

1

THE BIOLOGY OF CHANGE

In this introductory chapter I discuss a number of background issues for developmental cognitive neuroscience, beginning with historical approaches to the nature-nurture debate. Constructivism, in which biological forms are an emergent product of complex dynamic interactions between genes and environment, is presented as an approach to development that is superior to accounts that seek to identify pre-existing information in the genes or external environment. However, if we are to abandon existing ways of analyzing development in terms of “innate” and “acquired” components, this raises the question of how we should best understand developmental processes. One scheme is proposed for taking account of the various levels of interaction between genes and environment. In addition, a dissociation is introduced between innate representations and architectural constraints on the emergence of representations within neural networks. Following this, a number of factors are discussed that demonstrate the importance of the cognitive neuroscience approach to development, including the increasing availability of brain imaging and molecular approaches. Conversely, the importance of development for analyzing the relation between brain structure and cognition is reviewed. In examining ways in which development and cognitive neuroscience can be combined, three different perspectives on human functional brain development are discussed: a maturational view, a skill learning view, and an “interactive specialization” framework. Finally, the contents of the rest of the book are outlined.



1.1 VIEWPOINTS ON DEVELOPMENT

As every parent knows, the changes involved in the growth of children from birth to adolescence are truly amazing. Perhaps the most remarkable aspects of this growth involve the brain and mind. Accompanying the four-fold increase in the volume of the brain during this time are numerous and sometimes surprising



changes in behavior, thought, and emotion. An understanding of how the developments in brain and mind relate to each other could potentially revolutionize our thinking about education, social policy, and disorders of mental development. It is no surprise, therefore, that there is increasing interest in this new branch of science from grant funding agencies, medical charities, and even Presidential summits. Since the publication of the first edition of this book in 1997, this field has become known as *developmental cognitive neuroscience*.

Developmental cognitive neuroscience has emerged at the interface between two of the most fundamental questions that challenge humankind. The first of these questions concerns the relation between mind and body, and specifically between the physical substance of the brain and the mental processes it supports. This issue is fundamental to the scientific discipline of cognitive neuroscience. The second question concerns the origin of organized biological structures, such as the highly complex structure of the adult human brain. This issue is fundamental to the study of development. In this book I will show that light can be shed on these two fundamental questions by tackling them both simultaneously, and specifically by focusing on the relation between the postnatal development of the human brain and the cognitive processes it supports.

The second of the two questions above, that of the origins of organized biological structure, can be posed in terms of *phylogeny* or *ontogeny*. The phylogenetic (evolutionary) version of this question concerns the origin of species, and has been addressed by Charles Darwin and many others since. The ontogenetic version of this question concerns individual development within a life span. The ontogenetic question has been somewhat neglected relative to phylogeny, since some influential scientists have held the view that once a particular set of genes have been selected by evolution, ontogeny is simply a process of executing the “instructions” coded for by those genes. By this view, the ontogenetic question essentially reduces to phylogeny. In contrast to this view, in this book I argue that ontogenetic development is an active process through which biological structure is constructed afresh in each individual by means of complex and variable interactions between genes and their environments. The information is not in the genes, but emerges from the constructive interaction between genes and their environment (see also Oyama, 2000). However, since both ontogeny and phylogeny concern the emergence of biological structure, some of the same mechanisms of change have been invoked in the two cases.

FURTHER READING: OYAMA, 2000

The debate about the extent to which the ontogenetic question (individual development) is subsidiary to the phylogenetic question (evolution) is otherwise known as the nature–nurture issue, and has been central in developmental psychology, philosophy, and neuroscience. Broadly speaking, at one extreme the belief

is that most of the information necessary to build a human brain, and the mind it supports, is latent within the genes of the individual. While most of this information is common to the species, each individual has some specific information that will make them differ from others. By this view, development is a process of unfolding or triggering the expression of information within the genes.

At the opposing extreme, others believe that most of the information that shapes the human mind comes from the structure of the external world. Some facets of the environment, such as gravity, patterned light, and so on, will be common throughout the species, while other aspects of the environment will be specific to the individual. It will become clear in this book that both of these extreme views are ill conceived, since they assume that the information for the structure of an organism exists (either in the genes or in the external world) prior to its construction. In contrast to this, it appears that biological structure emerges anew within each individual's development from constrained dynamic interactions between genes and various levels of environment, and is not easily reducible to simple genetic and experiential components.

It is more commonly accepted these days that the mental abilities of adults are the result of complex interactions between genes and environment. However, the nature of this interaction remains controversial and poorly understood, although, as we shall see, light may be shed on it by simultaneously considering brain and psychological development. Before going further, however, it is useful briefly to review some historical perspectives on the nature–nurture debate. This journey into history may help us avoid slipping back into ways of thinking that are deeply embedded in the Western intellectual tradition.

