at each age except 15 years.

The curves illustrate the progressive divergence of MZ correlations from DZ correlations over age, as well as the strong upward trend in age-to-age correlations, which ultimately surpassed the MZ correlations. As intellectual functions consolidated and individual differences stabilized, the relative discontinuity of the early ages was replaced by a

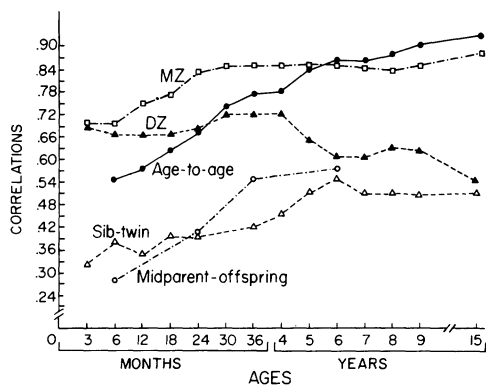


FIG. 4.—Mental development correlations for MZ twins, DZ twins, twin-sibling sets, parent-offspring sets; and for each child with itself, age to age.

strong year-to-year continuity. At this latter stage, the measures of intelligence for a single zygote—whether one child tested twice or a pair of replicates tested at the same time—approached a common high value in terms of concordance.

The twin-sibling correlations and midparent-offspring correlations began near .30, then moved into the mid-.50s by age 6. At that point all pairs of related zygotes in the family—whether DZ twins, twin-sibling sets, or parent-offspring sets—displayed concordance values averaging between .54 and .61. The concordance band broadened somewhat between 7 and 9 years, then narrowed to a common value in the low .50s at age 15.

When the concordance band is viewed in the opposite direction, the distance between the DZ curve and the twin-sibling curve at the earlier ages represented all those experiential factors that made DZ twins more alike than other two-zygote sets from the same family. This would include everything from the same date of testing to any concordance-enhancing experiences shared by the twins. As the curves showed, after the initial wide differences there was a pronounced funneling effect over age, with final convergence. Thus, the experiences enhancing DZ twin concordance in early mental development did not sustain the effect into the school years.

The message from these results seems clear: There is a strong developmental thrust in the growth of intelligence that continues through adolescence and is guided by an intrinsic template or ground plan. The template is rooted in genetic processes that act throughout childhood and adolescence.

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The effects are most dramatic in early childhood, when the rate of gain is sharpest and the spurts and lags most pronounced. But even during adolescence, as the integrative power of the brain approaches its maximum level, the end phase of this protracted sequence is still subject to maturational processes that are gene-controlled.

Gene segregation.—Just as the action of the genes is not completed until adulthood, so the effects of gene segregation within related zygotes may not be fully manifested until this late stage. In examining the degree of concordance among offspring from the same family, the ultimate test is their similarity after the developmental processes are completed.

As the present data show, DZ twins and twin-sibling sets converged toward each other during the early school years, but the final merger did not occur until adolescence. At that point, the collective factors that enhanced the DZ correlations and diminished the twin-sibling correlations were overridden by the shared genotype. In this sense, developmental genetic processes are most sharply displayed in the long term—they produce continuing refinements in the phenotype until the process is completed, and at that point the zygotes display concordance values closest to expectations from the genetic model.

It is worth mentioning that adoption studies show results comparable to these—adoptive children ultimately match their natural parents more closely than their adoptive parents, although at the early ages they may show an initial association with the qualities of the adoptive home. Furthermore, when two unrelated infants are adopted into the same home, they may show similarities in mental development at early ages, but at adolescence their correlation lapses to zero (Scarr & Weinberg, in this issue).

The cumulative effect of being raised together in the same home appears not to offset the developmental trend toward a level of similarity commensurate with the extent of shared genotype—in the case of these unrelated adopted siblings, close to zero. When this is viewed in the context of related zygote pairs converging toward an intermediate level of similarity at adolescence, it appears to reinforce the basic theme: Intelligence as ultimately realized in adolescence is powerfully affected by developmental genetic processes that steadily move each zygote toward a targeted end point.

