As developmental psychologists stand at the threshold of a new era in understanding the biological bases for human growth and continue to address fundamental questions about parenting influences, it is time for a new appreciation of the coactivity of nature and nurture in development. Beginning at the moment of conception, hereditary potential unfolds in concert with the environment. The dynamic interplay between gene action and environmental processes continues throughout life. Although their influences are so often distinguished in ancient philosophy and modern science, the inseparability of nature and nurture has profound implications for how we study and understand human development.\(^1\) In this chapter, we trace these implications drawing first on the literature on developmental behavioral genetics, then undertaking a discussion of molecular genetics. We close with a brief discussion of brain development, foreshadowing the focused attention that is given to this topic in Chapter 8.

Nature and nurture are partners in how developing people interact with the surrounding environment. Nature and nurture are partners also in

\(^1\)Although this chapter focuses primarily on genetic influences that contribute to individual differences among children, it is essential to remember that genetic influences also account for the characteristics that humans share as a species, such as upright walking and language. Indeed, the inseparability of nature and nurture is also reflected in the fact that both nature and nurture are required for children to acquire these and other attributes that all humans share.
the transactions between the gene and the variety of internal environments that surround it within the body (Greenough, 1991; Greenough and Black, 1992). The environment of the cell influences which of the tens of thousands of genes are expressed to affect cell characteristics. Hormones and growth factors in the cell can turn some genes on and turn others off. These substances can arise from the nucleus of the cell, its cytoplasm, or the surrounding cells or organs. The substances that influence gene expression arise also from the functioning of other genes within the cell (so-called regulator genes) and the products of earlier protein synthesis.

It is impossible to think of gene expression apart from the multiple environments in which it occurs. It is impossible to think of the manifestation of hereditary potential independently of the hierarchy of environments that shape its appearance. It is impossible to think of an organism that interacts with the environment without considering the genotypical uniqueness of that individual. It is impossible, in short, to consider nature apart from nurture.

Why, then, are these two forces of human development so persistently differentiated in efforts to understand human development? From ancient Platonic and Confucian philosophy to the present, the dichotomy between inherited capabilities and environmental incentives and pressures has guided human self-understanding in Western and Eastern thought. All contemporary scientists acknowledge the interaction of heredity and environment (see Elman et al., 1996, for a recent and sophisticated version of the interactionist view). Yet an emphasis on whether hereditary constraints or environmental incentives are the preeminent influence in human development can still be observed not only in scholarship in psychology but also, more significantly, in public discourse concerning the importance of parenting and early education, and in policy debates about early intervention programs, family support, delinquency and criminality, and other issues of child and family policy.

2Within the nucleus of every cell are chromosomes containing genes, which are segments of DNA. Genes direct the synthesis of proteins that are incorporated into the structure of the cell, regulate its biochemistry, and guide other genetic activity. Genes ultimately affect physical and behavioral characteristics through these influences on the cells within every living being. Although each cell contains genes that are identical to the genes of every other cell, not all genes function in the same way, and this accounts for why cells function differently from one another. Some genes act continuously, for example, while other genes in the same cells turn on temporarily, and others are never expressed. As one colorful description notes, if each gene is represented as a light bulb that is either activated or not, we would see a distinct twinkling of lights within each cell during its normal functioning (Leger, 1992). This is why organisms can have trillions of cells, all of which have the same DNA but many different forms and functions.
It is time to reconceptualize nature and nurture in a way that emphasizes their inseparability and complementarity, not their distinctiveness: it is not nature *versus* nurture, it is rather nature *through* nurture. If gene expression is inconceivable apart from the environment, then it is useless and potentially misleading to try to finely distinguish the relative importance of nature and nurture in the course of human development. Nature is inseparable from nurture, and the two should be understood in tandem. Moreover, by contrast with a traditional view that heredity imposes limitations and environments induce change in developmental pathways, research in developmental psychobiology shows that the coactivity of nature and nurture accounts for both stability and malleability in growth. This view is, indeed, one important way of integrating the science of early childhood development, and it is also reflected in recent scientific advances in some of the research fields that are currently generating greatest interest among developmental scientists: developmental behavioral genetics, molecular genetics, and brain development.