Throughout the seventeenth century there was an ongoing debate in biology between the so-called “vitalists,” on the one hand, and the “preformationists,” on the other. The vitalists believed that ontogenetic change was driven by “vital” life forces. Belief in this somewhat mystical and ill-defined force was widespread and actively encouraged by some members of the clergy. Following the invention of the microscope, however, some of those who viewed themselves as being of a more rigorous scientific mind championed the preformationist viewpoint. This view argued that a complete human being was contained in either the male sperm (“spermists”) or the female egg (“ovists”). In order to support their claim, spermists produced drawings of a tiny, but perfect, human form enclosed within the head of sperm (see figure 1.1). They argued that there was a simple and direct mapping between the seed of the organism and its end state: simultaneous growth of all the body parts. Indeed, preformationists of a religious conviction argued that God, on the sixth day of his work, placed about two hundred thousand million fully formed human miniatures into the ovaries of Eve or sperm of Adam (Gottlieb 1992)!

Of course, we now know that such drawings were the result of overactive imagination, and that no such perfectly formed miniature human forms exist in the sperm or ovaries. However, as we shall see, the general idea behind preformationism, that there is a pre-existing blueprint or plan of the final state, remained a pervasive one for many decades in biological and psychological development. In



Figure 1.1 Drawings such as this influenced a seventeenth-century school of thought, the “spermists,” who believed that there was a complete preformed person in each male sperm and that development merely consisted in increasing size.

fact, Oyama (2000) suggests that the same notion of a “plan” or “blueprint” that exists prior to the development process has persisted to the present day, with genes replacing the little man inside the sperm. As it became clear that genes do not contain a simple “code” for body parts, in more recent years, “regulator” and “switching” genes have been invoked to orchestrate the expression of the other genes. Common to all of these versions of the nativist viewpoint is the belief that there is a fixed mapping between a pre-existing set of coded instructions and the final form.

On the other side of the nature–nurture dichotomy, those who believe in the structuring role of experience also view the information as existing prior to the end state, only the source of that information is different. This argument has been applied to psychological development, since it is obviously less plausible for physical growth. An example of this approach came from some of the more extreme members of the behaviorist school of psychology who believed that a child’s psychological abilities could be entirely shaped by its early environment. More recently some developmental psychologists who work with computer models of the brain have suggested that the infant’s mind is shaped largely by the statistical regularities latent in the external environment. While such efforts can



reveal hitherto unrecognized contributions from the environment, it will become evident in this book that these computer models can also be an excellent method for exploring types of interaction between intrinsic and extrinsic structure.

FURTHER READING: BATES & ELMAN, 2002

The viewpoints discussed above share the common assumption that the information necessary for constructing the final state (in this case, the adult mind) is present prior to the developmental process. While vitalists' beliefs were sometimes more dynamic in character than preformationists', the forces that guided development were still assumed to originate with an external creator. Preformationism in historical or modern guises involves the execution of plans or codes (from genes) or the incorporation of information from the structure of the environment. Oyama (2000) argues that these views on ontogenetic development resemble pre-Darwinian theories of evolution in which a creator was deemed to have planned all the species in existence. In both the ontogenetic and phylogenetic theories of this kind a plan for the final form of the species or individual exists prior to its emergence.

A more recent trend in thinking about ontogenetic development is constructivism. Constructivism differs from preformationist views in that biological structures are viewed as an emergent property of complex interactions between genes and environment. Perhaps the most famous proponent of such a view with regard to cognitive development was the Swiss epistemologist Jean Piaget. The essence of constructivism is that the relationship between the initial state and the final product can only be understood by considering the progressive construction of information. This construction is a dynamic process to which multiple factors contribute. There is no simple sense in which information either exclusively in the genes or in the environment can specify the end product. Rather, these two factors combine in a constructive manner such that each developmental step will be greater than the sum of the factors that contributed to it. The upshot of this viewpoint is not that we can never understand the mapping between genetic (or environmental) information and the final product, but rather that this mapping can only be understood once we have unravelled some of the key interactions that occur between genetic and environmental factors during ontogeny. Unfortunately, this means that there are unlikely to be quick breakthroughs in understanding the functions of regions of the human genome for psychological development.

FURTHER READING: PIAGET, 2002

Until recently the constructivist view suffered from the same problem as vitalism, in that the mechanisms of change were poorly specified and the emergence of new



structures from old resembled the conjuror's trick of making a rabbit appear from a hat. Even the "mechanisms" proposed by Piaget appeared somewhat elusive on closer inspection. Another problem with the constructivist approach was that, despite its emphasis on interaction, it was unclear how to analyze development in the absence of the traditional dichotomy between innate and environmental factors. By taking a cognitive neuroscience approach to psychological development, in conjunction with a number of new theoretical approaches, we will see that it is now possible to flesh out the constructivist approach to development and to provide new ways to analyze cognitive and brain development.



