

Seventh Edition

HANDBOOK OF
CHILD
PSYCHOLOGY AND
DEVELOPMENTAL
SCIENCE

VOLUME 2

Cognitive Processes

Volume Editors

Lynn S. Liben
Ulrich Müller

Editor-in-Chief

Richard M. Lerner

WILEY

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Volume 2 *Cognitive Processes*

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LYNN S. LIBEN
ULRICH MÜLLER

Editor-in-Chief

RICHARD M. LERNER

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Foreword to the *Handbook of Child Psychology and Developmental Science*, Seventh Edition

WILLIAM DAMON

THE *HANDBOOK*'S DEVELOPING TRADITION

Development is one of life's optimistic ideas. It implies not just change but improvement, progress, forward movement, and some sense of positive direction. What constitutes improvement in any human capacity is an open, important, and fascinating question requiring astute theoretical analysis and sound empirical study. So, too, are questions of what accounts for improvement; what enhances it; and what prevents it when it fails to occur. One of the landmark achievements of this edition of the *Handbook of Child Psychology and Developmental Science* is that a full selection of top scholars in the field of human development have offered us state-of-the-science answers to these essential questions.

Compounding the interest of this edition, the concept of development applies to scholarly fields as well as to individuals, and the *Handbook*'s distinguished history, from its inception more than 80 years ago to the present edition, richly reveals the development of a field. Within the field of human development, the *Handbook* has had a long and notable tradition as the field's leading beacon, organizer, and encyclopedia of what's known. This latest *Handbook* edition, overflowing with insights and information that go well beyond the scientific knowledge available in previous editions, is proof of the substantial progress made by the field of human development during its still-short (by scholarly standards) history.

Indeed, the history of developmental science has been inextricably intertwined with the history of the *Handbook*. Like many influential encyclopedias, the *Handbook* influences the field it reports on. Scholars—especially younger ones—look to it to guide their own work. It serves as an

indicator and as a generator, a pool of received findings, and a source for generating new insight.

It is impossible to imagine what the field would look like if Carl Murchison had not assembled a ground-breaking collection of essays on the then-almost-unknown topic of child study in his first *Handbook of Child Psychology*. That was 1931, at the dawn of a scholarly history that, like every developmental narrative, has proceeded with a combination of continuity and change. What does this history tell us about where the field of developmental science has been, what it has learned, and where it is going? What does it tell us about what's changed and what has remained the same in the questions that have been asked, in the methods used, and in the theoretical ideas that have been advanced to understand human development?

The First Two Editions

Carl Murchison was a star scholar/impresario who edited the *Psychological Register*, founded important psychological journals, and wrote books on social psychology, politics, and the criminal mind. He compiled an assortment of handbooks, psychology texts, and autobiographies of renowned psychologists, and even ventured a book on psychic phenomena (Sir Arthur Conan Doyle and Harry Houdini were among the contributors). Murchison's initial *Handbook of Child Psychology* was published by a small university press (Clark University) in 1931, when the field itself was still in its infancy. Murchison wrote:

Experimental psychology has had a much older scientific and academic status [than child psychology], but at the present time it is probable that much less money is being spent for pure research in the field of experimental psychology than is being

spent in the field of child psychology. In spite of this obvious fact, many experimental psychologists continue to look upon the field of child psychology as a proper field of research for women and for men whose experimental masculinity is not of the maximum. This attitude of patronage is based almost entirely upon a blissful ignorance of what is going on in the tremendously virile field of child behavior. (Murchison, 1931, p. ix)

Murchison's masculine allusion is from another era; it might supply good material for a social history of gender stereotyping. That aside, Murchison was prescient in the task that he undertook and the way that he went about it. At the time this passage was written, developmental psychology was known only in Europe and in a few forward-looking U.S. labs and universities. Nevertheless, Murchison predicted the field's impending ascent: "The time is not far distant, if it is not already here, when nearly all competent psychologists will recognize that one-half of the whole field of psychology is involved in the problem of how the infant becomes an adult psychologically" (Murchison, 1931, p. x).

For this first 1931 *Handbook*, Murchison looked to Europe and to a handful of American research centers for child study—most prominently, Iowa, Minnesota, University of California at Berkeley, Columbia, Stanford, Yale, and Clark—many of which were at the time called *field stations*. Murchison's Europeans included a young "genetic epistemologist" named Jean Piaget, who, in an essay on "Children's Philosophies," cited data from his interviews with 60 Genevan children between the ages of 4 and 12 years. Piaget's chapter would provide U.S. readers with an introduction to his soon-to-be seminal research program on children's conceptions of the world. Another European, Charlotte Bühler, wrote a chapter on young children's social behavior. In her chapter, which still is fresh today, Bühler described intricate play and communication patterns among toddlers—patterns that developmental scientists would not rediscover until the late 1970s. Bühler also anticipated critiques of Piaget that were to be again launched during the sociolinguistics heyday of the 1970s:

Piaget, in his studies on children's talk and reasoning, emphasizes that their talk is much more egocentric than social . . . that children from three to seven years accompany all their manipulations with talk which actually is not so much intercourse as monologue . . . [but] the special relationship of the child to each of the different members of the household is distinctly reflected in the respective conversations. (Bühler, 1931, p. 138)

Other Europeans include Anna Freud, who wrote on "The Psychoanalysis of the Child," and Kurt Lewin, who wrote on "Environmental Forces in Child Behavior and Development"—both would gain worldwide renown in coming years.

The Americans that Murchison chose were equally notable. Arnold Gesell wrote a nativistic account of his twin studies—an enterprise that remains familiar to us today—and Stanford's Lewis Terman wrote a comprehensive account of everything known about the "gifted child." Harold Jones described the developmental effects of birth order, Mary Cover Jones wrote about children's emotions, Florence Goodenough wrote about children's drawings, and Dorothea McCarthy wrote about language development. Vernon Jones's chapter on "children's morals" focused on the growth of *character*, a notion that was to become mostly lost to the field during the cognitive-developmental revolution, but that has reemerged in the past decade as a primary concern in the study of moral development.

Murchison's vision of child psychology included an examination of cultural differences as well. His *Handbook* presented to the scholarly world a young anthropologist named Margaret Mead, just back from her tours of Samoa and New Guinea. In this early essay, Mead wrote that her motivation in traveling to the South Seas was to discredit the claims that Piaget, Lévy-Bruhl, and other "structuralists" had made regarding what they called *animism* in young children's thinking. (Interestingly, about a third of Piaget's chapter in the same volume was dedicated to showing how Genevan children took years to outgrow their animism.) Mead reported data that she called "amazing": "In not one of the 32,000 drawings (by young 'primitive' children) was there a single case of personalization of animals, material phenomena, or inanimate objects" (Mead, 1931, p. 400). Mead parlayed these data into a tough-minded critique of Western psychology's ethnocentrism, making the point that animism and other beliefs are more likely to be culturally induced than intrinsic to early cognitive development. This is hardly an unfamiliar theme in contemporary psychology. Mead offered a research guide for developmental field workers in strange cultures, complete with methodological and practical advice, such as the following: (1) translate questions into native linguistic categories; (2) do not do controlled experiments; (3) do not try to do research that requires knowing the ages of subjects, which are usually unknowable; and (4) live next door to the children whom you are studying.

Despite the imposing roster of authors that Murchison had assembled for this original *Handbook of Child*

Psychology, his achievement did not satisfy him for long. Barely 2 years later, Murchison put out a second edition, of which he wrote: “Within a period of slightly more than 2 years, this first revision bears scarcely any resemblance to the original *Handbook of Child Psychology*. This is due chiefly to the great expansion in the field during the past 3 years and partly to the improved insight of the editor” (Murchison, 1933, p. vii). The tradition that Murchison had brought to life was already developing.

Murchison saw fit to provide the following warning in his second edition: “There has been no attempt to simplify, condense, or to appeal to the immature mind. This volume is prepared specifically for the scholar, and its form is for his maximum convenience” (Murchison, 1933, p. vii). It is clear that Murchison, despite his impresario urges, was willing to sacrifice accessibility and textbook-level sales for scientific value in this instance.

Murchison exaggerated when he wrote that his second edition bore little resemblance to the first. Almost half of the chapters were virtually the same, with minor additions and updating. (For the record, though, despite Murchison’s continued use of masculine phraseology, 10 of the 24 authors in the second edition were women.) Some of the authors whose original chapters were dropped were asked to write about new topics. So, for example, Goodenough wrote about mental testing rather than about children’s drawings, and Gesell wrote a general chapter on maturational theory that went well beyond his own twin studies.

But Murchison also made certain abrupt changes. He dropped Anna Freud entirely, prompting the marginalization of psychoanalysis within U.S. academic psychology. Leonard Carmichael, later to play a pivotal role in the *Handbook* tradition, made his appearance as author of a major chapter (by far, the longest in the book) on prenatal and perinatal growth. Three other physiologically oriented chapters were added as well: one on neonatal motor behavior, one on visual–manual functions during the first 2 years of life, and one on physiological “appetites” such as hunger, rest, and sex. Combined with the Goodenough and Gesell shifts in focus, these additions gave the 1933 *Handbook* a more biological thrust, in keeping with Murchison’s long-standing desire to display the hard-science backbone of the emerging field.

The Early Wiley Editions

Leonard Carmichael was president of Tufts University when he organized Wiley’s first edition of the *Handbook*. The switch from a university press to the long-established

commercial firm of John Wiley & Sons was commensurate with Carmichael’s well-known ambition; and indeed Carmichael’s effort was to become influential beyond anything that Murchison might have anticipated. (The switch to Wiley meant that what was to become known as Wiley’s first edition was actually the *Handbook*’s third edition—and that what is now called the seventh edition is really the *Handbook*’s ninth.) Carmichael renamed the volume the *Manual of Child Psychology*, in keeping with Carmichael’s intention of producing an “advanced scientific manual to bridge the gap between the excellent and varied elementary textbooks in this field and the scientific periodical literature” (Carmichael, 1946, p. vi).

Despite the small title change, there was significant continuity between the Murchison and Carmichael’s editions. Carmichael acknowledged this in the prefaces to both of his editions, the 1946 and 1954 *Manuals*:

Both as editor of the *Manual* and as the author of a special chapter, the writer is indebted. . . . [for] extensive excerpts and the use of other materials previously published in the *Handbook of Child Psychology, Revised Edition*. (Carmichael, 1946, p. vi)

Both the *Handbook of Child Psychology* and the *Handbook of Child Psychology, Revised Edition*, were edited by Dr. Carl Murchison. I wish to express here my profound appreciation for the pioneer work done by Dr. Murchison in producing these handbooks and other advanced books in psychology. The *Manual* owes much in spirit and content to the foresight and editorial skill of Dr. Murchison. (Carmichael, 1954, p. v)

The first quote comes from Carmichael’s preface to the 1946 edition, the second from his preface to the 1954 edition. It is not known why Carmichael waited until the 1954 edition to add the personal tribute to Carl Murchison. Perhaps a careless typist dropped the laudatory passage from a handwritten version of the 1946 preface and its omission escaped Carmichael’s notice. Or perhaps 8 years of further development increased Carmichael’s generosity of spirit. It is also possible that Murchison or his family complained. In any case, Carmichael always acknowledged the roots of his *Manual*, if not always their original editor.

Leonard Carmichael took his 1946 *Manual* in the same direction established by Murchison back in 1931 and 1933. First, Carmichael appropriated five Murchison chapters on biological or experimental topics such as physiological growth, scientific methods, and mental testing. Second, he added three new biologically oriented chapters on animal infancy, on physical growth, and on motor and behavioral maturation (a tour de force by Myrtle McGraw that

instantly made Gesell's chapter in the same volume obsolete). Third, he commissioned Wayne Dennis to write a chapter that focused exclusively on physiological changes associated with puberty. Fourth, Carmichael dropped Piaget and Bühler, who, like Anna Freud years earlier, were becoming out of step with then-current experimental trends in U.S. psychology.

The five Murchison chapters on social and cultural influences in development were the ones Carmichael retained: two chapters on environmental forces on the child (by Kurt Lewin and by Harold Jones), Dorothea McCarthy's chapter on children's language, Vernon Jones's chapter on children's morality (now entitled "Character Development—An Objective Approach"), and Margaret Mead's chapter on "primitive" children (now enhanced by several spectacular photos of mothers and children from exotic cultures around the world). Carmichael also stuck with three other psychologically oriented Murchison topics (emotional development, gifted children, and sex differences), but he selected new authors to cover them.

Carmichael's second and final *Manual* in 1954 was very close in structure and content to his 1946 *Manual*. Carmichael again retained the heart of Murchison's original vision, many of Murchison's original authors and chapter topics, and some of the same material that dated all the way back to the 1931 *Handbook*. Not surprisingly, the chapters that were closest to Carmichael's own interests received the most significant updating. As Murchison had done, Carmichael leaned toward the biological and physiological whenever possible. He clearly favored experimental treatments of psychological processes. Yet Carmichael still retained the social, cultural, and psychological analyses by Lewin, Mead, McCarthy, Terman, Harold Jones, and Vernon Jones, even going so far as to add a new chapter on social development by Harold and Gladys Anderson and a new chapter on emotional development by Arthur Jersild.

In 1946, when Carmichael had finished his first *Manual*, he had complained that "this book has been a difficult and expensive one to produce, especially under wartime conditions" (Carmichael, 1946, p. vii). But the project had been well worth the effort. The *Manual* quickly became the bible of graduate training and scholarly work in the field, available virtually everywhere that human development was studied. Eight years later, now head of the Smithsonian Institution, Carmichael wrote, in the preface to his 1954 edition: "The favorable reception that the first edition received not only in America but all over the world is indicative of the growing importance of the study of the

phenomena of the growth and development of the child" (Carmichael, 1954, p. vii).

The Murchison and Carmichael volumes make fascinating reading, even today. The perennial themes of the field were always there: the nature/nurture debate; the generalizations of universalists opposed by the particularizations of contextualists; the alternating emphases on continuities and discontinuities during ontogenesis; and the standard categories of maturation, learning, locomotor activity, perception, cognition, language, emotion, conduct, morality, and culture—all separated for the sake of analysis, yet, as authors throughout each of the volumes acknowledged, all somehow joined in the dynamic mix of human development.

These things have not changed. Yet much in the early *Handbooks/Manuals* is now irrevocably dated. Long lists of children's dietary preferences, sleeping patterns, elimination habits, toys, and somatic types look quaint and pointless through today's lenses. The chapters on children's thought and language were done prior to the great contemporary breakthroughs in neurology and brain/behavior research, and they show it. The chapters on social and emotional development were ignorant of the processes of social influence and self-regulation that soon would be revealed through attribution research and other studies in social psychology. Terms such as *cognitive neuroscience*, *neuronal networks*, *behavior genetics*, *social cognition*, *dynamical systems*, *information processing*, and *developmental psychopathology* were unknown. Margaret Mead's rendition of the primitive child stands as a weak straw in comparison to the wealth of cross-cultural knowledge available in today's "cultural psychology."

Most tellingly, the assortments of odd facts and normative trends were tied together by very little theory throughout the Carmichael chapters. It was as if, in the exhilaration of discovery at the frontiers of a new field, all the facts looked interesting in and of themselves. That is what makes so much of the material seem odd and arbitrary. It is hard to know what to make of the lists of facts, where to place them, which ones were worth keeping track of and which ones are expendable. Not surprisingly, the bulk of the data presented in the Carmichael manuals seems not only outdated by today's standards but, worse, irrelevant.

Carmichael's second and final *Manual* had a long life: Not until 1970 did Wiley bring out a third edition. Carmichael was retired by then, but he still had a keen interest in the book. At his insistence, his own name became part of the title of Wiley's third edition: The edition

was called, improbably, *Carmichael's Manual of Child Psychology*, even though it had a new editor and an entirely new cast of authors and advisors.

Mussen's Transformation

Paul Mussen was editor of the 1970 edition; once again the project flourished. Now a two-volume set, the 1970 third edition swept the social sciences, generating widespread interest in developmental psychology and its related disciplines. Rarely had a scholarly compendium become both so dominant in its own field and so familiar in related disciplines. The volumes became essential sources for graduate students and advanced scholars alike. Publishers referred to Mussen's 1970 *Carmichael's Manual* as the standard against which other scientific handbooks were compared.

By 1970, the importance of theory for understanding human development had become apparent. Looking back on Carmichael's last *Manual*, Mussen wrote: "The 1954 edition of this *Manual* had only one theoretical chapter, and that was concerned with Lewinian theory which, so far as we can see, has not had a significant lasting impact on developmental psychology" (Mussen, 1970, p. x). The intervening years had seen a turning away from the norm of psychological research once fondly referred to as "dust-bowl empiricism."

The 1970 handbook—still called, as noted above, *Carmichael's Manual*—had an entirely new look. The two-volume set carried only one chapter from the earlier books, Carmichael's updated version of his own long chapter on the "Onset and Early Development of Behavior," which had made its appearance under a different title way back in Murchison's 1933 edition. Otherwise, as Mussen wrote in his preface, "It should be clear from the outset . . . that the present volumes are not, in any sense, a *revision* of the earlier editions; this is a completely new *Manual*" (Mussen, 1970, p. x).

And it was. In comparison to Carmichael's last edition 16 years earlier, the scope, variety, and theoretical depth of the Mussen volumes were astonishing. The field had blossomed, and the new *Manual* showcased many of the new bouquets that were being produced. The biological perspective was still strong, grounded by chapters on physical growth (by J. M. Tanner) and physiological development (by Dorothy Eichorn), and by Carmichael's revised chapter (now made more elegant by some excerpts from Greek philosophy and modern poetry). But two other cousins of biology also were represented, in a chapter on ethology

by Eckhard Hess, and a chapter on behavior genetics by Gerald McClearn. These chapters were to define the major directions of biological research in the field for at least the next three decades.

As for theory, Mussen's *Handbook* was thoroughly permeated with it. Much of the theorizing was organized around the approaches that, in 1970, were known as the "three grand systems": (1) Piaget's cognitive-developmentalism, (2) psychoanalysis, and (3) learning theory. Piaget was given the most extensive treatment. He himself reappeared in this *Manual*, authoring a comprehensive (some say definitive) statement of his own theory, which now bore little resemblance to his 1931/1933 catalog of children's intriguing verbal expressions. In addition, chapters by John Flavell, by David Berlyne, by Martin Hoffman, and by William Kessen, Marshall Haith, and Philip Salapatek, all gave major treatments to one or another aspect of Piaget's body of work.

Several other theoretical approaches were represented in the 1970 *Manual* as well. Herbert and Anne Pick explicated Gibsonian theory in a chapter on sensation and perception, Jonas Langer wrote a chapter on Werner's organismic theory, David McNeill wrote a Chomskian account of language development, and Robert LeVine wrote an early version of what was to become "culture theory."

With its increased emphasis on theory, the 1970 *Manual* explored in depth a matter that had been all but neglected in the *Manual's* previous versions: the mechanisms of change that could account for, to use Murchison's old phrase, "the problem of how the infant becomes an adult psychologically." In the process, old questions such as the relative importance of nature versus nurture were revisited, but with far more sophisticated conceptual and methodological tools.

Beyond theory building, the 1970 *Manual* addressed an array of new topics and featured new contributors: peer interaction (Willard Hartup), attachment (Eleanor Maccoby and John Masters), aggression (Seymour Feshbach), individual differences (Jerome Kagan and Nathan Kogan), and creativity (Michael Wallach). All of these areas of interest are still very much with us.

Wiley's fourth edition, published in 1983, was redesignated to become once again the *Handbook of Child Psychology*. By then, Carmichael had passed away. The set of books, now expanded to four volumes, became widely referred to in the field as "the Mussen handbook."

If the 1970 *Manual* reflected a blossoming of the field's plantings, the 1983 *Handbook* reflected a field whose

ground cover had spread beyond any boundaries that could have been previously anticipated. New growth had sprouted in literally dozens of separate locations. A French garden, with its overarching designs and tidy compartments, had turned into an English garden, unruly but often glorious in its profusion. Mussen's two-volume *Carmichael's Manual* had now become the four-volume Mussen *Handbook*, with a page-count increase that came close to tripling the 1970 edition.

The grand old theories were breaking down. Piaget was still represented in 1983 by his 1970 piece, but his influence was on the wane throughout other chapters. Learning theory and psychoanalysis were scarcely mentioned. Yet the early theorizing had left its mark, in vestiges that were apparent in new approaches, and in the evident conceptual sophistication with which authors treated their material. There was no return to dust-bowl empiricism. Instead, a variety of classical and innovative ideas were coexisting: ethology, neurobiology, information processing, attribution theory, cultural approaches, communications theory, behavioral genetics, sensory-perception models, psycholinguistics, sociolinguistics, discontinuous stage theories, and continuous memory theories all took their places, with none quite on center stage. Research topics now ranged from children's play to brain lateralization, from children's family life to the influences of school, day care, and disadvantageous risk factors. There also was coverage of the burgeoning attempts to use developmental theory as a basis for clinical and educational interventions. The interventions usually were described at the end of chapters that had discussed the research relevant to the particular intervention efforts, rather than in whole chapters dedicated specifically to issues of practice.

The Fifth and Sixth Editions

There was a long hiatus between the fourth edition in 1983 and the fifth edition, which was not to appear until 1998. The fifth edition fell to me to organize, and this was not at my own initiative. Two Wiley editors—Herb Reich, a legendary figure in academic publishing, and Kelly Franklin, an up-and-coming innovative star—approached me about reviving the project, which they correctly believed had a vital tradition behind it, but that they also believed was in danger of falling by the wayside. I had been editing the Jossey-Bass series that I founded, *New Directions for Child and Adolescent Development*, and the two Wiley editors believed that if we could impart a “new directions” tone to a new *Handbook* edition, the project could regain its

past appeal. I agreed, and I proposed that this next edition be organized in an intuitively simple four-volume design: a theory volume, a volume on cognitive and linguistic development, a volume on social and personality development, and a volume on child psychology in practice. When Wiley accepted my proposal, my first action as general editor was to invite an incredibly talented group of volume editors—Nancy Eisenberg, Deanna Kuhn, Richard Lerner, Anne Renninger, Robert Siegler, and Irving Sigel—to collaborate on the selection and editing of chapters. The edition was to become the result of a partnership among all the editors; and the same team collaborated again to produce the sixth edition of the *Handbook* in 2006, with Richard Lerner assuming an added role as my co-editor-in-chief. The 2006 edition closely followed the model of the 1998 edition, with some important additions, such as chapters on the positive youth development approach, on artistic development, and on religiosity and faith in human development.

Our team approached the 1998 and 2006 editions with the same purpose that Murchison, Carmichael, and Mussen before us had shared: “to provide,” as Mussen wrote, “a comprehensive and accurate picture of the current state of knowledge—the major systematic thinking and research—in the most important research areas of the psychology of human development” (Mussen, 1983, p. vii). We assumed that the *Handbook* should be aimed “specifically for the scholar,” as Murchison declared, and that it should have the character of an “advanced text,” as Carmichael defined it. We expected that our readership would be interdisciplinary, given the tendency of scholars in human development to do work across the fields of psychology, cognitive science, neuroscience, history, linguistics, sociology, anthropology, education, and psychiatry. In Volume 4, we hoped that research-oriented practitioners would be among the scholars for whom the *Handbook* had value.

By the time of the 1998 and 2006 editions of the *Handbook*, powerful theoretical models and approaches—not quite unified theories like the “three grand systems” that had marked earlier editions—were again organizing much of the field's research. There was great variety in these models and approaches, and each was drawing together significant clusters of work. Among the powerful models and approaches prominent in the 1998 and 2006 *Handbooks* were the dynamic system theories, life-span and life-course approaches, cognitive science and neural models, the behavior genetics approach, person–context interaction theories, action theories, culture theory, ecological models, and neo-Piagetian and Vygotskian models.

Although some of these models and approaches had been in the making for some time, by the end of the 20th century they had fully come into their own: researchers were drawing on them more directly, taking their implied assumptions and hypotheses seriously, using them with specificity and control, and exploiting all of their implications for practice.

The Present

The seventh Wiley edition of the *Handbook* continues and strengthens the trends toward specific theoretical analyses of multiple developmental processes, even highlighting this focus by including the term “processes” in three of the four volume’s titles, a designation new to the *Handbook*’s history. The volumes present a rich mix of classic and contemporary theoretical perspectives, but I believe it is fair to say that the dominant views throughout are marked by an emphasis on the dynamic interplay of all relational developmental systems that co-act across the life span, incorporating the range of biological, perceptual, cognitive, linguistic, emotional, social, cultural, and ecological levels of analysis. At the same time, the chapters together consider a vast array of topics and problems, ranging from sexuality and religiosity to law, medicine, war, poverty, and education. The emerging world of digital experience is also given a fuller treatment than in any previous *Handbook* edition, commensurate with our present-day technological revolution. All this gives this seventh edition of the *Handbook* a timely feel.

The present *Handbook*’s combination of theoretical and methodological sophistication and topical timeliness resolves an old tension evident in the *Handbook*’s prior cycling between theoretical-methodological and problem-centered approaches. My impression is that, rather than leaning in one direction or the other, this *Handbook* manages to be *both* more theoretical-methodological *and* more topical than the previous editions. As a developmental phenomenon, this puts the *Handbook*

in a class of organisms that develop toward adaptive complexity rather than toward one or another contrasting polar dimension.

I wonder what Carl Murchison would think of the grown-up child that he spawned before the field of human development had become a mainstream endeavor in research and teaching around the world. Murchison’s idiosyncratic assortment of fascinating studies bears little resemblance to the imposing compendium of solidly grounded knowledge in the present *Handbook*. Yet each step along the 83-year way followed directly from what had gone before, with only occasional departures or additions that may have seemed more like gradual revisions at the time. Over the long haul, the change in the *Handbook* has been dramatic, but the change process itself has been marked by substantial continuities. If Murchison were to come back to life today, he may be astonished by the size and reach of his child, but I believe he would recognize it—and proudly so.

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2014

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Preface

Across its editions, the title of this handbook has changed, now, five times: *A Handbook of Child Psychology*; *Manual of Child Psychology*; *Carmichael's Manual of Child Psychology*; *Handbook of Child Psychology*; and *Handbook of Child Psychology and Developmental Science*. As well, the field of scholarship represented in the handbook has also been labeled differently: child psychology, child development, developmental psychology, and, today, developmental science. The rationales for the use of these labels involve historically changing ontological and epistemological assumptions.

During the latter years of the 19th century and for much of the past two thirds of the 20th century, and perhaps especially in the United States and Western Europe, the study of human development was a visible subfield of psychology (see Cairns & Cairns, 2006, for a review; see also Damon, in the Foreword to this edition of the *Handbook*). In this literature, and its antecedents in philosophy (see Baltes, 1983; Overton, 2006 for reviews), development was envisioned to be a life-span phenomenon (e.g., Erikson, 1959; Hall, 1904, 1922). However, the majority of the scholarship about human development in the United States and Western Europe was focused on the early years of life (infancy and childhood) (e.g., Binet & Simon, 1905a, 1905b; Gesell, 1929; Piaget, 1923; Preyer, 1882; Terman, 1925).

As a consequence, across this historical period, child psychology emerged as a specific subarea of psychology, spurred on by the research of scientists studying this age period; by the founding of several university centers and institutes devoted to the study of children (e.g., in Iowa, involving scholars such as Boyd R. McCandless; and in Minnesota, involving scholars such as Dale B. Harris); and by the work in the field of home economics, which was focused on children (and families), that was occurring within land-grant universities in the United States

(Cairns & Cairns, 2006; Lerner & Simon, 1998). At the same time, many of the contributors to child psychology also created a purportedly multidisciplinary instantiation of scholarship devoted to the study of children, that is, child *development*. In 1933, the Society for Research in Child Development (SRCD) was founded to promote such a multidisciplinary approach to the study of children (and to the application of child development research) but, in actuality, SRCD was from its outset and remains today dominated by scholars whose training is in psychology. It is not surprising, then, that, whether labeled child psychology or child development, the study of the early portion of the life span was approached in very similar ways by scholars studying children.

At its inception, the child development (or child psychology) field was framed by Cartesian-split conceptions of change across ontogeny and by reductionist accounts of the bases of human development (Overton, 2013a, 2013b; Overton & Müller, 2013). The core conceptual issues of child development were the nature-nurture, the continuity-discontinuity, and the stability-instability controversies (Lerner, 2002), and “solutions” to these debates involved, for instance, reducing development to being a phenomenon explained by either nature variables (genes or maturation; e.g., Hamburger, 1957) or by operant or respondent stimulus-response connections (e.g., Bijou & Baer, 1961). This split, reductionist ontology about development meant that the epistemological route to learning about the basis of development was to identify the essential (nature *or* nurture) explanatory variable(s). Accordingly, the study of development was also marked by variable-centered analyses, as exemplified by the tables of contents of the editions of this *Handbook* published during this period (e.g., Carmichael, 1946, 1954; Murchison, 1931, 1933; Mussen, 1970, 1983; see also Damon, in the

Foreword to this edition), as well as by the tables of contents of other major compendiums published during this period (e.g., Reese & Lipsitt, 1970; Stevenson, 1963).

However, as early as 1970, Mussen, the editor of the third edition of the *Handbook* published by Wiley, pointed to the potential meaning of a growing interest among some scientists to move away from a reductionist approach, involving descriptions of the variables purportedly accounting for ontogenetic structure and function, and toward an approach that viewed development as involving interrelations among variables (from multiple levels of organization). Mussen (1970) said that “the major contemporary empirical and theoretical emphases in the field of developmental psychology . . . seem to be on *explanations* of the psychological changes that occur, the mechanisms and processes accounting for growth and development” (p. vii). By pointing to the interest in change processes, Mussen was implying that we needed something more to explain the process of development, unless we believed that nature or nurture variables explained themselves in structure or function.

That “something more” was already emerging within the study of development—for instance, at a series of conferences held at the University of West Virginia in the late 1960s and early 1970s about the nature and implications of a life-span view of human development (e.g., Baltes & Schaie, 1974; Nesselroade & Reese, 1973; Schaie, 1970). These West Virginia University conferences, the edited books that derived from them, and the associated articles published in both theoretically oriented journals (e.g., *Human Development*, *Developmental Review*) and empirically oriented journals (e.g., *Child Development*, *Developmental Psychology*, *International Journal of Behavioral Development*, and *Journal of Research on Adolescence*) discussed the philosophical, theoretical, and methodological problems associated with split/reductionist accounts of development. In addition, they introduced ideas about the potential for plasticity (i.e., the potential for systematic change) in development across life, and pointed to the role of potentially mutually influential relations between individuals and their normative age- and history-graded experiences and, as well, their non-normative experiences, in instantiating this plasticity. Finally, they underscored the fundamental necessity of studying intraindividual changes (and interindividual differences in intraindividual changes) involved in these individual-context relations in order to describe, explain, and optimize the course of human development. These ideas would act synergistically with growing scholarship

in Europe that provided theory and data fostering a “reversal” of focus for developmental inquiry—from variable-centered to person-centered approaches to human development (e.g., Magnusson, 1999). These ideas were also synergistic with work in sociology that demonstrated that the course of life was shaped by historical events that one encountered at particular times and in particular places (Elder, 1974).

When taken together, the dimensions of human development scholarship that crystallized and coalesced between the 1970s and 1990s pointed to the vacuity of split/reductionist models (and their attendant methodologies). In turn, these ideas underscored the importance of time and place, person–context relations, plasticity, and the need for a focus on longitudinal (change-sensitive) methods to study intraindividual change across life and, as well, the diverse life paths of these intraindividual changes. These ideas, when considered together, presented a major challenge to the then-dominant metatheoretical and theoretical ideas in the field. Indeed, the new ideas about human development that found an impetus at the West Virginia University conferences grew in influence across the field and together, across the last three decades of the 20th century, created a Kuhn-like (Kuhn, 1962) paradigm shift (Overton, 2013a, 2013b; Overton & Lerner, 2012).

The shift in conceptual and empirical foci attendant to this paradigm shift was multifaceted. As I noted, Mussen (1970) observed that the field had been primarily descriptive and normative (Mussen, 1970), with the norms usually generated by studying only a small portion of humanity (i.e., European American middle-class children in the main; Hagen, Paul, Gibb, & Wolters, 1990). In addition, the “paradigm” framing this research was as likely (if not more likely) to use cross-sectional research to study development as it was to employ longitudinal methods. The use of cross-sectional designs (and data analysis methods, e.g., R-technique analyses; e.g., see Cattell, 1966, and for more current versions of these ideas see Molenaar & Nesselroade, 2014; Nesselroade & Molenaar, 2010) was predicated on the assumption of the applicability of the ergodic theorem (e.g., Molenaar, 2007; Molenaar & Nesselroade, 2014). The ergodic theorem holds that data sets are marked by: (a) homogeneity across individuals in a three-dimensional matrix that involves persons, variables, and time; and (b) stationarity of individuals’ scores on variables across time (Molenaar, 2007).

In contrast, the approach to the study of human development that was evidenced by the life-span and life-course perspectives involved research that documented the

presence of systematic variation in trajectories of intraindividual change, both within and across people. As such, the assumptions of homogeneity and stationarity of the ergodic theorem were rejected and developmental scientists placed greater importance on not only person-centered research but, as well, change-sensitive methodologies for both descriptive and explanatory efforts (Molenaar, 2007, 2010). What was distinctive about this research, however, was that it was both derived from and promoted diverse attempts to create theoretical models of human development associated with an emergent, relational paradigm (Overton, 2013a, 2013b; Overton & Müller, 2013), a conception that focused on the individual and on the course of his or her trajectories of reciprocal bidirectional relations with the multiple levels of the ecology of human development (represented as individual $\longleftrightarrow$ context relations). Examples were the bioecological model of Bronfenbrenner (e.g., 1979), the dialectical model of Riegel (e.g., 1975), the developmental contextual approach of Lerner (1982), the developmental systems concepts of Gottlieb (1997, 1998) and of Ford and Lerner (1992), the model of individual development proposed by Magnusson (1999), and the embodiment model presented by Overton (1994, 1997).

In short, these “strands” of theory merged in the 1970s, 1980s, and 1990s and shifted the predominant developmental “paradigm” away from reductionism, Cartesian-split conceptions, and methods predicated on ergodicity, and created a focus on models emphasizing the mutually influential relations between individuals and their contexts, on person $\longleftrightarrow$ context relations (Cairns & Cairns, 2006; Lerner, 2006). Such models involved the belief that time and place matter in regard to shaping the course of life (Bronfenbrenner, 2005; Elder, 1998; Elder & Shanahan, 2006), and emphasized that the scientific study of human development needed to study both the individual and the diversity of people in order to understand human development.

In sum, the relational paradigm that framed conceptions of the bases of human development was associated with the generation of several, relational developmental systems models of human development (Lerner, 2006; Lerner & Overton, 2008; Overton, 2013a, 2013b; Overton & Müller, 2013), conceptions that were used to guide the study of individuals, contexts, and their dynamic interrelations across the life span. Table P.1 presents the defining features of such models.

This multilevel and multidisciplinary approach to studying human development was the basis of the view

that the field was best represented by the term developmental science. In turn, given this synergistic history of the links among theory, method, and research, it is not surprising that, at this writing, relational developmental systems theories are at the forefront of the study of human development (e.g., Lerner, 2012; Lerner & Benson, 2013a, 2013b; Overton & Lerner, 2012). Indeed, the fifth edition of the Wiley *Handbook* (Damon, 1998) had pointed to the growing prominence of such approaches to the study of human development and, in turn, the sixth edition (Damon & Lerner, 2006) noted that models derived from relational developmental systems thinking, and from a relational meta-model more generally, had become the predominant conceptual lens for the cutting-edge theory and methodological innovations guiding research in human development across the life span.

In the present seventh edition of the Wiley *Handbook*, this pathway of scholarly progression is continued. Key examples of relational developmental systems models are found across all four volumes of this seventh edition of the *Handbook*. Moreover, accompanying the use of these models are new methodologies to study individuals, to therefore capture the nonergodic character of human development and, as well, to study the developmental system within which individual $\longleftrightarrow$ context relations are embedded. Examples of these methods are also a prominent contribution of chapters in this edition of the *Handbook*.

Another key feature of the chapters in this edition of the *Handbook* is the applied use of relational developmental systems theoretical models. Based on ideas about the relative plasticity of individual $\longleftrightarrow$ context relations, this use of theory overcomes yet another traditional split within the study of human development—between theory-predicated explanations of human development and applications aimed at enhancing human development (Baltes, Reese, & Nesselroade, 1977; Lerner, 2002, 2012). For instance, to test explanations of developmental change, scholars need to institute or evaluate actions that are aimed at altering the bidirectional relations theoretically expected to produce changes in behavior and development. These actions must necessarily be embedded in the actual ecology of human development in order to have generalizability to the lived experiences of individuals (Lerner & Callina, 2014) and, as such, they constitute intervention (applied) research; at the same time, such research tests basic explanatory processes of human development. As such, in contemporary developmental science any splits between basic and applied research are regarded as anachronistic representations of the reductionist, Cartesian approaches of earlier eras.

TABLE P.1 Defining Features of the Relational Developmental Systems Paradigm**Relational Metatheory**

Predicated on a philosophical perspective that transcends Cartesian dualism and atomism, theories derived from the relational developmental systems paradigm are framed by a relational metatheory for human development. This focus includes an emphasis on process and a rejection of all splits between components of the ecology of human development (e.g., between nature- and nurture-based variables, between continuity and discontinuity, and between stability and instability). Holistic syntheses replace dichotomies, as well as reductionist partitions of the developing relational system, through the integration of three relational moments of analysis: the identity of opposites, the opposites of identity, and the syntheses of wholes. Deriving from the relational metatheory, relational developmental systems posit the organism as an inherently active, self-creating, self-organizing, and self-regulating nonlinear complex adaptive system, which develops through embodied activities and actions, as they co-act with a lived world of physical and sociocultural objects.

The Integration of Levels of Organization

Relational thinking, with the rejection of Cartesian splits, is associated with the idea that all levels of organization within the ecology of human development are integrated or fused. These levels range from the biological and physiological through the cultural and historical.

Developmental Regulation Across Ontogeny Involves Mutually Influential Individual $\leftrightarrow$ Context Relations

As a consequence of the integration of levels, the regulation of development occurs through mutually influential connections among all levels of the developing relational system, ranging from genes and cell physiology through individual mental and behavioral functioning to society, culture, the designed and natural ecology, and, ultimately, history. These mutually influential relations may be represented generically as Level 1 $\leftrightarrow$ Level 2 (e.g., Family $\leftrightarrow$ Community), and in the case of ontogeny may be represented as individual $\leftrightarrow$ context.

Integrated Actions, Individual $\leftrightarrow$ Context Relations, Are the Basic Unit of Analysis Within Human Development

The character of developmental regulation means that the integration of actions—of the individual on the context and of the multiple levels of the context on the individual (individual $\leftrightarrow$ context)—constitute the fundamental unit of analysis in the study of the basic process of human development.

Temporality and Plasticity in Human Development

As a consequence of the fusion of the historical level of analysis—and therefore temporality—in the levels of organization comprising the ecology of human development, the developing relational system is characterized by the potential for systematic change, by plasticity. Observed trajectories of intraindividual change may vary across time and place as a consequence of such plasticity.

Relative Plasticity

Developmental regulation may both facilitate and constrain opportunities for change. Thus, change in individual $\leftrightarrow$ context relations is not limitless, and the magnitude of plasticity (the probability of change in a developmental trajectory occurring in relation to variation in contextual conditions) may vary across the life span and history. Nevertheless, the potential for plasticity at both individual and contextual levels constitutes a fundamental strength of all human development.

Intraindividual Change, Interindividual Differences in Intraindividual Change, and the Fundamental Substantive Significance of Diversity

The combinations of variables across the integrated levels of organization within the developmental system that provide the basis of the developmental process will vary at least in part across individuals and groups. This diversity is systematic and lawfully produced by idiographic, group differential, and generic (nomothetic) phenomena. The range of interindividual differences in intraindividual change observed at any point in time is evidence of the plasticity of the developmental system, and gives the study of diversity fundamental substantive significance for the description, explanation, and optimization of human development.

Interdisciplinarity and the Need for Change-Sensitive Methodologies

The integrated levels of organization comprising the developmental system require collaborative analyses by scholars from multiple disciplines. Interdisciplinary knowledge is a central goal. The temporal embeddedness and resulting plasticity of the developing system requires that research designs, methods of observation and measurement, and procedures for data analysis be change- and process-sensitive and able to integrate trajectories of change at multiple levels of analysis.

Optimism, the Application of Developmental Science, and the Promotion of Positive Human Development

The potential for and instantiations of plasticity legitimate an optimistic and proactive search for characteristics of individuals and of their ecologies that, together, can be arrayed to promote positive human development across life. Through the application of developmental science in planned attempts (interventions) to enhance (e.g., through social policies or community-based programs) the character of humans' developmental trajectories, the promotion of positive human development may be achieved by aligning the strengths (operationalized as the potentials for positive change) of individuals and contexts.

Source: Based on Lerner (2006) and Overton (2013a, 2013b).

In short, the application of developmental science (optimization) is a co-equal partner with description and explanation within developmental science as it now exists. Once again, the chapters in this edition of the *Handbook* provide rich illustrations of the integrated foci of

developmental scholarship on the description, explanation, and optimization of human development across the life span.

Together, the metatheoretical, theoretical, methodological, and applied features of contemporary developmental

science that are represented across the four volumes of this seventh edition of the *Handbook* allow this reference work to continue its history of marking the best scholarship in our field and of specifying the key directions for scientific progress. These contributions of the *Handbook* emerge from the intellectual abilities and wisdom of the volume editors and the authors of the chapters involved in this edition. I am enormously indebted to Willis F. Overton and Peter C. M. Molenaar, editors of Volume 1, Lynn S. Liben and Ulrich Müller, editors of Volume 2, Michael E. Lamb, editor of Volume 3, and Marc H. Bornstein and Tama Leventhal, editors of Volume 4, for their broad and deeply erudite scholarship, vision, and leadership. Their knowledge and skills created and shaped the volumes they edited.

The volume editors and I are also profoundly grateful to the authors of the chapters in this edition. Their singular levels of expertise and mastery of their areas of scholarship are richly and compellingly conveyed in this edition. The work of these colleagues represents the best scholarship in developmental science, and we are deeply grateful for their truly field-defining contributions to this edition.