**DEVELOPMENTAL BEHAVIORAL GENETICS**

In animal species, the importance of genetic influences on behavior can often be studied directly through selective breeding research. In humans, less intrusive procedures are necessary, and for the past several decades developmental behavioral genetics has provided a powerful means of understanding the strength of heritable influences on individual differences in human development, and the environmental contexts in which they are expressed (see Lemery and Goldsmith, 1999; Plomin et al., 1997a; and Rutter et al., 1999a, for overviews of this field). By taking advantage of naturally occurring variation in genotypes and environments, behavioral geneticists seek to partition behavioral variability into its genetic and environmental components and describe their interaction.

They have two primary research strategies for doing so. In adoption research, genetic contributions are estimated by comparing the characteristics of an adoptive child with those of the birth mother (to whom the child is genetically related, but they do not share an environment) and the adoptive mother (who shares the child’s environment, but not genes). Sometimes biologically related and unrelated siblings are also studied. The second approach is twin research. Because identical (monozygotic) twins are genetically identical, comparing the similarity of their characteristics with those of fraternal (dizygotic) twins, who on average share half their genes, is another way of estimating genetic contributions.

Twin and adoption research designs each have assumptions or limitations that can make the interpretation of findings difficult and sometimes controversial. In adoption research, for example, prenatal influences (e.g.,
teratogenic exposure) can also account for the resemblance of biological mothers to their offspring, and this can inflate estimates of genetic contributions. In addition, adoption designs assume that the selective placement by adoption agencies of children into the homes of parents who are like them (or their biological parents) does not occur. It is possible to estimate the potential biases introduced by selective placement or prenatal influences, but this is very difficult in most research designs. Twin studies also have certain assumptions: that identical twins do not share a more similar environment than do fraternal twins, and that the development of twin pairs is fairly representative of the growth of children in general. These assumptions, too, have been tested, with some researchers concluding that these assumptions are valid and others disagreeing.

Adoption and twin studies each provide means of estimating quantitatively the proportion of variance in human characteristics that is attributable to heredity and to the environment, and of examining how these influences interact in development. During the past decade, developmental behavioral genetics research has expanded considerably in sophistication and analytic methods, using variations on the basic adoption and twin research designs (sometimes combining these methods) and employing structural equations modeling and other quantitative model-fitting methods for estimating genetic and environmental contributions to behavioral variability. These efforts have yielded important new insights into the heritability of individual differences in cognitive abilities, extraversion, emotionality, self-control, and other characteristics and have shown how inherited propensities to childhood disorders like autism, schizophrenia, attention deficit hyperactivity disorder, and antisocial behavior need to be considered by practitioners (see reviews by Plomin et al., 1997b and Rutter et al., 1999b).

Even more important is how this research contributes to an appreciation of how nature and nurture influence development in concert. A recent study of the development of antisocial behavior in children by Ge, Conger, Cadoret, Neiderhiser, Yates, Troughton, and Stewart (1996) is exemplary. Using an adoption design, these researchers found that when biological parents had substance abuse problems or antisocial personality disorder, their adopted children were much more likely to be hostile and antisocial than were adoptees from troubled biological parents. Children’s inherited antisocial tendency may have been manifested as difficult temperaments, problems with emotional self-control, impulsivity, or other difficulties. It was not surprising, therefore, that children’s antisocial tendency was also associated with greater harshness and less nurturance and involvement by their adoptive mothers and fathers. This illustrates how children’s inherited characteristics can evoke complementary responses from their parents (called “gene-environment correlation”).

Parents and children in these adoptive families influenced each other.
Children with greater hostility tended to evoke more severe disciplinary responses, but harsh discipline also tended to exacerbate children’s antisocial behavior. Parents’ treatment of their adoptive offspring was influenced not only by the child’s demandingness, but also by influences that were found to be independent of the child’s inherited characteristics, such as the quality of the parents’ marital relationship (see Figure 2-1). Thus the development of antisocial behavior in children was influenced by heritable characteristics—which altered the childrearing climate of the home—and by family influences that arose independently of the child. Other studies offer a similar portrayal of the coactivity of nature and nurture in human development (see Cadoret et al., 1996; O’Connor et al., 1998; Pike et al., 1996; and Reiss, 1997).