1.2 ANALYZING DEVELOPMENT

Viewpoints on cognitive development that involve reducing behavior to information derived from genes, on the one hand, and/or information derived from the external environment, on the other, have commonly used the distinction between "innate" and "acquired" components. The term "innate" has rarely been explicitly defined, and has a somewhat chequered history in developmental science. Indeed, it has been dropped from use, and even actively banned, in many areas of developmental biology. The main reason for the term having been dropped from use in fields of biology such as ethology and genetics is because it is simply no longer useful since it has become evident that genes interact with their environment at many levels, including the molecular. One compelling example of this point, discussed by Gottlieb (1992), concerns the formation of the beak in the chick embryo.

The production of the (toothless) beak in the chick embryo results from the coaction of two types of tissue. However, if, in an experimental situation, one of these types of tissue (mesenchyme) is replaced with the same tissue from a mouse, then teeth will form instead of a beak! Thus, as Gottlieb (1992) points out, the genetic component that is necessary for the chick to produce teeth has been retained from the reptilian ancestry of birds. More generally, the phenotype that emerges from these chick genes can vary dramatically according to the molecular and cellular context in which they are located.

Thus, there is no aspect of development that can be said to be strictly "genetic," that is, exclusively a product of information contained within particular genes. If the term "innate" is taken to refer to structure that is specified exclusively by genetic information, it refers to nothing that exists in the natural world, except for genes themselves. In cognitive science, however, use of the term "innate" has persisted despite repeated calls for it to be dropped from use (e.g. Hinde, 1974; Johnston, 1988; Gottlieb, 1992; Oyama, 2000). Presumably its persistent usage reflects the need for a term to describe the interaction between factors intrinsic to the developing child and features of the external environment. In considering this issue, Johnson and Morton (1991) suggested that it is useful to distinguish between the various levels of interaction between genes and their environment. Some of

these are shown in table 1.1. Within this analysis, the term “innate” refers only to changes that arise as a result of interactions that occur within the organism, and does not equate with “genetic.” That is, it refers to the *level of the interaction between genes and environment, and not to the source of the information*. I will adopt this working definition of the term in this book. Interactions between the organism and aspects of the external environment that are common to all members of the species, the species-typical environment (such as patterned light, gravity, etc.), were referred to as “primal” by Johnson and Morton. Interactions between the organism and aspects of the environment unique to an individual, or subset of member of a species, were referred to as “learning.”

Based on a series of experiments on the effects on brain structure of rearing rats in impoverished or comparatively enriched early environments, Greenough, Black, and Wallace (2002) proposed a similar distinction between two types of information storage induced by the environment. Changes induced by aspects of the environment that are common to all members of a species were classified as “experience-expectant” information storage (= “species-typical”), and are associated with selective synaptic loss. The second type of information incorporated by the brain through interaction with the environment was referred to as “experience-dependent” (= “individual-specific”). This referred to interactions with the environment that are, or can be, specific to an individual and are associated with the generation of new synaptic connections. Clearly, the boundary between these types of experience is often difficult to ascertain, and there have been many instances from ethological studies where behaviors thought to be innate turn out to be primal on closer study.

FURTHER READING: GREENOUGH ET AL., 2002

Using this framework it is possible to analyze aspects of development into underlying components. Normally in developmental psychology this is done in terms of components of cognition or behavior. In a cognitive neuroscience approach, by contrast, we can use evidence from different components of brain structure to constrain our thinking about cognitive development. Specifically, we can inquire

Table 1.1 Levels of interaction between genes and their environment

<i>Levels of interaction</i>	<i>Term</i>
Molecular	Internal environment
Cellular	Internal environment (innate)
Organism–external environment	Species-typical environment (primal)
	Individual-specific environment (learning)



into the extent to which aspects of a given neural circuit are innate (defined above as the product of interactions within the organism, and not sensitive to experience). Different aspects of brain structure and function are probably differentially sensitive to the effects of postnatal experience. The following analysis, which for simplicity I apply to the example of a simple abstract neural network, will assist in the later discussion of brain development and plasticity. A similar, but more detailed, analysis is presented in Elman et al. (1996).

The human brain is composed of very complex neural circuits bathed in a variety of chemicals that can regulate and modulate function. Therefore, when considering ways to analyze plasticity in such circuits it is useful to start with a simpler system that shares the same general properties. Connectionist neural network models involve nodes (simplified neurons) and links that can vary in strength (simplified synapses and dendrites). Learning in such networks takes place by varying the strength or extent of connections between nodes according to learning rules, some of which approximate those thought to be used in real brains (such as “Hebbian” learning rules).