I wish to express particular gratitude to William Damon, for his thoughtful, illuminating, and generous Foreword to this edition of the *Handbook*. Professor Damon was the editor of the fifth and sixth editions of the *Handbook* and, as well, for five decades he has been a visionary intellectual leader of the field that we now term developmental science. He stands as a model of scholarly excellence, erudition, and wisdom, and I am deeply grateful to have his ideas frame the volumes in this edition.

In addition, as scholars contributing to reference works of the scope of the *Handbook* realize, their work cannot be crystallized, completed, or disseminated without the efforts of the professional editors and publishers who work with them. The editors and authors of the seventh edition have been exceedingly fortunate to have had superb support and, as well, collegial guidance, from our editors in the Institute for Applied Research in Youth Development at Tufts and at John Wiley & Sons.

Jarrett M. Lerner, the managing editor in the Institute at Tufts, was involved with the seventh edition since its inception. He has organized and advanced every facet of the editorial and production process. His professionalism, knowledge, organizational capacities, efficiency, commitment, and indefatigable, positive spirit were vital to the existence, and to any archival contributions, of this edition.

In addition, Patricia A. Rossi, the executive editor for psychology at Wiley, was a masterful and wise guide and

catalyst for the seventh edition, again from its inception. Her deep knowledge of the scholarly qualities that are required to produce a reference work that will set the standard of excellence for its field, and her enthusiasm and unflagging commitment to enabling editors and authors to attain this standard, were essential contributions to the development and completion of this edition. She and her colleagues at Wiley, who enacted a superbly organized, efficient, and invariantly high-quality production process, have enabled the scholarship of the authors and editors to be superbly presented to our readership.

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Finally, the volume editors and I want to thank the colleagues and students who will read the chapters in this edition of the *Handbook* and who, we hope, will gain from the work presented across its four volumes. Many of these colleagues will find their contributions to developmental science represented in the pages of this edition. We thank them for these contributions. As well, we are grateful to them for another reason. Many of these colleagues will also be training the next generation of developmental scientists, young scholars whom we hope will be inspired by this edition of the *Handbook* to undertake scholarship that will make subsequent editions even better and more useful.

We wish these younger scientists well in this intellectual journey. As such, with the hope that their scientific

aspirations will be realized, we dedicate this seventh edition of the *Handbook of Child Psychology and Developmental Science* to them.

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Volume 2 Preface

With the cognitive revolution that ended the dark area of behaviorism (as it is commonly characterized), cognition took center stage in psychology in general, and in developmental psychology in particular. During the 1960s and 1970s, this trend was evident in the rediscovery and popularity of Piaget's cognitive-developmental theory. Since then, research on cognition has flourished in developmental science. Developmental journals and research studies have exploded, demonstrating that cognition is complex, on a number of different levels. There are multiple cognitive processes such as categorizing, reasoning, thinking, decision making, and judgment. Many cognitive processes come into play in different domains such as the understanding of time, gender, and the social world. Cognition plays a role in the arts, play, and gesture. Cognitive development is inextricably intertwined with perceptual development, motor development, emotional development, and brain development. Finally, and as demonstrated repeatedly in this and the other three volumes of this *Handbook*, cognition does not take place within the confines of each individual's head. Rather it is embedded in biological and sociocultural contexts and develops through constant interchange with these contexts.

How can we capture this complexity without misleading simplification, without reducing cognitive development to its biological substrates, or viewing it as a passive socialization process? The challenge is to recognize that cognitive development is a relational phenomenon that can be studied only as part of a larger whole that sustains it. This makes the study of cognitive development a challenge, but makes it much more interesting as well. Thus, the study of cognitive development provides different vantage points from which to view phenomena (biological, social), but the resulting view cannot be taken as absolute. It must take into account and be compatible with views seen from different vantage

points (that is, looking out from, rather than toward biological and social groundings). Furthermore, we hold that each of these views must, in the end, be compatible with the idea that the child is an active agent who, through his or her embodied actions in the world, contributes to his or her own development.

Taken collectively, the contributions to the current volume offer just such a relational stance. Specific domains of cognitive development are contextualized with respect to biological processes and sociocultural contexts. Furthermore, the same themes and issues (e.g., the importance of symbolic systems and social understanding) are threaded across multiple chapters even though each chapter is focused on a different domain within cognitive development. Thus, both within and across chapters, the complexity and interconnectivity of cognitive development are well illuminated.

As coeditors, we have profited from and enjoyed one another's knowledge, styles, and differing (but happily not conflicting) editorial insights and peeves. We are thus grateful for the opportunity to have collaborated in bringing this volume from our initial scribbled lists of ideas to a completed set of chapters for print (and screen). We are likewise grateful to our cognitive-developmental colleagues for their willingness to accept (almost always enthusiastically) invitations to contribute chapters to this *Handbook*. We—and the entire field of cognitive development—are indebted to them for their thorough and thoughtful scholarship in reviewing vast bodies of work and for fulfilling the even more difficult tasks of first, selecting which theoretical and empirical work to describe and illustrate, and second, finding ways to communicate their insights, conclusions, and recommendations to an audience comprised of readers with dramatically varied backgrounds, interests, and goals.

We are also grateful to the editors of the other volumes, and especially to the editor-in-chief, Richard Lerner, for sharing ideas, encouragement, and inspiration over the years of this project. We are deeply appreciative for the friendly, skilled, and miraculously speedy support from Jarrett Lerner in his role as production manager of the *Handbook*.

Finally, we would like to thank publicly our respective partners, Roger Downs and Nadia Sangster, for their love,

support, and understanding as we absented ourselves from far too much of our local relational systems.

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CHAPTER 1

Reflections on Cognitive Development

LYNN S. LIBEN and ULRICH MÜLLER

The study of cognitive development has itself developed significantly since the first edition of this *Handbook* appeared in 1946. Early scholars often tried to catalogue which factors could account for what outcomes, and even when they identified multiple factors, they attempted to quantify the relative contributions of each. The term “independent variable” was perhaps overinterpreted to mean that variables could, indeed, be independent of one another. As well-reflected in all four volumes of this new edition of the *Handbook*, contemporary developmental scientists recognize the problems associated with reductionist models and with the failure to consider the role of the broader context in addition to the role of an individual’s self-directive processes. The alternative model, described elsewhere in this *Handbook*, first in brief (Lerner, Preface) and then in detail (Overton, Chapter 1, Volume 1), is a relational-systems view that examines any particular topic such as cognitive development within the broader biological and sociocultural context.

Given their relational perspectives, authors of this volume’s chapters reject models that argue for singular unidirectional effects (for instance, from action to cognition or from social context to cognition). Similarly, authors make it clear that one cannot divorce so-called peripheral from so-called central processes. As such, what were earlier viewed as “lower level” processes are no longer seen as automatic and overdetermined. They are instead conceptualized as integrated within the developmental system, and investigated as part of a more inclusive and conjoint range of biological and sociocultural processes.

Although each chapter in this volume is titled to name its focus on a relatively constrained topic, many chapters actually address shared issues. Illustrative are the importance of symbols (e.g., see chapters on concepts, language, literacy, mathematical reasoning, gesture, symbolic representation, play, and artistic development); the role of context in human development (e.g., see chapters on artistic development, gender development, atypical cognitive development, cognitive development and culture, and media and cognitive development); the power and pervasiveness of inferential or logical processes (e.g., see chapters on reasoning, conceptual development, memory, temporal cognition, mathematical reasoning, and scientific thinking); connections between cognition and emotion (e.g., see chapters on gender, executive function, and social understanding); and the importance of diversity, both in individuals’ own characteristics and in the cultural contexts that surround them (e.g., see chapters on artistic development, culture, scientific thinking, and atypical development). The importance of the human body, whether approached from the perspective of neuroscience or embodiment, does not end with the first chapter on the brain and cognitive development, but rather is threaded throughout discussions of virtually all the chapters in the volume.

In short, then, while focusing on the richness and importance of their assigned topics, authors nevertheless reflect a relational perspective in conceptualizing the role of their focal cognitive-developmental process within an integrated developmental system.

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If one begins from a relational systems approach to developmental science, one of the greatest editorial challenges is rooted in the linear nature of books. Pages necessarily follow one another, and it is far too easy for readers to infer that what comes first is meant to be thought of as foundational, and that the order of the chapters that follow is meant to convey a message about the conceptual layering of topics such that each builds, in turn, on the preceding more-fundamental one. As editors, we thus begin by explicitly rejecting these as intended messages. In our attempt to find a way to avoid this implication we considered multiple possible chapter sequences. In the end, though, we simply selected one, recognizing that our commitment to a relational perspective meant that there could, in fact, be no single best order. There are simply too many simultaneous and reciprocal connections among topics and processes. Fortunately, the authors have avoided presenting their substantive topics as if they were isolated, materialist, independent causal explanations of developmental outcomes. In the remainder of this introduction to Volume 2, we briefly highlight the focus of each chapter. Of course, a few lines of text cannot begin to do justice to the depth of these contributions and thus they are intended only to whet readers' appetites rather than to substitute for careful readings of the chapters themselves.

In the first chapter, Stiles, Brown, Haist, and Jernigan examine current knowledge about the links between the brain and cognitive development. They point out that as knowledge about brain development has increased, models of brain development have changed. Whereas several decades ago the dominant belief was that brain development is innately determined, current models hold that brain development proceeds as a result of the complex and dynamic interplay of molecular, cellular, and environmental systems. Stiles et al. describe the different imaging technologies used to study the brain and its development, appraising the specific strengths and weaknesses in terms of the informational detail each offers. They next summarize basics of pre- and postnatal brain development. The section on *Brain and Cognitive Development in the Postnatal Period* constitutes the heart of the chapter. Here Stiles and colleagues examine the relations between brain development and cognitive development in three domains: visuospatial processing, cognitive control, and language. The authors synthesize the data in a neurocognitive model of brain-behavior relations in a way that captures the dynamic changes in brain and behavioral systems, aligning theory and data from developmental neurobiology and developmental neuropsychology. The core idea of this

model is that neurobehavioral development involves a dynamic series of interactions between biological and environmental factors. The chapter ends with a series of reflections on themes, trends, and future directions that emerge from the reviewed work.

In the next chapter, Johnson and Hannon discuss perceptual development. They emphasize that infants' perceptual systems are the primary means for acquiring and interpreting knowledge about events, objects, and people in the world around them. The chapter begins with a discussion of theories of perceptual development and its consequences for children's cognitive and social development. The authors then discuss neural foundations of perception and the emergence and development of sensory systems before and after birth, followed by detailed sections on audition, vision, and intermodal perception. Throughout, they focus on questions of how the developing child extracts meaningful information from the sensory array—that is, how the observer detects, synthesizes, and interprets sensory input so as to yield perceptions of structured events and objects—and how effects of experience on perceptual development interact with developmental timing and what had already been acquired earlier. They focus also on developmental processes—growth, experience, and learning—and examine as well the malleability, or plasticity, of perceptual systems during development. The chapter concludes with a discussion of how different theoretical views may be reconciled in light of the fact that the child is developing in a wider context.

In the chapter on motor development, Adolph and Robinson suggest that the study of motor development provides an opportunity to integrate developmental domains that are typically studied in isolation. This substantive domain is particularly conducive to an integrative framing because motor development is a physical (embodied) phenomenon that occurs through the child's activities within particular physical environments, is intertwined with social interactions, and is affected by the larger sociocultural context. Adolph and Robinson examine motor development through the lens of 10 general developmental issues: (1) the function of incidental activity and its consequences for motor development; (2) the relation between similar behavior patterns that are displayed at different ages; (3) the role of intraindividual variability in motor development; (4) the way in which the passage of time contributes to developmental change; (5) the challenge that the ever-changing body poses for adaptation and developmental diversity; (6) the active contribution of children to their motor development; (7) the importance of prospective control for

motor behavior; (8) the role of perceiving and generalizing affordances for action in choosing the appropriate course of action; (9) the ways in which the social and cultural context affects motor development; and (10) the influence of motor development on perceptual, cognitive, and social development. Reflecting the fact that motor development is a biopsychosocial (and cultural) phenomenon, the issues are loosely organized into framing sections on embodied movement, embedded action, and enculturated interaction.

Ristic and Enns begin their chapter on attentional development by arguing that the field has undergone a seismic shift over the past decade with respect to first, the content of the empirical data being collected, and second, the theoretical ideas used to understand these data. They begin their description of this paradigm shift by first examining research during the latter half of the 20th century. Specifically, they argue that work at this time was dominated by the information-processing framework, which views attention as a localizable, domain-general, and situation-invariant cognitive faculty for which the primary role is filtering sensory information in the service of task goals. However, more recently, researchers have begun to study how individual, emotional, and social aspects of life influence everyday attentional behavior. Mounting evidence from those studies revealed that the classic information-processing framework could not provide a complete account of attentional development. Thus, at present, attention is viewed as a concept that cannot be isolated from social and emotional aspects of development. With regard to future directions, they outline a dynamic view of attention in which attention is conceptualized as a cognitive facility, integrating the demands of “cool” cognition (i.e., information processing capacities) with “hot” functions that span temperament, emotion, social communication, individual histories, and cultural context. The authors note that if this trend continues, attentional development in the next decade will be studied as the outcome of complex interactions among an individual’s biology, life history, and social environment.

In the following chapter on memory development, Howe begins with a brief review of 20th-century views about memory development and then turns to three issues that have been attracting attention in the early 21st century. The first moves the theoretical focus away from questions about the structure of memory and its development and towards questions about the adaptive function of memory. Research shows that at least some of the functional attributes of memory include extracting meaning, binding information into regular patterns, and using these patterns

to predict future outcomes. The second issue concerns how these adaptive memory systems develop. To address this issue, Howe reviews recent research examining correlated changes in neurobiological and cognitive functioning. The final question he raises concerns whether humans share adaptive memory development with other animals, which he addresses by reviewing the comparative literature on memory development. Howe argues for the adaptive view of memory, which holds that memory’s function is not simply to remember the past, but also to understand the present and to anticipate the future.

Callaghan and Corbit focus their chapter on symbolic representations. They view these as communicative behaviors that set humans apart from other species, and that bind people together in communities and other social groups. More specifically, they focus on the developmental use of external symbols to communicate with others. They begin the chapter by considering the varieties of definitions, theoretical approaches, and recurring themes that have emerged from classic and contemporary work. They then use dominant themes from contemporary work to guide their review of the empirical findings from studies of language (including gesture), pretense, and material artifacts (including scale models, pictures, video, and maps). They argue that comparative research and cultural developmental studies provide important ways to deepen understanding of the origin of human symbolic representation, and thus they review such studies in their chapter. They end by discussing challenges faced by researchers who would like to move beyond offering insightful descriptions of symbolic development to providing process accounts of symbolic development.

In the next chapter on language development, MacWhinney observes that the modern study of children’s language is influenced by two contrasting perspectives. The first, the theory of Universal Grammar, emphasizes the role of innate abilities in a core language module. The second, Emergentism, instead views language learning as the result of processes of variation, competition, and generalization that operate across a diverse set of space-time scales ranging from online processing to long-term patterns of social and genetic consolidation. MacWhinney reviews language development on seven levels of emergent structure: articulatory phonology, auditory phonology, lexicon, morphology, syntax, mental models, and conversation, with the analysis for each addressing the role of input language structure, neural processes, and social mechanisms. On each level, MacWhinney articulates ways in which the initial learning of specific items gives rise to

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subsequent pattern extraction and generalization and then examines the neuronal basis of language control in terms of structures and methods that allow highly interactive online processing among the seven components. This model provides developmental science with ways of understanding both developmental language disorders and the learning of multiple languages at different stages in development.

Goldin-Meadow addresses the topic of gesture and cognitive development, arguing that one important feature of gesture is that it has the potential to reveal information about how speakers think, information that may not be evident in their words. A central claim of the chapter is that gesture not only provides information that might not otherwise be revealed about the speaker's state of mind, it also plays a central role in the development of communication and cognition. The chapter begins by discussing the relation between gesture and other nonverbal behaviors. The next sections describe the development of gesture in children who acquire language following the typical course, as well as in children whose course is atypical. These sections demonstrate that gesture is instrumental in language acquisition and that it can take on many different forms and functions. The next section shows that gesture continues to play a role in promoting skill learning even after language is developed, and provides a window into the learner's thoughts. The final sections examine the mechanisms that underlie gesturing and the functions of gesturing.

Carpendale and Lewis discuss the development of social understanding, emphasizing that understanding others is an essential aspect of being human. They review research and theory on the development of a range of skills constituting social understanding, beginning in infancy with gaze-following and gestures such as pointing. Given the importance attributed to false belief understanding in preschoolers, they review accounts of this development and criticisms of these accounts. Likewise, they discuss debates about claims of infants' understanding of false beliefs—claims that raise questions about the nature and origins of social awareness. Carpendale and Lewis also discuss later-developing social skills that are still relatively neglected in the literature as well as contributions of neuroscience to the study of social cognitive development. Noting that there are many links between social cognition and children's social relations, the authors explicitly focus on the key role of language in social cognitive development. They also review ways in which social understanding may influence social conduct, issues of trust and deception, and cooperation and moral development. Throughout the

chapter, the authors highlight ways that research traditions are influenced by worldviews or preconceptions about the nature of mind, meaning, and knowledge, and emphasize the interconnections between social understanding and all other aspects of human life.

To begin her chapter on play, Lillard notes that children spend a significant amount of time engaged in play, and illustrates the broad range of play activities. Despite its pervasiveness, play's role in development is not well understood. After discussing and evaluating the various definitions of play that have been used, Lillard reviews major theories of play, and then overviews the developmental course of various types of play (sensorimotor play, physical play, rough and tumble play, exploratory play, construction play, symbolic play). Lillard next covers some contemporary debates in play research that concern the relation between pretend play and theory of mind and symbolic understanding, children's ability to discriminate between fantasy and reality, the role of pretend play in promoting development, and the ways that children are initiated into the practice of pretend play. In the next section she reviews gender and cultural differences in play, and discusses play in atypically developing children. She closes by highlighting particularly important issues that remain in need of further research.

For his chapter on conceptual development, Sloutsky guides his review by using the following five principles: (1) There are diverse conceptual behaviors that range from simple and universal to complex and uniquely human; (2) simpler forms are more universal and exhibit earlier onset in the course of individual development; more complex forms are later appearing and depend on other aspects of cognitive development, including the development of attention and memory; (3) the development of more complex forms of conceptual behavior is more likely to be affected by language and instruction than is the development of simpler forms; (4) the age at which conceptual categories are acquired is affected by the structure of the input; and (5) conceptual development progresses from less-structured representations to more-structured representations.

Using these principles as a framework, Sloutsky reviews the history of the study of concepts and of theoretical approaches to concepts. Next, he discusses the multiplicity of conceptual behavior and its biological foundations. In the remainder of the chapter he addresses conceptual development in human infancy, the role of language in conceptual development, acquisition of semantic knowledge and of conceptual hierarchies, and the role of concepts

in reasoning. In the concluding section, Sloutsky revisits the principles of conceptual development outlined at the beginning of the chapter.

Ricco's chapter on the development of reasoning begins with a review of the course of development for deductive and inductive forms of reasoning across childhood and adolescence, followed by a critique of key theoretical accounts of that developmental course. The development of deduction is considered primarily with respect to syllogistic and conditional reasoning. Mental-logic, metacognitive, and mental-model accounts of deduction are contrasted and compared and the potential for rapprochement is identified. The development of inductive reasoning is discussed with respect to three primary types of induction—category-based induction, causal induction, and inductive processes in scientific thinking. The discussion of the development of reasoning provided in this chapter is situated within a dual systems or dual process account of cognition. According to this account, human cognition consists of two distinct systems (1 and 2) or types of processing, with the primary basis for the distinction being the engagement of working-memory resources. By adopting this framework, it becomes possible to shed light on the processes that underlie deductive and inductive reasoning and to trace how the development of each type of reasoning is related to changes in these underlying processes. Among the key conclusions of the chapter is that while the development of certain aspects of system 1 processing contributes to age-related changes in performance on reasoning tasks, the most significant changes in both deductive and inductive reasoning result from key developments in system 2 processing.

In the next chapter, on the development of executive function, Müller and Kerns examine theories of and empirical research on executive function. They show that research on executive function has grown dramatically over the last three decades. Even though the term emerged only 40 years ago, the concept of executive function can be traced back to far earlier clinical and empirical research on the frontal lobes. Müller and Kerns review influential theories of executive function, working memory, inhibition, computational modeling, and hierarchical accounts. They next review the development of the prefrontal cortex, which is considered the neural basis of executive function, and summarize research on particular component processes of executive function. In the next sections they address, in turn, the methodological challenges in research on executive function; sources of the development of executive function, with particular emphasis on the

ways in which social factors and language facilitate its development; and summaries of research of executive function in two other domains of functioning—social understanding and academic achievement. They conclude the chapter with the suggestion that executive function should be studied as a distributed process that develops as a result of the child's embodied interactions within a social context.

McCormack divides her chapter on the development of temporal cognition into two major sections, reflective of two basic ways in which time features in everyday thought and action, and in cognitive-developmental psychology. The first section addresses time as duration (i.e., time as a dimension of stimuli or events). In this section McCormack describes methods that are used to assess the accuracy of processing duration at different ages. She also reviews developmental changes in the accuracy of duration-processing across infancy and childhood, and discusses models and theories proposed to explain its development. The second part of the chapter deals with time as a framework within which events can be located, that is, as a framework that allows one to locate events in the past, present, or future and to recognize the systematic before–after relations inherent in the temporal locations of events. McCormack examines empirical research addressing the origin and development of children's understanding of time as a framework and summarizes the theoretical approaches that have been proposed to explain these developmental progressions.

In the next chapter, which discusses the development of scientific thinking, Lehrer and Schauble introduce three views of science that ground research and education on the development of scientific thinking: science-as-reasoning, science-as-conceptual change, and science-as-practice. They observe that there is now increasing emphasis on science as an integrated set of epistemic practices. For example, new science education standards in the United States highlight the importance of students' participation in scientific practices—communally recognized and supported ways of generating, revising, and critiquing scientific knowledge. Based on reviews of the history, philosophy, and psychology of science, Lehrer and Schauble argue that the defining practice of science is modeling, and that it is useful to conceive of other scientific practices in relation to this foundational one. Accordingly, they trace the ontogeny of representational and material practices of modeling and summarize the development of seven scientific practices (e.g., constructing and interpreting data; developing explanations and arguments) that are

intimately related to modeling. This perspective identifies fruitful areas for additional research that can inform ways of describing and supporting the development of scientific thinking.

In their chapter on the development of children's mathematical reasoning, Nunes and Bryant note that psychological research on this topic has focused either on children's understanding of quantities or on their knowledge of number. A synthesis of these two foci can be achieved by acknowledging that numbers have two meanings: a representational meaning, defined by their use as signs for quantities or relations between quantities, and an analytical meaning, defined by the conventions in the number system. In the introduction, the authors explicate these two meanings of numbers and explore the connections between them. In subsequent sections they analyze how children's mathematical knowledge develops in terms of an increasing ability to use different numerical representations (e.g., from the use of fingers to represent quantities to the use of conventional signs), a growing understanding of invariant relations between quantities (e.g., realizing that, given a fixed number of cookies, the more people sharing the cookies the fewer cookies each receives), and an increasing awareness of the relevance of specific concepts to different situations (e.g., understanding the relevance of division to solving problems connected to multiplication). Throughout the chapter, the connection between the nature of quantities and their numerical representations is explored. In the final section, Nunes and Bryant focus on the use of numbers to quantify space and relations between spatial dimensions, arguing that understanding relations among different dimensions in space (e.g., length and width) is crucial to quantifying space. They end their chapter with a brief discussion of directions for future research.

In the chapter on literacy development, Lonigan argues that the acquisition of literacy skills (i.e., reading and writing) is the most important educational attainment because it constitutes the foundation on which the acquisition of knowledge in multiple domains is built in school and throughout life. Lonigan begins by defining reading, and then details the skills and processes required for successful reading, including decoding skills and linguistic comprehension skills. He next reviews developmental changes in and influences on reading skills. In the next section he describes emergent literacy skills, the developmental precursors to conventional forms of reading and writing, and the types of reading problems children experience

and the methods used to identify reading impairments. He concludes the chapter with a discussion of historical perspectives, current approaches, and empirical evidence concerning reading instruction.

In the next chapter, Leaper presents contemporary theory and research on children's gender development from a social-cognitive perspective. First, he examines contemporary social-cognitive theories and conceptual models pertinent to the study of gender development. These include cognitive-developmental, information-processing, intergroup, and motivational approaches. Second, he summarizes the development of children's gender cognitions and examines their ramifications for a variety of areas, including gender stereotyping, attitudes, prejudice, self-concepts, and gender as a social identity. Third, he considers possible causes and consequences of gender-typed play. In the fourth section, Leaper reviews research on gender similarities and differences in children's competencies in academic achievement (including verbal, spatial, mathematical, science, and artistic domains), athletic achievement, interpersonal competence, and intrapersonal competence, among others. Fifth, he highlights some of the individual and social-relational influences on gender-related variations in performance and achievement. Leaper closes the chapter by advocating for future work that offers more theory-bridging and replications of prior empirical research.

Gauvain and Perez discuss cognitive development and culture, noting that cognitive development always occurs in cultural context. Accordingly, they describe the complex and multifaceted connections between culture and cognitive development and how these unfold across child development. Sociocultural theory, which is unique in its focus on cognitive development in relation to culture, provides the conceptual foundation of the chapter. Following discussion of the historical foundations of contemporary research on culture and cognitive development, the authors describe how culture has been studied in psychological research, the importance of a developmental approach for understanding culture-cognition connections, and some considerations in studying the sociocultural basis of cognitive development. They discuss capacities that human beings have that underlie participation in culture, reviewing current understanding of relevant neural functioning and brain development, and the social-cognitive capabilities through which children learn from others. To illustrate the defining role of culture in human cognition, the authors describe empirical research in four areas of cognitive development: memory, executive functions, spatial

cognition, and problem solving. They offer general conclusions on theory and research about culture and cognitive development and suggestions for future research.

The next chapter focuses on artistic development in both the visual arts and music. The authors, Milbrath, McPherson, and Osborne, begin by presenting archaeological evidence that indicates that modern humans have been making music, portable art, and cave-wall paintings as far back as 35,000 years ago. Drawing and song are also the first two art forms in which young children take an active part. The authors review what is known about children's artistic development in the visual arts and music, focusing on the historical and theoretical grounding of artistic development, the psychological and physical attributes of the developing child that play a role in children's artistry, and the sociocultural contexts in which child art and development occur. In each of the two major sections—one on the visual arts and the second on music—the authors begin by describing the known inceptions of the art form and the historical and contemporary approaches to children's development in them, and then review research on children's developmental achievements and competencies in the domain. They also present studies of atypically developing children and inquiries into children's understanding and aesthetic experience of the art form. They conclude each major section with a discussion of cultural differences in artistic practice and the influences these different practices have on children's artistic outcomes.

Anderson and Kirkorian discuss media and cognitive development, noting that by the time children reach adulthood, they will have spent more time using electronic screen media than in formal school settings. Thus screen media have enormous potential to influence cognitive development, for good or ill. The authors describe popular concerns about media impact, using *Sesame Street* as a case study. They provide current estimates of children's use of media and discuss data on engagement in multitasking behavior. They review empirical research on children's cognition during media use and then outline potential direct and indirect pathways of longer-term media influences on cognitive development, focusing on effects on cognitive skills and academic achievement. The authors conclude the chapter with a critical analysis of extant research and identify areas that are especially in need of further study.

In the final chapter of the volume, Pennington discusses atypical cognitive development. In addition to reviewing the history of earlier research, he reviews current issues

and findings in the study of atypical cognitive development organized around the following five key questions: (1) How general versus specific are mechanisms of cognitive development and individual differences in cognition? (2) What is the etiology of cognitive development and of individual cognitive differences? (3) How do these etiologies act on structural and functional brain development? (4) How malleable are developmental and individual cognitive outcomes? (5) Does age moderate the answers to these questions, and if so, how? A key issue that runs through the chapter is the role of nature versus nurture in the development of physical and psychological forms. Pennington argues that the resolution to this issue is found in the principles of probabilistic epigenesis, constructivism, and complex systems that self-organize to yield emergent properties. The chapter uses a multilevel, interdisciplinary approach to understanding atypical cognitive development. In addition to behavioral and cognitive development, these levels include consideration of etiology (genetic and environmental influences and their interplay) and brain mechanisms. Specific examples of atypical cognitive development (e.g., amblyopia, orphanage rearing, genetic syndromes) are described to illustrate these levels of analysis and to address key issues. The chapter concludes with a summary of current answers to the five key questions and implications for future research.

Collectively, the contributions to this volume offer convincing evidence that the complexity of cognitive development cannot be captured adequately by studying particular aspects of cognition in isolation as if they were encapsulated modules unfolding along a genetically predetermined timetable. Different cognitive processes are intrinsically linked to one another and to emotional processes. Thus, advances in the domain of cognitive development are of interest not only to those who are fascinated with cognitive development per se, but also to those whose major interests lie elsewhere. Connections among different aspects of cognitive development, in turn, must be examined in the context of biological, physical, social, and cultural contexts. Even though taking such complexity into account may at first appear daunting, in the long run, only relational approaches can produce a satisfactory and useful understanding of cognitive development.

Authors who contributed to this volume have demonstrated important continuities with work from earlier eras while simultaneously offering exciting new methodologies and findings that escort us into the future. As captured in the concluding sections of each chapter, the field has

8 Reflections on Cognitive Development

made important strides in understanding key domains of cognitive development. Theoretical and methodological advances should allow developmental scientists to become increasingly adept in describing, explaining, and optimizing developmental outcomes in the years to come. We invite readers to taste or devour the chapters that

follow. They offer much food for thought, not only about individual topics traditionally studied under the umbrella of cognitive development, but also about broader ideas that must be considered as developmental science continues to grapple with theoretical, empirical, and applied pursuits.

CHAPTER 2

Brain and Cognitive Development

JOAN STILES, TIMOTHY T. BROWN, FRANK HAIST, and TERRY L. JERNIGAN

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INTRODUCTION

Research over the past several decades has greatly expanded our understanding of cognitive and brain development. The many chapters of this *Handbook* reflect the breadth and richness of the psychological studies (e.g., see Marshall, Chapter 7, Volume 1). From the elaboration of

This chapter is the product of the collaborative efforts of experts representing different areas of neurocognitive development. As such, the substance of this chapter reflects the equal and independent contributions of the four authors. As senior author, Joan Stiles was responsible for the overall outline and organization of the chapter, minding of deadlines, and correspondence with editors. Beyond that, order of authorship is arbitrary and does not indicate the level of contribution.

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¹Color versions of Figures 2.6, 2.8, 2.9, and 2.10 are available at <http://onlinelibrary.wiley.com/book/10.1002/9780470147658>.

stochastic learning processes, joint attention, and phonological processing in young infants to the effects of cultural practices, peer interaction, and schooling on older children, our knowledge of how children come to know about and interact in the world has grown and changed significantly. We have made comparable progress in understanding the basic processes of brain development. Our models of brain development have changed considerably through discoveries about everything from the molecular mechanisms for neural stem cell differentiation and early patterning of the embryonic neural system to studies demonstrating the critical role of experience in pre- and postnatal brain development. Over this course of time, knowledge gained in these two critically important areas of developmental research progressed largely independently of one another. Studies linking behavioral development to change in underlying neural systems are comparatively limited. One consequence of this lack of interdisciplinary integration is a divergence in the theoretical models of development that each field offers to account for the observed changes. One important aspect of those theoretical differences concerns the issue of biological inheritance and the role it plays in development.

Models of Neurobehavioral Development

The central debate within developmental psychology for many decades focused on the question of whether and to what extent humans are innately prepared to interpret and act in the world, and to what extent they rely on learning and/or experience. Nativists propose the existence of a core set of innate concepts that form the necessary foundation for later learning (Gelman, 2000; Spelke & Kinzler, 2007). Proponents of traditional nurture-based views (represented, for example, by ecological, neoconstructivist, and information processing perspectives) argue that complex concepts emerge from more primitive, yet innate, sensory, motor, and learning abilities (Elman et al., 1996; S. P. Johnson, 2003; Sirois et al., 2008). Both sides in the psychological debate assume that innate factors originate within the organism and are presumably part of the biological endowment, while learned behaviors originate outside the organism and result from experience in the world. Thus, at issue in the traditional psychological nature-nurture debate is not whether there are innately specified behaviors, but rather whether there exists a privileged set of “core concepts” (Gelman, 2000) that should be included among the class of innately specified behaviors.

The dominant model of brain development 40 years ago was strongly deterministic. Brain development was the product of an intrinsic, innately determined maturational pathway (Gottlieb, 1976; Johnston, 2001). Contemporary models present a distinctly different view of inheritance and brain development. What is inherited at conception is quite specific: (a) the DNA, and (b) the first cell with the cellular machinery for translating the information in the nucleotide sequences of DNA into proteins (the active agents in all biological processes). Biological inheritance provides essential tools, but neither the genes nor environmental factors prescribe outcomes. Rather brain development proceeds via the complex interaction of molecular, cellular, and environmental systems and elements. The biological state of the organism at any moment is the product of developmental processes that involve an intricate interplay among complex cascades of gene expression interacting with influences from an ever-expanding range of environmental factors. Under this model, it would be a mistake to construe intrinsic factors as deterministic and extrinsic factors as modulatory. Rather, the complex interaction of many elements interacting dynamically over time brings about the progressive differentiation and specification of the nervous system.

The lack of alignment between the psychological and biological theories of inheritance and development presents

a difficult and important problem. The theories from both disciplines intend to provide an account of human development. Yet, the differences in the assumptions about very basic processes lead to a divergence in focus and direction. Psychological theories include elements that are presumed to be innately specified and, thus, do not need to be explained. Biological theories underspecify the richness and range of input. In fact, humans are biological beings with brains that mediate their thoughts, feelings, and actions, *and* the development of stable, functioning neural networks depends critically on the experience of the individual and his or her actions in the world. Integrating theories of neural and cognitive development into a single model of neurocognitive development is essential for a full understanding of human development. Seeking such integration is the guiding principle for this chapter.

The Plan of the Chapter

The remainder of this chapter explores the current state of knowledge about the relationship between brain and cognitive development. The overarching goal is to forward an integrated account of how complex neurocognitive processes arise in humans. The study of the development of brain-behavior relationships is still in its infancy. Many areas of neurocognitive processing remain largely unexplored and more questions remain than have been resolved. Nonetheless, research in a number of different domains has progressed and the growing body of work in those areas can serve as a model for approaching these kinds of substantively and technically difficult interdisciplinary questions. We do not and cannot exhaustively review all extant knowledge about brain-behavior relationships across the range of cognitive domains. Rather, we focus on three cognitive domains for which a substantial body of neurocognitive data is available and more integrated models of neurocognitive development are emerging. These domains include studies of visuospatial processing of faces, cognitive control, and language.

One obstacle to interdisciplinary dialogue is that the methods of interrogation in the behavioral and neurosciences are very different. This makes evaluation of data from related fields difficult. Cognitive neuroscience relies on a range of clinical and neuroimaging methodologies that may be less familiar to behavioral scientists. This chapter begins with a Methods of Interrogation section to bridge this part of the interdisciplinary divide with a brief overview of the major investigative tools available for studying brain-behavior relations in developing children.

Any discussion of the nature of brain-behavior relationships assumes a substantial knowledge of the basics of development within both systems. Training in psychology has not historically included intensive instruction in the fundamentals of brain development. The section entitled Major Milestones in Anatomical Brain Development provides an overview of the basics of pre- and postnatal brain development. Brain development begins in the third week postconception and extends at least through late adolescence, and arguably throughout the lifespan. Contemporary models of brain development portray a dynamically developing system that relies absolutely on genetic, systemic, and experiential factors, all interacting in complex ways. An understanding of how brain systems emerge through the interaction of all of these factors is critical to the formulation of any model of neurocognitive development.

The sections that constitute the heart of this chapter, Brain and Cognitive Development in the Postnatal Period, follow the discussion of brain development. Three primary cognitive domains are considered. The discussion of visuospatial processing focuses on a well-studied aspect of visual processing, face processing (for a more extensive discussion of visuospatial processing, see Johnson & Hannon, Chapter 3, this *Handbook*, this volume). The review of cognitive control focuses on the development of attention, working memory, and inhibitory control. The section on language focuses on acquisition in late infancy and the early toddler period as well as later mastery of complex grammar and discourse skills.

All of the studies considered in this section rely on imaging or recording technologies of one type or the other. The age of the children under study and the particular empirical questions typically dictate the choices of imaging modality used. Discussions within each domain include as wide an age range as is possible, beginning as early in infancy as data are available and extending through late childhood or adolescence. Most studies are cross-sectional in design, thus providing snapshots of the state of the neurobehavioral system at specific points in time. Inclusion of multiple age groups within a single study allows for some extrapolation to developmental trajectories, but only with caution. The detailed study of developmental trajectories using longitudinal designs is rare but, as discussed in the closing sections of this chapter, will eventually need to become a critical part of the database.

A Neurocognitive Perspective on Human Development, the fourth section of the chapter, integrates the data reviewed in the earlier two sections, and offers a

neurocognitive perspective on the nature of brain-behavior relationships. This section captures the dynamic nature of change in both brain and behavioral systems, and provides a means of aligning theory and data from developmental neurobiology and developmental neuropsychology. At the heart of this model is the idea that neurobehavioral development involves an ongoing and robust series of interactions among biological and environmental factors. It views development as a continuous process of adaptation shaped by genetic, environmental, and temporal constraints.

The chapter ends with a series of reflections on themes, trends, and future directions that emerge from the work reviewed in this chapter. This section attempts to synthesize common threads that emerge in the discussion of each domain separately. It begins with a discussion of trajectories of neurocognitive change, and considers commonalities and differences in the patterns of change in the neural networks that support particular functions as well as differences in the timing of those changes across domains. Next, the importance of multimodal and multidimensional approaches to the study of human development is considered. The models of neurocognitive development discussed in this chapter make clear the need for multidisciplinary approaches that integrate data from genetics to neural systems to behavior and the environment into a comprehensive and aligned system. That requires coordinated, multidimensional approaches to everything from data collection to model building. We emphasize the importance of the study of individual differences in development. It is likely that the “modal child” is a myth, an artifact of our statistical analyses. Our understanding of neurocognitive development will likely rely as much on our knowledge of the nature of the variability in trajectories of development as it does on our understanding of the common principles of development.

METHODS OF INTERROGATION

Historically, the major source of data for mapping brain-behavior relationships came from adult patient studies; yet, the application of these methodologies to developmental issues is complex and provides only limited information on typical trajectories of development. Advances in neuroimaging modalities now provide the tools necessary to precisely define developmental trajectories in structure, connectivity, and functional responsiveness over the entire brain in typical development. The following sections

provide a brief overview of the major methods for the study of brain-behavior relationships in developing children.

The Lesion Method

Historically, studies of adults with localized brain injury have been a major source of data about brain-behavior relationships. This approach typically uses the logic of subtraction to define the function of a brain area. That is, the functional loss observed after injury to a particular brain area defines the original function or role supporting a function of that brain area. However, the adult lesion method does not work for developmental questions because the brain systems have not yet organized to mediate the targeted behavioral functions. Instead, the study of children with localized brain lesions provides a window on the processes of early brain plasticity and the capacity of the neural system to develop alternative patterns of organization as a means of adapting to injury (Stiles, Reilly, Levine, Trauner, & Nass, 2012). While important for informing our understanding of the dynamic nature of brain development, child lesion data provide limited information on typical trajectories of neurocognitive development.

Neuroimaging Methods

Understanding the associated development of behavior and brain requires multidimensional brain measures assessing changes across a substantial range of space and time. Spatial measures must span resolutions from the submillimeter to millimeter range to capture neurons, neuronal columns, and cortical layers, to the centimeter range to estimate regional maps, through to whole brain resolution to assess integrated brain systems. Temporal measures must span resolutions in the range of milliseconds to hours to capture dynamic brain activity through to days, months, and years to appreciate changes across the lifespan. Tools to measure typical human development must be noninvasive, or so minimally invasive that the cost of the information gained far exceeds the risk to the participant. The present day armamentarium of noninvasive techniques available to developmental researchers allows for the analysis of development across this vast breadth of spatial and temporal domains. The following provides a brief description of many of the most significant structural (anatomical) and functional (physiological) neuroimaging tools presently used in developmental cognitive neuroscience.

While modern neuroimaging has revolutionized our understanding of brain-behavior relationships across development, these techniques are not panaceas. Any single neuroimaging technique provides only a narrow window onto the complexity of developmental brain-behavior relationships; that is, each brain imaging technique has specific strengths and weaknesses in terms of spatial and temporal resolution. For example, structural MRI (sMRI) provides incredibly precise measures of brain anatomy from the near microscopic level to whole brain, yet a structural MRI scan provides only a single snapshot in time of brain status. Functional MRI (fMRI) can measure dynamic traces of neuronal activity from submillimeter resolution through to whole brain within seconds after stimulation and provide a highly dynamic description of brain function related to a cognitive task. Yet, the temporal resolution of fMRI that is measured in seconds necessarily suggests that we are observing an echo of brain activity that occurred within milliseconds to several hundred milliseconds after stimulation. Electroencephalography (EEG) and magnetoencephalography (MEG) can observe dynamic brain activity at millisecond resolution, but because these measures are acquired at the scalp, they lack unique or precise spatial resolution of the underlying brain generators of the response. Developmental cognitive neuroscientists are in complete agreement that comprehensive descriptions of brain-behavior relationships across development require multimodal imaging strategies of collecting data with multiple techniques to increase the observation power through converging methods with strengths across different spatial and temporal ranges.

Applying imaging methodologies to child populations is challenging. Many of the methodologies are sensitive to various kinds of movement that can render the data uninterpretable. Methods are emerging to address motion issues, yet even with these improvements, some neuroimaging techniques continue to present a challenge for testing infants and young children. Thus, the application of methodologies is not uniform across ages. In many cases, the absolute signal to noise of imaging techniques is low. This often necessitates the collection of many observations or stimulus repetitions to obtain reliable brain signals. Obtaining sufficient data requires time that may challenge the ability of children to sustain their attention and vigilance. Thus, researchers must frequently sacrifice multifactorial experimental designs to focus on essential variables to ensure sufficient data acquisition, particularly during tasks where performance may differ between younger and older participants.