These studies have important practical implications. Since parenting and other environmental influences can moderate the development of inherited tendencies in children, efforts to assist parents and other caregivers to sensitively read a child’s behavioral tendencies and to create a supportive context for the child are worthwhile. A good fit between environmental conditions and the child’s characteristics is reflected, for example, in family routines that provide many opportunities for rambunctious play for highly
active children, or in child care settings with quiet niches for shy children to take a break from intensive peer activity. Thoughtfully designed caregiving routines can incorporate helpful buffers against the development of behavior problems among children with inherited vulnerabilities by providing opportunities for choice, relational warmth, structured routine, and other assists. Interventions to assist children at risk for other psychological disorders must also be individualized and emphasize the creation of a good fit between inherited vulnerabilities and behavioral demands, especially for children at greater heritable risk for problems like antisocial behavior, depression, and attention deficit hyperactivity disorder.

Heritability

Twin and adoption research designs each permit behavioral geneticists to calculate a heritability statistic ($h^2$), which is an estimate of the proportion of variability in individual characteristics that is due to genetic differences. A heritability of .45, for example, indicates that 45 percent of the measured variability in a particular characteristic is due to genetic differences in the sample. There are comparable statistics that estimate environmental contributions to individual characteristics. Unfortunately, the distillation of many complex findings in behavioral genetics research to a single heritability figure has led to considerable misunderstanding of its meaning, especially when heritability estimates in the range of 30 to 70 percent are derived from studies of the genetic contributions to individual differences in intelligence, personality, and psychopathology. This misunderstanding derives, in part, from the traditional tendency to seek to distinguish the effects of nature and nurture in development. Thus it is important to appreciate several principles:

- **Heritability estimates are proportions based on environmental as well as genetic diversity.** As a proportion, heritability reflects the extent of environmental influences as well as genetic influences. On one hand, if the environment could be made the same for everyone, heritability would inevitably be large because individual differences would then be due entirely to genetic factors (Lemery and Goldsmith, 1999; Plomin et al., 1997b). On the other hand, if people are studied in environments with diverse influences on them (varying significantly in socioeconomic status, ethnicity, or culture, for example), environmental contributions are magnified and heritability is lower. In short, a heritability estimate is uninterpretable without an appreciation of the extent of the environmental variability that also influences behavior in a particular sample.

- **Heritability estimates are sample- and context-specific.** Heritability estimates reflect the environmental diversity of the sample under study, as
well as their genetic diversity. Heritability estimates tend to be higher in samples with greater variability in relevant genetic influences and, conversely, lower in samples that are genetically homogeneous. Because research samples can vary in both their environmental and genetic diversity, a heritability estimate must always be understood as pertaining to observed differences between individuals in a particular sample at a particular time in a specific environment.

- **Heritability estimates change with development.** A characteristic that is highly heritable at one age may not be particularly heritable at another (Lemery and Goldsmith, 1999). There are many reasons for this, including the changes that occur in gene activation with human growth, changes in environmental influences with increasing age, and changes in the nature of a person's engagement with the environment over time. The heritability of variations in general cognitive ability tends to increase with age, for example, as does the heritability of certain behavioral difficulties, such as those associated with antisocial behavior (Goldsmith and Gottesman, 1996; Plomin et al., 1997b). Heritability estimates are thus not consistent over the course of development.

- Perhaps most important, **heritability estimates describe what is in a particular population at a particular time, rather than what could be** (Plomin et al., 1997b). Changes in either genetic influences or environmental influences are likely to alter the relative impact of heredity and environment on individual characteristics. Phenylketonuria is a highly heritable genetic disorder that leads to mental retardation. But with a combination of early detection and environmental interventions, retardation can be completely prevented (Birch et al., 1992). Thus contrary to the common belief that highly heritable characteristics are impervious to environmental modification, interventions that alter the relevant environment—such as educational opportunities, therapeutic support, improved nutrition—can significantly alter the development of that characteristic.

Moreover, it is important to remember that a heritability estimate describes influences on individual differences in a characteristic. Environmental influences can have a profound effect on that characteristic, however, even when heritability is high. During the past century, for example, there have been significant increases in average height owing to improved nutrition and medical care, even though individual differences in height are strongly influenced by heredity. This is because environmental changes (such as improved diet and medical care) have markedly increased average height from one generation to the next, while individual differences in height have remained highly heritable (i.e., smaller parents still have smaller children; see Figure 2-2). In a similar manner, other research (see Chapter 10) indicates that the socioeconomic status of adoptive homes has a powerful effect in elevating the IQ scores of adopted children, even though the
heritability of individual differences in IQ remain high (see Maccoby, 1999; Schiff et al., 1982).