FURTHER READING: MUNAKATA & STEDRON, 2001; BATES & ELMAN, 2002

Figure 1.2 shows a simple connectionist neural network. There are a number of ways it could be sensitive to training. First, the basic architecture of the network could alter as a result of experience. This could involve a change in the number of nodes, the learning rule, or the extent to which the nodes are interconnected. There are, in fact, a few neural network models that change in this way. Another possibility is that while the basic architecture of the network is fixed, the strength of the connections between the nodes varies according to a weight-adjustment

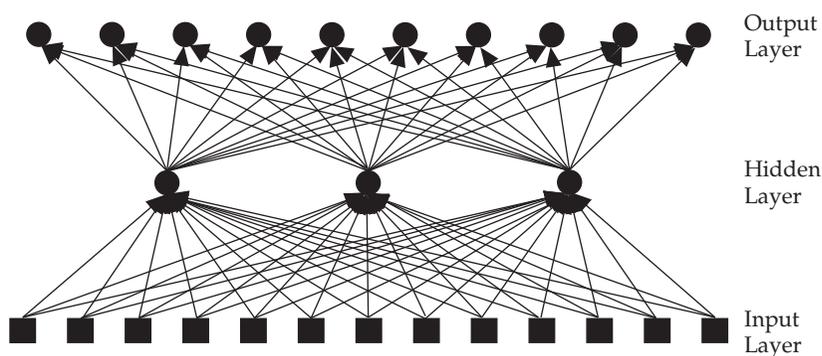


Figure 1.2 A simple three-layered connectionist neural network in which groups of nodes are joined by links. Changes in the strength of links as a result of training are determined by a learning rule.

learning rule. This is the way that most connectionist neural networks encode information. Since representations in artificial connectionist networks are dependent on the particular pattern of link strengths between nodes, allowing these to vary with the input means that different representations may emerge as a result of experience. In terms of the brain, we can think of these changes as residing in the details of microcircuits and synaptic efficacy. When the basic architecture of the network is fixed but the link strengths vary, we may say that the network shows an *innate architecture*. *More specifically, the representations that emerge as a result of training are constrained by the architecture of the network.* In chapter 2 we will review evidence consistent with the view that the primate cerebral cortex imposes architectural constraints on the development of representations.

Within this framework, there are, however, also two other possibilities. The first of these is that both the basic architecture of the network and the patterns and strengths of links between nodes are innate (as defined in table 1.1), and thus insensitive to external input. I will refer to this as the network possessing *innate representations*. In later chapters we will see that there is little evidence that the human neocortex possesses innate representations. The second alternative possibility is that both the architecture and the detailed pattern and strength of links are malleable as a result of training. In the next chapter we will see that only under extremely atypical environmental conditions, or in cases of genetic atypicality, do we see changes in the basic architecture of the primate brain.



1.3 WHY TAKE A COGNITIVE NEUROSCIENCE APPROACH TO DEVELOPMENT?

Until the past decade, the majority of theories of perceptual and cognitive development were generated without recourse to evidence from the brain. Indeed, some authors argued strongly for the independence of cognitive-level theorizing from considerations of the neural substrate (e.g. Morton, Mehler, & Jusczyk, 1984). Evidence from the brain was thought to be either distracting, irrelevant, or hopelessly complex. However, our understanding of brain function has improved significantly over the past twenty years or so. Accordingly, many believe that the time is now ripe for exploring the interface between cognitive development and brain development, and a spate of books on the topic have appeared (e.g. Nelson & Luciana 2001; Johnson, Munakata, & Gilmore, 2002; de Haan & Johnson, 2003). Further, the integration of information from biology and cognitive development sets the stage for a more comprehensive psychology and biology of change than was previously thought possible: a developmental cognitive neuroscience. By the term “cognitive neuroscience” I include not only evidence about brain development, such as that from neuroanatomy, brain imaging, and the behavioral or cognitive effects of brain lesions, but also evidence from ethology. Ethology, a science pioneered by Tinbergen, Lorenz, and others in the 1940s and 1950s, concerns the



study of a whole organism within its natural environment (see Tinbergen, 1951; Lorenz, 1965; Hinde, 1974). We shall see that ethology is a powerful complement to neuroscience, and that the two fields combined can change the way we think about critical issues in perceptual and cognitive development.

In general, insights from biology have begun to play a more central role in informing thinking about perceptual and cognitive development, for a number of reasons. First, a range of powerful new methods and tools have become available to cognitive neuroscientists. These techniques permit questions to be asked more directly than before about the biological basis of cognitive and perceptual development. One set of tools relate to neuroimaging – the generation of “functional” maps of brain activity based on changes in either cerebral metabolism, blood flow, or electrical activity. Some of these imaging methods, such as positron emission tomography (PET), are of limited utility for studying transitions in cognitive development in normal infants due to their invasive nature (requiring the intravenous injection of radioactivity-labeled substances) and their relatively coarse temporal resolution (on the order of tens of seconds). In contrast, two current techniques are readily applied to development in normal children – high-density event-related potentials (HD-ERPs) and functional magnetic resonance imaging (fMRI).