Structural Magnetic Resonance Imaging (sMRI)

Structural MRI (sMRI) was the first application of MRI to developmental brain research and remains one of the most commonly used methods today. The tissue contrast of sMRI reflects tissue-specific variation in density and relaxation of magnetized protons in water molecules. Specifically, sMRI produces detailed images of sulcal and gyral patterns of the cerebral cortex and cerebellum because of strong signal contrast between the myelinated fibers of the brain's white matter and adjacent gray matter. The visual appearance of the brain on sMRI therefore changes appreciably over the first 2 to 3 years of life, and these changes mirror the orderly pattern of early myelination in white matter regions. Major advances have been made in quantitative sMRI morphometry techniques in the past two decades, and these have allowed investigators to detect subtler changes in brain structure that continue well past this age. A particular challenge for the interpretation of results from pediatric anatomical imaging is the dramatic change in gray-white contrast that occurs across the childhood age range. We discuss this issue briefly later in the chapter.

Diffusion Tensor Imaging (DTI)

Diffusion weighted imaging (DWI) is an MRI technique that measures the diffusion of protons in water molecules through brain tissue. This form of brain imaging yields several measures that exhibit strong age dependence during postnatal development, because myelination of brain fibers and other biological changes across development increasingly limit the diffusion of water molecules. The most common DWI index is a measure of the rate of diffusion called diffusivity. A common use of DWI involves fitting a tensor at each location that estimates the rate of diffusion along three orthogonal axes; that is, the tensor estimates diffusivity in different directions. Researchers refer to this method as diffusion tensor imaging (DTI) (see Figure 2.1). Tensors from locations in fluid-filled areas in the brain exhibit high, isotropic diffusivity; that is, diffusion occurs freely in all directions (Figure 2.1a). Diffusivity in gray matter is lower, because of restriction by cellular structures, but is also relatively isotropic (Figure 2.1b). In voxels that contain fiber bundles, the rate of diffusion is relatively higher along the long axis of the fibers. This phenomenon is measured as an index of *anisotropy*, usually as fractional anisotropy (FA). High FA is illustrated in the elongated structure shown in Figure 2.1c.

DTI and related methods provide information about the directionality of proton diffusion (Figure 2.1c) allowing

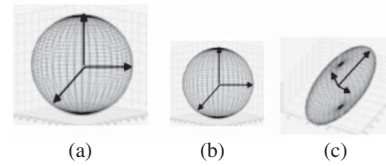


Figure 2.1 Diffusion Tensors: (a) Illustration of tensor from region with high isotropic diffusivity, as in cerebrospinal fluid. (b) Tensor exhibiting isotropic, but lower diffusivity, as in gray matter. (c) Elongated tensor exhibiting anisotropy, as in fiber tracts.

researchers to trace the apparent courses of major fiber tracts within individual brains, an approach called tractography (Mukherjee, Berman, Chung, Hess, & Henry, 2008; Mukherjee, Chung, Berman, Hess, & Henry, 2008). Tractography can define tract regions of interest (ROIs) in order to estimate diffusion parameters specific to particular tracts, and it is sometimes used to try to determine the pattern of connectivity itself.

All sMRI methods are sensitive to participant motion. However, recent methodological advances allow investigators to reduce significantly the degradation of image quality associated with motion in children (Brown et al., 2010; Kuperman et al., 2011; White, Roddey, et al., 2010).

Functional Magnetic Resonance Imaging (fMRI)

Functional magnetic resonance imaging (fMRI) includes a range of methods using MRI measurements of physiological responses to neuronal activity. These typically target the dynamic moment-to-moment changes in brain signals related to mental activity and its associated blood flow response. In 1990, Ogawa and colleagues (1990) described a technique for *in vivo* measurement of a particular aspect of the hemodynamic response to neural activity: the intrinsic blood oxygen-level dependent or BOLD signal. While other fMRI measures are available (e.g., brain perfusion using arterial spin labeling; Buxton et al., 1998), BOLD signal studies are the most commonly used in basic and clinical research.

The BOLD signal arises from a complex relationship between biophysical properties of the local ratio of paramagnetic deoxygenated hemoglobin to nonparamagnetic oxygenated hemoglobin, and physiological properties of cerebral blood flow, cerebral blood volume, and cerebral oxygen metabolism changes related to neuronal activation. Researchers typically apportion the BOLD response into three phases: the initial transient decrease in BOLD signal, the main increased BOLD signal response, and the BOLD signal undershoot. The second phase BOLD

signal is the most frequent dependent variable in fMRI studies, beginning a few seconds after the initiation of neuronal activity and peaking many seconds later (e.g., 4–8 seconds). This phase begins with the increase of local blood flow that produces an increase in the volume of oxygenated hemoglobin thereby increasing the oxygenated to deoxygenated hemoglobin ratio (Fox & Raichle, 1986). It is now understood that all excitatory and inhibitory activity within local circuitry (neurons, glia, interneurons) contributes to the BOLD hemodynamic response function (Logothetis, 2002). While most developmental studies using BOLD focus on describing regional activation, there is growing interest in characterizing brain activation within networks, a style of analysis commonly called functional connectivity analysis.

The most significant challenge in pediatric fMRI is compliance, specifically the ability to remain motionless during a data acquisition period lasting several minutes and a session lasting up to an hour. Beyond compliance, physiological factors such as blood flow and neuronal metabolism, together with structural factors such as differences in capillary bed distribution, may influence developmental BOLD signal differences not tied to task or resting state factors (for review, see Harris, Reynell, & Attwell, 2011). Finally, important differences in resting state activation may influence the baseline BOLD signal from which task and other effects are measured (Haist, Adamo, Han, Lee, & Stiles, 2013).

Electroencephalography/Event-Related Potentials (EEG/ERP)

Electroencephalography (EEG) offers particularly sensitive measures of the timing aspects of brain activity. EEG records the electric potentials generated by neurons from electrodes placed on the scalp with millisecond resolution. Scalp-recorded EEG activity is believed to reflect the intermittent synchronization of extracellular current flows within small populations of neurons predominantly on the gyral surfaces of the cortex (Nunez, 1981). EEG cannot precisely localize activity to its cerebral sources because the electric potentials are smeared, distorted, and deflected as they conduct through different types of tissue (e.g., brain, dura, skull, scalp; Cuffin & Cohen, 1979). It is not possible definitively to identify the exact sources of the EEG signal (Pascual-Marqui & Biscay-Lirio, 1993), although modern source analysis tools can suggest the best source solution given certain assumptions. EEG data can be analyzed within both the frequency and event-related domains, extracting effects such as coherence or synchrony

within particular frequency bands or averaged in relation to the repeated presentation of some time-locked stimulus of interest. Researchers refer to the latter averaged response as the evoked or event-related potentials (ERP). Different sensory, perceptual, and cognitive processes produce unique ERP components, which are traditionally labeled according to the polarity (positive or negative voltage deflection) and timing of the peak in relation to the stimulus (Polich, 1993). For example, the N170 is a negative-going deflection peaking at about 170 ms (in adults) following the presentation of a visual face stimulus. The P600 is a positive deflection peaking at about 600 ms that has been linked to cognitive operations in language and memory. ERP components are examined for changes in amplitude, latency, and scalp topography in relation to the manipulation of sensory, cognitive, or subject factors of interest such as clinical group or age.

The rapid development of EEG technology will allow it to be used freely outside the laboratory setting, a unique feature amongst brain imaging methods, and thus offers tremendous promise for use in developmental research. Systems coming to market allow for the easy user-friendly application of multiple electrodes that provide built-in analog-to-digital (A/D) converters paired with wireless transmitters (e.g., Bluetooth or Wi-Fi). Thus, researchers can acquire EEG and ERPs in diverse settings (i.e., schools) on easily portable machines such as laptops, tablets, and smartphones.

Magnetoencephalography (MEG)

Magnetoencephalography (MEG) is a technique similar to EEG. MEG measures fluctuations in the magnetic fields induced by voltage-gated and ligand-gated neuronal current flows with submillisecond resolution, limited only by the digitization rate (Cohen & Cuffin, 1983). MEG sensors, called SQUIDs (superconducting quantum interference devices), are contained within the helmet-shaped dewar that surrounds the participant's head. Unlike EEG, the spatial relationship between brain activity sources and the sensors is reasonably straightforward because magnetic fields pass through biological tissues with essentially no perturbation as they emanate from the brain (Cohen & Cuffin, 1991; Cohen et al., 1990; Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Nevertheless, MEG source localization still requires inferences based on careful modeling because measurements are made at the scalp some distance from the brain. Many researchers now using MEG employ model constraints using information from an MRI from the subject. Noise-normalized,

anatomically constrained statistical parametric maps of MEG-derived brain activity show strong spatial correspondence with recordings from intracranial EEG for a variety of stimulus types and sensory and cognitive components (Dale & Halgren, 2001; Halgren, 2004). MEG has several practical advantages for use with children and infants. MEG does not require the placement of scalp electrodes, which can be time consuming and tiresome for young subjects. The MEG scanner is an entirely passive instrument and is quiet. And it allows either supine or upright data collection. Thus, it can be used when MRI is contraindicated.

Positron Emission Tomography (PET)

Positron emission tomography (PET) is an imaging technique used to measure chemical and physiological activity in a variety of body organs and has been used in developmental studies from neonatal ages and above (Phelps & Mazziotta, 1985). PET uses radiotracers that contain positron-emitting isotopes that are injected into the bloodstream. The emitted positrons immediately collide with negatively charged electrons leading to the destruction of both particles. This “annihilation event” releases energy in the form of two photons traveling in opposite directions. A PET scanner consists of a ring of scintillation sensors that detect and localize where these events occur. Using H_2O^{15} (“oxygen-15 water”) as the isotope allows the researcher to quantify regional cerebral blood flow (rCBF), and by inference, localized changes in brain activity. PET can also track the synthesis of specific proteins or the uptake and binding of particular neurotransmitters. Since glucose and oxygen are fundamental to meeting the energy demands of the brain, many PET studies of early development have measured age changes in these substrates. Local cerebral metabolic rates for glucose undergo dramatic maturational changes in most parts of the brain, particularly in the cerebral cortex, and these changes continue over a protracted period (Chugani & Phelps, 1991; Chugani, Phelps, & Mazziotta, 1987).

The major limiting feature of PET for typical development studies is that it requires the injection of ionizing radiation, thereby making it one of the most invasive of the neuroimaging tools for studying development. Thus, developmental PET studies are most frequently reported from clinical populations with neurological diagnoses, such as pediatric cancer (see Jadvar, Connolly, Fahey, & Shulkin, 2007), seizure disorders (Kannan & Chugani, 2010), or neurodevelopmental disorders such as autism (see Chugani, 2012) and attention deficit hyperactivity disorder (see Mana, Paillere Martinot, & Martinot, 2010).

Near-Infrared Spectroscopy (NIRS)

Near-infrared spectroscopy (NIRS) is a noninvasive optical imaging method that measures the state of hemoglobin oxygenation in the brain that is modulated by regional levels of cerebral blood flow and cortical activity. NIRS uses light projected into the brain from scalp-based illuminators and sensors (optodes) located nearby to measure hemoglobin oxygenation changes in external gyri measured with a resolution ranging from tenths of seconds to seconds. NIRS recording systems are portable, allow subjects to move, operate silently, and require little setup and calibration time. These factors make NIRS appealing for research with infants and young children. A limitation of NIRS is difficulty in developing standard ways of mapping the locations of brain activity sources. Also, idiosyncratic factors such as skull and skin thickness and even skin color may affect recordings.

MAJOR MILESTONES OF ANATOMICAL BRAIN DEVELOPMENT

The anatomical development of the human brain begins in the first weeks of gestation and extends into adulthood. The processes that underlie brain development are dynamic, with each step laying the foundation for the emergence of new neural structures and systems. Development at the cellular level is most evident in the changing array of cell types that arise at critical points and contribute in varying ways to the gradually emerging neural structure. Some classes of cells form the permanent structures of the brain, while others contribute to transient systems that support a specific aspect of brain development and then disappear. At the macro level, the morphology of the brain undergoes a dramatic series of changes in the prenatal period as the major neural structures differentiate and the primary neural pathways extend and are refined and stabilized. Although the basic elements of mature neural organization can be discerned by the postnatal period, brain development is far from complete. The brain volume of a newborn is approximately 25% that of an adult and will reach 90% of adult size by 6 years (Iwasaki et al., 1997; Kennedy, Makris, Herbert, Takahashi, & Caviness, 2002; Paus et al., 2001). However, change in volume does not tell the story of brain development. Significant changes in the size of cortical regions and areas, thickness of the neocortex, and stabilization of pathways continue through childhood and do not reach adult levels until middle to late

adolescence. Genetic factors contribute to and constrain the trajectories of brain development in both the pre- and postnatal periods. Inputs from the environment strongly influence all of these changes. The sections that follow will provide a brief overview of the major milestones of pre- and postnatal brain development. They are intended to convey the dynamic and interactive nature of the processes that underlie the development of this most critical and complex biological structure.

Prenatal Brain Development

Developmental change in the prenatal period involves two fundamental processes: (1) the progressive differentiation of neural elements, and (2) the progressive stabilization of those emerging neural components into functional neural systems. Both of these processes involve complex molecular and functional interactions among different cell populations that affect the subsequent regional development of the prenatal brain. There are two main prenatal periods. The embryonic period includes the first 8 weeks after conception, and the fetal period from week 9 to birth. By convention, weeks after conception are referred to as Gestational Weeks (e.g., GW8 for the eighth week postconception) and days after conception as Embryonic Days (e.g., E13 for the 13th day postconception). The basic neural cell lines are established and the major spatial axes of the nervous system are defined during the embryonic period. Rapid change in neural structure and organization during the fetal period gives rise to the basic areal organization of the neocortex and the establishment of the major brain pathways including the corticospinal tract, the corpus callosum, the thalamocortical pathway, and many of the major association pathways.

Prenatal Changes in Brain Morphology

Gastrulation: Differentiation of Neural Tissue. Brain development begins during the third week after conception (GW3). The embryo is a flat, slipper-shaped structure that is composed of two cell layers at the beginning of GW3. The upper layer contains *epiblast* cells and the lower layer *hypoblast* cells. The embryo is transformed through a set of processes that are referred to collectively as *gastrulation* into a three-layered structure by the end of the third week (Sadler & Langman, 2010; Schoenwolf & Larsen, 2009). Although this seems a simple change, the transformations of cell lines that occur during gastrulation set the stage for all subsequent developments in the embryo. The epiblast cells of the upper cell layer

will differentiate into the three primary *stem cell* lines that will eventually give rise to all of the structures in the developing embryo, while the hypoblast cells of the lower layer will form “extraembryonic” tissues such as the fetal component of the placenta and the connecting stalk. The neural stem cells are among the stem cell lines that emerge during gastrulation. The neural stem cells are capable of producing almost all of the different cells that make up the brain and central nervous system, and for this reason the neural stem cells are called the *neural progenitor cells*.

The appearance of a slit-like opening in the upper layer of the embryo called the *primitive streak* signals the first step in the gastrulation process. The primitive streak provides access to the lower regions of the embryo (see Figure 2.2a). Next, a subset of the epiblast cells detaches from the upper layer of the embryo and migrates toward the primitive streak. These cells change direction and pass through the primitive streak moving under the upper layer after reaching the opening (see Figure 2.2b). They change direction again and begin moving toward the rostral end of the embryo (see Figure 2.2c), which will develop into the baby’s head. The earliest migrating cells move to the most rostral/head positions in the embryo, later migrating cells move to successively more caudal regions that will develop into the neck and trunk of the body. The migrating cells form two new embryonic layers. The deepest is the *endodermal* stem cell layer which gives rise to structures of the gut and respiratory tract, while the intermediate *mesodermal* stem cell layer gives rise to muscle, bone, cartilage and the vascular system. The remaining epiblast layer cells transform into one of two types of *ectodermal* stem cells. *Epidermal ectodermal* stem cells give rise to skin, nails, and sweat glands, while *neuroectodermal* stem cells give rise to the brain and central nervous system. The neuroectodermal stem cells are the neural progenitor cells. The differentiation of all three types of embryonic stem cell lines involves complex cascades of molecular signaling, but only the differentiation of the neural stem cells (neural progenitors) are considered here.

At the beginning of gastrulation, the epiblast layer cells that differentiate into neural progenitor cells are located along the rostral-caudal midline axis of the two-layered embryo (the central rectangle in Figure 2.2d). The differentiation of these cells into neural progenitor cells is the result of complex molecular signaling that involves multiple gene products (i.e., proteins) produced by several different populations of embryonic cells. Recall that at the beginning of gastrulation, epiblast cells begin to migrate toward and then down through the primitive streak to

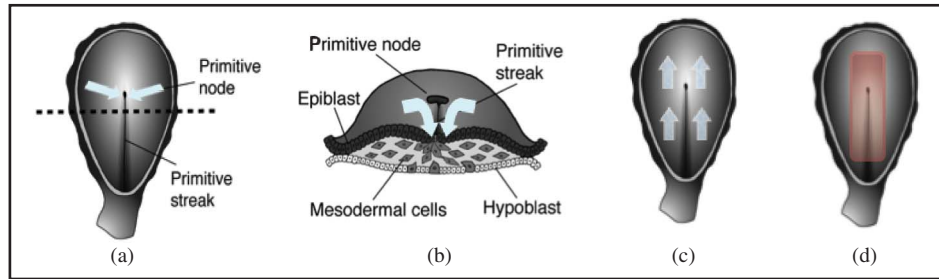


Figure 2.2 The major events of gastrulation occur between E13 and E20. (a) Gastrulation begins with the formation of the primitive streak and the primitive node. The primitive streak provides an opening to deeper embryonic layers. The primitive node is a critical molecular signaling center. On E13, cells from the epiblast layer begin to migrate toward the primitive node and streak (arrows). The dotted line indicates the cross-sectional view shown in panel B. (b) The migrating cells first move to the primitive streak and then move down and under the upper layer (arrows). As the cells pass the node they receive molecular signals that induce gene expression in the migrating cells. (c) Once under the upper layer, the cells change direction and begin migrating rostrally under the upper layer (arrows). The first cells to migrate form the most rostral regions of the newly forming endodermal and mesodermal layers. Later migrating cells form progressively more caudal regions of the layers. (d) Cells that migrate along the axial midline send molecular signals that induce cells in the overlying epiblast layer to differentiate into neuroectodermal cells (central rectangle) which are the neural progenitor cells. Migrating cells also receiving a second set of signals from the node that induce anterior or posterior fate in different subpopulations of the neuroectodermal cells. Early migrating cells signal anterior fate in the progenitor cells, while late migrating cells signal posterior fate.

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form the lower embryonic layers. As the cells that migrate along the rostral-caudal midline of the embryo approach the opening, they pass another structure called the *primitive node*, which is a molecular signaling center (see Figure 2.2a). Primitive node cells send a molecular signal to the subset of cells that migrate along the rostral-caudal midline of the embryo and that signal, in turn, triggers gene expression in the migrating cells. Gene expression in the migrating cells produces a protein that is secreted into the space between the migrating cells and the cells remaining in the midline region of the upper epiblast layer. The secreted protein binds to receptors on the surface of cells in the upper layer of the embryo, sending a signal that leads to the differentiation of the epiblast cells into the neural progenitor cells.

In addition to providing the molecular signaling leading to the transformation of the overlying epidermal cells into neural progenitor cells, the primitive node generates a second set of signals that *change* over the course of gastrulation and serve to establish the basic rostral-caudal organization of the embryonic nervous system. Recall that the earliest migrating epidermal cells move to the most rostral/head end of the embryo and later migrating cells move to successively more caudal locations. In addition to the basic neuralizing signal, the primitive node provides each successive wave of migrating cells a second signal that specifies the regional identity for the neural progenitors. Thus, primitive node signals *early* migrating epidermal

cells to produce molecular signals for the cells in the overlying epiblast layer to differentiate into neural progenitors capable of producing cells appropriate for forebrain structures, while later migrating cells signal differentiation of neural progenitors capable of producing cells appropriate for midbrain, hindbrain, or spinal cord structures.

In summary, by the end of gastrulation, cells located along the midline of the upper layer of the embryo have transformed into neural progenitor cells (central rectangle in Figure 2.2d). These cells are further specified to produce the kinds of neurons that are needed within the particular region of the developing neural system in which they are positioned. The differentiation of neural progenitor cells requires complex genetic signaling among at least three cell populations: the cells of the node, the migrating epiblast cells, and the cells that will become the neural progenitors. In the absence of this complex signaling, the prospective neural progenitor cells differentiate into *epidermal* ectodermal progenitor cells, leading to catastrophic failure of brain development.

Neurulation: The Formation of the Neural Tube.

The formation of the neural tube, the first well-defined neural structure, is the next major step in brain development. The neural tube forms during the GW4, between E20-27. By the end of gastrulation, the neural progenitor cells have differentiated and are positioned along the rostral-caudal midline of the upper layer of the three-layered embryo in a region called the *neural plate*.

The first sign of neural tube development is the appearance of two ridges, or folds, that form along the two sides of the neural plate (Figure 2.3a). The neural progenitor cells lie between the two ridges. Over the course of several days, the ridges rise, fold inward, and fuse to form a hollow tube (Copp, Greene, & Murdoch, 2003). Fusion begins in the center of the developing neural tube and proceeds in rostral and caudal directions (Figure 2.3b and c). The *anterior neuropore* at the rostral end of the neural tube and the *posterior neuropore* at the caudal end, are the last segments to close, on E25 and E27, respectively (Figure 2.3d).

The neural progenitors form a single layer of cells that line the center of the neural tube immediately adjacent to the neural tube's hollow center when it is complete. The hollow center of the neural tube is cylindrical in the embryo, like the center of a straw. The shape of the hollow cavity changes to form the ventricular system of the brain and the central canal of the spinal cord as the brain becomes larger and more complex. Because the neural progenitors are located in the region that become the ventricles, the region is called the "ventricular zone" (VZ). The neural progenitor cells in the most rostral region of the neural tube give rise to the brain, while more caudally positioned cells give rise to the midbrain, hindbrain, and spinal column.

Differentiation of the Neural Tube. The embryo undergoes rapid growth over the next month. The embryo is 3 to 5 mm long at the end of neurulation (E28), and undergoes a tenfold increase in size to 27 to 31 mm by the end of the GW8. The shape of the primitive nervous system changes dramatically during this period. The anterior end of the tube expands to form the three primary *brain vesicles*, or pouches, just before neural tube closure (Figure 2.3e). The most anterior of these vesicles, called the "prosencephalon," is the precursor of the forebrain. The middle vesicle is the "mesencephalon," which is the precursor of midbrain structures. The posterior vesicle is the "rhombencephalon," which becomes the hindbrain. These three segments subdivide so that five secondary brain vesicles are present at the end of the embryonic period (Figure 2.3f). The prosencephalon divides into the "telencephalon" and the "diencephalon," and the rhombencephalon divides into the "metencephalon" and "myelencephalon." The mesencephalon does not further divide. These five subdivisions are complete by the end of GW6 and aligned along the rostral-caudal axis of the embryo to establish the primary organization of the central nervous system (Stiles, 2008).

Formation of Gyri and Sulci. The human brain begins as a smooth, "lissencephalic" structure that gradually develops the characteristic mature pattern of gyral and sulcal folding. The formation of gyri and sulci follows an orderly sequence. Primary sulci are first seen as grooves positioned in specifically targeted brain regions, secondary branches then begin to form off the primary sulci, followed by the tertiary branches. The longitudinal fissure that separates the two cerebral hemispheres is the first fissure to form. Its development begins in rostral regions as early as GW8 (Chi, Dooling, & Gilles, 1977) and proceeds caudally until it is complete at GW22. Other primary sulci form between GW14-26. These include: Sylvian, Cingulate, Parieto-Occipital, Calcarine in GW14-16, the Central and Superior Temporal in GW20-24, and Superior Frontal, Precentral, Inferior Frontal, and Postcentral, Intraparietal in GW25-26. Secondary sulci emerge between GW30-35; formation of tertiary sulci begins during GW36 and extends well into the postnatal period.

Cellular Elements

Neural Progenitor Cells. The human brain contains nearly a hundred billion neurons most of which are produced by mid-gestation as well as many more billions of support cells (Bayer, Altman, Russo, & Zhang, 1993; Rakic, 1995). The neural progenitor cells produce most of these cells. However, the pool of neural progenitor cells specified at the end of gastrulation is far too small to accommodate cell production on this scale. Thus, there must be a means of increasing their number. Unlike neurons, neural progenitors are mitotic cells; that is, they can divide to form new cells. The population of neural progenitor cells divides by a "symmetrical" mode of cell division from the end of gastrulation through E42 in humans. Symmetrical cell division produces two identical neural progenitor cells. Symmetrical cell division provides the means for augmenting the size of the neural progenitor pool over multiple rounds of cell division between E25 and E42.

Programmed cell death refers to a ubiquitous cell-intrinsic molecular program that leads to the destruction of the cell. All classes of neural cells exhibit programmed cell death as a means to regulate cell numbers, correct for cellular errors, and to eliminate cell populations that play a transient role in brain development. Most neuron production is complete by mid-gestation. Programmed cell death in progenitor populations begins to occur in small numbers early in the period of cortical neurogenesis (GW7), and increases across the fetal period,

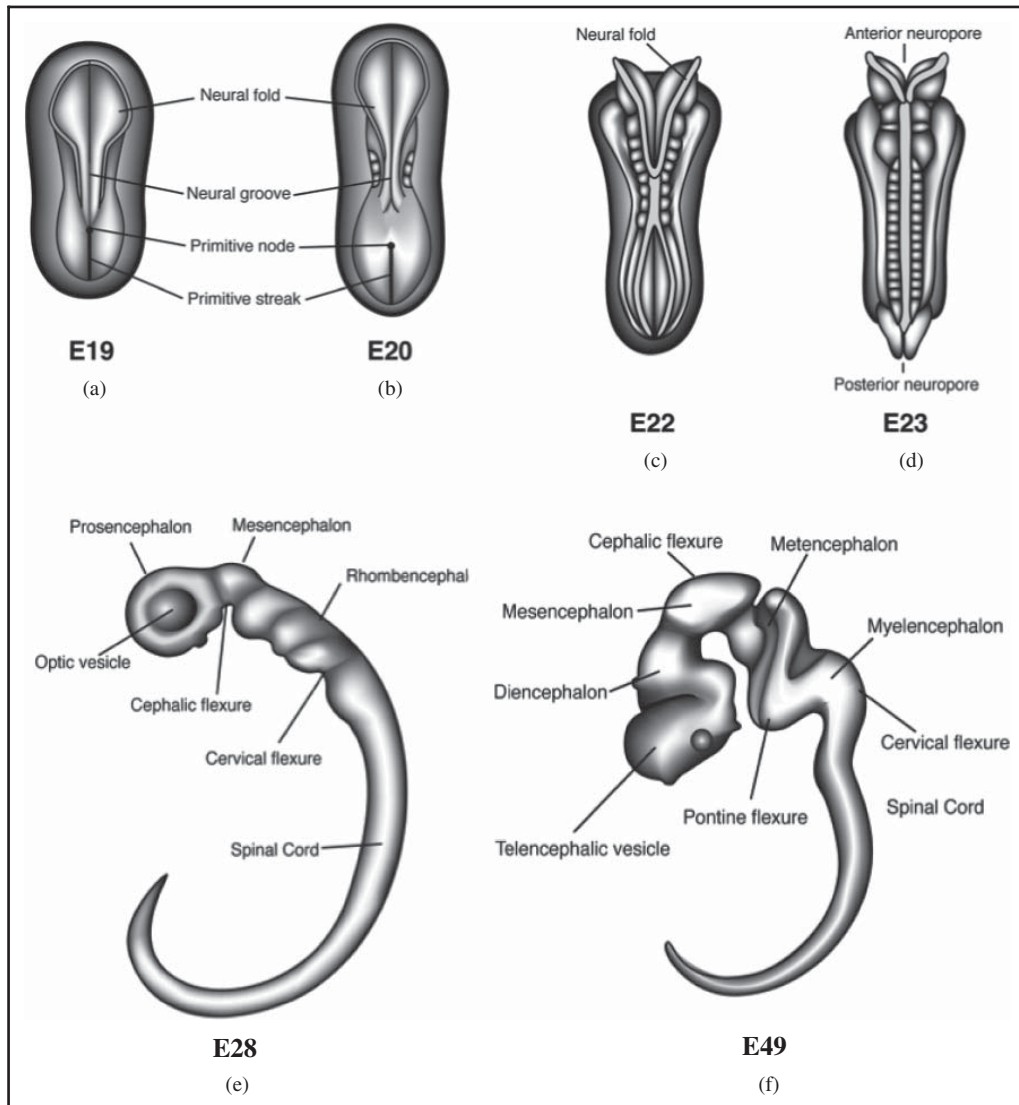


Figure 2.3 Changes in the morphology of the embryo in the embryonic period. (a) The emergence of the neural folds is observed on E19. (b) The ridges fold over to begin the process of neural tube formation. (c) Closure of the neural tube begins on E22 in central regions of the newly forming neural tube. (d) Closure continues in rostral and caudal direction. (e) Following the closure of the neural tube, the embryo begins to expand particularly in anterior regions. The primary vesicles are evident by E28. (f) By E49 the secondary vesicles emerge.

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resulting in cell death of 50%–70% of progenitors by the end of gestation (de la Rosa & de Pablo, 2000; Yeo & Gautier, 2004).

Neurons: Production, Migration, and Differentiation.

In humans, neuron production begins on E42. It involves a shift in the mode of cell division from symmetrical to asymmetrical. Asymmetrical cell division in neural progenitors produces one neural progenitor and one neuron (Wodarz & Huttner, 2003). The new progenitor

cell remains in the proliferative zone and continues to divide, while the neuron, which is postmitotic and no longer capable of dividing, leaves the proliferative zone to take its place in the developing neocortex. The shift to asymmetrical cell division in the progenitor population is gradual and initially includes only a small proportion of progenitors. Those numbers increase dramatically by the end of cortical neurogenesis. In humans the production of cortical neurons or “cortical neurogenesis” is mostly

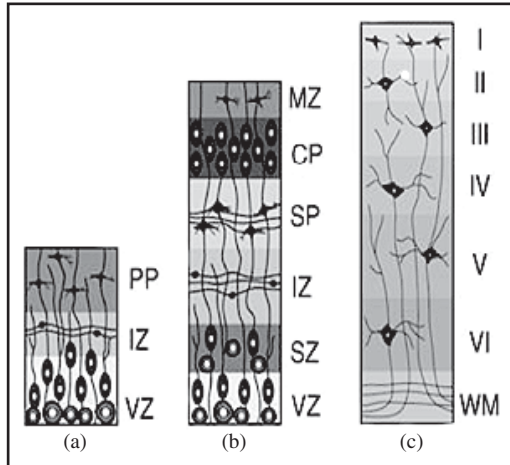


Figure 2.4 Development of the neocortex. (a) The earliest produced neurons migrate from the ventricular zone (VZ) to form the preplate (PP). (b) The next neurons split the PP into the marginal zone (MZ) and the subplate (SP), both transient brain structures. (c) The mature brain has six well-developed cortical layers (I–VI), but none of the embryonic structures (MZ, SP, VZ). The intermediate zone (IZ) becomes a mature white matter layer (WM).

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complete by approximately E108 (Clancy, Darlington, & Finlay, 2001).

Most neurons are produced in the VZ and an adjacent later developing region called the subventricular zone (SVZ). They migrate radially from the VZ/SVZ in the center of the brain out to the developing neocortex (see Figure 2.4). The great majority of neurons migrate from the VZ/SVZ to the cortex along a kind of cellular scaffold that was originally called the radial glial cell (Rakic, 1972). The cell bodies of RGCs are anchored in the VZ. These cells extend a kind of filament composed of the cell's wall called the cellular process that fastens to the far side of the developing cortical plate (CP). Newly produced neurons attach themselves to this cellular scaffold to migrate from the VZ/SVZ to the CP (Nadarajah & Parnavelas, 2002). Each glial scaffold can support the migration of many neurons.

A second proliferative zone is located in the region of the ventral telencephalon that will later develop into the basal ganglia (Anderson, Marin, Horn, Jennings, & Rubenstein, 2001; Nery, Fishell, & Corbin, 2002). These neurons migrate via “tangential migration,” traversing the contour of the developing cortical mantle. Tangentially migrating neurons use a number of guidance molecules

produced in local regions along their migratory route to direct their movement into the cortex (Marin & Rubenstein, 2001; Valiente & Marin, 2010).

The mature neocortex is a thin mantle of cells that covers the surface of the brain. The organization of the neocortex is well conserved across regions, indeed across mammalian species. Cortical thickness ranges between 2 and 5 mm, and all regions contain six layers of cells. The six-layered organization emerges with development, and is the product of the orderly migration of neurons from the VZ/SVZ in the developing neocortex (Cooper, 2008). Early migrating neurons form the deepest layers of cortex and later migrating neurons form successively more superficial layers (see Figure 2.4) such that the order of migration is “inside-out,” with one exception. The very earliest set of migrating neurons is the exception to the inside-out rule. These first neurons to leave the proliferative zone initially form a primitive structure called the preplate (PP; see Figure 2.4a). Once the preplate is complete, the next wave of migrating neurons splits the preplate into two separate regions: the marginal zone (MZ) and the subplate (SP). These neurons begin to form a new region between the MZ and SP that is the emerging cortical plate (CP; see Figure 2.4b). The first neurons to arrive in the CP are the cells that will form cortical layer 6, the deepest layer of cortex, subsequently migrating cells will form progressively more superficial layers of cortex.

Both the MZ and the SP are transient cortical layers that play a critical role in the development of the cortex, but both largely disappear by the end of the fetal period (see Figure 2.4b and c). The MZ contains an important class of cells, the Cajal-Retzius cells (CR) that control the positioning of neurons into the correct layers of cortex. The CR cells produce Reelin, a molecular signal that is part of the pathway that signals neurons when to stop migrating and take up their positions in the cortex (Huang, 2009; Valiente & Marin, 2010). Each new wave of migrating neurons bypasses the previous wave. When they reach the most superficial position within the developing CP, they move into the zone of Reelin signaling and receive the cue to stop and take up their position in the neocortex. Neurons in the subplate layer do not participate in the formation of cortical layers, but as discussed later, they are essential for establishing the primary sensory pathways of the developing brain.

The young neurons become part of information processing networks once they reach the cortex. To do that, these neurons develop neuronal processes (axons and dendrites) that allow them to communicate with other neurons. Axons are the principle means of sending signals from the neuron,

whereas dendrites are major sites for receiving input from other neurons. Each cell has many dendrites that form dense “arbors” in the immediate vicinity of the cell, and a single axon that can extend for some distance away from the cell. The tip of each axon has a structure called a growth cone, which is the site of axon elongation and extension (Brown, Keynes, & Lumsden, 2001). The growth cone samples the local environment for guidance molecules that direct the axon toward its target as the axon extends. Some guidance cues are attractive and signal movement toward a source; others are repulsive and guide movement away. Connections called synapses form with the target cell once the axon has reached its target. Synapses allow for the transmission of electrochemical information that is the essential means of communication in the brain.

Production of the Brain’s Glial Cells. Glial cells are much more numerous than neurons in the mature brain, yet make up only about half of the mature brain volume because they are smaller than neurons. The timing and duration of gliogenesis is quite different from neurogenesis. Neurons are produced before glia in most brain regions. Neurogenesis is largely complete by midgestation, while gliogenesis extends well into postnatal life. Astrocytes and oligodendrocytes are produced by the same neural progenitor cells that produce neurons in the early stages of glial development (Sun, Martinowich, & Ge, 2003), but spatially and temporally distinct subsets of neural progenitors appear to be responsible for production of different types of glial cells. Oligodendrocyte precursor cells (OPCs) arise in multiple proliferative sites within the dorsal and ventral telencephalon (Kessaris et al., 2006). In humans, OPCs are first observed at about GW19-20 concentrated largely within the SVZ. A second population of OPCs is present in the subplate regions late in gestation. OPC production of oligodendrocytes appears to extend through the lifespan (Richardson, Young, Tripathi, & McKenzie, 2011). Astrocyte production follows a different course. Although astrocytes derived from radial glial cells and from the SVZ populate the cortex during the prenatal period, in the immediate postnatal period, there is a very large and rapid increase in numbers of astrocytes. In the cortex, this increase involves symmetrical cell division that produces new cells that become functionally integrated into local glial networks (Ge, Miyawaki, Gage, Jan, & Jan, 2012).

Neural Patterning in the Prenatal Period

Patterning of the nervous system begins early in the embryonic period. The patterning observed by the end of the

embryonic period provides only a primitive map of eventual nervous system organization, yet it sets the stage for later developments (Sur & Rubenstein, 2005). Embryonic patterning affects all brain regions from the forebrain through the spinal column. By the end of the embryonic period major compartments within diencephalic and midbrain regions have differentiated (Kiecker & Lumsden, 2004; Nakamura, Katahira, Matsunaga, & Sato, 2005), dorsal-ventral structures have begun to segregate, and the segmental organization of the hindbrain and spinal column have been specified (Gavalas, Ruhrberg, Livet, Henderson, & Krumlauf, 2003).

Neocortical patterning also begins in the embryonic period. The mature neocortex is partitioned into well-defined structurally and functionally distinct “areas” differentiated by their cellular organization and patterns of neuronal connectivity. Areal patterning of the neocortex begins during the embryonic period with primitive specification of the major sensorimotor areas. Initial patterning of neocortex into cortical areas results from different molecular signals present in different regions of the neocortical proliferative zone. While a number of signaling molecules are now known to contribute to this early neocortical patterning (O’Leary & Sahara, 2008; Sansom & Livesey, 2009), the *Emx2* and *Pax6* molecules, which play an essential role in the early patterning of the presumptive neocortex, illustrate these important early processes (see Figure 2.5).

Emx2 and *Pax6* are produced in opposite gradients along the anterior-posterior extent of the neocortical proliferative zone (see Figure 2.5a). The concentration of *Emx2* is highest in posterior and medial regions, and lowest in anterior lateral regions; *Pax6* has the opposite expression pattern. The interaction of these two gradients contributes to early patterning of the neocortex (Bishop, Rubenstein, & O’Leary, 2002; Hamasaki, Leingartner, Ringstedt, & O’Leary, 2004). High concentrations of *Pax6* combined with low *Emx2* induces progenitors to produce neurons appropriate for motor cortex (M1), while the inverse concentrations induce production of neurons for visual cortex (V1). Somatosensory cortices (S1) emerge at intermediate levels of both factors. Studies of mutant mice, for which expression of either *Emx2* or *Pax6* is reduced (thus altering the balance of signals across the cortical proliferative zone), show systematic shifts in the organization of cortical areas (Bishop, Goudreau, & O’Leary, 2000). These studies confirm that the interaction of the two signaling molecules induces change in the surrounding cell populations. When *Emx2* expression is reduced, visual

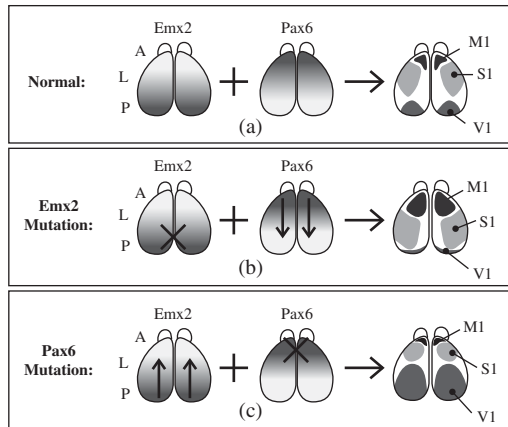


Figure 2.5 Emx2 and Pax6 are expressed in complementary concentration gradients within the neocortical proliferative zone. The combination of the two molecules at particular concentration levels determines the functional identity of the cortical region. Mutations affect the quantities of either molecule, alter cortical patterning. A = anterior, L = lateral, P = posterior, M1 = motor, S1 = somatosensory, V1 = visual.

Source: From “Regulation of Area Identity in the Mammalian Neocortex by Emx2 and Pax6,” by K. M. Bishop, G. Goudreau, and D. D. O’Leary, 2000, *Science*, 288(5464), pp. 344–349. Adapted with permission.

areas shrink and somatosensory and motor areas enlarge (Figure 2.5b); when Pax6 expression is reduced, visual areas enlarge while somatosensory and motor areas shrink (Figure 2.5c). Thus, the effect of the particular level of one molecular signal in combination with the level of another signal produces the classical pattern of sensorimotor organization in the developing cortex.

These graded patterns of molecular signaling occur in regions of the neocortical proliferative zone that were specified as “rostral” during gastrulation. This later patterning constitutes a regional elaboration or refinement of an earlier phase of neural patterning. Patterning within these regions is far from complete at the end of the embryonic period. Fundamental organizational features of the sensory and motor cortices do not arise until the late fetal period. The structural and functional identity of these basic brain areas remains malleable and subject to the effects of input and experience across the period of fetal and early postnatal development.

Formation of the Major Brain Pathways in the Prenatal Period

Studies of both monkeys and humans have documented widespread exuberant production of connections throughout all brain regions in the early postnatal period (Bourgeois, Goldman-Rakic, & Rakic, 1994; Huttenlocher & Dabholkar, 1997; Huttenlocher & de Courten, 1987;

Zecevic, Bourgeois, & Rakic, 1989). Exuberant connectivity occurs in pathways as diverse as the corpus callosum, thalamocortical pathways, corticospinal tract, and pathways linking the temporal lobe and the limbic system (Innocenti & Price, 2005; Stanfield & O’Leary, 1985). A wide range of factors affects the retention or elimination of pathways. Competition for resources, such as neurotrophic factors, plays a significant role in selection of pathways. Importantly, afferent input plays a critical role in modulating the stabilization or elimination of pathways. This section considers the initial formation of several major pathways in the prenatal period.