High heritability therefore does not mean low malleability. Environmental interventions—which can include improved education, health care, nutrition, and caregiving—can significantly improve developmental outcomes for children, even though individual differences in those outcomes may be strongly influenced by genetic processes. Heritability does not imply constraints on change. It is instead more relevant to appreciating how developmental outcomes can be changed. In particular, heritability
may be relevant to considering the kinds of interventions that might be most effective in relation to the genetically based characteristics of children.

Some developmental behavioral genetics researchers are dissatisfied, however, with the heritability estimate because it provides a quantitative but frequently misunderstood index of genetic influence that distracts attention from the ways that behavioral genetics research can contribute to a better understanding of risk and protective factors in development (e.g., Rutter, 1997; Rutter et al., 1999a; Wahlsten, 1990; Wahlsten and Gottlieb, 1997). An authoritative review of this field noted (Rutter, 1997:391):

It has gradually come to be accepted that the precise quantification of heritability has little value because it provides no unambiguous implications for theory, policy, or practice. . . . There is little to be gained by merely quantifying the relative importance of the contributions of genetic and environmental influences because any estimates will be specific to the population studied and will be subject to change if environmental circumstances alter.

Shared and Nonshared Environmental Effects

Research in developmental behavioral genetics has also elucidated features of environmental influence on individual differences. In particular, researchers have helpfully distinguished between shared and nonshared environmental influences. Shared environmental influences are those that make individuals similar in their common environment. Nonshared environmental influences are those that distinguish among individuals within the same environment. Within a family, for example, shared environmental influences make siblings alike independent of their genetic similarity, while nonshared environmental influences make siblings different independent of genetic factors. For instance, parental divorce is a source of shared environmental influence if siblings within the family are affected similarly by this event (e.g., because of moving to a new neighborhood, loss of contact with one parent). Parental divorce can also be a source of nonshared environmental influence if siblings are affected differently by the same event (e.g., older and younger children may interpret their parents’ divorce differently). This example illustrates how the terms “shared” and “nonshared” refer not to events or people, but to the effects they have on different children within the family.

Both shared and nonshared environmental influences can be estimated from adoption and twin research designs, although in different ways and with different assumptions. Within each design, however, shared and nonshared environmental effects are inferred from the resemblances among genetically related family members and are rarely observed directly or experimentally manipulated. This has caused some scholars to criticize how
shared and nonshared environmental influences are estimated (see, e.g., Baumrind, 1993; Rutter et al., 1999a) and to caution that direct measurement is necessary before firm conclusions can be drawn about shared and nonshared influences (e.g., Plomin et al., 1997b).

Like heritability estimates, the difference between shared and nonshared environmental influences is often misunderstood. Some studies have shown, for example, that within families the most important environmental influences are nonshared, making siblings different from each other (Plomin and Daniels, 1987; Rowe, 1994). Some commentators have interpreted this to mean that conventional portrayals of parenting influences (such as the view that parents who use reasoning and gentle sanctions raise responsible children, or that parents who read frequently inspire their offspring to do so) are no longer valid because the important parental influences are those that make siblings different rather than alike in their characteristics (e.g., Rowe, 1994; Scarr, 1992; see also Harris, 1995, 1998). But parenting influences have long been understood by developmental scientists as sources of differences between siblings for many reasons (Collins et al., 2000; Maccoby, 1999). Parents develop unique and special relationships with each of their offspring, their childrearing efforts are experienced differently by siblings because of each child's distinctive characteristics (e.g., temperament, personality, gender, age), and good parents take these characteristics into account in adapting their general childrearing practices to their specific encounters with each child (Grusec and Goodnow, 1994). Indeed, even when parents use the same child-rearing practices with different children, they evoke different reactions because of each child's temperament, age, and other characteristics. These influences contribute to why, as every parent knows, siblings develop unique and distinctive characteristics, and parental practices help to account for these differences.