FURTHER READING: CASEY, THOMAS, & McCANDLISS, 2001; NELSON & MONK, 2001

HD-ERP is a method of recording the electrical activity of the brain by means of sensitive electrodes that rest on the surface of the scalp. These recordings can either be of the spontaneous natural rhythms of the brain (electroencephalography – EEG), or the electrical activity time-locked to a stimulus presentation or action (ERPs). Since the ERP from many trials is averaged, the spontaneous natural rhythms of the brain that are unrelated to the stimulus presentation average to zero. However, there has also been recent interest in rapid bursts of high-frequency EEG that appear to be related to stages of information processing in the brain (event-related oscillations) (Csibra, Davis, Spratling, & Johnson, 2000). With a high density of electrodes on the scalp, algorithms can be employed which infer the position and orientation of the brain sources of electrical activity (dipoles) for the particular pattern of scalp surface electrical activity. Some of the assumptions necessary for the successful use of these algorithms are actually more likely to be true of infants than adults. For example, lower levels of skull conductance and fewer cortical convolutions may improve the accuracy and interpretability of HD-ERP results in infants relative to adult subjects (but see Nelson, 1994, and Johnson et al., 2001, for discussion of this methodology as applied to infants).

Functional-MRI allows the non-invasive measurement of cerebral blood oxygen levels with the prospect of spatial resolution on the order of millimeters and temporal resolution of several seconds, using MRI machines commonly available

in modern medical facilities. This technique is being applied to children in several laboratories, though factors such as noise, vibration levels, and enclosure still make it difficult to use with healthy infants (see Casey et al., 2001, for details).

In addition to this armory, a technique that holds promise for the future is near infra-red spectroscopy (NIRS). This is a form of optical imaging, meaning that it depends on measuring tiny changes in the scatter or bending of weak light beams as they pass through the skull and brain (see Meek 2002). Changes in blood oxygenation can be detected with this method, and therefore it could provide an excellent alternative to fMRI for use with young infants. At the time of writing, however, the technique is still being developed in several laboratories.

Another useful tool for linking brain development to behavior is the “marker task.” This method involves the use of specific behavioral tasks which have been related to one or more brain regions in adult humans and non-human primates by neurophysiological and/or brain imaging studies, and preferably by more than one method. By studying the development of performance on the task at different ages and in different contexts, the researcher can gather evidence about how the observed behavioral change is accounted for by known patterns of brain development.

In this book, I will survey several lines of inquiry which illustrate the marker task approach. There are also weaknesses of the marker task approach, such as that findings from one task sometimes don’t generalize to others, and it can be difficult to compare results from pools of participants that differ significantly. Another challenge stems from the design of a task that is sufficiently limited in its demands as to give interpretable results with infants or young children, and yet sufficiently demanding to call upon “interesting” cognitive capacities. Moreover, since different brain regions may be critical for the same task at different ages (Goldman-Rakic, 1971), the interpretation of results is made more complex. Nevertheless, the marker task approach is a useful methodology that promises to provide insight into the development of neurocognitive systems.

Marker tasks need to be based on the cognitive abilities of young infants. Obviously, behavioral tasks involving verbal instruction or output are not feasible. Further, young infants only have a short attention span in terms of the length of time they are prepared to cooperate with the experimenter. Consequently, studies involving extensive training are not feasible either. Fortunately, however, a number of methods have been developed for testing infants that utilize their natural tendencies to look at conspicuous and novel visual stimuli. One of these procedures, called “preferential looking,” involves presenting paired visual stimuli, and recording the time that the infants choose to look at each. Another procedure, called “habituation,” involves showing the same stimulus repeatedly until the infant shows a clear decrease in the time she spends looking at it. When a certain criterion for the looking decrement is reached, a novel stimulus is presented and the increase or recovery in looking time is recorded. If there is significant recovery of looking time, we may infer that the infant can discriminate between the two stimuli. If there is little or no recovery, we may infer that the infant is unable to



discriminate between them. Other techniques for eliciting discriminative responses from young infants include using rate of sucking to measure habituation, the use of an eye-tracker to determine exact patterns of looking, and the use of heart rate measures.