Corticospinal Tract. The typical mature corticospinal tract (CST) originates in the frontoparietal cortices. The tract travels through the anterior half of the posterior limb of the internal capsule (the dense white matter system connecting cortex with the brainstem) forming the cerebral peduncles before reaching the brainstem. The CST crosses the midline to the contralateral side forming the medullary pyramid decussation in the lower medulla. The contralateral CST travels down the spinal cord synapsing on motor neurons (Armand, 1982). CST neurons initially exhibit an “exuberant distribution” during development (O’Leary & Kroll, 2009). The CST initially forms bilateral connections, in contrast to the mature pattern of contralateral organization (e.g., right motor cortex controls the left side of the body). The CST is discernable as early as GW13 (Eyre, 2007; Huang et al., 2009), and by GW24 projections originating in the motor cortex innervate *both* ipsilateral and contralateral spinal motor neurons creating dual pathways that are detectable through the first 3 months of postnatal life (Eyre, 2007). Thereafter, progressive withdrawal of the ipsilateral projections occurs resulting in clear contralateral dominance by 18 months. The CST forms a conduit between the motor cortex and the limbs of the body, such that activity in the motor cortex depends on the motor activity of the limbs and vice versa. This activity drives the maturation of the CST and modulates the balance between projection and withdrawal of contralaterally and ipsilaterally projecting CST axons (Eyre, 2007; Martin, 2005).

Corpus Callosum. The corpus callosum (CC) connects neurons in the two cerebral hemispheres and is the largest pathway in the brain. Its principal function is the coordination and transfer of information between the hemispheres. Critical events during the early embryologic period set the stage for CC development. During the differentiation of the telencephalon, the single vesicle of

the prosencephalon expands and divides into two compartments creating the characteristic two-vesicle structure of the telencephalon. The two cerebral hemispheres emerge from the vesicles of the embryonic telencephalon. The ventral portions of the two hemispheres are initially fused, but it is not until the end of the embryonic period that more dorsal regions also fuse, creating a substrate for the developing CC (Jovanov-Milosevic, Culjat, & Kostović, 2009; Richards, Plachez, & Ren, 2004).

Cortical layer 3 neurons are the principal source of the axons that make up the CC in primates. These neurons extend axons from the neocortex ventrally into the intermediate zone near the ventricles. The axons then change direction following the medial wall of the ventricle across the midline of the brain and from there they grow toward their cortical targets in the contralateral brain hemisphere. A large number of guidance molecules direct the axons' movement through these various brain compartments (Jovanov-Milosevic, Culjat, & Kostović, 2009; Richards et al., 2004). The first CC axons approach the midline by GW 11. All the major components of the CC (genu, body, splenium) are present by GW 18–20 (Huang et al., 2009; Jovanov-Milosevic et al., 2009). The CC structure is similar in shape and position to that of an adult by GW 19, although it is smaller in rostral-caudal extent and thinner. An areal cross section of the CC at GW19 is 5% the size of a 5-year-old, but by birth the cross section is 50% of a 5-year-old. Connectivity in the developing CC is extremely dynamic, exhibiting the kind of synaptic exuberance and pruning that is characteristic of many brain areas (Innocenti & Price, 2005; Paul, 2011). LaMantia and Rakic (1990) reported that the CC of a newborn Rhesus monkey contains 3.5 times the number of axons of a mature CC. Development of the CC is protracted, extending well into adolescence (Paul, 2011).

Thalamocortical Pathway. The thalamocortical pathway (TCP) relays visual, auditory, motor, and somatosensory information from the receptors in the retina, cochlea, muscle, or skin to the sensorimotor regions of the neocortex via the thalamus, the major subcortical sensorimotor relay center. The corticothalamic pathway (CTP) completes the feedback loop by transmitting information from cortex back to the thalamus. These essential pathways begin forming in the later part of the second trimester in humans, and are complete by GW26 (Kostović & Jovanov-Milosevic, 2006). The cells of the transient subplate layer of the developing brain play an essential role in establishing these pathways (see Figure 2.4b). TCP axons do not immediately

make connections with neurons in the primary input layer of cortex (layer 4) when they arrive at the developing cortex during GW22. Rather, they make connections with the neurons of the subplate layer. The TCP-subplate connections last for approximately 4 weeks, during which time the subplate neurons make connections with neurons in cortical layer 4. The subplate neurons appear to provide instructive input to the TCP neurons during this period. In the absence of subplate neuron signaling, normal patterns of connectivity between TCP axons and layer 4 cortical neurons do not develop. The CTP pathway follows a similar pattern of instructive connectivity. Subplate neurons extend axons to the thalamus and establish connections with thalamic neurons before the normal CTP connections between cortical layers 5 and 6 neurons and the thalamus are formed. It is thought that subplate connections serve to guide the CTP axons to their positions in the thalamus. The subplate neurons retract their connections and the cells gradually die off once the TCP and CTP pathways are complete.

The primary visual pathway includes both the optic pathway and the visual component of the thalamocortical pathway. The pathway begins with the retinal ganglion cells (RGC) in the eye and projects along the optic pathway to the optic chiasm. There, 50% of the projections cross and project to midbrain targets in the contralateral hemisphere, specifically the superior colliculus (SC) and the dorsal lateral geniculate nucleus of the thalamus (dLGN), while the remaining projections synapse on comparable ipsilateral midbrain targets (Leamey, Van Wart, & Sur, 2009; Reese, 2011). Connections to the SC and dLGN are initially imprecise but are gradually refined. Exuberant projections are pruned to more restricted regions within the SC. Initially mixed and imprecise RGC connections segregate into eye specific domains within the dLGN (Haupt & Huber, 2008). Initial projections from the dLGN to occipital cortex along the optic component of TCP exhibit similar initial imprecision. Though controversial (Katz & Crowley, 2002), recent evidence suggests that waves of spontaneous retinal activity are necessary for this fine-tuning of the visual system connectivity (Huberman, Speer, & Chapman, 2006).

The auditory pathway includes both the brainstem auditory pathway and the auditory component of the TCP. The brainstem auditory pathway begins with the spiral ganglion cells (SGC) in the cochlea and projects to the cochlear nuclei in the brain stem (Appler & Goodrich, 2011; Moore & Linthicum, 2007). From there, the pathway extends to the olivary complex, to inferior colliculi (IC), and from the IC to the medial geniculate nucleus (MGN) of the thalamus.

The brainstem pathway is well established by the end of the second trimester. The auditory TCP is established during early third trimester, but undergoes considerable development postnatally. The auditory pathway exhibits tonotopic organization with cells responsive to different frequencies arranged in a linear fashion. Tonotopy is evident throughout much of the pathway including the cochlear nuclei, MGN, and primary auditory cortex. Although the mechanisms that underlie the functional development of the auditory pathway are not as well understood as those of the visual pathway, it is presumed to follow similar developmental principles. There is evidence, however, that the initial tonotopic mapping within the auditory system may be more precise than the retinotopic mapping of the visual system (Appler & Goodrich, 2011).

Association Pathways. Association pathways connect cortical areas within each cerebral hemisphere. Most of the major association pathways can be identified in the prenatal brain, although they emerge at different points in development. The external capsule can be traced as early as GW15, while the inferior longitudinal fasciculus, inferior fronto-occipital fasciculus, and the uncinate cannot be clearly traced until GW19. The superior longitudinal fasciculus, an important pathway connecting frontal and parietal brain areas, is late developing, and is not evident at the end of the prenatal period (Huang et al., 2009).

Postnatal Brain Development

The human brain exhibits dramatic postnatal biological development. *In vivo* brain imaging of infants and children provides much of the information about the nature and timing of alterations during this exuberant brain growth and maturation period. Nevertheless, the specific biological processes giving rise to the effects observed via imaging remain obscure. Developmental neurobiology also adds critical information about postnatal brain development. Importantly, estimates of the extent and time course of human developmental processes generally must extrapolate from data acquired in other species, often rodents, and from limited human postmortem material. The result is uncertainty about the scale and temporal extent of cell proliferation, migration, differentiation, and regression, and about the relationship of these processes to each other, during the human postnatal period.

Progressive Processes in Postnatal Brain Development

The production and migration of neurons are largely prenatal events. Nonetheless, evidence shows that neurogenesis

continues to a very limited degree postnatally in the subventricular zone, where new neurons continue to emerge and migrate to the olfactory bulb, and in the dentate gyrus of the hippocampus. These exceptional forms of neurogenesis produce only a small percentage of the neuronal population. By contrast, glial progenitors proliferate and migrate vigorously during the immediate postnatal years, and these processes continue for a protracted period. Indeed, progenitor cells (oligodendrocyte precursor cells, or OPCs), persist indefinitely in the adult brain in a wide anatomical distribution, and can differentiate in response to injury. Glial progenitors mostly proliferate in the forebrain subventricular zone and migrate radially and laterally into the overlying white matter and cortex, striatum, and hippocampus, where they differentiate into oligodendrocytes and astrocytes. Unlike neural progenitors, glial progenitors continue to proliferate as they migrate (Cayre, Canoll, & Goldman, 2009).

Initially, astrocytes in cerebral cortex arise from radial glial cells in the VZ and glial progenitors in the SVZ. However, evidence from rodent models suggests that, once established in cortex, these early differentiated astrocytes produce most cortical astrocytes through local symmetrical division. Astrocyte numbers increase rapidly during the immediate postnatal period in widely distributed brain areas (Ge et al., 2012).

Some OPCs begin to differentiate into oligodendrocytes by extending processes and upregulating myelin protein expression upon reaching their destinations. The new processes begin to form membrane wraps around nearby axons. The oligodendrocytes eventually form tightly wrapped multilayered sheaths from which most of the cytoplasm has been extruded. The best understood functional consequence of myelination is the effect on axonal conduction velocity; however, observations of functional interactions between oligodendrocytes and neurons suggest that they are complex and dynamic. Oligodendrocytes synthesize a number of trophic factors that contribute to the maintenance of axonal integrity and neuronal survival, and neuron-oligodendrocyte interactions influence neuronal size and axon diameter (McTigue & Tripathi, 2008).

An intriguing new line of evidence also suggests that a subset of the OPCs dispersed throughout the brain form excitatory and inhibitory connections with neurons, and thus may contribute actively and directly to neural signaling (Lin & Bergles, 2004). These cells, also sometimes referred to as nerve/glial antigen 2 or NG2 cells, account for most cell proliferation and differentiation in the postnatal and adult brain. They are dispersed roughly evenly

within white and gray matter regions and migrate over long distances postnatally (Mangin & Gallo, 2011). Many questions remain about these interesting brain cells. While they clearly contribute to the oligodendrocyte population that myelinates neuronal axons, there is growing evidence they may have other important functions as well in the nervous system (Mangin & Gallo, 2011).

Research has also focused on the so-called microglia, the bone marrow derived population of brain resident cells that colonize and persist in the central nervous system. Microglia, particularly in an immature amoeboid form, are present during fetal development. However, their numbers increase dramatically in early postnatal life and a protracted process of postnatal maturation occurs during which these cells disseminate throughout all regions of the brain and assume a highly ramified phenotype characterized by long, thin processes. The final distribution of cells suggests relatively nonoverlapping surveillance territories. Although maturation of this cell population is not well understood, there is evidence suggesting that microglia functions during development extend beyond their established role in immune activation to possible roles in regulation of neurogenesis, gliogenesis, synaptic remodeling, and myelination (for review, see Harry & Kraft, 2012).

In summary, proliferation and migration of glial precursors and maturation of astrocytes and oligodendrocytes, as well as ongoing maturation of microglia, are processes that extend long into the postnatal period. The full scope of their impact on neural dynamics remains unclear. Research continues to uncover additional molecular interactions between neurons, oligodendrocytes, astrocytes, and microglia. The existence of these interactions implies that the postnatal maturation of glial and microglial populations probably has widespread functional implications for developing neural systems.

Regressive Processes in Postnatal Brain Development

Brain development is characterized by early overproduction of neurons and glial cells, neural processes, and synapses. Although programmed loss of neurons has its peak during prenatal life, apoptosis in glial cell populations has a time course corresponding to the protracted postnatal time course of differentiation from glial precursors. Many excess oligodendrocytes undergo apoptosis within a few days after differentiating during the initial myelination period, and evidence suggests this process depends on signals from nearby axons, such that the number of surviving oligodendrocytes matches the local axonal surface area (for review, see McTigue & Tripathi, 2008).

Much of the regressive remodeling that occurs in the postnatal brain involves elimination or pruning of neuronal processes, i.e., axonal and dendritic processes, spines, and synapses. Studies of monkeys and humans reveal excess connections throughout distributed gray matter regions in the early postnatal period (Bourgeois, Goldman-Rakic, & Rakic, 1994; Bourgeois & Rakic, 1993; Huttenlocher & Dabholkar, 1997; Huttenlocher & de Courten, 1987; Zecevic et al., 1989). Several axonal pathways, especially in the corpus callosum, but also in thalamocortical pathways, corticospinal tract, and pathways linking the temporal lobe and the limbic system show exuberant connectivity (Innocenti & Price, 2005; Stanfield & O'Leary, 1985; Stanfield, O'Leary, & Fricks, 1982). The process of pruning excess connectivity is not fully understood. Influences such as competition for neurotrophic factors and the presence or absence of afferent input are implicated in this process. Studies using video microscopy reveal that neuronal processes continuously sample the surrounding space, forming and retracting synaptic connections dynamically, probably to varying degrees throughout the lifespan (Hua & Smith, 2004).

Imaging Studies of Brain Morphology

MRI studies reveal dramatic changes in the tissues of the developing brain during the postnatal brain growth spurt. These changes presumably reflect proliferation and maturation of oligodendrocytes, astrocytes, and microglia as well as the deposition of myelin. The changes provide information about the timing and anatomical distribution of these processes (Barkovich, 2000, 2005). Myelination changes first appear in sensorimotor pathways and commissural tracts and gradually spread throughout the white matter. The earliest MRI morphometry studies comparing children and adults revealed that gray matter volumes in the cerebral cortex and subcortical nuclei are considerably larger in school-aged children than in young adults (Jernigan & Tallal, 1990; Jernigan, Trauner, Hesselink, & Tallal, 1991; Pfefferbaum et al., 1994). This suggested more protracted tissue alterations related to brain maturation than was previously supposed. Although subsequent studies confirmed and extended these findings (for review, see Toga, Thompson, & Sowell, 2006), the underlying cellular changes remain a matter of speculation. MRI measurements indicate that cranial vault volume increases dramatically with age after birth but very little after the first decade. Evidence from MRI suggests that effects of waning progressive changes throughout childhood and adolescence, associated with continuing maturation of

glial populations and neurotrophic effects, are opposed by regressive changes, perhaps associated with “pruning” of neuronal processes. These observations are consistent with ample histological evidence for ongoing myelination across this period (Yakovlev & Lecours, 1967), and evidence for the reduction of synaptic density in cortex during childhood (Huttenlocher & Dabholkar, 1997). Nonetheless, it remains unclear to what extent these factors, or other tissue changes that occur concurrently, contribute to the changing morphology observed with MRI.

Employing mapping methods for visualizing the spatial pattern of age-related change across the late childhood range provides greater anatomical detail to MRI morphometry studies (Giedd, Snell, et al., 1996; Giedd, Vaituzis, 1996; Sowell et al., 1999; Sowell, Trauner, Gamst, & Jernigan, 2002). Such studies confirm the protracted course of postnatal white matter growth and the declining volume of tissue with the MR signal characteristics of “gray matter” in the cerebral cortex and some deep nuclei. These studies also seemed to indicate a modal pattern of childhood and adolescent change in the morphology of the cerebral cortex with growth, or thickening, of the cortex in the early years, followed by widespread cortical thinning (Gogtay et al., 2004; Sowell et al., 2004). One problem in interpreting these mapping studies is distinguishing the contribution of changes in cortical surface area from those in cortical thickness. The separation of these effects is a difficult computational problem, but is critical during the first decade of life when brain volume is increasing and the two effects could be strongly dissociated. The evidence from mapping studies suggests that apparent cortical thinning occurs first in primary sensory-motor cortex and then progresses into secondary, multimodal, and finally supramodal cortical areas throughout childhood and adolescence. Ostby et al. (2009) confirmed these observations in a large cross-sectional sample of participants aged 8 to 30 years with more advanced methods that provided concurrent estimates of cortical surface area and cortical thickness. Modest decreases in cortical surface area accompanied the more dramatic decreases in cortical thickness across this age range. Unfortunately, that study provided no information about the early postnatal period during which thickness and surface area are likely to exhibit distinct developmental trajectories.

The preschool years are still undercharacterized in brain imaging research; however, advances in MRI methods make it increasingly feasible to image younger children. Multimodal brain imaging was acquired in approximately 1,400 typically developing individuals between 3 and 20

years old in the Pediatric Imaging, Neurocognition, and Genetics (PING) study (Brown et al., 2012). This multisite study applied prospective head motion correction that significantly reduced lost data and artifacts from motion in the youngest children (Brown et al., 2010; Kuperman et al., 2011; White, Roddey, et al., 2010). Data from the PING study extend and clarify results of previous imaging studies of postnatal development beyond 3 years of age. Age-related change in cortical surface area and thickness are best presented in the maps of annualized rate of change shown in Figure 2.6a and b. Annualized rate of change is defined by a measure of the age-varying developmental slope across a 1-year age band, and is calculated at every point across the brain surface, displayed here as a map

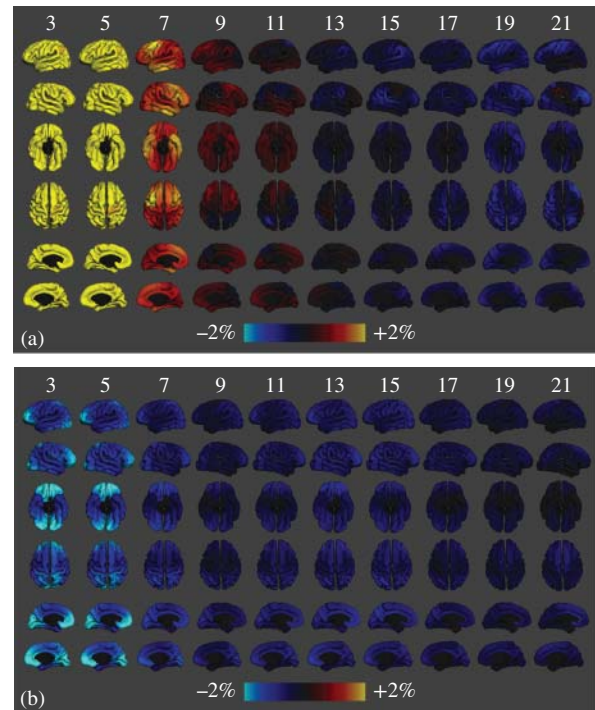


Figure 2.6 Annualized rates of developmental change in surface area (panel a) and thickness (panel b) across the human cerebral cortex. For each age conveyed, estimated instantaneous rate of change for a 1-year interval is shown at every cortical location, calculated as a percentage of the total measure at the lowest age within that interval. Both socioeconomic status and genetically derived ethnic ancestry are controlled for. Developmental changes in the average cortical surface geometry are also conveyed (note subtle lengthening with age). Yellow = 2% annualized increase; red = 1% increase; light blue = 2% decrease; dark blue = 1% decrease. Columns show results from ages 3 to 21 every 2 years (left to right). Rows show (from top to bottom) left lateral, right lateral, inferior, superior, left medial, and right medial views. Results were computed using 1109 subjects between the ages of 3.0 and 20.7 years. See footnote 1.

of changing characteristics of cortical surface area and thickness. As Figure 2.6a shows, there is significant expansion of cortical surface area during preschool ages and early school-age years. By 4 years, the greatest changes in area are occurring within higher order cortical regions such as prefrontal cortex and temporal association areas, still increasing but to a lesser extent are areas within primary sensory (visual, auditory) and sensorimotor cortex bilaterally. By the 10th year, some cortical regions begin to show decreases in area, especially within occipital and superior parietal lobes; however, continued cortical area expansion still occurs in some regions. From 10 to 16 years, the balance between contracting and late expanding areas shifts further until cortical area contraction is present throughout almost the entire cortex. These data show clearly that the peak of total cortical surface area at around 10 years represents the net effect of waning expansion in some regions and early contraction in others.

In stark contrast to cortical area, apparent cortical thickness shows no developmental increase at any point across this age range. In fact, thickness measures decrease throughout the cortex into young adulthood (Figure 2.6b). From 3 to 6 years, cortical thickness apparently decreases by about 2 percent each year within medial and polar occipital and prefrontal regions, as well as within parietal cortex. At these ages, the remainder of the cortical surface shows an annual decrease in thickness of about 1 percent that continues to age 20 years and likely beyond. Previous imaging studies have characterized developmental changes in the volume of cortical gray matter (Giedd, Snell, et al., 1996; Jernigan & Tallal, 1990; Jernigan et al., 1991). However, the PING study demonstrates why it is important to deconstruct volume into thickness and area, as they have different developmental trajectories overall and within different cortical regions (see also Sowell et al., 2004). Area and thickness may relate to cognitive and behavioral development differentially given their separate neurobiological origins, including evidence for distinct genetic factors influencing them (Panizzon et al., 2009). In summary, there is an early period of striking, widespread, but regionally varying surface area expansion that gives way gradually to contraction around puberty, while apparent cortical thickness decreases continuously across the childhood years.

The relationship of these effects to myelination is a germane issue. At the basic level, cortical “thinning” could simply reflect increased myelination in the white matter tracts coursing within and near the deepest layer of cortex. In other words, the “gray” signal of the unmyelinated

fibers could simply be becoming more “white” as myelin is deposited. This is clearly part of the cortical thinning measured with morphometry, especially in preschool aged children. However, there is evidence that true regressive changes also occur in some structures—probably due to loss or simplification of neuronal processes (dendrites and/or axons). This is inferred from the fact that the progressive changes that are expected to result from continuing myelination do not seem to increase cranial volume in late childhood (as though they were opposed by regressive factors). Indeed, cortical surface area decreases slightly. Additionally, there are modest but significant CSF volume increases adjacent to the cortical surface and in the ventricular system over this age-range, as might be expected, *ex vacuo*, in the wake of the loss of neural elements in the adjacent tissues (Jernigan et al., 1991; Sowell et al., 2002).

The functional correlates of these changes in the neural architecture are unclear. It is possible that the functional changes resulting from myelination of fiber tracts stimulate cortical thinning, or conversely, that increasing activity due to intrinsic cortical maturation stimulates myelination of the axons in the maturing network. Neuron-glia signaling mechanisms mediate effects of action potentials on oligodendrocyte differentiation and myelination (for review, see Fields & Burnstock, 2006). Unfortunately, the interactions among these factors in developing brain tissues of children remain obscure. In any event, it is clear that ongoing maturation of fiber tracts plays a key role in the functional maturation of the brain.

Diffusion Imaging of Brain Development

Diffusion weighted imaging (DWI) has made it possible to examine the maturation of fiber tracts directly (Basser, Mattiello, & LeBihan, 1994; Mori & van Zijl, 1995). Diffusivity declines dramatically in the brain during postnatal development, in a widespread distribution that includes both gray and white matter structures (Cascio, Gerig, & Piven, 2007; Hermoye et al., 2006). Diffusivity in white matter of human newborns is high, and exhibits low FA (Hermoye et al., 2006). As the fiber tracts mature, and myelination proceeds, diffusivity declines, and FA increases. The denser packing of axons, their tightly wrapped myelin sheaths, and increasing axon diameters are factors likely to alter these parameters by reducing the extracellular space (Suzuki, Matsuzawa, Kwee, & Nakada, 2003); however, how these and possibly other factors, such as fiber morphology, contribute is still poorly understood.

Changes in diffusion parameters continue throughout childhood and adolescence in a regionally varying pattern

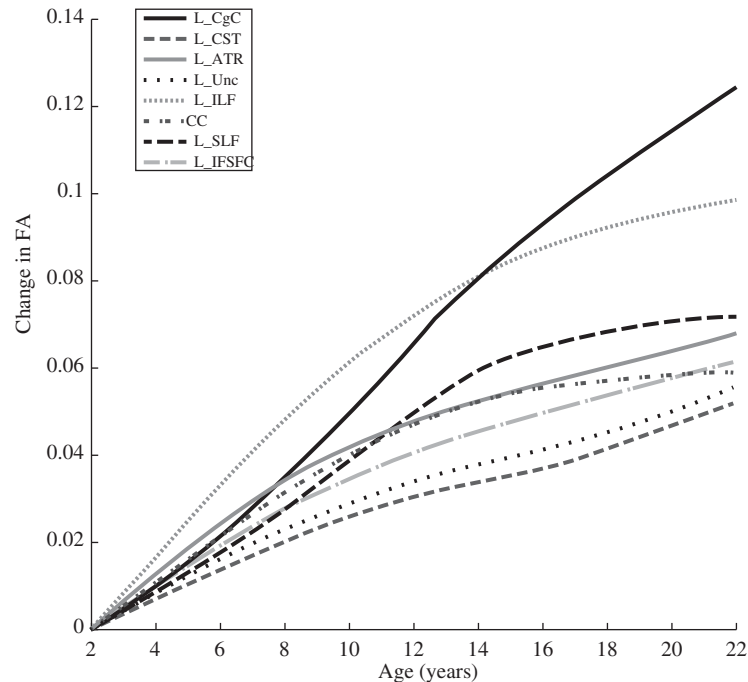


Figure 2.7 Relative age changes in fractional anisotropy (FA) by white matter tract. Spline-fit nonlinear curves are shown for the changes in FA with age for eight white matter fiber tracts, normalized to the earliest time point to reveal relative differences across time. Tracts are: corpus callosum (CC); left cingulum, main (L_CgC); cortico-spinal (L_CST); anterior thalamic radiations (ATR); uncinata (Unc); inferior longitudinal fasciculus (ILF); superior longitudinal fasciculus (SLF); and inferior frontal to superior frontal cortex (IFSFC). Trajectories were computed using 1,105 subjects between the ages of 3.0 and 20.7.

(Barnea-Goraly, Menon, et al., 2005; Schneider, Il'yasov, Hennig, & Martin, 2004; Snook, Paulson, Roy, Phillips, & Beaulieu, 2005). For example, FA reaches asymptote earlier in long projection and commissural than in association fibers, the latter continuing to exhibit age-related FA increases well into adulthood (for reviews, see Cascio et al., 2007; Huppi & Dubois, 2006; Mukherjee & McKinstry, 2006). Lebel et al. (2008) compared diffusion parameters in a large group of typically developing children to those in young adults. They observed robust increases in FA across the age-range from 5 to 12 years within multiple fiber tracts with varying time courses. This group also reported individual trajectories of tract FA obtained with repeated imaging of school-aged children (Lebel & Beaulieu, 2011). These data confirmed increases in FA over a period of 2 to 4 years within individual children, and highlighted wide individual differences in the pace of these changes across children.

The PING study (Brown et al., 2012) measured tract FA across a wider age range than previous studies and derived smooth age functions using generalized additive models (GAMs). GAMs allow for more data-driven, biologically plausible nonlinear estimates of developmental

trajectories. The developmental changes observed in FA within eight major fiber tracts are shown in Figure 2.7. Here, normalized FA values at the youngest age convey the differences among the tracts in the degree and time course of FA change across the studied age range.

Although less often a focus of developmental studies than changes in fiber tracts, age-related decreases in diffusivity and increases in FA are also measurable in most deep gray matter structures, for example, in diencephalon and striatum (Barnea-Goraly, Eliez, Menon, Bammer, & Reiss, 2005; Hermoye et al., 2006; Lebel & Beaulieu, 2011; Lebel et al., 2008). The biological mechanisms that underlie these gray matter changes in diffusivity are not well understood, but investigators have speculated that changing cell density or neurite structure might play a role, for example, glial cell proliferation, increased neuronal or glial cell sizes, or increased dendritic density.

Developmental Changes on Positron Emission Tomography (PET)

Local cerebral metabolic rates for glucose (ICMRGlc) are about 30% lower at birth compared to adult rates across the entire brain but rapidly increase to adult levels by

about the second year of life (Chugani & Phelps, 1991; Chugani et al., 1987). These increases continue through the preschool ages, exceed adult levels by about three years old, and plateau from about the age of 4 to 9. At their peak, glucose metabolic rates are highest within the cerebral cortex, where they are twice the value of adult rates. In brainstem and cerebellum, ICMRGlc does not exceed adult values and appears to be relatively metabolically mature at birth. Other subcortical structures, such as the thalamus and basal ganglia, show intermediate glucose metabolic rate increases over adult values. At around the ages of 8 to 10 years, ICMRGlc begins to decline and comes to resemble adult levels by about 16 to 18 years of age.

Based on the developmental trajectories of synaptic proliferation and elimination, and on clinical observations of behavioral plasticity in children with brain damage, Chugani et al. (1991) proposed that early increasing ICMRGlc rates are directly related to the period of rapid overproduction of synapses and nerve terminals thought to occur within a similar timeframe. The cause of the plateau during which glucose metabolic rates far exceed adult levels may be a transient increased cerebral energy demand from this overly elaborated connectivity. Likewise, subsequent developmental decline in metabolic rates may correspond to the later period of selective elimination (i.e., activity-dependent “withering”) of many of these connections, marking a time when plasticity seems to notably diminish. Chugani et al. (1991) have found support for these hypotheses in developmental studies with nonhuman animals.

Developmental Changes on Resting State Functional MR (rs-fcMRI)

Researchers using fMRI have developed techniques to look at brain network properties expressed as modulated interregional hemodynamic activity correlations measured at waking rest, in the absence of the presentation of any time-locked stimuli. Similar in concept to frequency domain analyses of EEG and MEG, resting state fMRI analyses look at correlated activity fluctuations on a much slower time scale, limited by the vascular BOLD response as a stand-in for neuronal activity. Resting state functional connectivity MRI (rs-fcMRI) has come to play a prominent role in neuroimaging research in both adults and children (Biswal et al., 2010; Snyder & Raichle, 2012). Resting functional connectivity studies of children have produced interesting developmental findings comparing school-age children to adolescents and young adults. From about 7 to 30 years of age, linked resting functional networks

shift from a predominantly “local” organization in young children to a more “distributed” architecture in young adults (Fair et al., 2009). With development, greater overall connectivity is observed (Fair et al., 2010), characterized by significant weakening of short-range connections and strengthening of long-range functional connections with development (Power, Fair, Schlaggar, & Petersen, 2010). However, several large-scale studies have concluded that resting interregional activity correlations undergo a prominent developmental shift from “diffuse to focal activation patterns,” seemingly contradicting findings that the functional organization develops from local to distributed (Supekar et al., 2010; Uddin, Supekar, Ryali, & Menon, 2011). This discrepancy may reflect an imprecision in the descriptive terminology, or it may relate more directly to the results themselves, but some reconciliation seems warranted (e.g., for discussion of the use of the term “diffuse,” see Brown, Petersen, & Schlaggar, 2006).

It is important to note that head motion may cause particularly insidious artifacts in resting state connectivity studies (Van Dijk, Sabuncu, & Buckner, 2011). Thus, systematic differences in head motion from early childhood into young adulthood may underlie some of the major developmental effects (Power, Barnes, Snyder, Schlaggar, & Petersen, 2013). A rigorous characterization of the nature and scope of this problem is important because of the application of resting state functional connectivity to a wide range of child and adult clinical groups. These include studies of autism (Lee et al., 2009), attention disorders (Mennes et al., 2011), schizophrenia and psychosis (Alonso-Solis et al., 2012; White, Schmidt, Kim, & Calhoun, 2010), early deprivation (Behen et al., 2009), childhood epilepsy (Mankinen et al., 2012), fetal alcohol spectrum disorders (Wozniak et al., 2011), preterm and low birth weight children (Gozzo et al., 2009), pediatric Tourette syndrome (Church et al., 2009), and childhood mood disorders (Cullen et al., 2009). If children and adults with clinical issues systematically produce more motion in the scanner than people without these problems, these groups may spuriously appear to have more “immature” patterns of functional connectivity. This is a recurring theme in these studies. Reconciling these issues is an important area of research in rs-fMRI.

The Role of Experience in Brain Development

The events of the prenatal period serve to establish the core compartments of the developing nervous system from the spinal cord and hindbrain to the cortical structures of

the telencephalon. These early events also provide initial patterning within each of the major subdivisions of the brain, but this early patterning, particularly in the neocortex, is both underspecified and malleable. The mature organization of the neocortex emerges slowly during the postnatal period, and it requires diverse forms of input. Some of this input arises from within the organism in the form of molecular signaling and cross-regional activity. However, the specific experience of the individual organism also plays an essential role in establishing the mature organization of the neocortex. The development of normal brain organization requires input via all of the major sensorimotor systems. When specific aspects of input are lacking, alternative patterns of brain organization can and do emerge. These alternative patterns of organization reflect the effects of altered neural competition and capture a fundamental property of mammalian brain development, the capacity for plastic adaptation.

The Role of Input on Brain Development

Greenough, Black, and Wallace (1987) introduced the term “experience expectant” development to capture the idea that the early experience of the organism plays an essential role in normal brain development, particularly in the early postnatal period. Although cortical patterning begins in the embryonic period, it remains malleable for an extended period. Typical, expected, postnatal experience is necessary for the emergence of normal patterns of neocortical organization. When that input is lacking, brain areas develop differently, and the specific pattern of development reflects the kinds of input that the organism actually received. At later ages, the developing—and even the mature—nervous system continues to require input to acquire new knowledge and to develop functional neural systems. Greenough has termed this later phase of development “experience dependent” learning. These two important constructs suggest that experience plays an essential role in establishing and refining neural organization in ways that allow the organism to adapt to the contingencies of the world in which it lives throughout development. Studies that systematically manipulate the specific experience of the young organism provide insight into the dynamic and adaptive nature of brain development.

Two simple ways to alter input are enrichment and deprivation. Both have dramatic effects on the structural and functional organization of the developing brain. Greenough has shown that simply rearing animals in either impoverished (standard laboratory cage) or enriched environments (large enclosures with interesting and changing

landmarks and multiple littermates) affects the development of a wide range of brain structures and functions (Black, Sirevaag, & Greenough, 1987; Greenough & Chang, 1988; Markham & Greenough, 2004). Animals reared in complex environments show enhancement in density of cortical synapses, increases in the number of brain support cells, and even augmentation of the complexity of the brain vascular system. Further, many of the effects of rearing in the complex environment persist even when the animal is returned to more impoverished conditions.

Sensory deprivation has more selective effects that target particular cortical sensory systems. The seminal studies of Hubel and Weisel (Hubel, 1982) showed that monocular visual deprivation in the early postnatal period could substantially alter basic patterns of organization within primary visual cortex (PVC). Within the typical primary visual pathway, inputs from the two eyes remain segregated from the retina to the thalamus to PVC. In PVC, the inputs from the two eyes form a distinctive banded pattern, called ocular dominance columns (ODC) that give the input layer of PVC a striped appearance. Suturing one eyelid closed produces striking effects on ODC organization. The bands representing the active eye widen and expand into the territory of the deprived eye; the bands representing the deprived eye shrink to thin stripes. The monocular reduction in activity introduced by the suturing procedure alters the competitive balance of input from the two eyes. The inputs from the active eye invade and subsume territory that would normally have received input from the deprived eye.

Neural Pathology and Input

The enrichment and deprivation studies provide powerful evidence of the role of experience on brain development. However, experimental studies can be more invasive, introducing procedures that directly affect or eliminate specific brain areas. These studies provide evidence that plasticity in developing neural systems can extend to the capacity to develop fundamentally different patterns of organization and function in the face of injury. For example, Sur and colleagues (Pallas, Roe, & Sur, 1990; Sur, Garraghty, & Roe, 1988) surgically eliminated the major input pathway to the primary auditory cortex (PAC) in 1-day-old ferrets to determine what would happen to this important sensory area in the absence of input. In the normal course of early development, the visual pathway from the retina extends what are typically transient connections to PAC, in addition to the normal connections to PVC. The retina-PAC connections are typically pruned

as part of the normal competitive processes. However, in the absence of competition, the inputs from the retina stabilize and form a functional visual pathway to PAC. PAC takes on patterns of internal organization that, while cruder, are characteristic of PVC (Sur & Leamey, 2001) and the “rewired” PAC functions as a visual area in behavioral testing (von Melchner, Pallas, & Sur, 2000). Thus, the altered early experience of the organism results in fundamental functional and structural reorganization of a primary sensory area, providing robust evidence for the role of neural plasticity in early brain development.

BRAIN AND COGNITIVE DEVELOPMENT IN THE POSTNATAL PERIOD

Over the past several decades, our understanding of how both cognitive and neural systems develop has made great progress. However, the advances in the two fields have been largely independent of one another. As a result, the role of change in biological systems is poorly specified in cognitive models, and the impact of emerging cognitive systems is underestimated in neurobiological models. Yet, these are interdependent systems. What develops over time is an integrated neurocognitive system that cannot be fully described in the absence of either behavioral or neurological data. This balkanization of scientific disciplines finds its origins in the complexity of the data within each area, and in the technical challenges of designing robust measures that can bridge and ultimately unify these complex data sets. The advances in neuroimaging technologies offer a means of approaching these very difficult and complex issues. The remainder of this section focuses on three cognitive domains for which a substantial body of neuroimaging data is available, and is beginning to be incorporated into more integrated models of neurocognitive development. These domains include studies of visual processing of faces, cognitive control, and language.

Development of the Brain Systems for Visual Processing of Faces

Faces are arguably the most important visual stimuli in our social environment. It is not surprising, therefore, that typically developed adults are expert face processors. Adult face expertise is characterized by the near universal ability to rapidly and accurately discriminate individuals from among thousands of highly similar faces

encountered routinely and to extract extensive information about individuals from brief exposures to face stimuli.

Adult Face Processing Expertise

Advances in functional neuroimaging are largely responsible for the significant increase in our understanding of the mature brain architecture for human face processing in typical and atypical populations (Haxby, Hoffman, & Gobbini, 2002; Kanwisher & Yovel, 2006). Based chiefly on neuroimaging studies, two overarching systems have been proposed to capture the complexity of visual face processing. The “core” face system processes the invariant aspects of faces, such as facial features and identity (Haxby, Hoffman, & Gobbini, 2000). This system includes the functionally defined fusiform face area (FFA) in the fusiform gyrus (Kanwisher & Yovel, 2006), the occipital face area (OFA) in the lateral inferior occipital gyrus (Gauthier et al., 2000), and the posterior superior temporal sulcus (pSTS) (Haxby, Hoffman, & Gobbini, 2000). Recent evidence suggests that the fusiform gyrus may include multiple face processing regions occupying the posterior and anterior aspects of the fusiform gyrus (Pinsk et al., 2009). We use the acronym FFA to refer to all regions within the fusiform gyrus that show a functionally defined preference to faces. One critical feature of the mature core system, particularly the FFA and OFA, is that these regions are activated when viewing faces largely regardless of specific task demands. That is, activation is observed whether the task requires active face processing, such as remembering or matching specific faces (Gauthier, Curby, Skudlarski, & Epstein, 2005; Yovel & Kanwisher, 2005), passive viewing (Grill-Spector, Knouf, & Kanwisher, 2004; Haist, Lee, & Stiles, 2010), or implicit presentation when faces and other visual stimuli are presented in a fashion that precludes conscious perception (Morris, Pelphrey, & McCarthy, 2007). Activation of the pSTS is most closely associated with dynamic feature processing, such as monitoring eye gaze and mouth movements, and is thus observed in tasks in which these actions are factors (Ishai, Schmidt, & Boesiger, 2005; Rolls, 2007).

Recruitment of the “extended” face system regions tends to be task specific (Haxby, Hoffman, and Gobbini, 2000). For example, the amygdala, insula, and other limbic regions are recruited when tasks require the analysis of the emotional aspects of a face (Ishai, Pessoa, Bickle, & Ungerleider, 2004). The retrieval of semantic knowledge for faces may engage the inferior frontal gyrus, whereas episodic memory retrieval may recruit the precuneus, posterior cingulate cortex, and medial temporal lobe

(Gobbini & Haxby, 2007). Analysis of intentions can activate the region of the temporal-parietal junction, whereas processing attitudes and mental states recruits the anterior cingulate cortex (Redcay et al., 2010). The anterior temporal pole may be active in tasks requiring individuation of faces and biographical information retrieval (Nestor, Plaut, & Behrmann, 2011). In summary, the differential activation of extended face network brain regions stems from the fact that many face tasks require processing of a wide array of information beyond the general appearance of the face.

Development of Face Processing Expertise

The ability to process faces as distinctive visual stimuli begins in the first year of life. Newborns show a preference for and can discriminate faces from other classes of objects and abstract stimuli (Johnson & Morton, 1991). By 3 months, infants categorize faces by gender, race, and attractiveness (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Slater, Quinn, Hayes, & Brown, 2000), and by 5 to 7 months they begin to rely on both the specific features of faces (featural information) and the arrangement of those features on the face (configural information) for face identification (Cohen & Cashon, 2001). Despite this evidence of early face processing abilities, the preponderance of behavioral evidence clearly suggests that expertise in face processing develops slowly and over many years (see Lee, Quinn, Pascalis, & Slater, 2013). For example, children have difficulty processing featural and configural information relevant to face identification through the school-age period. The pattern of children's featural processing reaches adult levels at about 10 to 11 years, before which they first rely on outer face features for face identification and then gradually shift to rely on inner face features (Want, Pascalis, Coleman, & Blades, 2003). Extraneous features such as clothing and hairstyle easily distract children under 10 to 11 years when identifying individual faces (Mondloch, Le Grand, & Maurer, 2002).

The emerging consensus from neuroimaging studies indicates that mature face processing expertise is the result of a protracted developmental process. Cognitive electrophysiological studies using event-related potentials (ERP) have shown that the N170 waveform, a putative marker for face processing manifest as a negative voltage deflection recorded at posterior scalp electrodes occurring approximately 170 ms after the presentation of a face, emerges early in childhood (de Haan, Johnson, & Halit, 2003b). However, the N170 in children is significantly delayed and is smaller in amplitude than the adult N170.

The N170 gradually shifts in time and increases in amplitude throughout development, reaching the adult form in the mid-teens (de Haan, Pascalis, & Johnson, 2002).