The distinction between shared and nonshared family influences is important to refining an understanding of how family processes affect children. Most importantly, it emphasizes that parental practices and family events are unlikely to have uniform effects on offspring because of how children experience, understand, and respond in individualized ways. But the distinction between shared and nonshared influences does not radically change current views of the importance of parental influences in the context of genetic individuality (see Box 2-1). Moreover, until findings about the nature of shared and nonshared family influences are based on observational and experimental studies, strong conclusions from developmental behavioral genetics research about how parents influence their children in shared or nonshared ways must remain tentative. Furthermore, current research indicates that it is extremely difficult to identify objective features of the environment that are "shared" or "nonshared" between siblings, and that shared and nonshared effects may depend, in part, on the hereditary
BOX 2-1
Understanding—and Misunderstanding—Parenting Influences

Most parents are concerned about doing the right things for their children. In recent years, however, they have had reason to question whether what they do really matters. In public (Harris, 1998) and scholarly forums (Rowe, 1994; Scarr, 1992), some developmental scientists have called into question whether parenting influences are as significant in the lives of children as commonly believed.

Most of the reason for questioning the impact of parenting comes from developmental behavioral genetics research. Studies emphasizing the importance of nonshared family influences suggest that it is not how parents treat offspring similarly that matters (such as their childrearing style, parental income or education, or socioeconomic status); it is their differential treatment of siblings that is developmentally influential. This is contrary to how most parents understand their influence on offspring. Moreover, behavioral genetics researchers observe that traditional studies of parenting confound the influence of heredity with the influence of childrearing practices. Children become interested in reading, for example, not only because of a home environment in which parents model reading, but also because of shared genes related to intelligence, activity level, and other characteristics that underlie reading interest and ability. From this view, therefore, parents’ most significant contributions to the development of children are the genes they contribute, not the home environment they create.

Clearly, parents respond to the genetically driven characteristics of their offspring (a phenomenon called a “gene-environment correlation”). Indeed, doing so is a characteristic of good parenting. Adults should treat their offspring differently because of their unique personalities, age, sex, and other characteristics. But gene-environment correlation typically accounts for only a small part of the variability in children’s characteristics, and parental behavior remains a large independent influence on offspring (Plomin et al., 1997b; Rutter et al., 1999a; see, e.g., Ge et al., 1996). The importance of parenting is further underscored by experimental studies that directly modify parental practices to create changes in the behavior of children that cannot be explained by the hereditary characteristics of offspring (Baumrind, 1993; see, e.g., van den Boom, 1994). This means that when parenting changes significantly (independently of gene-environment correlation), the behavior of children adjusts accordingly.

In the end, research shows that parenting does matter to children’s development (Collins et al., 2000; Maccoby, 1999). At the same time, developmental scientists are increasingly recognizing the need to consider the influence of a child’s heredity characteristics as moderators of parental influence, and to incorporate into their research designs attention to hereditary influences. As a result, a new generation of parenting research is emerging that more thoughtfully illustrates the developmental integration of nature and nurture in the family environment.
characteristics of the child (Rutter, in press; Rutter et al., in press; Turkheimer and Waldron, 2000). This form of gene-environment interaction is discussed in the next section.

Like the focus on the heritability estimate, a strong emphasis on the relative influence of shared and nonshared family influences risks missing the important conclusion of developmental behavioral genetics research: specifically, that the action is in the interaction between heredity and environment. The manner in which the family environment accommodates to and modifies a child’s heritable characteristics shapes the development of those characteristics in a family environment that is also evolving over time.

**MOLECULAR GENETICS**

Developmental behavioral genetics examines nature and nurture indirectly through the behavioral characteristics of genetically related and unrelated individuals. But it would be far more informative if researchers could identify specific, individual genes associated with distinctive human characteristics, examining their behavioral consequences in concert with particular environmental influences. That goal is slowly being realized because of advances in molecular genetics, a relatively new science that is based on significant technological advances in mapping the human genome and conceptual advances in studying the connections between genes and behavior.

Molecular genetics begins with the scientifically complex task of identifying DNA markers for specific genes and connecting genes and behavior through relative linkage studies and association strategies (for overviews of these procedures, consult Plomin et al., 1997a; Plomin and Rutter, 1998; Rutter et al., 1999a). There have been significant advances in molecular genetics during the past decade owing to advances in mapping the human genome and the development of less intrusive and expensive technologies for extracting and genotyping DNA from human biological samples. There is every reason for confidence that further advances in genetic mapping and in linkage and association studies will soon provide a strong foundation for the integration of molecular genetics into the behavioral research of psychologists.