Beyond neuroimaging and the marker task, techniques exist in molecular genetics which allow the lesioning of particular genes from the genome of an animal. An example of this is the deletion of the alpha-calcium calmodulin kinase II gene which results in so-called “knockout” mice being unable to perform certain learning tasks when adults (Silva, Paylor, Wehner, & Tonegawa, 1992; Silva, Stevens, Tonegawa, & Wang, 1992). This method opens new vistas in the analysis of genetic contributions to cognitive and perceptual change in animals, and may be particularly fruitful when applied to well-studied animal models of development such as visual imprinting in chicks and song learning in passerine birds. These animal models may also be useful when investigating the role of genetic deletions/atypicalities for neurocognitive development in disorders of known genetic origin.

FURTHER READING: PENNINGTON, 2001, 2002; TAGER-FLUSBERG, 2003

Animal models are another way that the cognitive neuroscience approach can contribute to the study of development. A number of animal models of behavioral development have reached a stage where some of the principles discovered may be applicable to aspects of human development (see Blass, 1992). One example discussed later in this book is work on the neural basis of visual imprinting in the chick (see Horn, 1985; Johnson, 1991, for reviews). This line of research has implicated particular regions of the chick brain in visual imprinting, and has identified electrophysiological, neuroanatomical, and molecular correlates of this process. A neuronal network model of one of these brain regions has been developed, allowing the computational analysis of such phenomena as sensitive periods for learning (O'Reilly & Johnson, 2002). Further, the dissociation of neural systems underlying components of filial preference behavior in the chick has been used to argue for a similar dissociation in the development of face recognition in human infants (see chapter 5). In another example of the application of animal data to human development, comparisons between the behavioral development of humans and other primates can illuminate the importance of language to changes in other domains of cognition (see chapter 7). Consequently, while homologies between species must be made with great care, well-studied animal models increasingly provide useful theoretical and empirical insights into cognitive development in humans.

FURTHER READING: OVERMAN & BACHEVALIER, 2001; O'REILLY & JOHNSON, 2002

Importantly, theories which incorporate and reveal relationships between brain structures and cognitive functions will be useful in understanding the effects of early brain injury or genetic disorder on cognitive development. Evidence derived from infants with congenital and acquired brain damage will be discussed throughout later chapters. Beyond its clinical utility, this line of evidence can also contribute to the development of theories about functional specification, critical periods, and plasticity in the brain. Thus, there is a two-way interaction between clinical evidence and basic research in developmental cognitive neuroscience.



1.4 WHY TAKE A DEVELOPMENTAL APPROACH TO COGNITIVE NEUROSCIENCE?

Ontogenetic development is the constructive process by which genes interact with their environment at various levels to yield complex organic structures such as the brain and the cognitive processes it supports. The study of development is necessarily multi-disciplinary since new levels of structure that emerge as a result of this process (such as particular neural systems) often require different levels and methods of analysis from those that preceded them. The flip side of this is that development can be used as a tool for unraveling the interaction between seemingly disparate levels of organization, such as that between the molecular biology of gene expression and the development of cognitive abilities such as object recognition. Further, the human adult brain, and the mind it sustains, is composed of a complex series of hierarchical and parallel systems which has proven very difficult to analyze in an exclusively “top-down” manner. Brain damage induced by surgical lesions, or by accident or stroke, is unlikely to cleanly dissociate different levels of hierarchical organization. The developmental approach may allow different levels of hierarchical control to be observed independently. Specifically, it presents the opportunity to observe how various neurocognitive systems emerge and become integrated during development. For example, in chapter 3 we will see how different brain pathways underlying eye movement control emerge and become integrated during development.



1.5 THE CAUSE OF DEVELOPMENTAL CHANGE

Those inclined to see development as the unfolding of pre-existing information in the genes tend to adopt a maturational view of developmental psychology in which infants have reduced versions of the adult mind which increase by steps as particular brain pathways or structures mature. In contrast, taking a constructivist view of development involves attempting to unravel the dynamic relations between intrinsic and extrinsic structure which progressively restrict the phenotypes that can emerge. The distinction between these two approaches has also been



noted by Gottlieb (1992), who refers to them as “predetermined epigenesis” and “probabilistic epigenesis.” Predetermined epigenesis assumes that there is a unidirectional causal path from genes to structural brain changes to brain function and experience. In contrast, probabilistic epigenesis views the interactions between genes, structural brain changes, and function as bidirectional:

Predetermined epigenesis:

(Unidirectional structure–function development)

genes → brain structure → brain function → experience

Probabilistic epigenesis:

(Bidirectional structure–function development)

genes ↔ brain structure ↔ brain function ↔ experience

(Source: Gottlieb, 1992)

Thus, by the predetermined epigenesis view the infant mind is viewed as being comparable to adults with focal brain injury. That is, specific cognitive mechanisms are either present or absent at a given age. For example, parallels have been drawn between infants and patients with frontal lobe deficits. This view shares common assumptions with the “marker task” method discussed earlier, and is commonly associated with a maturational viewpoint. Circuits that support components of the adult system are assumed to come “on-line” at various ages. However, while this approach is likely to provide a reasonable first approximation for normal developmental events, it is unlikely to provide a full account in the long run.