The overwhelming majority of developmental fMRI studies have focused exclusively or primarily on the core face network, specifically the FFA. The preponderance of evidence indicates that while the FFA can be observed in 5- to 7-year-old children (Cantlon, Pinel, Dehaene, & Pelphrey, 2011; Pelphrey, Lopez, & Morris, 2009), the FFA shows an extended developmental trajectory extending into mid-adolescence as measured by volume of the fusiform gyrus occupied (Golarai et al., 2007; Haist et al., 2013), the intensity of BOLD activation (Cohen Kadosh, Henson, Cohen Kadosh, Johnson, & Dick, 2010), and the spatial location of the FFA within the fusiform gyrus (Haist et al., 2013). A similarly prolonged developmental trajectory has been described for the other core face network areas of the OFA (Scherf, Behrmann, Humphreys, & Luna, 2007) and superior temporal gyrus/sulcus (Golarai, Liberman, Yoon, & Grill-Spector, 2010).

The prolonged developmental path to reach mature face processing expertise is supported additionally by the analysis of functional connectivity, or the interaction between face preferential brain regions. Cohen Kadosh et al. (2011) evaluated effective connectivity (i.e., directional functional connectivity) within the core face network. They scanned younger (7–8 years) and older (10–12 years) children and adults during face identity, emotion, and gaze detection tasks and found that all groups produced the same basic network pattern of the inferior occipital gyrus (i.e., occipital face area) that influenced activation in the fusiform gyrus (i.e., fusiform face area) and the superior temporal sulcus (STS). This suggested that an integrated core face network is observed in children as young as 7 years. However, the magnitude of effects among the child groups differed from adults. The old and young child groups exhibited weaker connectivity between inferior occipital gyrus (IOG) and fusiform gyrus (FG), and no significant connectivity between IOG and STS. Furthermore, the effects of task demand differentiated the adults and children. Different tasks selectively modulated network patterns in adults; specifically, the identity task increased IOG influence on FG, whereas the expression task increased IOG influence on STS. Children did not show such selective task effects. Thus, although the rudimentary structure of face-processing networks is observable in young school-age children, the interaction of the regions and their response to task effects is not mature.

The status of the developmental trajectories in the extended face network is currently very limited. Recently, Haist et al. (2013) reported findings from a developmental study of whole brain activity that used regression analysis across a continuous sample of age spanning 7-year-olds to adults. They found wide ranging hyperactivation of multiple regions of the extended face network in children that included the anterior temporal pole, amygdala, insula, inferior frontal gyrus, and lateral parietal cortex (see Figure 2.8). Moreover, these regions showed a reliable negative linear trend across age, indicating that younger participants produced the greatest activation in these regions and adults did not activate the extended network. They interpreted their findings as suggesting that development of face processing expertise is characterized by increasing modulation of the extended network so that regions are engaged in a task-appropriate fashion with increased expertise.

In summary, behavioral and functional neuroimaging data are in very good agreement that face processing abilities begin early in development and have an extended developmental trajectory. Mature levels of face expertise are not found until mid-adolescence. These effects cut across both the core and extended face networks.

Development of Brain Systems for Cognitive Control

Perhaps no other domain of functioning exhibits more dramatic and protracted development throughout childhood than do the processes that allow children to regulate and control their perceptual processes, thoughts, and actions in the context of goal-directed behavior. This review will focus on developmental research examining the neural bases of three forms of such control: working memory, spatial attention, and inhibitory functions. In each case, we describe relevant models of the neural circuitry of these functions drawn from animal and adult human studies, followed by the neurobehavioral observations obtained in studies of children.

Working Memory

Working memory has been conceptualized as a mental system used to transiently hold information in mind in order to attend to it, manipulate it, or act on it in relation to psychological and behavioral goals. Working memory is distinguished from so-called short-term memory by its active, goal-oriented, top-down nature, as opposed to a more passive, bottom-up trace maintenance. In a widely

cited and elaborated theoretical model of working memory, Baddeley (1974) proposed a hierarchical, multicomponent system made up of a central executive that controls several slave systems, which include a phonological loop, a visuospatial scratchpad, and an episodic memory buffer (for review, see Baddeley, 2012). Across all models of working memory, there is agreement that it is a limited capacity system closely related to executive control, critical to a wide range of complex cognitive functions, and that ties together perception, attention, and memory (Cowan et al., 2005; Just & Carpenter, 1992; Postle, 2006; Roberts & Pennington, 1996).

Working memory relies on a distributed network of brain regions heavily involving lateral prefrontal and posterior parietal areas. Although task paradigms used in neuroimaging studies vary considerably, all require that the subject hold information in mind for a brief period, either to make a decision or response, to manipulate it, or to perform active transformations on it. For example, a simple spatial working memory task might require remembering a briefly cued location during a delay in order to retrieve a reward from that location after the delay. Often experimenters vary the duration of time the information is held “online,” the type or number of bits of information, or the type or difficulty of manipulations that must be performed. Jacobsen (1936) first showed that lesions to the lateral prefrontal cortex impair working memory performance in monkeys. Fuster (1973) found that firing in individual prefrontal neurons during the delay period of a working memory task predicted the successful memory-based retrieval of food. Research with nonhuman primates has shown that similar delay-active neurons also exist in the posterior parietal cortex and in several subcortical structures including the thalamus and parts of the basal ganglia (i.e., globus pallidus, head of the caudate; Goldman-Rakic, 1995). This work also revealed the central role in working memory of recurrent excitatory glutamate pathways involving pyramidal cells within this network of brain regions.

Human adult functional neuroimaging studies of working memory show consistent involvement of lateral prefrontal and posterior parietal cortical regions, premotor and anterior cingulate cortex, the cerebellum, and the basal ganglia. Several PET and fMRI studies suggest a division of labor between ventrolateral and dorsolateral prefrontal cortex, with dorsolateral regions becoming increasingly involved when monitoring or manipulation of information is required, usually bilaterally, and ventrolateral regions supporting information maintenance (D’Esposito, Postle,

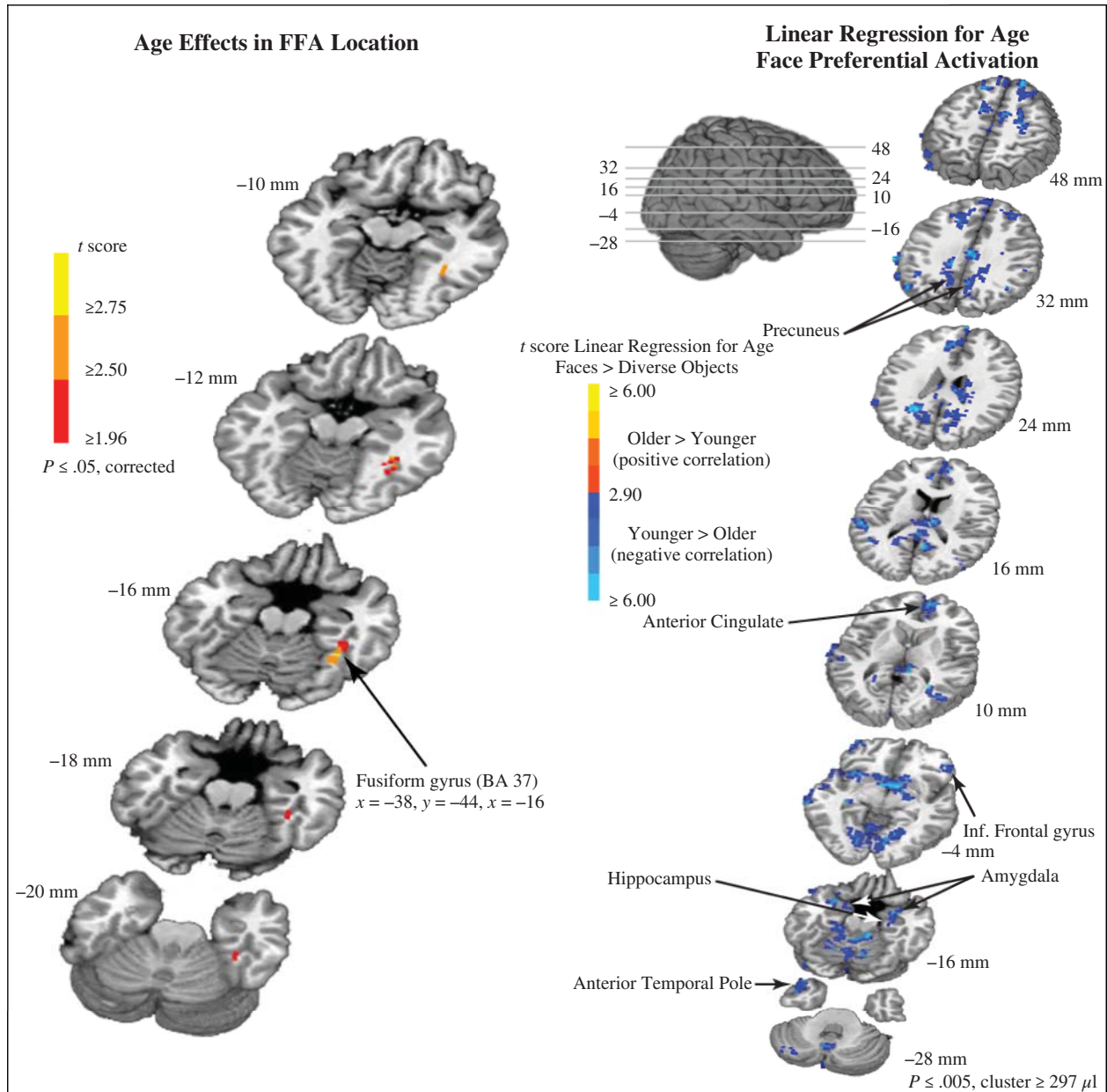


Figure 2.8 Example of fMRI findings for the development of face-processing expertise. These findings are drawn from a study of face processing that used a simple face and object viewing paradigm in a continuous age-sample of typical development from 6 years to adults ($N = 71$). The left panel shows the results from the first reported statistical analysis (logistic regression) of the developmental change in location of the fusiform face area (FFA). The region in the right middle fusiform gyrus (BA 37) produced a positive relationship with age (warm colors) indicating that this most commonly activated face preferential area across adult studies of face processing has a protracted developmental trajectory. That is, this region increasingly becomes specialized for face processing through development that extends into middle adolescence. The right panel shows the analysis of whole brain (voxelwise) activation using linear regression analysis for age. Cool blue colors indicate regions that showed a negative relationship with age, meaning that younger participants (i.e., children) activated these regions more than older participants (i.e., adults). Many of the regions indicated are part of the extended face processing network that adults typically use in a task-specific fashion. The passive nature of this task suggests that the “hyperactivation” of extended face network regions in younger participants results from immaturity in modulating brain activity for task specific purposes. See footnote 1.

Source: From “The Functional Architecture for Face-Processing Expertise: FMRI Evidence of the Developmental Trajectory of the Core and the Extended Face Systems,” by F. Haist, M. Adamo, J. Han, K. Lee, and J. Stiles, 2013, *Neuropsychologia*, 51, 2893–2908. doi:10.1016/j.brainres.2013.01.001. Reprinted with permission.

& Rypma, 2000; Jonides et al., 1998; Passingham & Sakai, 2004; Wager & Smith, 2003).

A common task used in working memory studies is the so-called “n-back” task. In the n-back task, participants are presented a sequence of individual symbols (e.g., numbers, letters) or spatial locations, and the subject must recall the identity or location of the item that was presented several items previously (e.g., 1-back, 3-back). This allows a parametric manipulation of processing load, providing sensitive within-subjects comparisons and task adaptation for different levels of functioning. In a meta-analysis of fMRI studies using the n-back task, Owen, McMillan, Laird, and Bullmore (2005) found consistency across 24 studies in the involvement of dorsolateral and ventrolateral prefrontal, posterior parietal, anterior cingulate, premotor, and cerebellar regions. Comparing n-back tasks requiring subject attention to the location of objects versus their identity, they found that premotor activation was reported significantly more often during spatial working memory tasks (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Haxby, Petit, Ungerleider, & Courtney, 2000; Postle, Stern, Rosen, & Corkin, 2000). For spatial working memory tasks, the activation foci in prefrontal regions have been observed in both right and left DLPFC, and whether spatial working memory is lateralized remains an issue of debate (Leung, Oh, Ferri, & Yi, 2007; Lycke, Specht, Ersland, & Hugdahl, 2008; Owen et al., 2005; Srimal & Curtis, 2008).

Working Memory in Infancy. In infancy, scientists have used simple hiding tasks to evaluate the development of working memory (Diamond, 1990; Jacobsen, 1935). EEG studies comparing baseline EEG levels to working memory task-related levels report generalized increases in EEG power and coherence during the first year of life as well as age-related changes in both indices between 5 and 10 months of age (Bell, 2012; Bell & Wolfe, 2007; Cuevas & Bell, 2011). Longitudinal investigation of the infants in Cuevas and Bell’s study showed a shift in the location of EEG changes between 8 months and 4.5 years. Specifically, while 8-month-old infants showed task-related increases in both power and coherence for all electrode sites (16 right and 16 left sites), by 4.5 years these same children showed task-related changes in EEG power in the medial frontal region only, and task-related changes in coherence for medial frontal-posterior temporal, and medial frontal-medial occipital electrode pairs only. Thus, EEG measures suggest generalized task related increases in brain activity during the first year of life that localizes

to fronto-parietal and fronto-occipital brain regions by the preschool period.

Later Working Memory Development. In typical development, working memory performance improves throughout childhood, showing changes in speed of processing, maintenance duration, capacity, and robustness to interference. From the ages of about 6 to 10, children show linear increases in performance on visual and auditory n-back tasks (Vuontela et al., 2003). In this study, working memory performance for visual stimuli was higher than for auditory tasks across age, and girls consistently outperformed boys. Comparing several verbal and spatial working memory and other putative “frontal lobe” tasks, Conklin, Luciana, Hooper, and Yarger likewise found consistent, monotonic performance increases across adolescence for tasks believed heavily dependent on prefrontal cortical areas (Conklin et al., 2007).

Developmental fMRI studies have found qualitatively similar patterns of brain activity in school-age children and college-age adults during performance of the same working memory tasks, with some regional location and activity amplitude differences (Casey et al., 1995; Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006; Klingberg, Forssberg, & Westerberg, 2002; Kwon, Reiss, & Menon, 2002). For example, during a spatial n-back task performed by children aged 8 to 10 years and young adults, both groups activated similar right dorsolateral prefrontal and parietal regions, but children additionally engaged left precuneus and bilateral inferior parietal lobule (Thomas et al., 1999). In several developmental fMRI studies, Klingberg and colleagues showed that the superior frontal sulcus and intraparietal cortex in particular are involved in visuospatial working memory in both school-age children and young adults (for review, see Klingberg, 2006). These studies have also demonstrated that the peak amplitudes of brain activity in the fronto-parietal network increase across these ages independent of performance, and that greater activity in these locations is related to higher working memory capacity (Klingberg et al., 2002). Structural brain development also relates to improving working memory skills from childhood into adolescence. For example, diffusivity parameters within white matter tracts (linked to biological maturation), particularly within fronto-parietal connections, show significant correlations with task performance (Bava & Tapert, 2010; Nagy, Westerberg, & Klingberg, 2004; Olesen, Nagy, Westerberg, & Klingberg, 2003; Vestergaard et al., 2011). In 7- to 13-year-old children, better spatial working memory performance was

specifically associated with increased fractional anisotropy in the superior longitudinal fasciculus, a tract connecting temporoparietal to prefrontal cortices (Vestergaard et al., 2011). Diffusion parameters in the left hemisphere tract exhibited stronger associations with spatial working memory than did the right hemisphere tract, and the associations were independent of age effects, or effects attributable to global white matter differences. Thus, the associations may have reflected individual differences in the pace of maturation in spatial working memory networks.

Spatial Attention

There exists a large scientific literature on the neural systems involved in spatial attention in adults, and research specifically on the endogenous (top-down) control of spatial attention has provided great insight into certain aspects of cognitive control. Most research has focused on aspects of visual attention rather than attention in other sensory modalities (e.g., auditory, tactile). Seminal behavioral studies conducted by Posner et al. (for reviews, see 2012; 1982; 1998; Raz & Buhle, 2006), using a simple but powerful spatial cuing paradigm, showed that directing a person's attention to a specific location in space facilitates subsequent processing of information at that location, resulting in faster response times. Related studies with stroke patients demonstrated a strong association between the functioning of parietal cortex and spatial attention operations, particularly the ability to actively disengage attention from an attended location (Posner, Walker, Friedrich, & Rafal, 1984). ERP studies subsequently helped to explain the temporal dynamics and neurophysiological bases for Posner's findings, demonstrating that the brain's sensory response to information at a particular spatial location is enhanced when attention is shifted to that location (Hillyard & Anllo-Vento, 1998; Mangun & Hillyard, 1991).

Landmark PET and fMRI studies have identified the principal neural systems involved in spatial attention in adults, which include right and bilateral posterior parietal cortex (especially intraparietal sulcus), the temporal-parietal junction, bilateral frontal eye fields within premotor cortex, anterior cingulate, and subcortical circuits (Corbetta, Miezin, Shulman, & Petersen, 1993; Coull & Frith, 1998; Nobre, Sebestyen, Gitelman, & Mesulam, 1997). Rapid event-related fMRI studies have identified several networks that contribute to different aspects of spatial attentional control. These include an anterior network involving the anterior cingulate, related to conflict resolution in attention; a dorsal fronto-parietal system

involved in the allocation and maintenance of attention to a particular location; and a more ventrally lying, primarily right hemisphere, fronto-parietal network specific for disengaging attention (Corbetta, Kincade, & Shulman, 2002; Jack, Shulman, Snyder, McAvoy, & Corbetta, 2006; Thiel, Zilles, & Fink, 2004). The neural substrates for visual and auditory spatial attention may involve the same key networks, as several studies have found evidence that these systems are supramodal, maintaining representations of space that are independent of sensory modality and motor response (Downar, Crawley, Mikulis, & Davis, 2000; Driver & Spence, 1998; Farah, Wong, Monheit, & Morrow, 1989; Macaluso, Eimer, Frith, & Driver, 2003; Shomstein & Yantis, 2004).

A growing number of studies have investigated spatial attention and its functional neuroanatomy in infants and children. Infants 3 to 4 months old can shift visual-spatial attention (for review, see Johnson, 2001), and the speed and efficiency of attention functions increase significantly throughout childhood and adolescence (Enns & Brodeur, 1989; Ridderinkhof & van der Stelt, 2000; Schul, Townsend, & Stiles, 2003). The "zoom lens hypothesis" of attention posits that the field of attended space expands and contracts as a function of task demands, and that processing efficiency increases as the size of this field declines (Eriksen & St. James, 1986). Several researchers have suggested that the ability to control the contraction and expansion of the spatial attention field improves from the preschool into school-age years (Enns & Girgus, 1985; Pastò & Burack, 1997). As with working memory and other tasks requiring cognitive control, age-related differences and changes in cerebral functional organization have been shown for spatial attention processing (Johnson, 2001, 2003). Johnson suggests that the cortical mechanisms for spatial attentional control are different in infancy than they are in adulthood, relying relatively more on frontal cortex in their early form, and shifting to more posterior (i.e., parietal) control, and he posits that this might reflect a general learning mechanism by which frontal activity decreases as proficiency increases. An fMRI study compared school-age children and young adults during the reorienting of spatial attention and found very different patterns of activation despite similar levels of accuracy on the task. Although adults showed significant involvement of right inferior frontal gyrus, right temporal-parietal junction, and bilateral parietal lobes, children aged 8 to 12 years showed greatest activity in left superior frontal gyrus, right occipital-temporal gyrus, and left occipital gyrus (Konrad et al., 2005). Townsend, Haist, Adamo, and

Stiles also found developmental functional organization differences between school-age children and young adults for spatial attention processing (Townsend et al., 2003). During shifts of attention not accompanied by eye movements, adults showed bilateral intraparietal sulcus activity that was greater on the right, including activation in inferior temporal cortex. Children, in contrast, showed greatest activity in prefrontal and inferior temporal cortex, with weaker activation of parietal cortex, providing additional support for Johnson's front-to-back learning hypothesis.

One recent study examined associations between diffusion parameters and speed of responding in a simple spatial attention task in children between 7 and 13 years. Madsen et al. (2011) used a simple spatial choice reaction time task to measure response latencies to stimuli that appeared at one of five locations. Reaction time to the spatial stimuli decreased dramatically across this age range. Independent of age, however, faster five-choice reaction times were associated with lower diffusivity in the corticospinal tracts, putamen, and caudate. Although these effects were bilateral in the corticospinal tracts and putamen, right (relative to left) caudate diffusivity showed the stronger relationship to task performance. The results suggest a link between visuo-motor performance variability in children and diffusivity in motor and attention systems perhaps related to individual differences in the phase of fiber tract and neostriatal maturation in children of similar age.

Response Inhibition

Models of Motor Response Inhibition. An important aspect of behavior regulation involves the ability to suppress execution of a planned action in response to a relevant cue from the environment. In recent years, motor response inhibition has been studied extensively in adults and clinical populations, using Go/No-Go, antisaccade, and stop-signal tasks (Chambers, Garavan, & Bellgrove, 2009). All of these tasks involve the suppression of a primed, or prepotent, motor response. The stop-signal task has been especially useful for examining individual differences in inhibitory functions because it is designed to provide a continuous measure estimating the amount of time a participant needs to suppress the response (Logan, Cowan, & Davis, 1984). Studies using this task in adults have implicated several brain structures in a neural network subserving response inhibition. Execution of volitional motor responses is linked to activity in a premotor-striatal-pallidal-motor cortical network (Chambers et al., 2009). A primarily right-lateralized network, involving the inferior frontal gyrus, presupplementary

motor area, and subthalamic nucleus has been implicated in response inhibition (Aron et al., 2007; Aron & Poldrack, 2006); and fMRI studies have shown that inhibiting a prepotent response activates this network in adults (Aron et al., 2007; Aron & Poldrack, 2006; Aron, Robbins, & Poldrack, 2004; Chevrier, Noseworthy, & Schachar, 2007; Rubia, Smith, Brammer, & Taylor, 2003) as well as in children (Cohen et al., 2010).

Studies of Inhibitory Functions in Children. Studies in children reveal dramatic improvement in performance on motor inhibition tasks throughout childhood and adolescence (Liston et al., 2006; Luna, Garver, Urban, Lazar, & Sweeney, 2004; Madsen et al., 2010; Williams, Ponesse, Schachar, Logan, & Tannock, 1999). Individual differences in children's inhibitory function correlate with diffusion imaging indices of maturation within the neural circuitry outlined above. Liston et al. (2006) reported an association between faster reaction times in demanding conditions of a Go/No-Go task and higher FA in fronto-striatal white matter tracts of children and young adults. Madsen et al. (2010) employed the stop-signal task in a study of 7- to 12-year-old children and reported that better response inhibition was associated with higher FA and lower diffusivity in white matter of both inferior frontal and presupplementary motor regions of the right hemisphere (see Figure 2.9). Moreover, both of these effects remained significant after controlling for age and global white matter diffusivity parameters. Interestingly, the measures from the two regions contributed additively to the prediction of performance variability. Many questions complicate the interpretation of these kinds of associations. They could reflect links between individual differences in behavior and individual differences in the pace of fiber tract maturation. Alternatively, other effects on the neural architecture, unrelated to the pace of brain development, could map onto performance differences, such as experience-driven biological effects on the fiber tracts or genetically mediated differences in patterns of connectivity.

In contrast to the evidence from studies cited earlier, showing that motor response inhibition approaches adult proficiency during adolescence, there is considerable evidence for elevated risk-taking behavior during this age range. Epidemiological evidence confirms that high-risk behaviors such as unsafe driving, drug use, and sexual behavior are more prevalent during adolescence than at other times in the lifespan (Somerville & Casey, 2010; Steinberg, 2008). Such behavior would appear to suggest poor inhibitory function, since there is evidence that

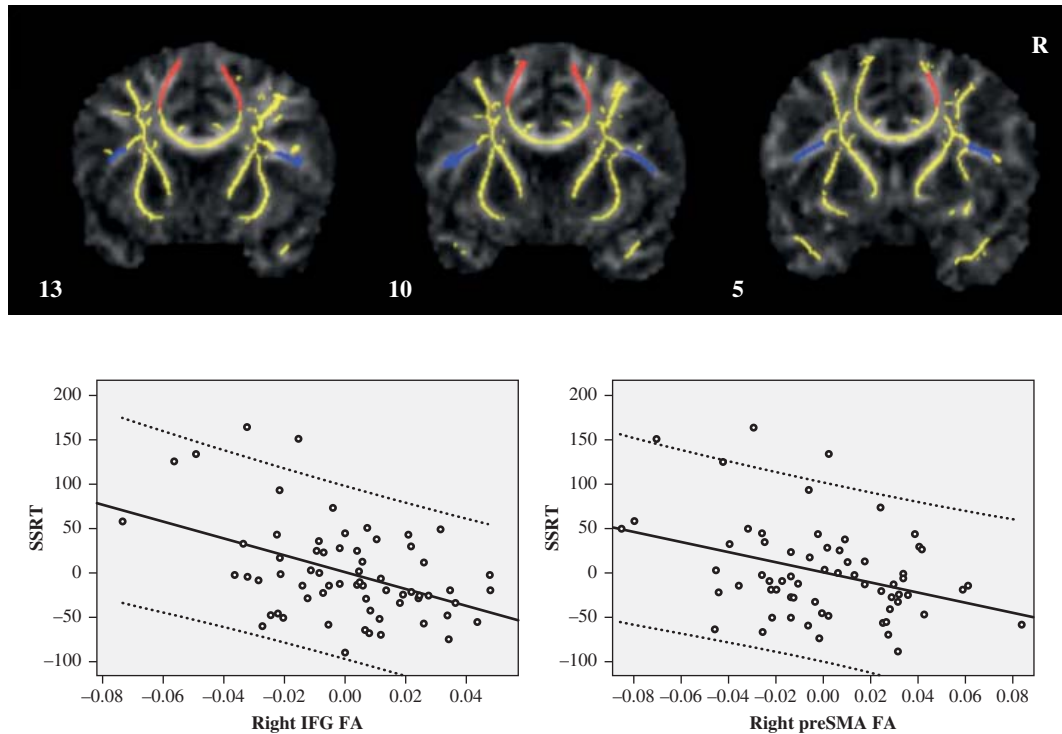


Figure 2.9 Fractional anisotropy in a region of interest (ROI) in the right inferior frontal gyrus (blue in right hemisphere) and in a right pre-SMA ROI (red) contributed additively in a regression model explaining individual differences in stop-signal performance in children (independent of age and other covariates). See footnote 1.

Source: From “Response Inhibition Is Associated with White Matter Microstructure in Children” by K. S. Madsen et al., 2010, *Neuropsychologia*, 48(4), pp. 854–862. Reprinted with permission.

adolescents are well aware of the risks and capable of strong reasoning about such risks (Steinberg, 2008). However, as confirmed by Shenoy and Yu (2011) in their computational work with the stop-signal task, inhibitory behavior is influenced by reward sensitivity as well as by cognitive and perceptual processes. Indeed, studies employing experimental risk-taking tasks, while confirming that adolescents are less risk-averse than both younger children and adults, suggest that this effect may be more strongly related to reward sensitivity than to risk evaluation. Cauffman et al. (2010), using the Iowa Gambling Task, showed that adolescents exhibited a stronger “approach” response to positive feedback on the task than either younger children or adults, whereas “avoidance” engendered by negative feedback increased more linearly with age. Thus, the form of disinhibition manifest in adolescent behavior may arise because of selectively heightened sensitivity to the positive rewards associated with risk.

Several studies have investigated the neural bases of such age-specific behaviors of adolescence. Somerville and Casey (2010) reviewed results of work conducted by Casey and associates and proposed a model accounting for adolescent risk-taking as emerging from altered processing

of appetitive and aversive cues. These alterations are further attributed to interactions between developing striato-limbic and prefrontal cortical brain systems. Specifically, using fMRI and a task requiring participants to process emotional faces, Hare et al. (2008) showed greater emotion-related amygdala activation in adolescents than in either younger children or adults. Similar findings of increased amygdala activation to negative cues in adolescents were reported by Ernst et al. (2005). Other studies have assessed the degree of ventral striatal response to appetitive cues in adolescents. Studies in adults have consistently shown activation in ventral striatum associated with anticipation of reward (Knutson, Momenan, Rawlings, Fong, & Hommer, 2001; O’Doherty, Deichmann, Critchley, & Dolan, 2002). Imaging studies in adolescents suggest heightened sensitivity to reward and more vigorous or prolonged reward-related activation of ventral striatum, relative to adults or children (Ernst et al., 2005; Galvan et al., 2006; May et al., 2004).

Functional imaging studies of emotion regulation suggest that successful regulation is associated with stronger prefrontal activation, and stronger functional connectivity between limbic and prefrontal regions (Pezawas et al., 2005; Phillips, Drevets, Rauch, & Lane, 2003). Somerville

and Casey (2010) note that, in contrast to the developmental effects observed in studies of reward sensitivity that suggest adolescents exhibit distinct differences from younger children in reward responses of ventral striatum, developmental change in both structure and function of prefrontal cortical regions appears to be more gradual and linear. Integrating these observations, the hypothesis that these authors advance is that the unique quality of inhibitory, or risk-taking, behavior in adolescents arises because of dynamic interactions between an accelerated course of development in brain systems subserving reward and punishment and a more gradual course of development in late-developing cortical functions involved in emotion and behavior regulation. The outwardly focused, and reward-seeking adolescent phenotype, which may have evolutionary advantages, gives way to a more cautious adult phenotype with a more measured approach to risk, presumably through the growing influence of learned associations better formed and retrieved with a more mature prefrontal cortex.

Development of the Brain Systems for Language

Language is a complex, multifaceted ability mastered over many years. Left-lateralized frontotemporal networks primarily mediate the major components of language for most adults. The majority of brain imaging studies of children have tried to determine whether these same core brain networks support language in children and whether there is systematic change in the patterns of activation with age.

The Neural Architecture of Language Processing in Adults

Individual studies of language typically focus on a single aspect of linguistic processing, ranging from decoding the acoustic/phonological signal, to semantic processing of words or phrases, to syntax and sentence or text level processing. A full account of the brain networks that support the different aspects of language processing is beyond the scope of this section (for comprehensive reviews, see Price, 2012; Vigneau et al., 2006). However, a meta-analysis by Vigneau et al. (2006) provides a means of summarizing the major findings. They created a brain map illustrating the distribution of activation for three categories of language tasks: phonological (blue), semantic (red), and syntactic/sentence processing (green) based on 729 data points defined from peak activations taken from 129 published imaging papers (see Figure 2.10a). It is clear that while the activation points for the different kinds of tasks are

overlapping, they tend to segregate into spatially distinct fields. Imaging studies also help define the neural pathways that connect the task-specific brain regions to form processing networks. Figure 2.10b provides a consensus view of the major language pathways. The arcuate fasciculus (AF) is among the important association pathways subserving language functioning, though its relationship to another major language pathway, segment III of the superior longitudinal fasciculus (SLFIII), remains unclear (Dick & Tremblay, 2012). Other language pathways include the uncinate fasciculus (UF), the extreme capsule fiber system (ECFS), the inferior longitudinal fasciculus (ILF), and the inferior frontal occipital fasciculus (IFOF). We discuss the functional significance of these pathways below.

Phonological processing of speech sounds (blue) is concentrated along the superior temporal sulcus (STS, Brodmann's area [BA] 22) near Heschl's gyrus (BA 41, primary auditory cortex; DaCosta, 2011) and the planum temporale, both areas previously shown to be involved in phonological decoding (Friederici, 2011; Price, 2012). Further, the posterior STS (BA 22 posterior) has been shown to connect via the AF to premotor cortex, supporting auditory-motor ("sound to articulation") integration (Friederici, 2011).

Activation during semantic processing (red) involves frontal, temporal, and parietal regions. The inferior frontal gyrus (IFG) has long been associated with semantic processing. Different components of the IFG play somewhat different roles. Specifically, the pars opercularis (BA 44, see Figure 2.10b) has been associated with lexical decision (Heim et al., 2009), the pars orbitalis (BA 47) with semantic retrieval (Demb et al., 1995), the ventral region of the pars triangularis (BA 45) is associated with semantic processing, and the dorsal region supports phonological working memory (Hautzel et al., 2002). The angular gyrus (AG, BA 39) of the parietal lobe, regions of the anterior fusiform (BA 37 anterior), and anterior temporal pole (BA 38) within the temporal lobe are all involved in semantic processing (Vigneau et al., 2011). The network is connected by the ILF that links the posterior STS and angular gyrus to the temporal pole; the temporal pole is connected to the IFG via the UF (Catani, Howard, Pajevic, & Jones, 2002), thus creating a fronto-temporal-parietal network for constructing meaning. In addition, Friederici (2011) has proposed a second frontotemporal semantic pathway extending from the STG (BA 22 anterior) to the pars triangularis (BA 45) via the ECFS pathway. This subnetwork functions to transfer sound to meaning.

The neural systems for syntactic or sentence processing (green) show great overlap with other processing systems,

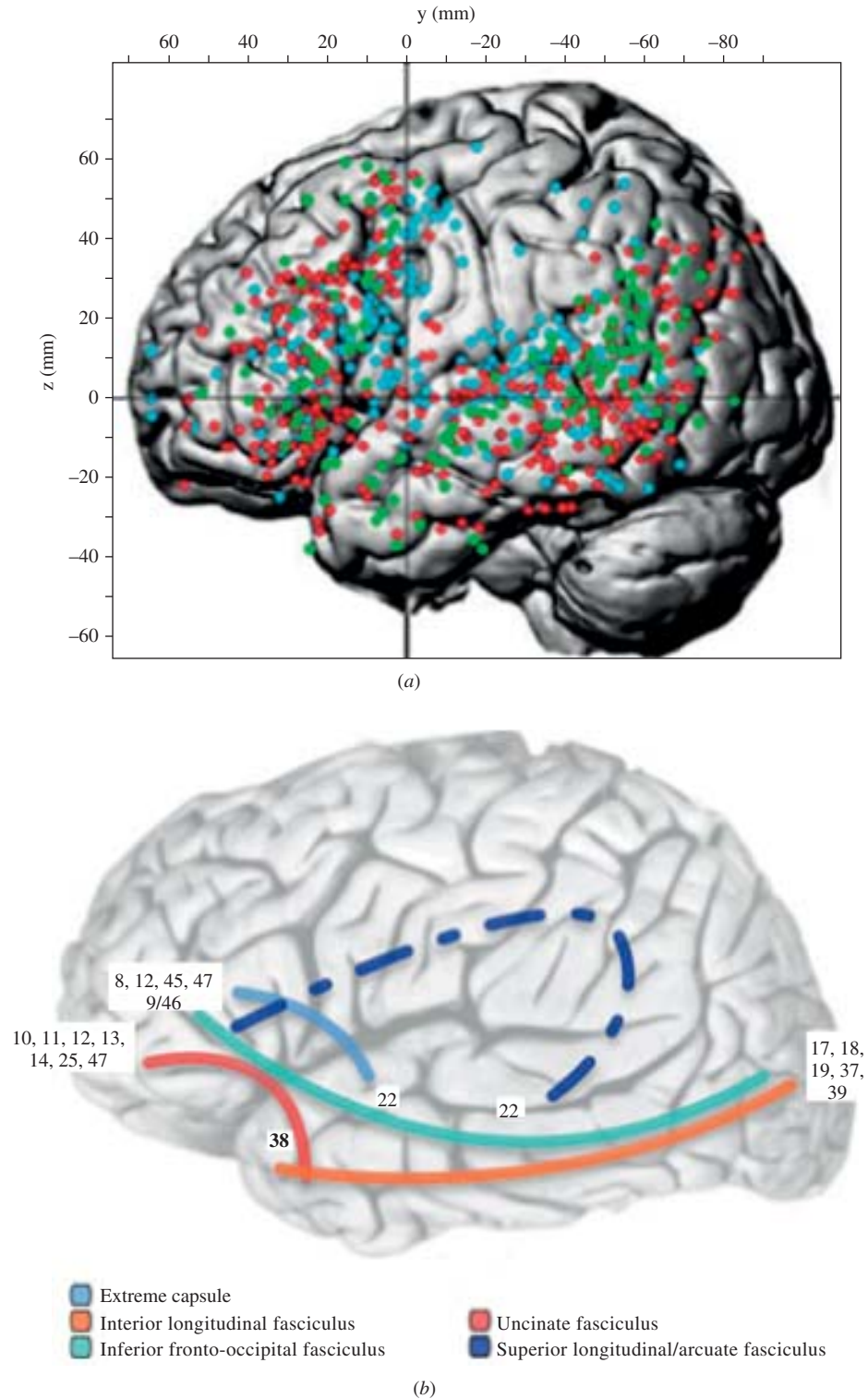


Figure 2.10 Overview of the neural networks for language in adults. (a) Summary of task specific patterns of activation during language processing. Each activation peak is color-coded according to its contrast category: phonology (blue), semantic (red), and syntax (green). (b) Summary of the major perisylvian pathways for language processing. The connectivity profile of the SLF/AF remains a focus of debate, and is thus represented as a single pathway (dashed line). Numbers indicate Brodmann areas. See footnote 1.

Source: (a) From “Meta-Analyzing Left Hemisphere Language Areas: Phonology, Semantics, and Sentence Processing,” by M. Vigneau et al., 2006, *Neuroimage*, 30(4), pp. 1414–1432. Reprinted with permission. (b) From “Beyond the Arcuate Fasciculus: Consensus and Controversy in the Connectional Anatomy of Language,” by A. S. Dick and P. Tremblay, 2012, *Brain*, 135(Pt 12), pp. 3529–3350. Adapted with permission.

in part due to the difficulty in separating sentence structure from meaning. Activations are observed widely within the frontoparietal networks, but few distinct networks have yet to be definitively identified. One possible candidate is a pathway between pars opercularis (BA 44) and posterior STS (BA 22) via the AF (Friederici, 2011). This pathway appears to support processing of nonadjacent elements in complex sentences, thus reflecting syntactic processing demands.

Most imaging studies examining the brain networks for language processing report stronger activity amplitudes within the LH than in the RH. Historically, two roles have been noted for the RH in language tasks, specifically prosody (Beaucousin et al., 2007) and the construction of meaning (Bookheimer, 2002; Lindell, 2006). In a recent metareview, Vigneau (2011) reanalyzed the data from his 2006 paper on LH activation, to look for explicit evidence of the RH engagement in the kinds of phonological, semantic, and syntactic processing tasks examined in the earlier review. He defined bilateral activation as activation of homologous regions of the two hemispheres, and unilateral activation as activity in only one hemisphere. Overall, RH activation in the language studies was low. Further, to the extent that there was RH activation, brainwide activity tended to be bilateral, unlike the pattern of predominantly unilateral activation in the LH. It is worth noting that defining brain activity as either activated or not according to an arbitrary threshold creates what might be a misleading dichotomy. To be clear, studies of language processing tasks frequently find significant engagement of right hemisphere regions as well, compared to baseline. However, the activity amplitudes within the left hemisphere are often relatively greater and so may be the only regions visible on thresholded activation maps.

Early Language Acquisition: Milestones and Brain Changes

Sublexical Level. The first steps toward the acquisition of language require the decoding of basic acoustic and phonological information during infancy (for reviews see Friederici, 2006; Kuhl, 2010). Among the many skills infants must master to build a foundation for receptive language are the abilities to differentiate speech from non-speech sounds, to use the contours of speech intonations to parse structural units, and to identify and discriminate among the phonemes of their native tongue. Functional neuroimaging studies of brain responses during passive listening to speech sounds in young infants have found generally greater activity in the left hemisphere than in

the right. Comparing forward speech to speech played backwards, sleeping newborns showed larger increases in oxygenated hemoglobin over left temporal brain regions than in right, as measured by optical imaging of cortical blood flow (Peña et al., 2003). At 3 months old, brain activity amplitudes measured with fMRI for forward speech were also greater in the left hemisphere and involved primary auditory cortex within Heschl's gyrus, the superior temporal sulcus, and extended to association areas in the left temporal pole (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002). Interestingly, this study also found an active region within right prefrontal cortex, but only for infants who were awake, which the authors interpreted as related to attention.

The intonational contours of speech are also important cues for the infant, allowing the segmentation of auditory input into the structural units of language. During natural speech, breaks in prosody signal phrase boundaries, providing critical information about the syntax of the language that is to be learned. Using fMRI, investigation of the brain bases of prosodic processing in young infants revealed a similar functional neuroanatomy for normal and prosodically flattened speech, which included activity in bilateral temporo-parietal and frontal cortical regions for both conditions (Homae, Watanabe, Nakano, Asakawa, & Taga, 2006). However, a direct voxel-wise statistical comparison of brain activity during normal versus flattened speech showed significantly greater involvement of right temporo-parietal regions for normal speech, suggesting that the rightward hemispheric asymmetry for processing the pitch envelope that has been documented in adults is already evident at 3 months of age. ERP studies of infant prosodic processing demonstrate a qualitatively similar topographical brain organization between 8-month-old infants and adults, but reveal that the timing aspects of these cognitive operations undergo significant changes with development, showing delayed activity peaks in babies (Pannekamp, Weber, & Friederici, 2006).

Another class of acoustic information that must be parsed by the developing infant is the collection of phonemes for a given language. Each language uses a unique set of about 40 distinct sound elements that are combined to make whole words (Ladefoged & Maddieson, 1996). In order to begin acquiring words and their associated meanings within a given language, the infant must first make progress identifying and distinguishing among these foundational phonemic categories. During the first half of the first year of life, infants show a universal perceptual ability to distinguish all of the phonemes of all

languages. Between the ages of about 6 to 12 months, their ability to distinguish nonnative phonetic units declines. At the same time, perceptual abilities for native speech increase, demonstrating a learning mechanism that is tuned by the language experience of the individual (Best & McRoberts, 2003).