For developmental psychologists of the future, therefore, molecular genetics offers the remarkable possibility of identifying the genetic markers associated with specific behavioral propensities in children and examining the manifestations of these propensities in relation to environmental factors, developmental changes, and the influence of other genes. Molecular genetics will also enable researchers to develop more powerful analytic methods and theoretical models for understanding the influence of heredity on behavioral development. Perhaps most important, molecular genetics will help developmental psychopathologists understand the genetic bases
for childhood disorders, which will include a better appreciation of the
continuities between typical variability in personality functioning and atypical
deviation, improved detection of continuities in psychopathological risk
across developmental transitions, and the potential of reconceptualizing
clinical syndromes according to their genetic bases (Plomin and Rutter,
1998). There have already been promising discoveries, such as advances
toward the identification of a susceptibility gene for autism and autistic-like
characteristics, and research findings suggesting inherited propensities to
attention deficit hyperactivity disorder through genes regulating neurotransmitter
receptors (Rutter et al., 1999b). Furthermore, impending discoveries
from molecular genetics studies will provide added evidence that: (a) hereditary influences are polygenic and multifactorial, involving the impact of
multiple genes coacting with environmental influences to increase the like-
lihood of certain behavioral propensities; (b) genetic bases for developmen-
tal disorders reflect, in most cases, extreme variations on a continuum that
includes normal variants of the same characteristics; and (c) genetic effects
on behavior are probabilistic (rather than predetermined) because they
increase the likelihood that certain characteristics will occur, but do not
directly cause them (Plomin and Rutter, 1998).

Consistent with the more complex portrayal of nature and nurture
emerging from molecular genetics is a new appreciation of the importance
of gene-environment interaction. Gene-environment interaction indicates
that genetic susceptibility may increase an individual's sensitivity to specific
environmental influences. Such an interaction is especially important in
understanding hereditary vulnerability to environmental stresses that might
lead to psychopathology. Gene-environment interaction is demonstrated
when researchers find, for example, that there is small to moderate risk for
antisocial behavior in individuals who have either a genetic susceptibility
for this disorder or grow up in a stressful environment, but for individuals
with both genetic and environmental risk for antisocial behavior, the prob-
ability of pathology is sharply higher (Cadoret et al., 1995a, 1995b, 1996;
Rutter et al., 1999b).

Comparative studies with animals can specify these gene-environment
interactions more precisely. In one investigation, for example, rhesus mon-
keys with a specific genetic vulnerability affecting neuroendocrine function-
ing who grew up under adverse (peer-rearing) conditions consumed more
alcohol in experimental conditions (Campbell et al., 1986a) than did mon-
keys without this vulnerability. However, monkeys raised under advanta-
geous (mother-reared) conditions with the same genetic vulnerability con-
sumed less alcohol than those without it, suggesting that a genetic risk
factor under adversity was a protective factor in advantaged conditions.
Other forms of gene-environment interaction were apparent with respect to
dominance-related assertive behavior in this sample, showing that positive
early rearing significantly buffered the detrimental social impact of specific genetic vulnerability in young rhesus monkeys (Bennett et al., 1998; Suomi, 2000). These studies underscore how significantly developmental outcomes depend on the interaction of heredity and environment, rather than the direct effects of either. They also indicate how the behavioral effects of genetic vulnerability can be altered in the context of positive or negative early rearing.

As this research shows, the identification of gene-environment interaction is important not only to understanding developmental psychopathology but also to its prevention, since it indicates how individuals with a genetic propensity to the development of a disorder may be buffered from its emergence if their environments are made more protective. A child with an inherited vulnerability to antisocial personality is much less likely to develop this disorder in supportive, nonstressful family, school, and community environments.