Genotype-environment correlation.—Scarr and Grajek (1982) have interpreted the dispersion among siblings at adolescence as an illustration of active genotype-environment correlation, whereby each individual begins to select environments that fit his or her capabilities and interests (“niche” picking). With increasing age, it takes precedence over the earlier passive genotype-environment correlation, in which the young child was simply exposed to advantages or disadvantages at home reflective of family SES.

It is undoubtedly true that niche picking occurs, but it is important to note that it is driven by developmental genetic processes that propel each offspring in a particular direction. Starting from a common home environment, the offspring disperse in selecting their niches, and the directions reflect the range of intrinsic capabilities represented among the offspring.

These capabilities only become fully realized by adolescence; so the dispersion among offspring in measured intelligence and in niches selected likewise becomes fully manifested at this stage. For related offspring, the dispersion spreads around a midpoint value near .50; for unrelated adopted children, the extent of similarity in their intelligence and niche selection seems to depend more on chance similarities in their biological parents than on the cumulative influences of the adoptive home.

Does this suggest that the quality of the home environment is unimportant? Not at all. The contribution of the parents, whether natural or adoptive, is in potentiating the child's inherent capabilities, in creating an atmosphere of enthusiasm for learning, and in adapting their expectations to the child's capability. The wide diversity within families emphasizes the importance of giving each child full opportunity for development and indeed of making sure that the opportunity is taken. The ultimate goal is the maximum realization of each child's intelligence coupled with a sense of satisfaction and personal accomplishment in its use. There is no better way to foster such development than by a supportive and appropriately stimulating family environment (Wilson, 1977).

Prospectus.—If these results are in any sense persuasive in making a case for developmental behavior genetics, then the entire area of developmental psychology is opened up to some powerful and far-reaching concepts. The recent advances in neurobiol-

ogy and genetics are so compelling in their implications for brain functioning and behavior that they will significantly reshape how we think about this area. Some of the implications are glimpsed briefly elsewhere (Cowan, 1979; Purves & Lichtman, 1980; Suomi, 1982; Wilson, in press), and there can be no doubt that developmental psychology will be affected profoundly by these advances. Perhaps a brief overview can highlight some of the most provocative findings.

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 a thoughtful overview of his work (1971), 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 in an enormously intricate guidance program that involves millions, perhaps billions, of different, chemically distinct brain cells. Each fiber in the brain pathways has its own preferential affinity for particular prescribed trails in the differentiating surround. The probing fiber tip eventually locates and connects with certain other neurons, often far distant, that have appropriate molecular labels. . . . In general outline at least, one could now see how it would be entirely possible for behavioral nerve circuits of extreme intricacy and precision to be inherited and organized prefunctionally solely by the mechanisms of embryonic growth and differentiation. [Pp. 30-32]

Exactly how this precise wiring is coded in the DNA of the genes and then translated into cell-to-cell connections remains an unsolved problem (Hubel, 1979). 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 (1979).

In addition, recently it has become apparent that the development of many brain regions is sculpted by tightly programmed phases of cell death. Many more neural cells are generated than ultimately survive, and

this dieback of cells serves to adjust the quantity of neurons to the size of the target field they innervate.

It would appear that for some finite period there is an overabundance of cells fated to develop into a specific neural structure. If development proceeds normally, these surplus cells are sloughed off; but if some cells become aberrant or damaged, the remaining pool can furnish replacement cells to sustain the developmental process. This characteristic recalls one of Waddington's criteria—that developmental processes are buffered against disruptions and tend to resume their original course, even if deflected.

Following this stage of cell dieback, there is a subsequent adjustment in the number of synaptic processes each neuron maintains. After initially establishing multiple synaptic connections, many cells then progressively eliminate surplus connections with other cells, until only one neuron-to-neuron connection remains.