ERP studies of this transition from universal to native-specific phonemic abilities during infancy have commonly used the mismatch negativity (MMN) as a neural correlate of auditory discrimination skills. The principal generators of the MEG analog of the MMN in adults have been localized to bilateral primary auditory cortex (Alho et al., 1998). In ERP studies of adults, the mismatch response is always expressed as a negative-going deflection, but infants have been found to display either a negativity or a positivity, with somewhat varying scalp distributions and peak latencies (Cheour et al., 1998; Friederici, Friedrich, & Weber, 2002). In accordance with behavioral studies, brain indices of language-specific phonemic discrimination place the shift in these abilities between the ages of about 6 and 12 months (Cheour et al., 1998; Rivera-Gaxiola, Silva-Pereyra, & Kuhl, 2005). While infants younger than 6 months old show brain electrophysiological measures that discriminate among phonemic contrasts for both native and nonnative languages, older infants display discrimination brain response components only within their native language (Kuhl, 2004).

Early perceptual language abilities are intimately tied to the development of expressive language skills. Learning to produce the sounds characteristic of an individual's "mother tongue" is particularly challenging and requires a protracted period of accumulating expertise, typically not fully mastered until well into the school-age years (Ferguson, Menn, & Stoel-Gammon, 1992). As with receptive language, there is hierarchical regularity to the development of language production. Vocal imitation can be elicited from babies by about 20 weeks of age (Kuhl & Meltzoff, 1982), and by about 10 months of age infants raised in different countries can be distinguished from one another by their babbling sounds (de Boysson-Bardies, 1993). Kuhl and Meltzoff suggest that the close ties between infant language perception and production are linked by shared sensory and motor mechanisms within the brain. Sensory experience with a particular language lays down auditory traces stored in memory that are unique to that language, and these representations guide an infant's verbal motor attempts until a match is produced (Kuhl & Meltzoff, 1996). The ability to produce vocal imitations has also been suggested to depend on a specific

brain system for social interaction, which, guided by joint attention, facilitates "mirroring" behaviors of various types and involves a complex network of brain regions bringing together visual, auditory, attention, and motor information (Hari & Kujala, 2009; Rizzolatti & Craighero, 2004).

Lexical and Semantic Level. Functional neuroimaging and recording studies of infants processing single words have shown, relative to adults, that young brain responses show generally longer latencies (i.e., slower timing to activity peaks after stimulus presentation) and often higher activity amplitudes, but age comparisons of the functional topography have varied widely by task paradigm, imaging modality, and analysis methods. ERP studies have demonstrated differential brain responses between known and unknown words in 11-month-olds (Thierry, Vihman, & Roberts, 2003) and 14- to 20-month-olds (Mills et al., 2004). Both of these studies found a negative component occurring between 200 and 400 ms after presentation of a word that was larger in amplitude for familiar than for unfamiliar words.

The N400 component has been used extensively in ERP research as an index of lexical semantic processing. Its amplitude and latency are modulated by several linguistic (and nonlinguistic) factors, such as word concreteness, frequency, class, repetition, and contextual integration difficulty (Kuhl & Meltzoff, 1996). N400 task paradigms typically involve presenting words auditorily within some context (e.g., at the end of a sentence or simultaneously with a picture), which allows for semantic congruity manipulation. In adults, the amplitude and latency of the N400 component are increased in relation to the degree to which the meaning of the word does not fit the context in which it is encountered. For example, a greater N400 modulation would result from the presentation of the word "mouse" simultaneously with an image of a car than with an image of a mouse. The primary neural generators of the N400 response in adults, measured with MEG, localize to bilateral anterior temporal cortex and left inferior frontal cortex (Halgren et al., 2002; Maess, Herrmann, Hahne, Nakamura, & Friederici, 2006). Similar task paradigms using fMRI have found significant activity within bilateral middle and superior temporal gyrus with greater activity in the left hemisphere, bilateral inferior frontal gyrus, as well as bilateral basal ganglia (Friederici, Ruschemeyer, Hahne, & Fiebach, 2003; Kotz, Cappa, von Cramon, & Friederici, 2002; Kuperberg et al., 2000; Mummery, Shallice, & Price, 1999). Overall, activity within frontal cortex appears to be heavily dependent on task demands, whereas temporal

cortical involvement seems tied directly to lexical semantic processes.

ERP studies of 1-year-olds demonstrate enhanced negativity over lateral, anterior electrodes from about 100 to 500 ms after word onset modulated by congruous versus incongruous pictures, suggesting an early form of the N400 (Friedrich & Friederici, 2004, 2005). The presence of this early N400 brain response at 19 months of age was shown longitudinally to discriminate children with age-adequate expressive language abilities from children with poor language skills at 30 months old (Friedrich & Friederici, 2006). Within ERP studies, the functional brain organization of lexical semantic processing appears to change from relatively bilateral at around 12 months old to somewhat more left lateralized by 20 months of age (Mills, Coffey-Corina, & Neville, 1997). A recent MEG study of the magnetic analog of the N400 found a qualitatively similar topographical organization in 12- to 18-month olds as has been previously reported in young adults, showing activity within frontotemporal cortex that was stronger in the left hemisphere (Travis et al., 2011). However, consistent with previous ERP research, the infant brain responses to processing words was delayed, commonly peaking around 550 ms (Holcomb, Coffey, & Neville, 1992).

Functional Neuroimaging Studies of Language Processing in School-Age Children and Adolescents

Imaging studies of the brain organization for language in adults have confirmed over a century of work from neuropsychological patients that a left lateralized frontotemporal and perisylvian network primarily mediates the major components of language (Rasmussen & Milner, 1977). Brain imaging studies of children primarily focus on whether these adult core brain regions support language in children and to what extent there is developmental change within these regions. The degree of left laterality in children is a central question.

Studies of Regional Brain Associations to Language Development. Most studies support a general pattern of increasing lateralization with development. Nevertheless, the findings reveal noteworthy task and age differences. Younger left lateralized activity patterns are typically found for passive lexical processing tasks (Balsamo, Xu, & Gaillard, 2006; Everts et al., 2009; Gaillard et al., 2003; Lidzba, Schwilling, Grodd, Krageloh-Mann, & Wilke, 2011) as compared to tasks assessing more complex aspects of language production, such as verb generation (Holland et al., 2001; Ressel, Wilke, Lidzba, Lutzenberger, &

Krageloh-Mann, 2008; Szaflarski, Holland, Schmithorst, & Byars, 2006). On both passive and controlled types of lexical tasks, there are significant functional neuroanatomical changes in the spatial extent and/or amplitude of activity within traditional language areas, particularly in frontal regions (Brown et al., 2005; Gaillard et al., 2003). There is evidence for a developmental decline in task-related activity during language tasks for nonlanguage areas such as the ventral visual pathway (Balsamo et al., 2006; Schmithorst, Holland, & Plante, 2007) and right frontal regions (Brown et al., 2005).

On tasks requiring complex receptive and expressive language, the findings of robust increases in left lateralization are consistent. Verb generation tasks yield both developmental increases in activation within traditional left hemisphere language areas using fMRI (Ressel et al., 2008; Szaflarski et al., 2006) and MEG (Gummadavelli et al., 2013; Ressel et al., 2008), as well as developmental activation decreases in right hemisphere regions associated with attention and task performance (Szaflarski et al., 2006). Age-related increases in focal activity without age-related increases in laterality are reported within the superior temporal gyrus bilaterally using story comprehension tasks (Lidzba et al., 2011).

A NEUROCOGNITIVE PERSPECTIVE ON HUMAN DEVELOPMENT

The mature human brain is composed of approximately a hundred billion neurons that form trillions of connections, all in the service of orchestrating the equally complex processes that constitute human thought and behavior (Pakkenberg & Gundersen, 1997). The central question in the study of human development is how this remarkable neurobehavioral system comes into being. However, questions about how the brain and behavioral systems develop have been pursued largely independently, with neuroscientists focused on change in physical attributes of brain systems and behavioral scientists on addressing questions of change in specific aspects of behavior. The initial divergence of these paths of study was largely historical and attributable to the technical challenges of simultaneously studying the development of neural and behavioral systems in living human children. Nevertheless, the long-term consequence of this disciplinary divide is a lack of interdisciplinary integration of data and a divergence in the theoretical models of development that each field offers to account for the observed changes.

As illustrated by the studies reviewed in this chapter, recent advances particularly in brain imaging technologies have made it possible to begin to bridge this interdisciplinary divide. The findings that are beginning to emerge from this interdisciplinary work, coupled with existing data from studies of both brain and behavior, point to commonalities in basic principles of development that operate at very different levels of inquiry and analysis. The next two sections draw from the findings reported earlier in this chapter to provide a summary of the major developmental themes that arise, first, from current models of brain development and, then, studies of neurocognitive development. The final section examines commonalities in the themes that derive from these two bodies of data. It will argue that the principles that arise from the data on brain and behavioral development are consistent with a unified model of brain and behavioral development that is well characterized as dynamic and interactive; marked by progressive differentiation, elaboration, and gradual commitment of resources to neurocognitive structures that emerge slowly over the course of development.

The Dynamic Nature of Brain Development

The studies of brain development reviewed in this chapter support a strongly interactive model with genetic, physiological, behavioral, and environmental factors acting in concert as a complex and dynamic system that promotes the development of the brain (Stiles, 2008). Signals that support the processes of brain development arise from molecular sources in the form of gene expression, from interactions among individual cells, from electrical signaling between distant cell populations, and from signals arising in the external environment and transmitted to the developing organism. None of these factors acts in isolation to *determine* developmental outcome. Rather, each contributes to the many complex and multifaceted processes that underlie brain development. This is a view of neural development anchored in the *process* of development itself, with each step influenced by myriad cues arising from multiple levels of the emerging system. A few examples of the processes that are involved in cortical area formation illustrate this point.

Cortical area formation begins very early in the gastrulating embryo where multiple, sometimes migrating, cell populations engage in complex molecular signaling that alters the fate of the subset of cells that will become the neural progenitor cells for forebrain structures (Sadler & Langman, 2010; Schoenwolf & Larsen, 2009). The absence or alteration of any aspect of this signaling can

have dire consequences, suppressing head growth and even compromising the viability of the embryo. At the end of the embryonic period, molecular signals originating from multiple signaling centers in the ventricular zone and expressed in concentration gradients across the cortical plate, act in concert to establish the rudimentary sensorimotor area organization of the emerging neocortex. Alterations in the level of any one of the signaling molecules can dramatically alter the size and location of cortical areas.

The establishment of the thalamocortical (TC) pathway is essential for maintaining and refining cortical sensory areas in the fetal period. Multiple cell populations in the ventral telencephalon provide guidance signals to the developing TC axons as they project to the input layers of the neocortex (Kahler et al., 2011; Kostović & Jovanov-Milosevic, 2006). Alteration of cells in these signaling centers can divert TC axon path finding and disrupt cortical organization. The TC axons synapse with cells of the transient subplate layer once they arrive at cortex. The subplate cells play an essential role in establishing functional connections between the TC axons and the layer IV cortical cells, and between layer IV cells and the thalamus (Eyler et al., 2011). Destruction of subplate cells disrupts TC pathway formation.

At birth, environmental input is essential for establishing and maintaining specific features of cortical area organization. For example, binocular patterned visual input is necessary for ocular dominance column organization (ODC) in primary visual cortex (PVC). Binocular elimination of input suppresses ODC patterning, while monocular input induces dramatic changes in the balance of inputs in PVC (LeVay, Wiesel, & Hubel, 1980). An even more dramatic example of the role of early input in cortical area organization is seen in the cortical rewiring studies (Leamey et al., 2009; Sur et al., 1988). These studies showed that elimination of auditory inputs to fetal primary auditory cortex induces the stabilization of normally transient visual inputs and redefines the function of the area as visual.

Postnatal imaging studies document the protracted nature of cortical area development. Throughout the preschool and school-age periods, both progressive and regressive region-specific changes in cortical area and thickness are evident. Indices of cortical thickness suggest gradual region-specific thinning of the neocortex that extends through adolescence (Gogtay et al., 2004; Ostby et al., 2009; Sowell et al., 2004). Region-specific changes in cortical area exhibit early expansion followed by contraction. A notable feature of these postnatal events is

that different cortical regions exhibit different trajectories of development for surface area and thickness (Ostby et al., 2009). Differential trajectories of development are observed in the major brain pathways that connect these cortical regions. Thus, the essential components of the major brain networks that support complex behavior exhibit not only protracted development, but also continuing change in the *relative* maturity of different components of the networks, thus creating different functional states throughout development. Neurogenomic imaging studies of adults are defining the relationships between specific patterns of gene expression and differences in cortical arealization and thickness. Nonetheless, the specific nature of the gene action that gives rise to these patterns and the mechanisms of gene activity during development are poorly understood (Chen et al., 2012; Eyler et al., 2012; Panizzon et al., 2009).

Associations Between Brain and Behavioral Development

Neuroimaging studies have begun to map associations between behavioral changes and change in the neural systems that mediate behavior. As represented by the discussions in earlier sections of this chapter, most neuroimaging studies focus on higher cognitive functions that begin to emerge in the first year of life and continue to develop gradually over many postnatal years. Although healthy neonates possess the basic sensorimotor abilities that are essential for the later development of higher functions, data on the emergence of these very early behaviors are extremely limited. Studies documenting patterns of neurocognitive change in older children are more extensive. Data from each of the domains considered in this chapter document the complex and protracted trajectories that are characteristic of the development of higher cognitive functions.

Neonates are capable of both simple volitional motor activity and rudimentary sensory processing. By the time a human infant is born, the corticospinal tract (CST) system that supports central motor control (Armand, 1982; Eyler, 2007; Huang et al., 2009) and the thalamocortical tract (TC) system that supports the major sensory functions are largely established (e.g., Armand, 1982; Kostović & Judas, 2010). Indeed, there is some evidence that these systems begin to function in the prenatal period. Imaging studies of human fetuses have shown that soon after the establishment of the CST in GW 20, cortically based, bilateral movements are observed in the fetus, and between GW 26–32, independent movement of the extremities

is common. In the late fetal period generalized mouth movements (open, close, swallow, tongue protrusion) and rhythmic “mouthing” movements similar to those observed in later motor speech are observed (Prayer et al., 2006). There is evidence that sensory information impacts later development. Within the auditory domain, prenatal exposure to maternal or community language is associated with later preferences for the prenatally available language (May, Byers-Heinlein, Gervain, & Werker, 2011). Similar effects are reported for music exposure. Very recent data from rats suggest the visual system may also be sensitive to prenatal input. Dark rearing of pregnant mice during the late gestational period (E16–17, for a 20-day gestation) results in a reduction in the number of retinal neurons measured in the rat pup postnatally. The mechanism for the change is linked to effects on the fetal vasculature and level of photopigment in the rat pups, which jointly regulate neuron number (Rao et al., 2013).

As these examples illustrate, the neonate brings a range of functional somatosensory systems to the task of acquiring higher cognitive functions. Additionally, there is substantial evidence that the neonate is capable of quite powerful statistical learning of environmental information. Statistical learning refers to the ability of the organism to extract statistical regularity from environmental input. A large number of studies have documented statistical learning during the first year of life for a wide range of domains including words (Saffran, Newport, & Aslin, 1996), musical tones (Saffran, Johnson, Aslin, & Newport, 1999) and spatial shapes (Kirkham, Slemmer, Richardson, & Johnson, 2007). Recently, this work has been extended to newborns who showed evidence of statistical learning for novel shapes (Bulf, Johnson, & Valenza, 2011).

Each of the higher cognitive domains considered in this chapter illustrate the protracted nature of development through childhood and adolescence. Face processing is an important basic skill that is essential for human social interaction. Preferences for faces over other classes of objects are documented in neonates, and by 3 months, infants can categorize faces by gender and race. Despite these early emerging abilities, face processing undergoes a protracted period of development extending well into adolescence (Lee et al., 2013). The brain networks for face processing are complex. They consist of both a core network for face identification that is located in ventral temporal regions and includes the fusiform gyrus, the inferior occipital gyrus, and the superior temporal gyrus (STG), as well as an extended network that includes additional regions in the medial temporal lobe, frontal lobe,

parietal lobe, and subcortical structures. Imaging studies have shown that patterns of activation in both core and extended networks for face processing undergo systematic change throughout the school-age period (e.g., Haist et al., 2013). In addition, electrophysiology studies also provide evidence for systematic change in the neural signatures of face processing (Shibata et al., 2002), with the classic N170 response undergoing protracted change from infancy through adolescence (de Haan, Johnson, & Halit, 2003a).

Studies of working memory abilities also document a protracted period of development. There is now an extensive body of behavioral evidence documenting the early emergence and rapid development of basic working memory abilities during the first year of life that correspond to systematic change in associated neural responses (e.g., Bell, 2012; Cuevas, Raj, & Bell, 2012). Throughout childhood (Vuontela et al., 2003) and adolescence (Conklin et al., 2007), a linear improvement in working memory performance is observed for a wide variety of tasks. fMRI studies suggest that the brain networks serving these important functions mirror the basic adult networks from very early in development, but are more distributed and less differentiated. Improvement in working memory performance accompanies changes in the specificity of the underlying neural systems (e.g., Klingberg, 2006; Thomas et al., 1999).

Finally, language is a complex cognitive ability that requires mastery and integration of a range of processes. Fluent language users seamlessly process many aspects of language including the acoustic, phonological, lexical-semantic, morphological, syntactic, and discourse levels when listening to or producing speech. Acquisition of each of these components of language develops on somewhat different temporal trajectories, with early acquired skills such as acoustic or phonological processing proceeding and serving as the foundation for later skills such as lexical or syntactic processing (e.g., Cheour, Lepanen, & Kraus, 2000; Peña et al., 2003; Werker & Tees, 1999). Considerable progress has been made in mapping the brain substrates of language in adults. Studies of children suggest that the functional brain systems employed for the various aspects of language emerge early but undergo protracted developmental change and in general reflect developmental increases in the leftward lateralization of functions and developmental decreases in activity within a language-learning “scaffolding” that includes areas outside the classic adult language organization, including right frontal, temporal, and occipital cortex (e.g., Balsamo et al., 2006; Everts et al., 2009; Friederici, Brauer, &

Lohmann, 2011; Lidzba et al., 2011; Schlaggar et al., 2002; Szaflarski et al., 2006). These changes in the brain substrates for language presumably reflect the increasing specification and refinement of the neural systems for language that accompany the child’s growing mastery of this complex set of cognitive processes.

Common Developmental Principles

A number of common themes arise in reflecting on the patterns of data observed in studies of brain and neurocognitive development. The first is the idea of progressive differentiation of system elements, where initially rudimentary structures are elaborated, refined, and integrated into increasingly effective systems. The second related theme is that of progressive commitment of elements and networks to particular processes, thus creating stable and effective neurocognitive systems. The third theme has two complementary aspects. On the one hand is the idea that the process of neurocognitive development is dynamic and interactive; on the other hand is the essential complement to dynamism, which is constraint. There are three primary sources of constraint on neurocognitive development: genetic, environmental, and temporal, and each plays an essential role in constraining developmental trajectories. These themes are considered in greater detail next.

Progressive Differentiation. Progressive differentiation refers to the ongoing increases in the complexity of the organism, which is one of the hallmarks of any developing system. Organisms and behaviors begin small and are gradually elaborated over time. The phenomenon is clearly illustrated in the events of embryonic brain development. The embryo goes from a two-layered to a three-layered structure as new cell lines differentiate and become organized and integrated. Migrating cells that will eventually form the mesodermal and endodermal germ layers of the embryo also establish signaling pathways that promote the differentiation of the neural progenitor cell population in the ectodermal layer. In addition, the progressive differentiation of neural progenitors has a spatial component that is critical for establishing the basic functional organization of the embryo. Concurrent with the signaling that promotes the differentiation of the neural progenitor cell lines, more specific signaling induces neuroectodermal cells in rostral regions to become forebrain progenitors, and more caudally positioned cells to become spinal and hindbrain progenitors. A few weeks later, the graded expression of multiple transcription factor proteins in the rostral progenitor cell population will promote

further differentiation within cell populations destined to form the major sensorimotor areas of the emerging neocortex. Progressive differentiation, thus, brings increasing complexity at all levels of the neural system from cell lines to neural systems.

Progressive differentiation is also seen in neurocognitive systems. Language acquisition begins with the parsing of the acoustic stream and the differentiation of important speech sounds. The parsing of sounds sets the stage for identifying word boundaries. Combinations of words are linked in ways that serve simple specific meanings. Strings of meaningfully connected words and sentences combine to express complex ideas in discourse or text. Similarly with face processing, infants initially discriminate faces as an important class of stimuli, but it is several months before gender or race categories become salient. The basis for face discrimination remains fairly global for many years, as children rely more on external cues such as hairline or clothing rather than fine analysis of internal facial features. The neuroimaging studies of language and face processing suggest that the neural systems that support these developing behaviors undergo a concomitant shift from relatively imprecise engagement of system elements to increasingly specific, and presumably efficient, engagement. A critical aspect of progressive differentiation for both the brain and behavioral systems is that with each phase of development the processes of differentiation produce new structures that are essential for the next step in development.

Progressive Commitment. Progressive commitment refers to the stabilization of systems. Developing systems exhibit considerable plasticity and capacity to adapt to varying signals and contingencies. However, that plasticity declines with development as different neurocognitive elements become progressively committed to particular systems. We can see this phenomenon of progressive commitment in the course of brain development. Initially the cells of the embryo are totipotent, which means that they are capable of differentiating into any cell type in the body. Nevertheless, with development there is progressive restriction in that potential and therefore emerging constraints on plasticity. We also observe this kind of waning plasticity much later in development. Basic sensory areas in the neonatal brain retain the capacity to receive input that can fundamentally change their normally targeted function. Sur's (2001, 1990, 2005) neonatal rewiring studies demonstrated that when normal patterns of input are disrupted, primary auditory cortex retains the capacity to adapt to quite different modes of sensory input, in effect

becoming a visual area. Early synaptic exuberance, found throughout the developing brain, underlies this capacity for plastic adaptation. However, widespread exuberance of the sort that can support cortical rewiring is a phenomenon of early development. While the mature brain retains some capacity for plastic reorganization, it is considerably attenuated.

Evidence for progressive commitment for higher cognitive functions is best seen in studies that directly or indirectly examine cognitive expertise. One example comes from studies of late second-language learners. These studies show late second-language learners are less proficient in overall level of mastery of the newer language. There is also evidence that they may process the second language differently from native speakers, applying rules appropriate to their native language when engaged in second-language processing. These processing differences suggest that early commitment of neurocognitive resources to the particular structural constraints of one language makes learning a language with different constraints more difficult (Hernandez & Li, 2007; Kotz, 2009). Age-of-acquisition effects that show that second-language proficiency varies as a function of duration between first- and second-language acquisition suggest that commitment of neurocognitive resources is gradual and extends over many years (Hernandez & Li, 2007). In addition, fMRI and MEG studies suggest differences in the neural systems for processing first and second languages. These relate to age of acquisition and mirror the developmental functional neuroanatomical changes observed during first language learning, where later acquired languages, even if highly proficient, utilize more right hemisphere resources (Brown et al., 2005; Hernandez & Li, 2007).

A second source of data on the effects of progressive commitment of neurocognitive resources comes from studies of face processing. Specifically, the demands of sociocultural exchange require that humans become expert face processors. An index of this expertise comes from behavioral studies showing that adults tend to use the individual level as the entry point of processing faces, making the discrimination of large numbers of similar stimuli more efficient. By contrast the entry point for processing common objects is the basic level (Tanaka, 2001). Evidence that face expertise may reflect a protracted process of progressive commitment comes from studies of cross-race face processing. These studies show that processing of own race faces is faster and more accurate than processing of other race faces, reflecting long-term exposure to certain classes of face stimuli and the acquisition of

greater own-race face expertise. Differences in own- and other-race face processing are also seen at the neural level. EEG studies show that processing differences of own- and other-race faces are detected within the first 250 ms after the onset of the face stimulus (Tanaka & Pierce, 2009; Vizioli, Rousselet, & Caldara, 2010). fMRI studies have documented subtle differences in both the intensity and location of responses to own- and other-race faces within ventral occipitotemporal cortices (Golby, Gabrieli, Chiao, & Eberhardt, 2001).

Constraints on Development

The studies on brain and neurocognitive development presented in this chapter highlight the dynamic and interactive nature of brain development. Indeed, one might legitimately ask whether such a model is too dynamic. There are many degrees of freedom in these complex, interactive signaling cascades, but, if it is assumed that there is no specific mechanism for *determining* a particular outcome, then how is it that development proceeds with such uniformity to produce species-typical individuals? The answer to this question lies in the fact that while development is dynamic it also occurs within the context of very powerful constraints that originate from three principal sources: genetics, environment, and time.

Genes are the first factor that imposes constraints on the developmental process. Each species, each individual, has a specific set of genes that has been acquired across the course of evolution. The availability of specific gene products at particular points in development is essential for normal outcomes. Further, the particular quantity of a particular gene product is an essential factor in developmental outcomes. As illustrated by the work of O'Leary and colleagues, modulation of the level of transcription factor expression can fundamentally alter the emerging organization of somatosensory and motor areas of cortex (Bishop, Garel, Nakagawa, Rubenstein, & O'Leary, 2003; O'Leary & Kroll, 2009). Thus, genes provide powerful constraints on developmental processes and play a large and essential role in brain development.

The second source of constraint comes from the environment. Like genes, the environment imposes rigorous constraints on how an organism can develop. From an evolutionary perspective, development is an adaptation to the contingencies of the environment. Early ontological development relies on what Greenough has called experience expectant change (Black & Greenough, 1986; Greenough et al., 1987). Normal development requires normal input from the world to modulate and shape

the emerging functional organization of neural systems. Neural systems do not develop normally in the absence of typical environmental input. Studies of deprivation such as those illustrated in the work of Hubel and Wiesel provide powerful examples of the importance of normal, expected input on developing systems. The effects of environment play as powerful a role in the development of behavioral systems. Deprivation studies provide striking examples of the wide-ranging effects of impoverished conditions on all aspects of emotional and cognitive development (Nelson, Fox, & Zeanah, 2014; Pollak et al., 2010). Equally powerful are studies of the effects of behavioral interventions on the development of children in at-risk populations (Fletcher & Vaughn, 2009).

The third constraint is time. Development is a complex, multilevel process that unfolds over *time*. Biological and cognitive systems start out simple and become more complex over time. Across the entire period of brain development, the neural system depends on the availability of the right neural elements appearing at the appropriate moment in developmental time. Complex cognitive systems such as language develop in a similar temporal manifold (Elman, 2003). Often the emergence of a new element depends critically on the developmental events that immediately precede it. As such, the developing organism often creates as it goes the tools necessary for each successive step in development. Thus, time constrains what changes *can* occur and what factors *can* influence development. In that sense, development is a temporally constrained, self-organizing process.

Trajectories of Neurocognitive Development

One important aspect of the temporal constraint on development involves changing sensitivity of the organism to developmental signals. The level of development of the organism constrains the kinds of signals to which it can respond. At any point in time, the developing organism has both a state and a history that constrains its developmental potential. The history is the sum of all of the events that contributed to the current state of the organism. The state represents both the current structure and functional capacity of the organism, as well as its potential for further change. Sensitivity to a specific intrinsic or extrinsic influence depends on the current developmental state of the organism. For example, auditory input has no effect on the events of gastrulation, but is critical for the development of features such as tonotopy in primary auditory cortex. Similarly, language input is essential for normal acquisition of language skills but fluent language ability is robust to loss of input. Thus, the increasing variety

of structural elements (some permanent, some transient) creates diversity in the kinds of interactions that can be engaged in the complex signaling cascades that structure the developing neurocognitive system.

The state of the organism represents a “snapshot” at a single moment in developmental time. It is a temporally bound, two-dimensional cross section of a complex multidimensional developmental manifold. It is possible to specify the currently available elements of a system and their immediate relationships, but a critical factor missing from cross-sectional snapshots is the dimension of time. Even within the limited data considered in this chapter, it is clear, that each element within a given snapshot has its own developmental trajectory. Each individual brain area and neural pathway develops according to its own temporal trajectory (see Figures 2.7 and 2.11). That is also the case with sensory and motor systems, phonological and syntactic processing, and memory and inhibitory control. Further, each of these systems has its own subsystems that are also on individual temporal trajectories of development. This means that not only do the elements of the neurocognitive system differ at different time points; the relations among all of the elements also change with time. Thus, the

trajectory of neurocognitive development is determined over time by ongoing interactions across the multiple levels of the neurobehavioral system. The processes of progressive differentiation and commitment continuously modify the existing state of the organism, such that the system is reorganized not once, but many times across the course of development. In that sense, development can be construed as a process of continuous, successive reorganization. The product of these developmental processes is a relatively stable (though still plastic) end-state organization that is characteristic of the mature individual.

FUTURE DIRECTIONS

The preceding sections outline remarkable progress in human developmental neuroscience. However, many lacunas in our understanding remain, especially about the relationships between observations made with different methods, in different age ranges, sometimes within different cohorts, cultures, or genetic groups. In this concluding section, we make the case for a more intensely interdisciplinary, more collaborative paradigm in developmental

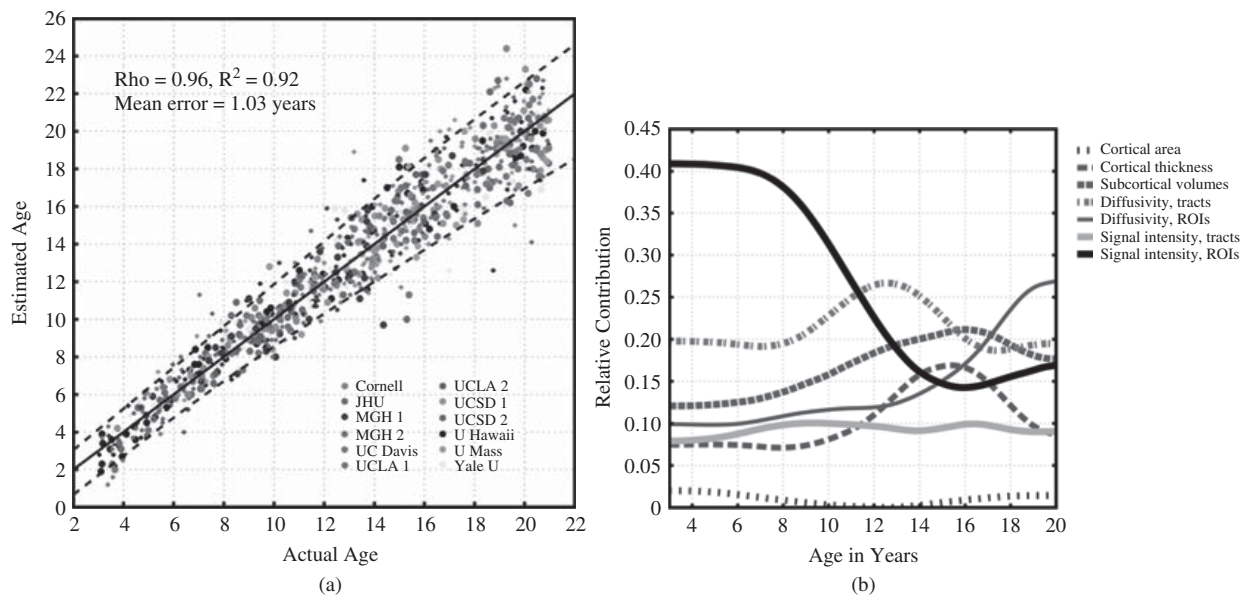


Figure 2.11 Multimodal imaging. (a) Multimodal quantitative anatomical prediction of age. For 885 individuals, estimated brain age is plotted as a function of actual chronological age. Symbol size represents subject sex (larger = female, smaller = male). A spline-fit curve (solid line) with 5% and 95% prediction intervals (dashed lines) is also shown. (b) Age-varying contributions of different imaging measures to the prediction of age. The relative contributions of separate morphological, diffusivity, and signal intensity measures within different brain structures are plotted as a function of age. Contributions are computed as units of the proportion of total explained variance.

science. This paradigm involves more studies employing multidimensional observations and multivariate modeling of developmental phenomena.

From Snapshots to Trajectories

Whether one focuses on the behavior, the neurobiology, or the structural and functional organization of the developing brain, the picture that emerges suggests multiple, parallel yet interacting processes that unfold over decades, and indeed are continuous across the entire lifespan. The confluence of these processes gives rise to an ever-changing, dynamic neurobehavioral system within each individual child. The typical assessment of a child produces a “snapshot” of this system, but this view cannot be understood absent an understanding of the history and continuing trajectory of these unfolding processes.

Emerging understanding of the meaning of the information coded in our genomes suggests that this information is less a recipe for our biology than a workshop for an always-adapting species, the hallmark of which is behavioral adaptivity itself. The code is therefore flexible, within the fitness limits set by our evolutionary history, and redundant, and is well tuned to the demands on members of our species to encode information available in the environment and to generate and update models of the world around them. In this context, if one is interested in the behavior, or the behavioral phenotype, of the child, it makes little sense to attempt to identify a level of representation of this dynamic system as “causal.” The developing mind-brain is an extraordinarily complex phenomenon, and meaningful representations of important attributes and dynamics of the phenomenon are almost certainly present at all levels of analysis, across which many forms of isomorphism exist. An important question for the field is how best to advance the sophistication of what is now an exceedingly shadowy and fragmented model of the developing behavioral phenotype.

Given the challenges, the field would do well to organize its efforts around a data-driven and multivariate approach. For the first time ever, developmental scientists are poised to bring to their study of developing children a multitude of new, noninvasive techniques for monitoring the biological and functional attributes of the brain, as well as ever-advancing methods for characterizing genomic and epigenetic variation, neuroendocrine and hormonal factors, and immunological markers. The importance of a multidimensional approach is well illustrated by recent evidence suggesting that gonadal steroid hormones may substantially modify late brain maturation, giving rise to

late emerging differences among youth in brain structure and connectivity (Perrin et al., 2008). Moreover, additional evidence suggests that these effects may interact with genotype (Peper, Hulshoff Pol, Crone, & van Honk, 2011; Perrin et al., 2008). Nonetheless, we need much more research to determine the behavioral implications of these effects, and of the well-known variability in pubertal trajectories among children.

Equally important are the increasingly sophisticated methods for complete assessments of the child in context and over time. New web-based, mobile, and wireless technologies are opening up opportunities for less obtrusive and higher dimensional assessments of the behavioral and physiological responses, experiences, activities, and environments of children. This new information promises to greatly augment data obtained from laboratory assessments. The developmental research community would do well to commit to collaborative efforts to aggregate information about developing children in large-scale, multidimensional databases. In the following section, we describe some examples of such multivariate approaches to aggregated data.

Multimodal and Multidimensional Approaches

There is an ever-growing and diverse collection of scientific tools available for noninvasively studying human brain development and relating it to behavioral and cognitive change. We have made significant progress using these technologies to characterize maturational differences and trajectories in structural and functional brain development. Despite these advances, however, across all types of imaging and recording methods, the vast majority of studies have investigated developmental changes within a single measurement modality; for instance, comparing brain features only *within* structural MRI, EEG, fMRI, DTI, or MEG. In order to begin to understand the complex interplay of anatomical and physiological growth and to better reveal the biological significance of our imaging measures, it will be necessary to study brain changes using integrated multimodal approaches that relate different kinds of measures to one another. Done rigorously, such studies will require more than just the addition of more variables to statistical models; the accurate spatial and temporal interrelation of multiple structural and functional brain measures demands the collaboration of researchers with expertise across difficult and diverse areas, including biophysics, signal processing, computational neuroscience, mathematical modeling and statistics, and the behavioral sciences. The technical demands and scientific promise

of multimodal imaging approaches are evident in the increasing publications using integrated brain measures. Successful examples of their application include integrating EEG and MEG data with structural MRI data (Dale & Sereno, 1993), MRI and MEG with fMRI data (Dale & Halgren, 2001; Dale et al., 2000), PET and fMRI (Gerstl et al., 2008), EEG and fMRI (De Martino et al., 2010; Oun, Numenmaa, Hämäläinen, & Golland, 2009), fMRI, MEG, and intracranial EEG (McDonald et al., 2010), resting state fMRI with DTI tractography (Uddin et al., 2010), and resting fMRI and DTI with voxel-based morphometry (Supekar et al., 2010). Besides just relating different kinds of measures, a major goal in integrating approaches is to capitalize on the relative strengths and bypass the relative weaknesses of each modality, for example, by combining the superior spatial resolution of fMRI with the millisecond-wise temporal resolution of MEG to study the detailed spatiotemporal dynamics of human memory and language processing (Dale & Halgren, 2001). Although usually developed first within studies of adults, integrated forms of multimodal structural and functional neuroimaging constitute an exciting prospect for future studies of child development.

A closely related but distinct issue involves the ability to model simultaneously the developmental change of a large number of biological or behavioral variables and relate them to each other in interpretable ways. Just as studies of brain development typically use measures from only one type of imaging, they also commonly characterize brain features and maturational trajectories only in isolation, as a list of separate, univariate dimensions along which developmental change occurs. For example, we know that there exist during school ages developmental increases in the volume of the thalamus, decreases in total diffusivity of the pyramidal white matter tracts, and decreases in cortical thickness. Nevertheless, how do these trajectories interrelate, and which types of changes are dominating at what ages? In developmental brain research, it remains a critical challenge to characterize the multidimensional nature of such features in a way that accurately conveys complex relations among them.

An example of such an attempt to characterize brain development integrating information from a set of multidimensional imaging phenotypes comes from the multisite PING Study. Using a regularized nonlinear modeling and cross-validation method, PING researchers developed an approach that quantifies the age-varying contributions of different biological change measures to the prediction of multidimensional developmental phase as defined by

chronological age (Brown et al., 2012). Using this new technique, different components of brain development were quantified and compared directly, showing their relative roles in the dynamic cascade of changing brain characteristics. This study found that the composite developmental phase of an individual person can be captured with much greater precision than has been possible using other types of biological measures or approaches. Using a multimodal set of 231 brain biomarkers assessed in 885 subjects between the ages of 3 and 20 years, Brown and colleagues were able to predict the age of every individual within about one year on average (Figure 2.11a). This result indicates that a highly age-sensitive composite developmental phenotype is present within a set of biomarkers that includes measures of brain morphology, tissue diffusivity, and signal intensity. It reveals the presence of a developmental clock of sorts within the brain—a complex latent phenotype for which the timing of maturation is more tightly controlled and more closely linked to chronological age than previously understood. This multidimensional biological signal cuts through the high individual difference variability across children and adolescents and explains more than 92% of the variance in age.

The new method employed in the PING study also revealed how the neuroanatomical features that contributed most strongly to the prediction of age changed over the age range (Figure 2.11b). Interestingly, from the preschool years until about 11 years of age, the changes in normalized MR signal intensities within subcortical regions, including gray matter, explained the most variance in age. From the ages of about 11 to 15 years, changes in the diffusivity of white matter tracts (such as FA and ADC) were the strongest age predictor. Volumetric measures of subcortical structures explained the most variance in the age range from about 15 to 17 years. As many researchers are not measuring diffusion within these structures, it was surprising that diffusivity within subcortical regions, including gray matter, was the strongest contributor to the prediction of age between 17 and 20 years. This pattern suggests that continuously throughout development changes in tissue biology are cascading across the brain in a way that is systematic even among different individuals, and that these specific changes may be relatively insensitive to experiential variability typical among healthy children. While this is an interesting discovery, it does not provide by itself information about the role of these tissue changes in functional development. It is possible, even likely, that other composite phenotypes such as brain activity measures would associate more strongly with the individual

differences observable among developing children of the same age. Future applications of this flexible approach should examine whether cognitive, behavioral, and clinical variables are reliably predicted using multidimensional sets of brain measures.

Defining the Individual in Developmental Terms

The PING study has provided an unusual opportunity to apply advanced multivariate methods to extract new information from high-dimensional data in a large cohort of children across a wide age range. However, more information acquired over time from the same children is of critical importance for the success of future data-aggregation efforts in developmental science. Therefore, the designs of contributing studies must be longitudinal, or cohort-sequential. This is critical for several reasons.

Developmental trajectories are likely to explain behavioral phenomena that cannot be accounted for with concurrent measurements of relevant variables alone. One example of this emerged from imaging genomics. Individual differences in gross brain morphology are highly heritable, with estimates of the heritability of brain size, cortical surface area, and average cortical thickness that often exceed .80 (Baaré et al., 2001; Panizzon et al., 2009). However, a recent longitudinal study of developing twins confirmed that the rate of cortical thinning between the ages of 9 and 12 years was itself heritable (van Soelen et al., 2012). These effects were regionally variable, and cross-age genetic correlations suggested that different genetic factors influenced the rate of thinning at different points in the childhood age range. Such genetically mediated differences in trajectories of cortical development are likely to be relevant to adult behavioral phenotypes, in part because they will alter the nature of interaction between the still-developing neural systems. Without longitudinal study designs these effects of genetically mediated developmental differences will be difficult to detect and define because the structure of the mature brain may mask differences in the timing of its maturation.

We need large longitudinal studies to thoroughly investigate the influence of environmental and experiential factors, especially as they interact with other factors at the level of the individual. These interactions are likely to have important implications for prevention and intervention. For example, an intensive reading intervention administered to children receiving normal classroom instruction but experiencing reading difficulties not only improved their reading performance, but appeared to normalize, at least in part, pretreatment differences in the biology of specific fiber

tracts (Keller & Just, 2009). These changes did not occur in a control group of poor readers or a control group of good readers who were assigned to normal classroom instruction. This study suggests that both the reading phenotypes of these children and the accompanying neural signature may reflect interactions between individual factors and the nature of the instruction they receive. Understanding these critical interactions is key to developing new interventions that prevent adverse outcomes in children.

The potential gains of better developmental models of behavioral phenotypes are immense. Because so much of previous research has focused on the modal course of development, and on the “net” effect of experiential variables on representative samples, very little is known about the interactions of experience with constitutional or genetic factors. Yet, virtually all “risk” phenotypes identified so far for adverse outcomes of development, such as academic failure, depression and anxiety disorders, substance-use disorders, social dysfunction, and other behavioral disorders, are heritable. This fact attests to the importance of detecting and explaining interactions of experience with genetic or other constitutional factors (such as early damage or toxic exposure of the brain). The languishing developmental phenotype of a child with a high risk for an adverse outcome may in many cases, and in many respects, be less a result of inherent limitations of the child’s nervous system than the expression of an unusual brain responding to environments and cultures shaped to promote the development of the modal child. To the extent that this is true, it implies that, tragically, many children may not escape the negative outcomes for which they have increased risk only because the environment is unsupportive. It also implies, however, that intelligent interventions for children at increased risk, interventions that modify their environments and experiences adaptively, may both dramatically reduce the risk of adverse outcomes in these children and also promote previously underdeveloped capabilities that they possess, and that may even travel (e.g., genetically) with those risks. Exploring these possibilities is the often-repeated mandate for our field, but we have far to go in developing the basic science foundations that are most likely to yield powerful models and interventions.