Typical research designs in developmental behavioral genetics lack power to detect these interactions and, in fact, they are often not measured at all (Lemery and Goldsmith, 1999), but molecular genetics research has the potential for identifying gene-environment interactions, as the susceptibility genes to personality characteristics become identified. Behavioral studies suggest the existence of many such gene-environment interactions, such as the heightened responsiveness of temperamentally fearful, inhibited young children to maternal discipline efforts (Kochanska, 1993, 1995, 1997), the stronger impact of mother-infant synchrony on the growth of self-control of temperamentally difficult children (Feldman et al., 1999), and other illustrations of what Belsky (1997) describes as children’s differential susceptibility to rearing influences. As the field of molecular genetics matures, in other words, it will become possible to understand how the hereditary characteristics of children influence their responsiveness to parental incentives, their susceptibility to environmental stresses and demands, and their vulnerability (in concert with environmental risk) to psychopathology.

Psychology is thus at the dawn of a new era. Not only will molecular genetics enable scientists in the near future to better understand how the interaction of multiple genes influences behavioral characteristics, but it will also illuminate how gene action can augment vulnerability or resistance to environmental demands. This view of the multifactorial origins of behavior, reflected especially in gene-environment interaction, is another reflection of the essential integration of nature and nurture in behavioral development.
BRAIN DEVELOPMENT

Brain development also reflects the coaction of nature and nurture. The traditional view of early brain development describes a process under tight genetic control, and to a great extent this portrayal is true. Important regulatory genes, such as the "homeobox" genes discovered in the fruit fly, control the timing of the expression of other genes and can direct the development of an entire segment of the insect's anatomy, such as an eye or a limb. Comparable genes have been shown to exist in mammals, including humans, which play similarly significant developmental roles. There is no question that there are genetically driven developmental processes that guide the basic organization of the body and the brain, and these processes influence the growth of single cells and entire systems.

But as the opening paragraphs of this chapter illustrate, gene expression always occurs within the context of the intracellular and extracellular environments within the body, and in the context of experience in the outside environment. These multilevel environmental influences are necessary to coordinate the complex behavioral and developmental processes that are influenced by heredity, as well as to provide catalysts to gene expression that enable behavior to become fine-tuned to the external settings in which the organism lives. When songbirds first hear their species' song, or when patterned light first hits the retina of the human eye, these experiences provoke a cascade of gene expression that commits neural development to certain growth patterns rather than others. This is because the genetically guided processes of neural development are designed to capture experience and to incorporate the effects of experience into the developing architecture of the nervous system. This is especially true of human brain development.

The purpose of a brain is to store, use, and create information. The amount, complexity, and contingency of the information required for humans is far greater than that of the fruit fly, and this is one reason why the strong regulatory influence of homeobox genes in the fruit fly provides a poor model for human brain development. A limited amount of information is required to enable a fruit fly to function successfully for a short life span, and much of the necessary information can be encoded genetically. By contrast, humans acquire information primarily from experience, including their systems for thinking, feeling, and communicating. Most of human knowledge cannot be anticipated in a species-typical genome (e.g., variations in culture, language, and technology), and thus brain development depends on genetically based avenues for incorporating experience into the developing brain. This developmental integration of nature and nurture enables humans to grow and adapt as a species in a manner unequalled by any other (fruit flies don't have books, movies, radio, or televi-
sion from which to learn, and the only webs available to them are dangerous ones), permitting unparalleled flexibility in behavior and development. The incorporation of experience into the genetically driven plan for human brain development helps to account for many of the unique qualities of the species.

Developmental neurobiologists have begun to understand how experience becomes integrated into the developing architecture of the human brain (see Chapter 8 for further details). First, developmental processes of brain growth are based on the expectation that certain experiences will occur that will organize and structure essential behavioral systems. These developmental processes have been called "experience-expectant" because normal brain growth expects and relies on these forms of environmental exposure (Greenough and Black, 1992). Not surprisingly, the experiences that are incorporated into normative brain development are ubiquitous in early life: exposure to patterned light and auditory stimulation are two of the best studied, and there are likely to be others (such as acquiring physical coordination in gravity). Deprivation of these essential forms of environmental exposure can cause life-long detriments in behavioral functioning.

Second, throughout life, new experiences also help to trigger new brain growth and refine existing brain structures. This is, in fact, how learning, memories, and knowledge are acquired and retained throughout the life course. These developmental processes are called "experience-dependent" because they rely not on species-typical environmental exposures but instead on the idiosyncratic and sometimes unique life experiences that contribute to individual differences in brain growth (Greenough and Black, 1992). For example, there is evidence that brain functioning is changed in subtle ways if a person is a stringed instrument musician, which can alter neural areas governing the finger movements of each hand (Elbert et al., 1995). Experience-dependent brain development is thus a source of the human brain's special adaptability and lifelong plasticity (Nelson, 1999). Each person has a unique history of experience-dependent influences on brain growth.