An alternative approach to investigating the relation between the developing brain and cognition is associated with a probabilistic epigenesis approach to biological development. This viewpoint assumes that development involves the progressive restriction of fate. Early in development a system, such as the brain/mind, has a range of possible developmental paths and end states. The developmental path and end state that result are dependent on the particular sets of constraints that operate. This type of analysis of ontogenetic development derives from work on the development of body structure by D’Arcy Thompson (1917) and C. H. Waddington (1975), among others.

Waddington (whose work greatly influenced Piaget) proposed that there are developmental pathways, or necessary epigenetic routes, which he termed “chreods.” Chreods can be conceptualized as valleys in an epigenetic landscape such as that shown in figure 1.3. Self-regulatory processes (which Waddington called “homeorhesis”) ensure that the organism (conceptualized as a ball rolling down the landscape) returns to its channel following small perturbations. Large perturbations, such as being reared in darkness, can result in a quite different valley route being taken, especially when these occur near a decision point. These decision points are regions of the epigenetic landscape where a small perturbation can lead to a different route being taken. Thus, while for the typically developing child the same end point will be reached despite the small perturbations that arise from slightly different rearing environments, a deviation from the normal path early in

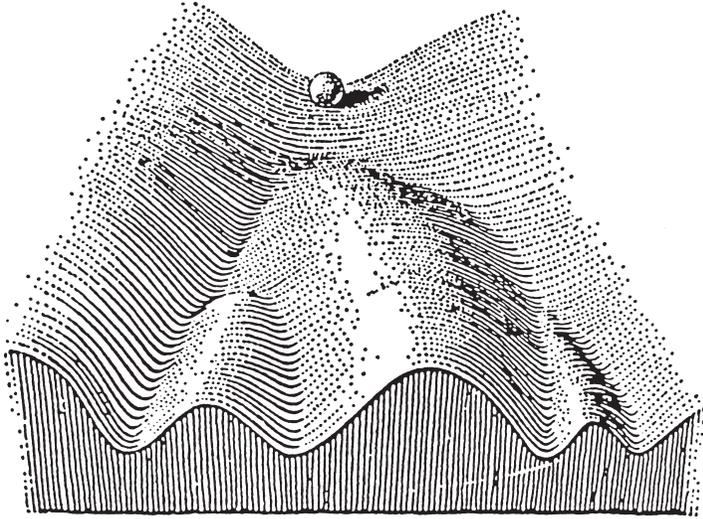


Figure 1.3 The epigenetic landscape of Waddington (1975).

development (high up the hill), at a decision point, or a major perturbation later in development, may cause the child to take a different developmental path and reach one of a discrete set of possible alternative end states (phenotypes).

Aside from Waddington's informal conceptualization, the constructivist (probabilistic epigenesis) approach to development is currently more difficult to work with since we have few theoretical tools for understanding emergent phenomena in complex dynamic systems. By this view, developmental disorders are possible developmental trajectories that are responses to different sets of constraints. This implies that from the moment when the developmental trajectory deviates from the normal one, a variety of new factors and adaptations will come into play, making it likely that some re-organization of brain functioning will take place. In contrast to the maturational approach (causal epigenesis), therefore, applying the mapping between brain regions and functions found in normal adults to such cases may be only partially informative. It should be stressed that the constructivist view just outlined does not seek to downplay the role of genetic factors. Rather, it seeks to understand the emergence of new structures and functions through the complex interactions between genes and their different environments.

1.6 THREE VIEWPOINTS ON HUMAN FUNCTIONAL BRAIN DEVELOPMENT

Relating the neuroanatomical changes that occur during the development of the brain to the remarkable changes in motor, perceptual, and cognitive abilities



during the first decade or so of human life presents a considerable challenge. Throughout this book, I will discuss evidence inspired by three distinct, but not necessarily incompatible, viewpoints on human functional brain development. These are: (1) a maturational perspective, (2) interactive specialization, and (3) a skill learning viewpoint.

As mentioned earlier, much of the research to date attempting to relate brain to behavioral development in humans has been from a maturational viewpoint in which the goal is to relate the “maturation” of particular regions of the brain, usually regions of the cerebral cortex, to newly emerging sensory, motor, and cognitive functions. Evidence concerning the differential neuroanatomical development of brain regions is used to determine an age when a particular region is likely to become functional. Success in a new behavioral task at this age may then be attributed to the maturation of this “new” brain region. By this view, functional brain development is the reverse of adult neuropsychology, with the difference that specific brain regions are added-in instead of being damaged.