In conclusion, we cannot overstate the urgency of a “big data” approach to investigation of the developing child. Large-scale, data-driven approaches have led to new discoveries, powerful predictive models, and intelligent and highly adaptive systems in physics, biology, engineering, and business. Yet, in spite of the enormous impact

such advances in human developmental research would have—for education, child welfare, and prevention and treatment of behavioral disorders—a large-scale, multidimensional study of the developing mind and brain has not yet been performed.

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CHAPTER 3

Perceptual Development

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INTRODUCTION

Sensory systems provide information about the environment so that we might prepare and enact actions appropriate for the context. Vision, audition, proprioception, taste, and smell work together to impart coherent interpretations of the identities, locations, and movements of objects and people in our surroundings. Consider, for example, the two scenes depicted in Figure 3.1. At left, two girls are seen on

a beach under a partly cloudy sky, a boat in the distance. At right, the same two girls are seen in New York City in Washington Square Park, a far more cluttered setting: trees, buildings, cars, other people, and so forth. The parents' responsibility to keep watch over the children is the same in these two settings, but the perceptual environments are quite different. At the beach, there are few other objects in view, a soundscape consisting of wind and waves, and the smell of the ocean. At the park, there are innumerable objects in view, a cacophony of street sounds, and the smell of exhaust and other miasma of the city.

These examples illustrate five important features of mature perceptual systems. First, perception is *active*: Attention is directed toward salient and meaningful objects

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Figure 3.1 Two scenes.

and events (J. J. Gibson, 1950) and in this respect is under the influence of both “bottom-up” and “top-down” control. Second, perception is *evaluative*: Objects and events are attended to by virtue of their importance for the observer (what E. J. Gibson, 1969, referred to as *affordances*). Third, perception is *context-sensitive*: Parents may be alert to the special dangers posed by oceans and cities, and vigilant to their children’s movements accordingly. Fourth, perception is *selective*: Irrelevant stimuli are filtered out and ignored, and relevant, attended stimuli are processed in detail. Fifth, perception is *multimodal*: The different senses often receive information simultaneously, and these inputs are characterized by unique “channels” for processing by discrete cortical networks. Yet rarely do we interpret the inputs as distinct—rather, they are generally integrated seamlessly.

How do these perceptual skills arise early in life? How do they contribute to developing systems of knowledge? As we note throughout this chapter, these five features of perceptual systems have motivated innumerable experiments on perceptual development in humans and other species. Recounting them all is impossible, and so our strategy in writing the chapter is to provide a narrative about the development of human infants’ perceptual systems as the primary means to acquire and interpret knowledge about events, objects, and people in the world around them. We focus also on developmental mechanisms—growth, experience, and learning—and we consider as well the

malleability, or plasticity, of perceptual systems during development.

THEORIES OF PERCEPTUAL DEVELOPMENT

Interest in infants’ perceptual development has been part of psychology at least since William James (1890) famously claimed that “The baby, assailed by eyes, ears, nose, skin and entrails at once, feels it all as one great blooming, buzzing confusion” and “... the undeniable fact being that *any number of impressions, from any number of sensory sources, falling simultaneously on a mind THAT HAS NOT YET EXPERIENCED THEM SEPARATELY, will fuse into a single undivided object for that mind.*” Furthermore, James recognized that perceptual and cognitive development proceed in tandem: “Infants must go through a long education of eye and ear before they can perceive the realities which adults perceive. *Every perception is an acquired perception*” (James, 1890, Vol. 1, p. 488, *emphases original*). These suggestions constitute both a hypothesis about the infant’s perceptual experience and a theory of development. The specifics of this hypothesis and this theory remain disputed, and they anticipate debates concerning perceptual development that continue today.

The theories reviewed here focus largely on object perception, but their principles in many cases pertain to auditory perception as well, to the extent that they attempt to account for perception of coherent entities requiring

integration of discrete parts. Consider, for example, our ability to track effortlessly almost any object of our choosing. The immediate visual array (i.e., the light that is reflected to the observer from visible surfaces in the environment) changes with every head or eye movement, and objects themselves frequently go out of sight and subsequently return to view. Objects may emit sounds and their movements introduce dynamic auditory trajectories, becoming softer and louder as they disappear and reappear, and causing echoes from other surfaces that themselves change over time. Yet our experience is not a world of fleeting, disembodied shapes and sounds, but rather a unified one of substance, volume, and depth.

There has long been fierce debate as to the best characterization of perceptual and cognitive development in infants and children. Most pertinent to this chapter, some of these debates have centered on the extent to which knowledge of objects is gained from visual or manual experience, or arises from inherent, organized, internally generated systems of thought.

Piagetian Theory

Jean Piaget's theory of cognitive development (1937) was organized around four broad themes: object, space, time, and causality (after Kant, 1767). Knowledge of these domains was proposed to develop together and as interdependent achievements. The principal explicandum of Piagetian theory was *objectification*: knowledge of the self and other objects as discrete, separate in space, and constrained by physical principles governing, for example, causality, solidity, and persistence. Objectification was thought to be an outcome of coordination of action systems. Importantly, the contributions of action systems to cognition are rooted in the child's recognition of her own body as an independent object and her own movements as movements of objects through space, akin to movements of other objects she sees, a transition from *egocentric* to *allocentric* reasoning. Things are detached from actions, and actions are placed in the ongoing, observed series of surrounding events, all encapsulated in the broader *construction* of the reality of time and space—that is, the gradual emergence of cognitive expertise with the accretion of experience with existing, lower-level manual and perceptual skills.

Initially, prior to the advent of these manual action skills, infants experience the visual environment as a “sensory tableaux” in which images without permanence or substance shift erratically and capriciously; objects, as we understand them, do not yet exist. Active search behavior emerges after 4 months, and enables the beginnings of

“true” object concepts. Over the next few months, infants reveal this knowledge, for example, by following the trajectory of thrown or dropped objects, and by retrieval of a previously seen object from under a cover. Later, infants search accurately for objects even when there are multiple potential hiding places, marking the advent of full “object permanence.” For example, it was through everyday play, by repeatedly hiding and revealing a toy under a blanket, that Piaget watched his daughter use her manual experience to identify spatial relations among objects (such as above, below, and behind). Similarly, infants who are learning to reach (at 4–6 months) soon discover which objects are and are not within reach, imparting a kind of depth perception. Parallax perception, achieved by moving the head back and forth, comprises an excellent means of seeing relative depth and becomes systematic by 8 to 10 months.

Piaget's theory views perception to supply “signifiers” that are given meaning by the overall embodied experience. For Piaget, there is meaning to perception before the coordination of vision and prehension, and meaning is tied to the schemes the perceptual event has been and can be assimilated to. Thus, perceptual events can be discriminated from each other, but they might not have functional, subjective meaning unless they can be assimilated to action schemes. In addition to this functional meaning contributed by action, the coordination of actions also results in a transformation of meaning. It leads to a distancing (objectification), and, importantly, it is the coordination of actions that leads to the perception of a sequence (e.g., causality). Building coherent entities and complete, permanent objects from disconnected images, therefore, comes from action and experience with objects over time. Piaget's theory emphasizes *construction* of cognition, and has come to be known as the first viable (if not always empirically supported) *constructivist* theory of development. Present-day constructivist theories, discussed subsequently as *neoconstructivism*, share some of the same goals as Piaget's theory (e.g., explaining the developmental process), but have the advantage of the accumulation of information about infants' perceptual and cognitive skills from several decades of empirical research and the insights afforded by a wealth of advances in theory and methods.

Gestalt Theory

The Gestalt psychologists, like Piaget, were active in the first half of the 20th century. Their work mainly concerned adults' phenomenological perception, but it included speculation about the developmental causes of the phenomena they observed. They posited that perceptual experience

corresponds to the simplest and most regular interpretation of a particular visual array, consistent with a general “minimum principle,” or *Prägnanz* (Koffka, 1935). When confronted with the scene depicted in the left panel of Figure 3.1, for instance, an adult observer will usually report perception of a continuous shoreline, despite partial occlusion by people standing on the beach. This determination can be made on the basis of the alignment of the edges to their left and right, and between (the Gestalt principle of good continuation), the resemblance of the visible portions of the shore’s surface (symmetry and similarity), and the regularity and simplicity of the shoreline in general (good form). Shapes that are defined by such principles are more coherent, regular, and simple than disconnected and disorganized forms. The minimum principle and *Prägnanz* were thought to arise from a tendency of neural activity toward minimum work and minimum energy (analogous to other physical systems), which drive the visual system toward simplicity (Koffka, 1935).

Because this predisposition is inherent in the visual system, according to the Gestalt view, it follows that young infants should experience the visual array in ways similar to adults, and so the roles of learning and experience were downplayed to an extent. In one of the few sections of Gestalt writings to focus on development, a “primitive mentality” was attributed to the human infant (Koffka, 1959/1928; Köhler, 1947), and there was a belief that perceptual experience is never one of disorganized chaos, no matter what one’s position in the lifespan. Hebb (1949), in addition, noted that an “intrinsic organization” characterized newborns’ brain activity when measured by the electroencephalogram, and this organization was postulated as a foundation of subsequent perceptual development. J. J. Gibson (1950) echoed the suggestion that visual experience begins with primitive or “embryonic meanings,” and Zuckerman and Rock (1957) argued that an organized world could not arise solely from experience because experience cannot operate over inherently disorganized inputs (cf. Fodor, 1983). Necessarily, therefore, the starting point of visual organization is inherently organized. Like Piaget, Gestalt psychologists proposed that development of object perception *per se* involved active manual exploration, which imparts additional information about specific object kinds (Koffka, 1959).

Nativist Theory

A central tenet of psychological *nativist* theories is that some kinds of knowledge form a central core around which

more diverse, mature cognitive capacities are elaborated. That is, some kinds of knowledge, including object concepts, are *innate*. Innateness may refer to skills or representational content that is present at birth, purely “genetic” or “biological” in origin, universal, constant across development, modular, unlearned, or some combination of these attributes (cf. Cowie, 1999; Elman, Bates, Johnson, Karmiloff-Smith, Parisi, & Plunkett, 1996). Nativist views are long-established; Plato and Descartes, for example, proposed that some ideas were universal and available innately because they were elicited in the absence of any direct tutoring or instruction, or were unobservable in the world, and thus unlearnable. Nativist views have grown increasingly sophisticated and nuanced with the advent of rigorous methods for testing infants and young children in the last century, as the idea of unlearned concepts spread from research on object perception to social development (e.g., Spelke & Kinzler, 2007).

Representations of objects as obeying commonsense, real-world constraints, such as persistence and identity across occlusion, solidity, and inertia, have led to arguments for three kinds of innate object concepts. First, early concepts seem to develop too quickly to have derived from postnatal learning. Second, infants’ detection of apparent violations of simple physical constraints has been proposed to arise from *contrastive evidence*, opportunities to observe conditions under which an object behaves in a manner consistent or inconsistent with a particular concept (Baillargeon, 1994). A concept of persistence across occlusion must be innate, so goes the reasoning, because there are no available opportunities to observe conditions under which an object goes out of existence (Aguilar & Baillargeon, 1999). Third, there is evidence from nonhuman animals and anatomical specialization in humans for commonality of function across species, and commonality of structure across individuals, suggesting a kind of pretermination of some concepts, such as detecting the number of items in small sets of objects, that is “programmed” via evolutionary pressure (Dehaene, 1997; Wynn, 1998). A related argument for nativist theory comes from evidence for mechanisms by which cortical structure emerges from intrinsic molecular and chemical mechanisms that operate prenatally. For example, neural connectivity patterns in early visual cortex (i.e., area V1) originate in part from spontaneous activity in retinal cells that passes, wavelike, to neighboring cells (Morgan, Soto, Wong, & Kerschensteiner, 2011; Wong, 1999). This loosely structured activity is conveyed, in turn, through to higher stages of subcortical processing until reaching the cortex,

imparting a close correspondence between activation of spatial layout of retina and the circuitry of V1. The result is a cortical map that encodes spatial position in the environment, already set up to encode the locations of visual stimuli once the infant is born.

Fundamental object concepts are, as far as we know, universal across individuals and societies, and emerge early in infancy. Nevertheless, there is clear evidence for developments in object knowledge across the first several months after birth. We do not know whether these changes are inevitable, arising, for example from the natural course of neural maturation, or whether they depend on exposure to the normal flow of activities and events in the everyday surroundings, and whether and how concepts are modified when development proceeds atypically (e.g., in blindness). A range of mechanisms provides a structured cortex at birth in humans, but their contributions to the neural circuits necessary for veridical object concepts are also unknown (see Elman et al., 1996). One possibility is that prenatal development results in a cortex without the fine-grained neural microcircuitries necessary to support object concepts (M. Johnson, 1997). On this view, object concepts are acquired, in part, by viewing objects in the environment, subsequent to onset of exposure to patterned light. The distinction between what is innate and what is learned becomes blurred at this level of analysis, and, notably, development is always a matter of building new structure upon the old, whether the structures under consideration are concrete, such as arrangements of neural connections, or more abstract, such as object concepts (in the words of Elman et al., 1996, “interactions, all the way down”). The infant is always an active perceiver, ready and able to acquire and retain information, prepared to discover the patterns and regularities in the events she views in the surrounding environment.

Information-Processing Theory

In many respects information-processing theory is the polar opposite of nativist theory. Rather than presuppose an unchanging, innate core of (conceptual) cognitive capacities, information-processing theorists posit a set of sensory, perceptual, and (nonconceptual) cognitive processes that are constant across development (Cohen, 1998; Cohen, Chaput, & Cashion, 2002). These processes include perceptual sensitivities to auditory and visual input, memory, attention, and categorization. On this view, complex and mature concepts are constructed from these more primitive mechanisms, and the principal developmental changes

occur in the *content* of information, and what constitutes a *unit* of information. Cohen et al. (2002) outlined six principles of information-processing and their development, as follows: (1) there is an innate information-processing system, (2) infants form higher from lower units in hierarchical fashion, (3) higher units serve as components for still-higher units, (4) there is a bias to attend to highest-formed units, although (5) lower-level units are still utilized depending on the context, and (6) this learning system applies throughout development and across domains.

Units of information naturally expand with improvements in information-processing skills: Initially, the information that is accessed is relatively simple, but with development, infants become able to integrate the lower-level units of information into a more complex, higher-level unit, these higher-level units serve as the components for even more complex units, and so on. Concepts are thus formed incrementally in a bottom-up fashion. This hierarchical approach to cognitive development is repeated across domains, underlying skill acquisition and proficiency over a range of tasks, and throughout the lifespan.

Experiments that examine developmental changes in infants' detection of correlations among stimulus attributes during a category formation task provide evidence for this approach. Experiments on categorization in infants must employ artificial categories the infant has not experienced previously, to avoid possible confounds of familiarity with stimulus materials, and manipulate category exemplars systematically to determine how the infant processes and organizes them (Cohen, 1998). Younger and Cohen (1983, 1986) adopted this strategy in studies in which infants were presented with line drawings of artificial animals. Features varied from animal to animal—ears, tail, body, and number and type of legs. In one set of experiments (Younger & Cohen, 1986) those feature values were tightly correlated with one another so that one animal always had fluffy ears, a horse tail, a giraffe-like body, and four long legs, while another animal always had antlers, a bunny tail, a bear-like body, and two short legs. Using a “switch” design, in which test stimuli contain novel combinations of familiarized features, the researchers showed that 4-month-old infants only responded to novel features but didn't seem to notice when familiar features were combined in novel ways. By contrast, 7- and 10-month-old infants seemed to respond to the animals as “wholes,” noticing changes in the relations among the features. In another, more difficult task, infants viewed sets of animals containing a subset of correlated features and other features that varied randomly. Now instead of having to recognize two animals, infants

had to recognize two distinct animal categories (i.e., four web-footed feathery animals versus four club-footed fluffy animals). This experiment again revealed that 4-month-olds relied on specific features while 10-month-olds responded to relations among features (in this case, categories). Seven-month-olds, despite being able to respond to relations among features in the simpler task, now responded like 4-month-olds when the task required categorization (which was relatively difficult). That is, the requirement to form categories “overloaded” the system for 7-month-olds, and they fell back to a simpler level of processing.

Experiments that corroborate the dynamic shifting between processing of higher-level concepts and processing of lower-level components were reported by Cohen and colleagues (Cohen & Amsel, 1998; Cohen & Oakes, 1993; Oakes and Cohen, 1990). Infants between 4 and 10 months of age were tested with stimuli in which an object moves across the display into the vicinity of a second object. If the objects make contact, and the second object moves away abruptly, adults report a causal relation between the two, a “launching” event. The likelihood of causal perception at any particular age is a function of event complexity. For example, 6.5-month-olds responded to causality, and not merely the movements of the individual components of the event, as long as the objects were simple shapes. With more complex objects, infants at this age responded solely on the basis of the spatial and temporal characteristics of the objects in the displays. Ten-month-olds responded to such displays on the basis of causality, but failed to detect causality when the objects themselves changed from trial to trial while maintaining a causal relation. Presumably, as the increasing complexity of stimuli constrains processing, infants are compelled to process events at a perceptual, rather than a conceptual level.

A substantial body of evidence, therefore, demonstrates that infants analyze motion patterns and configurations of stimulus components prior to organizing these components into higher-level structures or concepts. Information-processing theory provides a description of this developmental progression, but leaves missing an explicit characterization of how it occurs. For example, it remains unclear how, exactly, infants come to perceive connectedness of two visible parts of a scene, and how, exactly, infants come to perceive persistence of an object that has gone out of view (evidence is described in greater detail below). We know that these two processes mature postnatally, a crucial advance contributed by evidence consistent with information-processing theory, but what is still needed

is an explanatory account of the mechanisms that underlie successful performance at occlusion tasks, and how these mechanisms develop.

Gibsonian Theory

The Gibsonian (or *ecological*) view of perception and perceptual development was popularized by James J. and Eleanor J. Gibson (E. J. Gibson, 1988; J. J. Gibson, 1950, 1979). The Gibsons contested the extent to which perception could be understood with reference solely to the observer and the state of his or her knowledge base and its development over time. The focus of Gibsonian theory is on understanding and balancing these perceptual capabilities with the available information in the perceiver’s world. A central idea in this account is that mobile organisms are able to exploit visual information to maximum effect because motion and change provide important information for perception: The eyes rotate within the head, which moves relative to a body, which perambulates and explores the world. Moreover, motion of objects and events in the environment provide vital information about object properties, segregation, distance, and coherence. Different perceptual abilities may require varying contributions from native endowment, maturation, and learning. For example, although perceptual learning may be involved in calibration and fine tuning of sensory systems, the basic sensory mechanisms themselves are assembled via inborn and early maturing mechanisms, some of which are discussed in more detail in subsequent sections of this chapter.

Building on the idea that the actions of the developing child could promote learning about the visual world, E. J. Gibson (1988) posited several areas in which exploratory skills facilitate object knowledge. Newborns use visual scanning to obtain information about important events in the world, and over the first several months after birth, infants become increasingly skilled at coordinating eye movements with head movements. Coordination of visual and manual exploratory systems begins to develop around the fourth month, giving infants even more opportunities to learn about the distinctive features of objects. As self-locomotion begins around the eighth month, infants can use their own actions to situate objects within the three-dimensional world and discover the layout of an environment. In E. J. Gibson’s ecological approach, knowledge is grounded within action as the two form a mutual loop (E. J. Gibson, 1969). Actions take place, guided by simultaneously developing cognitive systems, and infants learn

and grow in a world of real, three-dimensional objects where they receive immediate feedback from their behaviors and learn the perceptual consequences of movements of eyes, head, limbs, and body. In addition, motor development is vital to revealing a number of important features of objects that cannot be learned easily through visual inspection without contact or active control (Bushnell & Boudreau, 1993). Action is constant, therefore, and inherently meaningful for the developing infant, due to its close links with perception, cognition, and learning.

Neoconstructivist Theory

The final theoretical view discussed in this section is neoconstructivism, a term intended to capture the constructivist goal of understanding developmental mechanisms, and at the same time reflecting dramatic advances in our knowledge of perceptual and cognitive development from neural, experimental, and computational perspectives (S. Johnson, 2010). As a consequence, this view acknowledges breakthroughs in methods, contributions from cognitive science (e.g., insights from connectionism, dynamic systems theory, and Bayesian networks), and findings from thousands of empirical studies. Together, these advances coalesce into a theoretical framework recognizing that Piaget's "fundamental idea seems now to have been absolutely right: that a biologically prepared mind interacts in biologically evolved ways with an expectable environment that nevertheless includes significant variation" (Newcombe, 2010, p. vi).

In common with Gibsonian and Gestalt theories, neoconstructivism stresses the vital contributions of a richly structured and predictable world, and perceptual systems

tuned to this structure, to developing cognitive systems. In common with information-processing theory, neoconstructivism highlights the substantial contributions of attention and learning mechanisms that are operational at birth and available throughout infancy, responsible for identifying, evaluating, storing, and synthesizing the environmental structure just mentioned. A sharp distinction between neoconstructivist and nativist theories is the emphasis on the need for organisms to, in the former case, *discover* structure in the environment—structure to perceive and learn, and from which to build knowledge—versus the need for organisms to, in the latter case, *possess* knowledge prior to encountering the structure—knowledge that is used to interpret what is experienced. The neoconstructivist solution to this "chicken or egg" problem is to propose key developmental mechanisms that can be investigated empirically and evaluated for their contributions to the constructive process (see Johnson, 2010, for details).

Foremost among the mechanisms important for early developments in perception and cognition are *action systems*—oculomotor, manual, postural, and ambulatory, and combinations of these systems—with which children explore the world. Individual differences in eye movement patterns, for example, were associated with *perceptual completion* of partly visible objects behind occluders (Johnson, Slemmer, & Amso, 2004; see Figure 3.2). That is, examining relevant object parts appears to facilitate perception of their unity. Likewise, individual differences in coordinated visual-manual exploration of objects, facilitated by the onset of unaided sitting (freeing the hands for holding and manipulating objects), were associated with 3D object completion, as when objects are perceived as coherent wholes in 3D space despite limited views

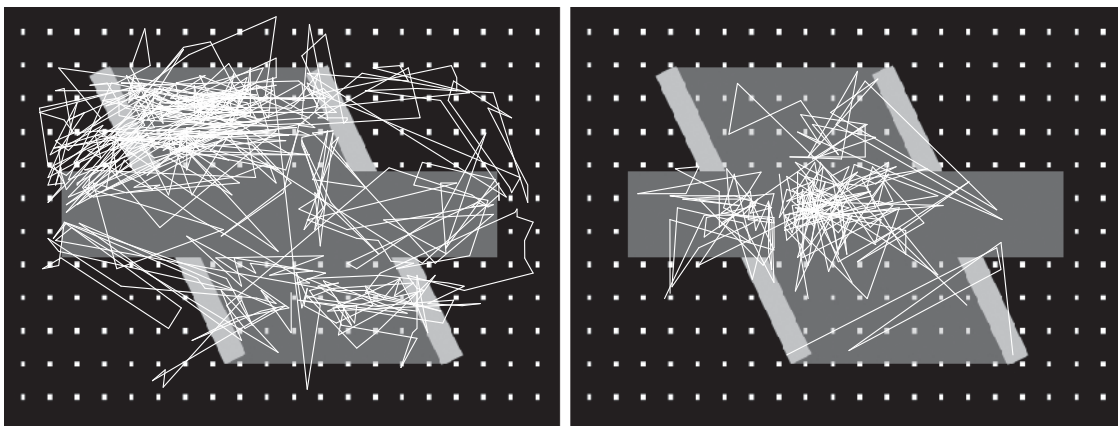


Figure 3.2 Recordings of oculomotor scanning of a display depicting a partly occluded object in motion. Left: This infant scanned more in the vicinity of the moving rod parts. Right: This infant appeared more interested in the stationary box than the moving object.

(Soska, Adolph, & Johnson, 2010). Finally, the onset of sitting, crawling, and walking, in turn, allow the developing child to determine whether a gap in a supporting surface is risky or safe to reach across, yet, interestingly, the level of risk must be learned again with the acquisition of each skill (Adolph, 2000). This “specificity of learning” of relations between action systems implies that experience with earlier-developing systems does not immediately translate into appropriate guidance of later ones; they must be learned and constructed anew.

A second important developmental mechanism can be described as “computational inference,” the examination of how knowledge is influenced by, and built from, evaluation of probabilities of perceived events. One currently popular approach is Bayesian statistical inference, a branch of mathematical probability theory that allows one to model uncertainty about the world and outcomes of interest by combining prior knowledge and currently observed evidence (Mareschal & Westermann, 2010; Tenenbaum, Kemp, Griffiths, & Goodman, 2011). As evidence accumulates for the match or mismatch between what is perceived and what is currently hypothesized, the hypothesis can be modified and used to predict future events, as when 12-month-olds assessed possible outcomes of complex scenarios involving objects moving out of a container with an occluded opening (Téglás et al., 2011). Infants’ expectations about these events revealed they were reasoning about prior observed temporal, spatial, and logical cues that predicted which objects would emerge. Statistical learning, likewise, contributes to computation of probabilities of events in patterns ranging from simple to complex (Romberg & Saffran, 2010), in stimuli ranging from tones, phonemes, and words (Saffran & Thiessen, 2007) to colored shapes (Kirkham, Slemmer, & Johnson, 2002) and human actions (Roseberry, Richie, Hirsh-Pasek, Golinkoff, & Shipley, 2011), and in ages ranging from newborns (Bulf, Johnson, & Valenza, 2010) to adults (Fiser & Aslin, 2002). Finally, social information serves an important function in neoconstructivist theory. For example, 9-month-old infants used social cues (direction of gaze) in conjunction with probabilistic information to determine which portions of objects were likely to be connected versus split (Wu, Gopnik, Richardson, & Kirkham, 2011). Linguistic information facilitates formation of perceptual categories for nonsense objects, perhaps because it directs children’s attention and highlights commonalities across perceptual features (Sloutsky, 2010).

Researchers of a neoconstructivist persuasion have highlighted three processes that characterize early perceptual development. The first is known as *perceptual tuning*,

a term that describes processes by which perception becomes increasingly sensitive to functionally significant or meaningful features of the world, while simultaneously insensitive to functionally insignificant features. For example, adults readily discriminate phonemes from their native language yet fail to discriminate or produce phonemes from a foreign language. This tuning process occurs during the first year (Werker & Tees, 1984) and also characterizes early development of face perception (e.g., own- versus other-species or other-race faces [Pascalis et al., 2005] and musical patterns [Hannon & Trehub, 2005b]). Perceptual tuning may contribute to “enculturation” of music and speech (Hannon, 2010), as described in greater detail subsequently, and perhaps other important social and communicative events. The second process is development of expertise, or *perceptual learning*, whereby observers come to detect ever more fine-grained structure with experience. Formation of perceptual categories (e.g., cats versus dogs), for example, relies in part on attending to and learning diagnostic features that help define the categories (e.g., shapes of the ears, proportions of the legs and bodies), even in advance of any conceptual knowledge of animal species (Quinn, 2010). Finally, infants attend to and exploit *multimodal* perceptual information, noticing commonalities in input structure and identifying invariant intersensory relations and correlations across modalities. Three factors have been suggested as particularly relevant to the learning process: *availability* of information, *coherence* of the information, and *sensitivity* to the information (Kirkham, 2010). For example, visual statistical learning of predictable locations is facilitated in 8-month-olds by the addition of color and shape information to individual items, but location information is not helpful to younger infants who may lack a spatial reference frame; 11-month-olds learn locations even in the absence of the additional information (Kirkham, Slemmer, Richardson, & Johnson, 2007).

NEURAL FOUNDATIONS OF PERCEPTUAL DEVELOPMENT

The brain consists of systems that take in and process sensory information, and control actions. Inputs from peripheral sensory systems are routed through the thalamus, located in the center of the cortex at the top of the brainstem. The thalamus sends projections to primary cortical regions, which are devoted to processing sensory inputs, for example the primary visual area (area V1, Figure 3.3). Primary areas in turn project to secondary areas (V2, V3,

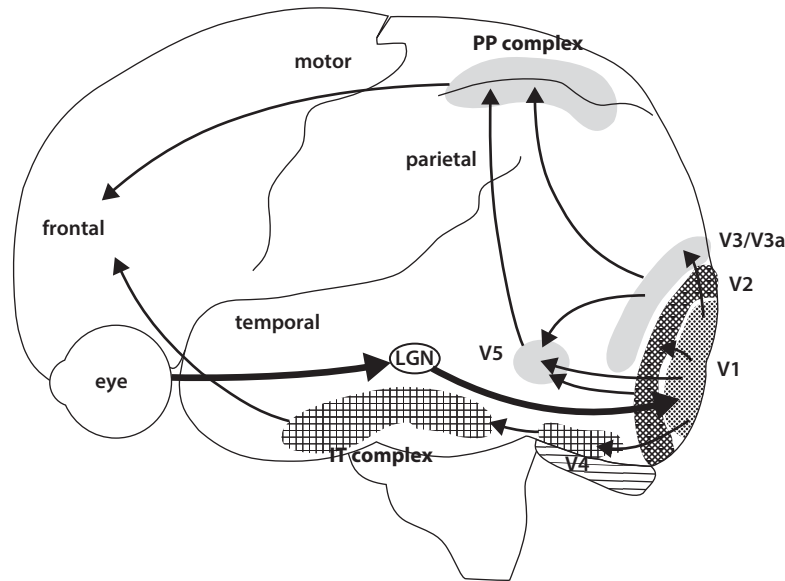


Figure 3.3 Major subcortical and cortical structures involved in visual processing, and the flow of visual input between structures. LGN, later geniculate nucleus; PP, posterior parietal; IT, inferior temporal.

Source: From *The Developing Visual Brain*, by J. Atkinson, 2000, New York, NY: Oxford University Press. Reprinted with permission.

V4, and so forth) for additional processing of low-level attributes such as color, form, and motion. From here, there are connections to regions responsible for evaluation and action planning, as seen in Figure 3.4, which depicts cortical networks for eye movements. Similar organizational schemes are in place for auditory (e.g., Weinberger, 2007) and somatosensory (e.g., Kaas, 1991) information. Aspects of neural development most relevant for understanding perceptual development include organization and

growth of subcortical structures and cortical networks, and plasticity and experience-dependent organization of cortical representations. These issues are covered extensively in Stiles, Brown, Haist, and Jernigan, Chapter 2, this *Handbook*, this volume (as is discussion of the proliferation and pruning of synaptic connections between neurons, not discussed here), and the topics we present below are accordingly selective.

Organization and Growth of Subcortical Structures and Cortical Networks

Perceptual systems begin to take shape early in prenatal development. Many major structures (neurons, areas, and layers) in sensory cortical and subcortical areas are in place by the end of the second trimester *in utero* (e.g., Zilles, Werners, Busching, & Schleicher, 1986). Later developments consist of the physical growth of neurons and their connections, which are, in part, activity-dependent (Greenough, Black, & Wallace, 1987; Huttenlocher, de Courten, Garey, & Van Der Loos, 1982). For example, the retina starts to form around 40 days after conception and is thought to have a relatively complete set of cells by 160 days, though the growth of individual cells (rods and cones) and their organizational structure continue to mature well past birth (Finlay, 2008; Finlay, Clancy, & Kingsbury, 2003). The distinction between the fovea (the central part of the retina) and other regions emerges early, but the topology and patterning of receptors and neurons continue to

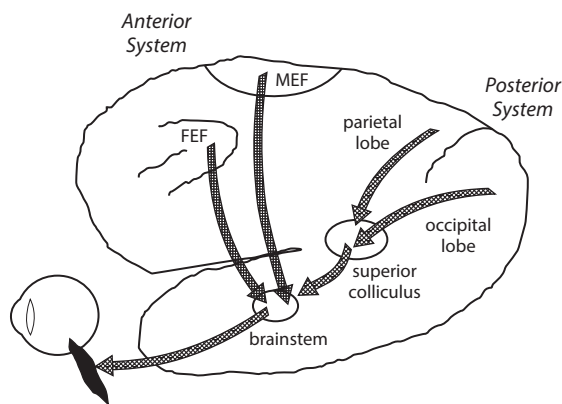


Figure 3.4 Major subcortical and cortical structures involved in oculomotor control. FEF, frontal eye fields; MEF, medial eye fields.

Source: From "Look and See: How the Brain Moves Your Eyes About," by P. H. Schiller and E. J. Tehovnik, 2001, in C. Casanova and M. Ptito (Eds.), *Progress in Brain Research*, Volume 134, pp. 127–142, Amsterdam, The Netherlands: Elsevier. Reprinted with permission.

change throughout prenatal development and the first year after birth. Photoreceptors in the fovea are over-represented in the cortical visual system, and detailed information about the visual environment is enabled by moving the eyes to different locations in the scene. The musculature responsible for eye movements develops before birth in humans, as do subcortical systems (e.g., superior colliculus and brainstem) to control these muscles (Johnson, 2001; Prechtl, 2001). However, cortical structures that impinge on these lower structures (Figure 3.4) develop during infancy.

Growth of the eye after birth presents a challenge to the developing visual system, because the retina changes shape as the eye gets larger, and the photoreceptors that receive visual information from specific regions relative to the point of gaze change. The number and types of photoreceptors also change: The fovea adds relatively fewer new cells than peripheral retina, matures more quickly, and becomes “wired” sooner; in addition, rod cells are initially overproduced and many die off in a protracted process (Finlay, 1992; Provis & Penfold, 1988). These developmental events necessitate plasticity in downstream developmental mappings of visual inputs to the central nervous system, as the visual angle corresponding to a particular set of retinal cells will undergo substantial change from birth to the first birthday (Aslin, 1993). A second way in which the growth of the eye requires plasticity is the need to match the length of the eye to the optical power of the lens and cornea (see Troilo, 1992). At birth, the focus of the image on the retina is rather variable, and it is tuned in part by experience (Howland & Sayles, 1985). As the image moves in and out of focus, the activity levels in the photoreceptors and the subcortical and cortical structures to which the eye connects likewise fluctuate, and under typical circumstances the system “settles” onto a solution that maximizes such activity. In addition, visual cortex can send an accommodative signal to the intraocular musculature to bring an image into focus and thus induce high retinal activity. As a consequence of such activity, the optics and length of the eye are matched and a signal is given to limit growth (Wallman, 1993).

Cortical sensory systems consist of richly interconnected yet functionally segregated networks of areas, each specializing in analyzing and processing different aspects of the input, and producing signals to assist in the determination of appropriate behavior. Visual cortex, for example, has distinct (yet connected) mechanisms for processing contours, motion, luminance, color, objects, faces, approach versus avoidance, and so forth. In somatosensory cortex, specific regions are dedicated to inputs from and

control of body parts (e.g., fingers, limbs). Areal patterns are present in rudimentary form during the first trimester but the final forms continue to take shape well after birth; like synaptic pruning, developmental processes are partly the result of experience. Some kinds of experience are intrinsic to the visual system, as opposed to outside stimulation. For example, spontaneous prenatal activity in visual pathways contributes to *retinotopic mapping* (Sperry, 1963), the preservation of sensory structure beginning in the retina and extending through the thalamus, primary visual cortex, and higher visual areas. Waves of coordinated, spontaneous firing of retinal cells have been observed in chicks and ferrets (Wong, 1999); these waves travel across the retinal surface and are then systematically propagated through to the higher areas. This self-organizing process might be one way by which correlated inputs remain coupled and dissimilar inputs become dissociated in the visual system, even prior to light exposure. A number of other sensory mapping mechanisms have been discovered (Fraser & Perkel, 1990; Udin & Fawcett, 1988), including mapping by proximity, temporal gradients, sorting statistical regularities from uncorrelated patterns, and trial and error, as when different motor sequences are enacted, evaluated, and retained (or discarded) to bring the hands nearer to a desired object (e.g., Thelen et al., 1993). Different mechanisms contribute to mapping at different developmental timescales (e.g., molecular signals are more important early, and activity-dependent organization late), and the balance varies by species. As noted by Finlay et al. (2003), the multiplicity of potential mechanisms should be instructive to developmental scientists who may be tempted to posit “the” mechanism of a particular developmental phenomenon!

Plasticity and the Role of Experience

As we discussed previously, competing theories posit different roles for experience-independent mechanisms that may yield areal specificity in the cortex, but this should not be interpreted to suggest that there is evidence for explicit genetic instructions for the wiring of the brain. Rather, the evidence is far stronger for cortical *plasticity*, the ability to reorganize in response to environmental pressures or inputs. The possibility that brain development is shaped by experience was first proposed by Hebb (1949), who noted that rats that had been brought to his home when young and kept for extended intervals as pets outperformed their lab-reared counterparts in problem-solving tasks. Superior performance appeared to be permanent in the

animals with enriched early experience. Hebb termed this phenomenon “use-dependent plasticity” (see Rosenzweig & Bennett, 1996, for a review of the animal literature), and there is abundant evidence that early experience also influences human cortical development (Webb, Monk, & Nelson, 2001), including adaptation to deprivation (e.g., Tottenham, 2012).

An important example of plasticity in perceptual development is the formation of *ocular dominance columns* in visual cortex, which are composed of alternating “stripes” of neurons that receive inputs from either the left or right eye (Figure 3.5) (see also Stiles, Haist, & Jernigan, Chapter 2, this *Handbook*, this volume). These are thought to be important for establishment of binocular vision and *stereopsis*, the perception of depth and distance from the disparity in views of objects received by the two eyes. Development of ocular dominance columns begins in the retina well before the onset of external visual experience. Retinal ganglion cells grow and they extend their axons soon after generation. These axons start to fire early on, and quickly influence their neighbors’ firing patterns; this activity coalesces into waves that are propagated into correlated activity all the way into visual cortex, once the axons have grown to sufficient length. Retinotopic mapping means that V1 in some ways preserves a representation of the spatial relations present in the visual array as seen by the observer with remarkable fidelity (Figure 3.6). However,

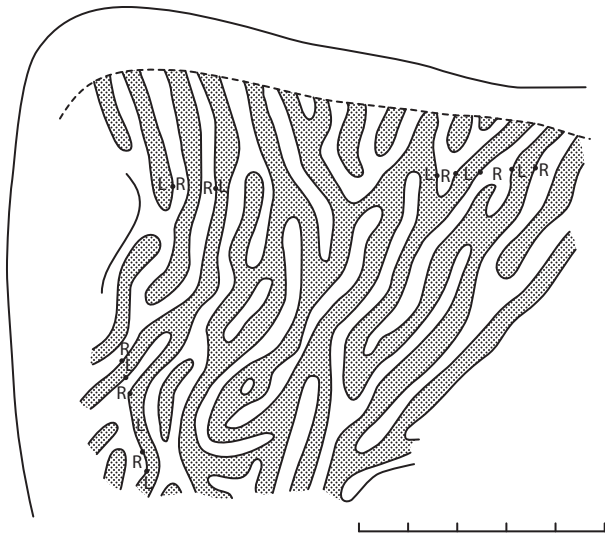
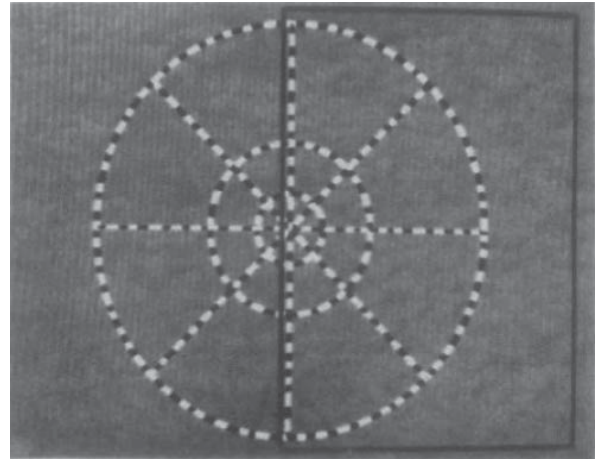
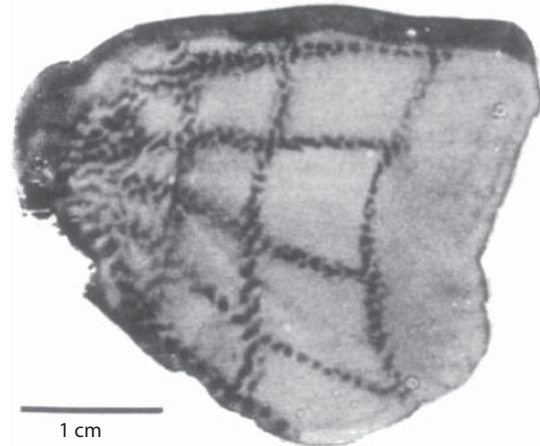


Figure 3.5 Ocular dominance columns in macaque visual cortex. Shaded stripes indicate tissue receiving input from the left eye; white stripes are from the right eye.

Source: From “The Pattern of Ocular Dominance Columns in Macaque Visual Cortex Revealed by a Reduced Silver Stain,” by S. LeVay, D. H. Hubel, and T. N. Wiesel, 1975, *Journal of Comparative Neurology*, 159, pp. 559–576. Reprinted with permission.



(a)



(b)

Figure 3.6 Top: Visual stimulus to which an anesthetized monkey was exposed for 25–30 min. Bottom: Pattern of activation in primary visual cortex yielded by exposure to the radial pattern, after staining with 2-Deoxyglucose.