Brain development therefore depends on an intimate integration of nature and nurture throughout the life course. Indeed, processes of brain development that were traditionally regarded as genetically hard-wired (such as visual capability) have now been discovered to depend on an exquisitely coordinated dance between experiential catalysts and the hereditary design for brain growth. Both nature and nurture are essential to the development of a brain of uniquely human capacities and potential. These developmental processes are discussed in further detail in Chapter 8.
CONCLUSION

The integration of nature and nurture, revealed in the findings of behavioral genetics, molecular genetics, and brain development research, should significantly influence how human development is understood. Contrary to the traditional view that heredity imposes constraints and environments induce change in developmental pathways, research in developmental psychobiology shows that nature and nurture are each sources of stability and malleability in human growth. More importantly, their coaction provides the impetus for development, whether it is viewed from the perspective of “experience-expectant” brain growth or the interplay between of genes and environments. The developmental action is in the interaction of nature and nurture.

Although work in developmental psychobiology has contributed most significantly to a revised view of hereditary influences, it also causes us to regard the environment in a different way. Most importantly, we now appreciate that how children respond to environmental incentives is based, in part, on hereditary predispositions (gene-environment interaction), that the social environment adapts itself to a child’s inherited characteristics (O’Connor et al., 1998), and that one of the most important ways of understanding environmental influences is how children are individually affected (the nonshared environment). Environmental influences are not just externally “out there”: a child’s responses to the family, the neighborhood, and the culture hinge significantly on genetically based ways of feeling, interpreting, and responding to environmental events. For parents and practitioners, this underscores the importance of taking into account each child’s individuality to create conditions of care that accord with the child’s inherited attributes and which, for some children, provide buffers to modify the expression of heritable vulnerabilities. Indeed, the importance of the goodness of fit between the environment and heritable characteristics also shows why human relationships are so profoundly important in early development, since human partners who know a child well are the environmental influences that can most easily accommodate helpfully to a child’s individuality.

The inextricable transaction between biology and experience also contributes to a better understanding of developmental disorders and the effects of early intervention. Hereditary vulnerabilities establish probabilistic, not deterministic, developmental pathways that evolve in concert with the experiential stressors, or buffers, in the family, the neighborhood, and the school. That is why early experiences of abuse, neglect, poverty, and family violence are of such concern. They are likely to enlist the genetic vulnerabilities of some children into a downward spiral of progressive dys-
function. By contrast, when children grow up in more supportive contexts, the hereditary vulnerabilities that some children experience may never be manifested in problematic behavior. Understanding the coaction of nature and nurture thus contributes to early prevention.

Early intervention, especially when it is well tailored to a child’s individual characteristics, can be helpful in shifting the odds toward more optimal pathways of later growth, but because the nature-nurture interaction is dynamic over time, there are no guarantees. Each new developmental stage provokes new forms of gene-environment transactions that may alter, or maintain, previous pathways. This means that giving young children a good early start increases but does not guarantee later success, and that children who begin life at a disadvantage are not doomed to enduring difficulty. The interaction of nature and nurture underscores the importance of creating current conditions of care that respect inherited characteristics, recognizing that nature-nurture is a source of continuing potential change across the life course.

Finally, research in developmental psychobiology emphasizes the continuity that exists between typical and atypical variability in human characteristics. One of the important emerging insights of molecular genetics is that many psychological difficulties arise not from single-gene mutations, but instead from extreme variations on a biological continuum that includes normal variants of the same characteristics. There is, in other words, a very broad range of individual differences in which the boundaries between the normative and the atypical are matters of degree rather than quality. This means that, in studying the growth of typical children, researchers gain insight into the developmental dynamics of atypicality and that, conversely, efforts to understand the challenges of children with developmental disorders yield insights into normative growth.

These conclusions are consistent with the broader themes of this report and of the findings of research on early childhood development. Taken together, they indicate that despite a long historical tradition of dissociating the effects of nature and nurture on human character and development, their influences are, in the end, indissociable.