Despite the intuitive appeal and attractive simplicity of the maturational approach, we will see during the course of this book that it does not successfully explain some major aspects of human functional brain development. Further, associations between neural and cognitive changes based on age of onset can be theoretically weak due to the great variety of neuroanatomical and neurochemical measures that change at different times in different regions of the brain.

In contrast to the above approach a specific constructivist viewpoint, “interactive specialization” (IS), assumes that postnatal functional brain development, at least within the cerebral cortex, involves a process of organizing patterns of inter-regional interactions (Johnson, 2001, 2002). According to this view, the response properties of a specific region are partly determined by its patterns of connectivity to other regions, and their patterns of activity. During postnatal development, changes in the response properties of cortical regions occur as they interact and compete with each other to acquire their role in new computational abilities. From this perspective, some cortical regions may begin with poorly defined functions, and consequently are partially activated in a wide range of different contexts and tasks. During development, activity-dependent interactions between regions hone the functions of regions such that their activity becomes restricted to a narrower set of circumstances (e.g. a region originally activated by a wide variety of visual objects may come to confine its response to upright human faces). The onset of new behavioral competencies during infancy will therefore be associated with changes in activity over several regions, and not just with the onset of activity in one or more additional region(s). I will expand further on this theory in chapter 10.

A third perspective on human functional brain development, skill learning, involves the proposal that the brain regions active in infants during the onset of new perceptual or motor abilities are similar, or identical, to those involved in complex skill acquisition in adults. For example, with regard to perceptual expertise, Gauthier and colleagues have shown that extensive training of adults with artificial

objects (called “greebles”) eventually results in activation of a cortical region previously associated with face processing, the “fusiform face area” (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). This suggests that the region is normally activated by faces in adults, not because it is prespecified for faces, but due to our extensive expertise with that class of stimulus. Further, it encourages parallels with the development of face processing skills in infants (see Gauthier & Nelson, 2001). While it remains unclear how far parallels can be drawn between adult expertise and infant development, to the extent that the skill learning hypothesis is correct, it presents a clear view of a continuity of mechanisms throughout the life span. Finally, skill learning is not necessarily incompatible with interactive specialization, and sometimes they make similar predictions.



1.7 LOOKING FORWARD

The next chapter reviews the current state of knowledge regarding the pre- and postnatal development of the human brain. While the general sequence of developmental events is very similar for all mammals, the timing of human development, and especially human postnatal development, is protracted. This extended period of postnatal development is associated with a greater extent of area of the cerebral cortex, in particular the prefrontal regions. The more extended postnatal development observed in humans reveals differential rates of development in aspects of brain structure (e.g. different cortical areas and layers). The more differentiated picture of postnatal brain development in humans has also been used to make predictions about the emergence of function.

Focusing on the cerebral cortex, neurobiological and brain imaging studies indicate that the cortex probably does not possess innate representations (in the sense discussed earlier). Rather, early in life large-scale regions of cortex have approximate biases that make them best suited to supporting particular types of computations. The fairly consistent structure–function relations observed in the cortex of normal human adults appear to be the consequence of multiple constraints both intrinsic and extrinsic to the organism, rather than of detailed intrinsic genetic specification. In the following chapters a number of domains of perceptual, cognitive, and motor development that have been associated with neural development are reviewed. In each of these domains I attempt to reveal some of the sources of constraint on the representations that emerge within cortical circuits. Examples of combinations of constraints from the correlational structure of the external environment, the basic architecture of the cortex, and the influence of subcortical circuits are discussed.

Although atypical development is not the primary focus of this book, throughout the review of normal development evidence from atypical development is discussed where relevant (see appendix). Focusing in particular on three developmental disorders (dyslexia, autism, and Williams syndrome), we see that specific



neurocognitive deficits can result from diffuse damage to multiple brain systems. Brain damage in prenatal development can divert the child from one developmental path to another. However, it is possible that different types of brain damage can result in the same adult end state (phenotype), somewhat like the discrete number of valleys in Waddington's epigenetic landscape. In contrast to this, brain damage in later life (perinatal and early postnatal) is commonly compensated for by other parts of the brain. Thus, at this later stage a focal brain lesion may have only mild diffuse cognitive consequences, resembling Waddington's self-organizing adaptation keeping the organism within a certain chreod and resulting in the same general phenotype.

In chapter 9, mechanisms and types of changes in representations during human postnatal development are discussed, and the IS viewpoint on human functional brain development is expanded further. The emergence of specific functions in cortical areas is seen as a product of interactions within the brain, and between the brain and its external environment. Just as the child develops within a social and physical environment, and the brain within a body ("embodiment"), each cortical area develops its functionality within the context of the whole brain ("embrainment"). In the final chapter a number of conclusions and recommendations for future research are made.