The latter point has been addressed recently by Purves and Lichtman (1980). They point out that the initial redundancy of connections is a strategy well suited to assuring that all target cells are innervated promptly. Once this is accomplished, the redundant connections are eliminated progressively to adjust the synaptic network to the number of target cells served. The authors propose that the elimination of multiple synapses may be the basis for the loss of plasticity or malleability in the developing central nervous system (CNS). They suggest that the early recovery of CNS function in the young after trauma and the progressive loss of such recovery with age may parallel the trend from multiple to single connections between neurons.

Regeneration of CNS Pathways

Whatever role is played by the above processes, the recovery of function and its relation to developmental processes has received a major impact from recent studies of brain recovery following early lesions. It now appears that, in infant mammals, central pathways within the brain can be regenerated and accurately reconnected even after damage (Kalil & Reh, 1979). The authors report that, when the pyramidal tract axons are cut in infant hamsters, "There is massive regrowth of the severed axons via a new brain-stem pathway to their appropriate terminal sites in the medulla and spinal cord. In contrast to previous studies, these results suggest that

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axons in the mammalian central nervous system damaged early in life may regenerate in a functionally useful way" (p. 1158).

The long-standing observation of greater recovery of function among the young after CNS injury now appears to have a possible foundation in the regeneration of neural connections. 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 (1976) surveyed a large number of studies with reference to the maturation of the nervous system and its effect on behavior. She notes that there is a strong interdependence of structure and function, even at the cellular level; many cells do not attain fully mature status and become functional until long after they originate.

For illustration, Goldman cites 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 extended even further (Conel, 1967).

These reviewed studies suggest a revised view of maturation that is closely coordinated with definable properties of the nervous system at every level from the cell upward. The functioning of the brain is dependent not just on the formation of cells or influx of experience but 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 (Goldman, 1976; Tanner, 1970).

Furthermore, maturational processes are subject to wide and pervasive individual differences; 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 on 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. 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 sponsor behavior.

Since all cells are initially equipotential in terms of genetic material, how is the commitment of each cell to a particular function determined? Caplan and Ordahl (1978) argue that such commitment is the result of irreversible repression of previously active genes. Drawing on the results of nuclear transplant experiments, they conclude: "As development proceeds, quadrants or groups of cells become 'fated' to differentiate and develop into cells of a specific organ. Thus, as the development of an organism proceeds, developmental potential of each cell (that is, its ability to differentiate into a number of different phenotypes) is severely restricted. This restriction seems to be irreversible. . . . We may assume . . . that the percentage of cells which retain a relatively unlimited potential progressively decreases as development proceeds" (pp. 121-122).

This basic pattern is clearly evident in brain tissue; if cells are transposed between two brain regions at an early stage, the transposed cells then develop normally as appropriate for the new region; but if transposed later, there is a defect (Cowan, 1979).

Under less dramatic circumstances than transposed tissue, the quote above suggests a prospective model for the greater recovery potential of young organisms, where a larger

number of cells might retain relatively unlimited potential and would subsequently be recruited to help restore a compromised function. As Goldman (1976, p. 68) has observed: "The evidence seems to indicate that the developing nervous system has a quantitatively greater capacity for reorganization than the mature nervous system, i.e., neuronal plasticity declines with age." Clinical and experimental data on brain injury and recovery of function seem to be emphatic on the same point (Hecaen & Albert, 1978, esp. chap. 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 ultimately depend on the retained potential of aggregate cell clusters to proceed toward their targeted end states.

These and related studies (Davidson, 1976; Garcia-Bellido, Lawrence, & Morata, 1979) bear witness to the extraordinary precision and detail of gene activity in regulating the course of development. Perhaps the crucial question for behavior genetics might be raised here: Is behavioral development guided by a genetic strategy analogous to that for biological development?

The answer would seem to be yes, both at the species level and in the realm of individual differences. If, as Carmichael (1970) 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.

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