Source: From “Deoxyglucose Analysis of Retinotopic Organization in Primate Striate Cortex,” by R. B. H. Tootell, M. S. Silverman, E. Switkes, and R. L. De Valois, 1982, *Science*, 218, pp. 902–904. Reprinted with permission.

activity in the two eyes is not correlated, and the brain must have some means of identifying which eye has produced which signal—hence ocular dominance columns, whose stripes are segregated and thus preserve eye-of-origin information. Visual areas “downstream” from V1, in turn, make use of this information and resolve the disparity that is frequently present but seldom noticed in our everyday visual experience. Formation of these columns is susceptible to experience. For example, the projections from the two eyes through the thalamus and into V1 may self-segregate via a competitive process;

if one eye is removed the other innervates cortical territory normally devoted to the now-inactive input (Shatz, 1990). If both eyes are sutured shut, so the animal never receives experience with patterned light, the segregation into ocular dominance columns is delayed but not prevented (LeVay, Wiesel, & Hubel, 1975). If an individual is strabismic (cross-eyed or wall-eyed), such that the two eyes never converge on the same point in visual space, the result is a substantial reduction in cells that process eye-of-origin (Hubel & Wiesel, 1965). Finally, ocular dominance columns can be created artificially: Striped input patterns were produced in frogs by implanting a third eye (Constantine-Paton & Law, 1978)!

As a final remark in this section, it is important to note that infants are born helpless in a physically and behaviorally altricial (immature) state, and require years of development before they are capable of leaving the family and surviving on their own. This delayed and protracted human maturation is often presented as a “design feature” endowed through evolutionary time, important for our unusual learning capacity relative to other species (e.g., Bjorklund, 2007). As noted, a substantial amount of brain development occurs after birth, but there is disagreement as to the extent to which human newborns are *neurally* immature. A statistical modeling approach that compared the developmental timing of neural events in humans and other mammals revealed that human neural development is actually relatively *advanced* at birth (Clancy, Darlington, & Finlay, 2000; Darlington, Dunlop, & Finlay, 1999; but see K. R. Gibson, 1990 for a different perspective). Relative to other primates, there is a mismatch of body and brain sizes in humans at birth; that is, the brain is large relative to the body. On this view, nonneural physical development lags behind brain development during gestation. For example, at 7 months postconception, neural tissue is comparatively developed (i.e., the majority of cortical cells and circuits are in place), but the lungs are not yet fully functional, subcutaneous fat deposits that provide postnatal insulation have not yet formed, and so forth. By contrast, the auditory system is functional and there is ample evidence for fetal learning and retention of speech and other auditory patterns (e.g., DeCasper & Spence, 1986; Mampe, Friederici, Christophe, & Wermke, 2009; van Heteren, Boekkooi, Jongsma, & Nijhuis, 2000). Finlay et al. (2003) suggested that this mismatch between the advanced neural and delayed somatic developmental timetables may give the human infant an “enforced,” relatively nonactive period to observe and assimilate information prior to the extensive motor activity that accompanies later

development. Perhaps this provides a foundation for later perception-action links during a developmental period in which the infant is protected by the parents from external harm, and harm to the self that might be engendered by attempts at actions (e.g., walking) for which he or she is not prepared.

INTERIM SUMMARY, AND A LOOK AHEAD

We have presented a theoretical and empirical backdrop for understanding early perceptual development and its neural foundations. A common theme emerges from these discussions and informs the remainder of the chapter: Understanding processes and mechanisms of development is vital for understanding any set of psychological constructs, including human perception, because development is, in an important sense, the *cause* of the construct. In the case of human perceptual development, it is clear that at its origins lie a combination of intrinsic (e.g., unlearned, experience-independent) and environmental (e.g., learned, experience-dependent) processes, and that developmental trajectories can be altered, often significantly, depending on the timing, interplay, and relative contributions of these influences. The theories that we discussed previously weight these processes somewhat differently. In the sections to follow, we focus on questions of how the developing child extracts meaningful information from the sensory array—that is, how the observer detects, synthesizes, and interprets sensory input so as to yield perception of structured events and objects—and how effects of experience on perceptual development interact with developmental timing and what has already been acquired.

AUDITION

The purpose of the auditory system is to transduce sound pressure waves from the atmosphere into neural signals that are relayed to the brain for processing and action planning. Waves are funneled through the ear canal to the tympanic membrane, and mechanically transduced through the middle ear into a fluid-filled chamber, which in turn connects to the inner ear, the site of initial neural transduction (see Figure 3.7). The outer ear consists of an external flap of tissue known as the pinna with a complex undulating surface that has the effect of creating

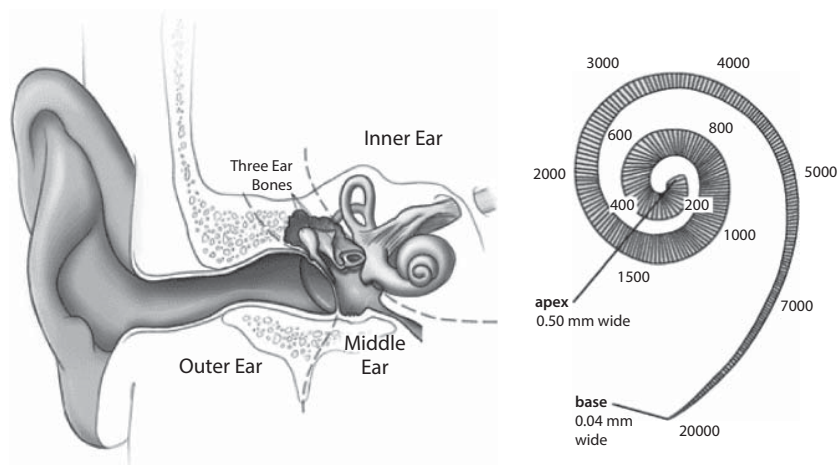


Figure 3.7 Left: major structures of the ear. Right: schematic depiction of the cochlea, illustrating the relation between sound frequencies (in Hz) and width of the basilar membrane.

Source: Retrieved from <http://science.education.nih.gov/supplements/nih3/hearing/guide/info-hearing.htm>

distinct reflections and delays between the two ears. The differences in these effects across the two ears can help the listener localize sounds. The tympanic membrane, or eardrum, receives vibrations traveling up the auditory canal and transfers them through three tiny bones (the smallest in the body), called ossicles, to the oval window, which divides the middle and inner ears. Vibration of the eardrum is transmitted to the oval window of the inner ear by means of a lever action of the ossicles working in tandem. The lever action is adjustable under muscular control (the acoustic reflex) and can attenuate loud sounds (higher than about 75 dB), for protection of the ear, by stiffening the chain of ossicles and reducing the efficiency with which vibrations are transmitted from the tympanic membranes to the inner ear. The inner ear consists of the snail-like structure known as the cochlea. It converts mechanical vibrations from the ossicles into nerve firings that are passed via the cochlear or auditory nerve to the medial geniculate nucleus (in the thalamus), and then are routed to auditory cortex. The cochlea consists of a spiral-shaped tube filled with a fluid known as perilymph, and lined with hair cells that when triggered send neural impulses down the auditory nerve. As the ossicles vibrate, they set up vibrations in perilymph, which in turn trigger hair cells whose lengths correspond to different frequencies of input, longer hair cells for lower frequencies, and shorter hair cells for higher frequencies (the so-called *tonotonic map*, corresponding to the visual system's retinotopic map described previously). These are located toward the base and the apex of cochlea, respectively (see Figure 3.7).

Hearing in the Fetus and the Neonate

The auditory system is more developed at birth than the visual system (e.g., Mastropieri & Turkewitz, 1999). Fetuses provide evidence that they can hear by about the seventh month of pregnancy (Groome et al., 2000), and the cochlea is known to be largely structurally mature by the end of pregnancy (Pujol & Lavigne-Rebillard, 1992). However, the intrauterine auditory environment is markedly different from the auditory environment outside the womb. Recordings taken within the womb reveal a predominance of low-frequency internal sounds (maternal heartbeat, breathing, etc.), with environmental sounds available at or above 60 dB SPL and frequencies attenuated above 250–500 Hz giving them a “muffled” quality (Abrams, Gerhardt, Huang, Peters, & Langford, 2000; Gerhardt & Abrams, 1996). Fetal hearing can be assessed by measuring heart rate deceleration, which is associated with discrimination of and attention to sounds (cf. Sroufe & Waters, 1977), though this measure is somewhat dependent on fetal state (e.g., periods of high and low variability; Lecanuet, Granier-Deferre, & Busnel, 1988). By 36–39 weeks, fetal heart rate responds differentially to rhythmic or pulsed sounds versus continuous sounds (Groome et al., 2000), and musical (complex) notes of different pitch (Lecanuet, Granier-Deferre, Jacquet, & DeCasper, 2000), and piano melodies versus recorded speech (Granier-Deferre, Bassereau, Ribeiro, Jacquet, & DeCasper, 2011; Kisilevsky, Hains, Jacquet, Granier-Deferre, & Lecanuet, 2004).

An interesting consequence of prenatal hearing is the opportunity it provides for learning. By the time of birth,

infants have been exposed to several months of maternal speech, and despite the filtered nature of the speech signal in utero, many aspects of speech are interpretable (Griffiths, Brown, Gerhardt, Abrams, & Morris, 1994). The fetus responds differentially to contrasted vowels (“ee” versus “ah”) (Zimmer et al., 1993), maternal versus nonmaternal voices (Kisilevsky et al., 2003, 2009; cf. DeCasper & Fifer, 1980), and native versus non-native language (Kisilevsky et al., 2009). Neonates also discriminate languages on the basis of prosodic rhythm (Nazzi, Bertoni, & Mehler, 1998), and they can remember specific passages of text read by the mother prior to birth (DeCasper & Spence, 1986). In neonates, the left superior temporal region of cortex (corresponding to Broca’s area) responds to speech, implying that cortical speech perception centers become specialized prior to birth (Imada et al., 2006).

Auditory Sensitivity

The minimum physical energy, or lowest intensity level (dB), at which a sound can be detected is called an *absolute threshold* (Gelfand, 1998). For adults, absolute thresholds are lower at high frequencies than at low frequencies. An *audibility curve* is a function relating absolute sensitivity to frequency, and it is one way of representing the relation between intensity and frequency (Figure 3.8). Thresholds have been measured from a few days after birth to 10 years of age, using pure tones, filtered noise bursts, and clicks (Berg, 1993; Schneider, Trehub, & Bull, 1980; Trehub, Schneider, & Endman, 1980; Weir, 1979). A few days after birth, thresholds tend to be about 30–70 dB higher than those of adults. The audibility curve is approximately

flat, which means that newborns’ thresholds are closer to adults in the lower frequencies than in the higher frequencies, since adults’ audibility curves tend to get lower (more sensitive) as frequency gets higher (Weir, 1979). Audibility curves become more adult-like (less flat) by 6 months, but thresholds are still elevated across the frequency range (Berg & Smith, 1983). The variability of the audibility curves is fairly similar for infants and adults, suggesting that differences between the populations reflect real changes in sensory capacities (Sinnott, Pisoni, & Aslin, 1983).

During the first year after birth, thresholds rapidly improve in the higher frequency range. At 6 months, thresholds are within 20 dB of adult thresholds for frequencies between 4 and 19 kHz, but are much higher for frequencies in the 200–2000 Hz range (Schneider et al., 1980; Trehub, Schneider, Morrongiello, & Thorpe, 1988). By 12 months, thresholds improve at lower frequencies (200–2000 Hz) by about 10 dB but are still well above adults’ low-frequency thresholds. At 24 months, infants have adult-like thresholds for very high frequencies (19 kHz) but thresholds even at 10 kHz are still significantly higher than adult thresholds (Schneider et al., 1980). The greater improvement of higher- over low-frequency thresholds continues until about 10 years of age. By the age of 10 years, children’s thresholds resemble adults’ thresholds across all frequency ranges and even surpass adult thresholds at very high frequencies, such as 20 kHz (Elliott & Katz, 1980; Schneider, Trehub, Morrongiello, & Thorpe, 1986; Trehub et al., 1988).

Behavioral changes in thresholds may result from the development of the ear and cochlea, changes in the

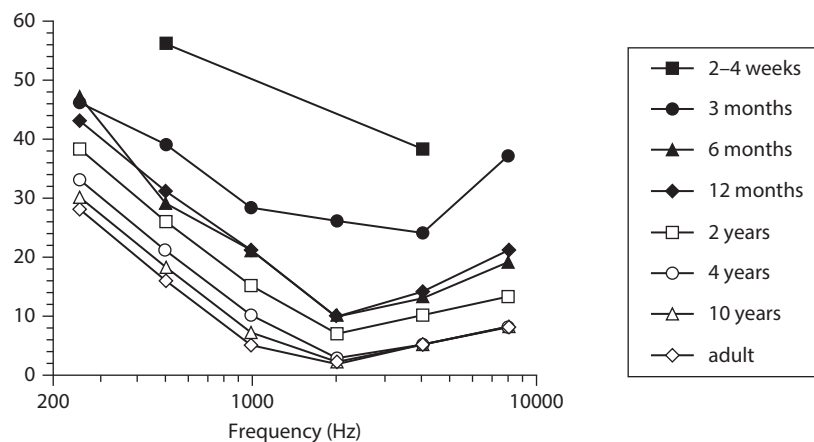


Figure 3.8 Development of the audibility curve.

Source: From “Human Auditory Development,” by L. A. Werner, in *The Senses: A Comprehensive Reference: Volume 3. Audition* (pp. 871–894), edited by R. Hoy, P. Dallos, and D. Oertel, 2007, St. Louis, MO: Elsevier. Adapted with permission.

auditory nervous system, or nonsensory processes such as attention and motivation. For example, the flatness of the newborn audibility curve resembles the flatness of an underwater audibility curve. In the latter case this is caused by the absence of middle ear conduction, leading to the suggestion that middle ear immaturity might cause the flatness of neonate audibility curves (Weir, 1979). Rapid development of high-frequency detection in the first 6 months has been related to changes in the cochlear tonotopic map. Developmental studies with chickens and rats suggest that a given cochlear position encodes progressively higher frequencies with age. This mapping can shift by as much as 15%: Rat pups can be trained to respond to an 8 kHz tone, but after 3 days this response “drifts” and is observed only for a 12 kHz tone (Werner & Gray, 1998). In addition, the changing size of the external ear may produce greater high-frequency resonance for younger, smaller ears than for older, larger ears, which may influence hearing throughout childhood and adolescence (Trehub et al., 1988).

Masked Thresholds

If a pure-tone signal or a signal with a narrow frequency band are presented within broadband background noise, the intensity level of the signal must be increased in order for it to be detected. This *masked threshold* (signal detection in the presence of other sounds) is higher than its absolute threshold (detection in silence). The masked threshold will vary with the bandwidth of the mask. When the mask is centered at the signal frequency, widening the bandwidth will increase masking only up to a certain point, after which no change in bandwidth will affect detection of the signal (Gelfand, 1998). This discovery introduced the idea of the *critical band* or auditory filter. The ability of an individual to respond to one frequency in a complex sound is called *frequency selectivity* or *frequency resolution* because the narrowness or wideness of the critical band reflects the fine-tuning of frequency processing. It predicts, in theory, how well a given frequency will be detected in the presence of noise.

Like absolute thresholds, masked thresholds decrease with age. Masked thresholds improve by 15 dB between 6 months and 10 years, by which time they are very similar to adult values (Schneider, Trehub, Morrongiello, & Thorpe, 1989). Developmental changes in frequency resolution during infancy depend on frequency range. When auditory brainstem response (ABR, recordings of electrical activity in the brain obtained via surface electrodes)

is used to measure tonal masking thresholds, 3-month-old infant and adult tuning curves are similar in shape and width at lower frequencies (1000 Hz), but at higher frequencies (4–8 kHz) tuning curves are broader until after 6 months (Abdala & Folsom, 1995). Frequency resolution improves between 7 months and adulthood for both very low (700 Hz) and very high (11.3 kHz) frequencies, implying that frequency resolution matures earliest in the mid-center frequency range, followed by the highest and lowest frequency ranges (Ponton, Eggermont, Coupland, & Winkelaar, 1992).

Because masked thresholds are so high, some have concluded that this must mean that auditory filters narrow, or frequency resolution improves, as individuals mature. However, contradictory findings arise when diverging methods are used to estimate resolution. Critical bands can be measured directly, by obtaining detection thresholds while varying the bandwidth of the masking noise centered at the signal frequency, or indirectly, estimated from the signal-to-noise ratio at the masked threshold (critical band = signal power/wide-band noise power). Indirect estimates suggest that infant critical bands are several magnitudes of order higher than adult critical bands. By contrast, direct measurements suggest that critical bands were never more than 50% larger than adults as early as 6 months of age, and that they do not narrow with age (from 2 to 20 years) (Schneider, Morrongiello & Trehub, 1990).

Masked thresholds are still elevated between 3 and 5 years, and psychometric functions (used to describe relations between percentage of correct detections to the intensity of the signal) are slightly shallower in slope for 5-year-olds than for adults (Allen & Wightman, 1994). However, the substantial variability of child responses suggests a likely role of attentional factors such as the child’s individual response strategy. Adults can lower their signal detection thresholds by as much as 8 dB by listening selectively within a chosen frequency band, whereas infants and children do not appear to listen selectively. Adults are much better at signal detection when signals are drawn from within a limited frequency range (predictable) than when they are presented in multiple frequency ranges (unpredictable). By contrast, infants and children up to 6 years of age show no advantage for predictable over unpredictable signals (Allen & Wightman, 1995; Bargones & Werner, 1994; Halliday, Taylor, Edmondson-Jones, & Moore, 2008). Thus, the observed changes in masked thresholds may arise from listening strategies and attention, rather than from any developmental changes in the shape or width of the auditory filter.

Loudness and Frequency Discrimination

Differential sensitivity is the ability to perceive a difference between two signals, measured as a *difference limen* (DL), also known as a *just noticeable difference* (jnd). Whereas adults detect intensity changes of 1.5–2 dB, infants 7–9 months old have intensity DLs from 3–12 dB (Sinnott & Aslin, 1985). Between 4 and 6 years, intensity DLs decrease to adult-like levels (Werner & Gray, 1998). As described earlier, developmental changes may be partially attributable to attentional factors, such as how interesting the child finds the stimulus.

Using measures such as sucking rate, heart rate deceleration, and event-related potentials (measuring *mismatch negativity* to oddball stimuli using electroencephalography, or EEG), infants from a few days to 4 months of age have been shown to detect frequency changes of 200–800 Hz in the 200–1900 Hz range (Alho & Cheour, 1997; Berg, 1974; Ceperoniene et al., 2002; Trehub, 1973). High-frequency discrimination matures sooner than low-frequency discrimination. Between 3 and 8 months of age, infants can discriminate high-frequency changes (1–3 kHz) on the order of 2%, which is very close to adult discrimination (Olsho, 1982; Olsho, Schoon, Sakai, Turpin & Sperduto, 1982). However, for lower frequencies such as 440 Hz, significant declines in DLs are not observed until Ages 4–6 years (Jensen & Neff, 1993).

There are at least two possible explanations for this (Werner, 2007). First, poor low-frequency discrimination may stem from immaturity of *periodicity* processing in the brain; high-frequency discrimination depends primarily on place of stimulation along the basilar membrane and auditory filter width, whereas low-frequency discrimination requires a temporal frequency code. Second, the ability to make use of periodicity representations may change with development. There is evidence from the ABR that periodicity processing is largely mature by Age 5 or 6 (Hall, 1992), yet both children and adults benefit from training when making low-frequency discrimination (e.g., Halliday et al., 2008; Harris, 1952). Thus, children may learn to optimize discrimination of low frequencies after periodicity processing has developed.

Perception of Timbre and Pitch

Timbre or “spectral shape” refers to the relative amplitude of frequency components that make up a complex sound. Most sounds in nature are not pure tones, but are composed of a fundamental frequency and many component frequencies above it, most of which are harmonically related to the fundamental. When the relative amplitudes of these

frequency components change, so does the timbre of the sound. Such distinctions allow listeners to discriminate, for example, between vowels or between different musical instruments.

As young as 7 months, infants discriminate vowels and complex tones on the basis of spectral shape (Marean, Werner, & Kuhl, 1992). After familiarization to a set of complex tones having identical spectral structures but varied fundamental frequency, intensity, and duration, infants discriminate novel tones on the basis of whether they conform to the previously familiarized spectral shape (Trehub, Endman, & Thorpe, 1990). Likewise, 7-month-olds discriminate a tone with a rising spectrum (an increase in intensity of successive harmonics), from a same-pitch tone with a falling spectrum (a decrease in intensity of successive harmonics) (Clarkson, 1996). Nevertheless, discrimination of tonal complexes has been shown to improve from chance levels at the age of 4 years to adult-like levels at the age of 9 years. With background noise, children require even higher intensity levels to successfully discriminate a complex tone from aperiodic noise, showing elevated performance (relative to adults) even at the age of 9 years (Allen & Wightman, 1992).

Spectral structure is also essential for the perception of *pitch*, which generally corresponds to the fundamental frequency of a complex tone. A well-studied phenomenon is the “missing fundamental,” which refers to the ability of adults to report the fundamental frequency of a complex tone even when there is no energy at that frequency, presumably because a coherent representation of pitch in the auditory system combines information from multiple frequencies (Gelfand, 1998). By 7 months, infants discriminate tones on the basis of missing fundamental frequencies, despite concurrent variations in the amplitudes of the spectral components (Montgomery & Clarkson, 1997). Like adults, infants need sounds that contain relatively low-frequency energy in order to perceive the missing fundamental (Clarkson & Rogers, 1995). Infants’ ability to perceive the missing fundamental improves with the number of harmonics: infants fail to discriminate tone complexes with only two harmonics, and get successively better as the number of harmonics increases (Clarkson, Martin, & Miciek, 1996).

High- and low-frequency maskers have distinct effects on perception of complex tones with missing fundamentals (Gelfand, 1998). A low-frequency noise does not disrupt perception of the missing fundamental in a complex tone, but it does disrupt perception of a sine tone at the same frequency. Conversely, high-frequency noise masks the missing fundamental but not the low-frequency sine tone,

suggesting that the missing fundamental results from analysis of the complex tone components. Like adults, 7-month-old infants can discriminate complex tones with different fundamental frequencies in the presence of a low-frequency masker, but not a high-frequency masker, implying a common pitch perception mechanism across infants and adults (Montgomery & Clarkson, 1997).

Temporal Integration

Temporal integration refers to detection threshold as a function of stimulus duration. The “time-intensity trade” describes the well-documented observation that when a signal is shortened by a factor of 10 (e.g., from 200 to 20 ms), the signal level must be increased by 8 to 10 dB to be detected by adults (Gelfand, 1998). Likewise, detection of a signal generally improves as the duration of that signal increases, up until about 300 ms. Traditionally, temporal integration has been viewed as a long-term process that integrates information over intervals of 200 or 300 ms, and it is the accumulation of sound over this interval that forms the basis of a detection decision (Berg & Boswell, 1995). However, this explanation cannot account for the temporal integration functions of infants, which are nearly twice as steep as those of adults.

Infants are much more sensitive than adults to duration increases. Increasing the duration of a sound improves performance for an infant nearly twice as much as it does for an adult. For 4 kHz and 500 Hz noise bursts, infant detection improves by 20 dB per decade of change in duration (Berg, 1991; Berg & Boswell, 1995). Differences between adult and infant temporal summation functions may be due to nonsensory processes such as attention: Infants are less likely to notice a signal that is very brief if they are inattentive a large proportion of the time (Bargones, Werner, & Marean, 1995; Werner & Marean, 1991). Alternatively, short-term temporal integration processes might be immature in infancy. Consistent with this possibility is the finding that infants are less sensitive to stimulus onsets than to continuous sounds; in addition, although increasing the number of pulses decreases adult and infant thresholds by about 10 dB, the slopes of infants’ temporal integration functions are much shallower for additional pulses than for equivalent increases in the duration of the signal (Berg & Boswell, 1995). This evidence challenges the traditional descriptions of temporal integration, and provides support for the idea that infants are selectively impaired for stimulus onsets, and perhaps for any transient stimulus that occurs over a shorter time constant.

Temporal Resolution

In some ways temporal resolution constrains all of audition, because even pitch perception (at low frequencies) depends on neurons phase locking to the periodicity of the signal. Here “temporal resolution” refers to the precision with which the auditory system can track changes in the amplitude envelope, which unfolds at a much slower rate.

One way of measuring temporal resolution is *gap detection*, when an ongoing noise is interrupted by brief silences; the smallest detectable silence is taken as a measure of temporal resolution. While adult gap detection thresholds range from 2 to 10 ms, 3-, 6-, and 12-month-old infants’ gap detection thresholds are as large as 60 ms (Werner, Marean, Halpin, Spetner & Gillenwater, 1992). Thresholds decline from 18 ms at Age 6 to adult levels by Age 12 (Irwin, Ball, Kay, Stillman, & Rosser, 1985). Detection is generally better for higher frequencies (1000–2000 Hz) than lower frequencies (500 Hz) (Irwin et al., 1985; Werner et al., 1992).

Duration discrimination tasks (of continuous tones, noise, or interstimulus intervals) also reveal developmental changes in temporal resolution. Mismatch negativity responses indicate detection of 100-ms changes of a 200-ms tone by the newborn brain (Ceponiene et al., 2002). However, detection tasks with infants reveal that the smallest detectable duration change is 20 ms at 6 months, 15 ms at 5 years, and 10 ms in adulthood (Morrongiello & Trehub, 1987). Other behavioral tasks (2AFC) yield highly variable performance among children 4–10 years of age, who require large changes (10%–90%) for accurate detection, especially for increases (rather than decreases) in duration (Elfenbein, Small & Davis, 1993). For a repeated temporal interval, such as a metronome, detection of changes in the speed or tempo improves from 15% in infancy (Baruch & Drake, 1997) to 5% in adulthood (Drake, Jones, & Baruch, 2000).

A third way to assess temporal resolution is through use of the *temporal modulation transfer function* (Hall & Grose, 1994). Here listeners must indicate which of two sounds is amplitude modulated (i.e., contains periodic fluctuations in the amplitude envelope). Greater amplitude changes (modulation depth in dB) are required for higher than for lower frequency sounds, and although this trend is evident from the ages of 4 through 10 years, much larger amplitude changes are needed for children than for adults (Hall & Grose, 1994).

Temporal resolution early in life may have implications for language learning. Typically developing children

have significantly smaller gap detection thresholds than children from families with a known history of language impairment (Benasich & Tallal, 1996). A longitudinal study found that infants with smaller gap detection thresholds at 6 months also had better language abilities 10–15 months later (Trehub & Henderson, 1996). Some accounts of developmental dyslexia posit a key role for deficits in processing amplitude modulation as well as rise time (i.e., detecting the rate at which the amplitude envelope changes) (Goswami, 2011).

Sound Localization

Orienting towards sound is one of the earliest behaviors observed in newborns. After only a few days, infants will orient their head in the direction of a laterally presented sound (Clarkson, Clifton, & Morrongiello, 1985). In the lab, infant localization can be measured by presenting sounds via a horizontal array of loudspeakers surrounding the infant at various degrees relative to midline. On a given trial, a sequence of tones or noise bursts is presented at midline, and then shifted to the right or left of the infant until the infant makes a direction eye or head movement, which is then rewarded. This yields an estimate of the *minimum audible angle* (MAA), the smallest angle for detection of a change in the position of a sound source (Ashmead, Clifton, & Perris, 1987). The MAA for adults is 1–2°, but for infants it is considerably larger, with 2- to 6-month-olds consistently responding to the general direction of a sound (i.e., right or left) but lacking precision within a hemifield (Morrongiello, Fenwick, Hillier, & Chance, 1994). At two days, newborn MAAs are approximately 30° (Morrongiello et al., 1994), improving to 20° at 5 and 6 months (Ashmead et al., 1987), 10° at 12 months (Ashmead, Davis, Whalen, & Odom, 1991), 4–5° at 18 months, and 1.5° at 5 years of age (Litovsky, 1997). Thus, sensitivity to the specific location of sounds appears to develop dramatically between birth and 5 years.

The primary cues for binaural localization are *interaural temporal disparities* (ITD) resulting from a sound arriving earlier at the nearer ear, and *interaural intensity disparities* (IID), which result from a sound being slightly louder at the nearer ear. Adults are sensitive to ITDs of 13–30 microseconds, depending on the frequency of the stimulus (Bernstein, 2001). In contrast, when infant ITD thresholds are measured in isolation (using headphones) they are not only worse than adult ITD thresholds, but are significantly larger than would be expected from performance in free-field sound localization (Ashmead et al., 1991).

Infants' use of intensity-based distance cues is also unclear. Six-month-olds reach in the dark for a sounding object that is closer than one farther away; however, unlike adults who use intensity as a localization cue, infants do this even when the farther sound is louder (Litovsky & Clifton, 1992).

An additional binaural processing phenomenon is called the *precedence effect*. This occurs when two similar sounds are presented from different locations with a very brief delay, and listeners perceive only one sound whose location is dominated by the first source (Litovsky, 1997). The functional explanation for the precedence effect is that it diminishes the perceptual impact of echoes so that the individual can accurately localize the original sound source. To measure the precedence effect, adult, 5-year-old, and 18-month-old MAAs were measured for the dominating versus lagging tone, separated over a range of delays (at the shortest delay only one sound is perceived, while at the longer delays, two sounds are heard). The precedence effect was significantly stronger in adults than in 5-year-olds, and stronger in 5-year-olds than in 18-month-olds (Litovsky, 1997). Although spatial hearing is less accurate in children, some 5-year-olds can localize stimuli in echo conditions at adult-like levels (Litovsky & Godar, 2010).

Several mechanisms may account for developmental changes in binaural processing. One explanation emphasizes physical growth: As head size changes, so do the size and quality of interaural localization cues (Ashmead et al., 1991). If so, then the representation of auditory space is somewhat unstable until the head reaches a fixed size, and the interaural timing and intensity differences also become fixed. A second explanation is that changes in localization accuracy may reflect maturational stages in auditory cortex (Werner & Gray, 1998).

Perceptual Grouping

The auditory system is confronted with a rich, complex, and unsegregated sensory signal. How do listeners determine which sounds are important, which parts of a complex sound belong together, and which sounds arise from separate sources despite their temporal simultaneity? *Auditory scene analysis* is one means by which individuals might parse sound environments into coherent “auditory objects” (Bregman, 1990). Adults tend to group incoming sound by spectral, pitch, intensity, and spatial information, and discrepancies in these features are used to determine whether sounds arise from separate or unified sources. For example,

frequency is a powerful grouping cue that can interfere with an adult listener's ability to discriminate a forward from a backward melody. If all notes of a melody are in the same frequency range, adults readily discriminate forward from backwards versions. By contrast, when the melody contains alternating high and low notes, the melody perceptually "splits" into separate high- and low-note streams, and adults then confuse forward and backward versions. Likewise, when habituated to a forward melody, infants 3 days to 3 months only dishabituate to backward melodies when all four pitches are in the same frequency range (Demany, 1982; McAdams & Bertoncini, 1997). Streaming by frequency also disrupts the ability to track temporal relationships between events in different streams. Like adults, 6- to 8-month-old infants are better at detecting a gap placed within a pitch-based perceptual group (e.g., AA AEEE) than they are at detecting the same gap between groups (e.g., AAA EEE) (Thorpe & Trehub, 1989; Thorpe, Trehub, Morrongiello, & Bull, 1988), implying that at least some aspects of stream segregation are present in infancy.

Relational Versus Absolute Information in Pattern Perception

Many aspects of melodic processing are adult-like during infancy. Like adults, 5-month-old infants recognize a melody when its pitch level is shifted up or down but interval relations between tones are preserved (transposition) (Chang & Trehub, 1977; Trehub, Thorpe, & Morrongiello, 1987). Seven- to 9-month-olds categorize melodies on the basis of *contour*, the pattern of upward and downward pitch change, ignoring concurrent changes in pitch level and interval (Trehub et al., 1987). Infants can even categorize melodies on the basis of relative duration (i.e., slow-fast-fast), responding only to rhythmic changes and ignoring concurrent pitch and tempo variations (Trehub & Thorpe, 1989).

Intervals and contour are aspects of *relative pitch*, which is critical for music processing in adults. By contrast, *absolute pitch* (sometimes referred to as "perfect" pitch) is the ability to name a pitch one hears and is rare in adults. Some evidence suggests that at least for some types of tasks, infants use absolute pitch information. For example, when standard and comparison melodies are not transposed, 9-month-old infants can detect small absolute pitch changes (Trehub, Cohen, Thorpe, & Morrongiello, 1986). In a statistical learning task 8-month-old infants could discriminate novel from familiar sequences of pitches on the basis of sequential relative and absolute pitch information

(Saffran & Griepentrog, 2001). When asked to provide similarity ratings for a standard melody and variations that preserved and violated relative or absolute pitch, the salience of absolute over relative pitch decreased from Age 5 to 12 (Stalinski & Schellenberg, 2010). This suggests that although relative pitch processing is possible during infancy, it also continues to develop throughout childhood.

Perception of Music

Few individuals are professional musicians, yet most of us have acquired a considerable amount of musical experience throughout our lifetime through passive exposure to the predominant music of our cultures. Developmental studies demonstrate how perceptual tendencies in musical experience change with increased cultural experience.

Musical Tone Perception

The ability to detect small frequency changes should perhaps follow predictably from the data on basic frequency resolution discussed previously. But this is not the case for the detection of mistunings in a musical context. Adults are much better at detecting mistunings placed in a melody or scale that is native to their culture than they are at detecting mistunings placed in a nonnative scale. For example, adults in Western cultures are better at detecting mistunings placed in a familiar Western scales, such as the diatonic major, than they are for mistunings placed in a less familiar Western scale context, such as the minor mode or augmented scale (Lynch & Eilers, 1992; Lynch, Eilers, Oller, & Urbano, 1990).

Infants, however, appear to be better than adults at detecting mistunings in unfamiliar scale contexts. Western 6-month-old infants were as capable of detecting mistunings in Western diatonic scales as they were for mistunings in the non-Western Javanese pelog scale and the Western minor and augmented scales (Lynch & Eilers, 1992; Lynch et al., 1990). Nine-month-olds are better at detecting mistunings in unequal-step scales than in equal-step scales, suggesting that there might be an inherent processing bias favoring unequal- over equal-step scales (Trehub, Schellenberg, & Kamenetsky, 1999). By 1 year of age infants respond to mistunings in a manner similar to adults, with better sensitivity in familiar Western scale contexts, suggesting that perceptual reorganization for musical tuning occurs some time between 6 and 12 months (Lynch & Eilers, 1992). A comparison of premature and full-term infants supports this claim, since this developmental change occurs after 6 months of postnatal experience

regardless of gestational age (Lynch, Short, & Chua, 1995). Children gradually exhibit sensitivity to implied harmony, performing equally well at detecting wrong notes that are in-key versus out-of-key at 5 years, but exhibiting superior performance on out-of-key changes over in-key changes at 7 years, just like adults (Trainor & Trehub, 1994). Similarly, although the scale mode of a tune can communicate a happy (major mode) or sad (minor mode) emotion, children are not sensitive to these emotion-mode associations until Age 6 (Dalla Bella, Peretz, Rousseau, & Gosselin, 2001).

Musical Enculturation

Exposure to the statistics of the environment alters infants' perceptual processes (Scott, Pascalis, & Nelson, 2007). One well-documented example comes from speech perception: Infants develop language-specific biases during the second half of the first year after birth. By 3–4 months of age, infants discriminate speech sounds from virtually all spoken languages, even those they have never heard (Eimas, Siqueland, Jusczyk, & Vigorito, 1971; Trehub, 1976). These early abilities change dramatically by the end of the first year, when infants only discriminate speech sounds that demarcate meaning in their native language, presumably because of their exposure to linguistic input containing disproportionately frequent exemplars of native-language categories (Werker & Lalonde, 1995; Werker & Tees, 1984).

Enculturation to musical structures is characterized by a similar developmental trajectory: Young infants discriminate musical structures that elude their parents, but begin to exhibit culture-specific declines by the end of the first year. A prominent example comes from perception of metrical (rhythmic) structure. Both isochronous (evenly spaced) and nonisochronous meters are common in traditional music from throughout the world, such as Africa, the Middle East, Eastern Europe, and South Asia (London, 2004; Clayton, 2000). Balkan rhythms, for instance, frequently consist of a mixture of isochronous (1:1) interval ratios (the temporal relations between the metrical hierarchy and the “beat”) and nonisochronous (3:2) ratios, as seen in Figure 3.9. Nonisochronous ratios are usually challenging for Western listeners to perceive and produce (Essens, 1986). A group of adults tested in North America detected temporal disruptions of a Balkan folk tune when it had an isochronous meter (with 2:1 ratios) but not when it had a nonisochronous meter (with 3:2 ratios; Hannon & Trehub, 2005a). By contrast, adults from Macedonia and Bulgaria performed equally well in both isochronous and

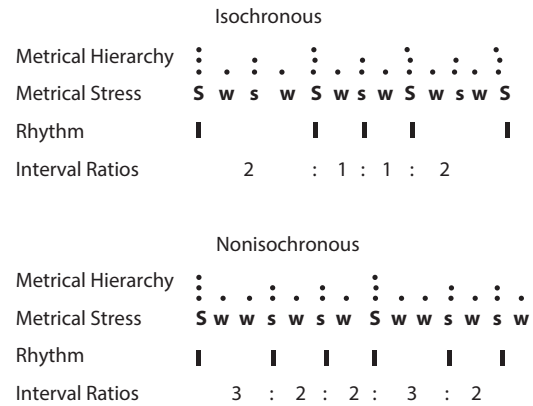


Figure 3.9 Schematic depiction of temporal relations between metrical hierarchies and metrical stress in isochronous and nonisochronous rhythms.

Source: Adapted from “Tuning in to Rhythms: Infants Learn More Readily Than Adults,” by E. E. Hannon and S. E. Trehub, 2005, *Proceedings of the National Academy of Sciences, USA*, 102, pp. 12639–12643.

nonisochronous conditions, presumably because both are equally familiar to these subjects.

Western adults may fail to detect disruptions to nonisochronous meters because there is a strong tendency to assimilate all patterns toward a familiar metrical template. This can be interpreted as evidence of acquired culture-specific knowledge of meter. After familiarization with the same folk tunes described previously, 6-month-olds exhibited a novelty preference for disrupted versions, whether the familiarization stimulus was isochronous or nonisochronous (Hannon & Trehub, 2005a). By 12 months, however, Western infants failed to discriminate rhythmic variations in the nonisochronous condition, even though they continued showing a novelty preference in the isochronous condition (Hannon & Trehub, 2005b). Thus, enculturation to musical rhythms—culture-specific metrical categories—changes infants' behavior and closely parallels trends observed in other domains, whereby initial discrimination abilities are maintained for familiar structures but decline for unfamiliar structures by the end of 1 year.

These developmental changes in infants' rhythm perception are presumably driven by exposure to Western music, where simple ratios are much more frequent than are complex ratios. Thus, culture-specific musical representations may arise simply from listening, in the same way that listening to native language and seeing familiar faces leads to declines in discrimination of unfamiliar speech and faces (Scott et al., 2007). Support for this possibility comes from a training study in which a brief period of exposure to foreign music (20 min of Balkan music per day for 2 weeks)

reversed the decline in performance in the nonisochronous condition (Hannon & Trehub, 2005b). More recent research used a similar passive exposure method with children between 5 and 11 years, and adults, and documented significantly greater improvement in meter discrimination in children younger than 9 relative to older children and adults (Hannon, der Nederlanden, & Tichko, 2012). Thus, culture-specific representations of musical rhythm and meter may continue to develop throughout childhood.

Perception of Speech

Although language acquisition has long been an important topic of study, development of speech perception has received somewhat less attention, perhaps because of very young infants' striking and precocious capacities for many aspects of speech perception. This may have led many past researchers to assume that speech perception abilities are already in place at birth, and that language learning occurs at a more abstract level of cognition independent of the sound patterns characteristic of speech (Jusczyk, 1997). More recently, researchers have found that while many aspects of infant speech processing are adult-like at an early age, there are several important developmental changes that take place over the first year after birth.

Perception of Vowels and Consonants

Like adults, even 2- to 3-month-old infants can discriminate the fine acoustical differences between phonemes such as /da/, /ba/, and /pa/ (Eimas, 1974). Infants shift their perceptions of phonemes in a manner similar to adults, in the sense that they detect some equal-sized acoustic changes along a continuum more readily than others. Some researchers have called this the *perceptual magnet effect*, because nonprototypic members of a phonemic category are "drawn toward," or perceived as more similar to, a phonetic prototype than to each other (e.g., American English /i/) (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992). Infants can also discriminate vowels very early in development. As early as 2 months, infants can discriminate vowels and ignore concurrent changes in other parameters, such as gender of the speaker and rising versus falling intonation (Marean, Werner, & Kuhl, 1992).

For some types of phonetic contrasts, young infants' performance is superior to that of adults. Adults discriminate phonetic contrasts that are used to differentiate meaning in their own language, but are poor perceivers of contrasts in other languages, an effect that likely stems

from perceptual tuning early in life. A classic example comes from Japanese adults, who often cannot perceive the difference between /r/ and /l/, let alone pronounce it. Adults also have a hard time discriminating contrasts that do occur in their own language but are not used to distinguish meaning, such as /da/ versus /sta/ without the [s]: Adults tend to hear the two as identical (Werker & Tees, 1999). Before about 6 months of age, infants can discriminate all consonant contrasts in native and nonnative languages, but by 10 to 12 months, perception becomes much more adult-like, with diminished perception for nonnative, but not native contrasts. This reorganization of consonant perception between 6 and 12 months has been observed for contrasts typical of Zulu but not English, contrasts typical of English but not Japanese, contrasts that exist in English but do not denote meaning (Werker & Tees, 1999), and synthesized as well as spoken contrasts typical of Hindi but not English (Werker & Lalonde, 1988).

This change in sensitivity to native over nonnative contrasts may develop earlier for vowels. When vowel contrast performance for Swedish and American 6-month-old infants were compared, both groups of infants showed the magnet effect only for contrasts in their native language (Kuhl et al., 1992). A second study showed that 4-month-old English-learning infants discriminated German vowel contrasts and English vowel contrasts, while 6-month-old English-learning infants only discriminated vowel contrasts typical of English (Polka & Werker, 1994). The general trend from "universal" discrimination abilities to language-specific abilities has led some researchers to speculate that during the first year infants are forming categorical representations for speech phonemes (e.g., Kuhl, 2004). Others have cautioned that infants' representations of phonemes may differ from adults' in important ways, perhaps characterized by much more rough, global differences, rather than any particular understanding of phonetic units as consonant-vowel combinations (Jusczyk & Derrah, 1987).

Perception of Global Prosodic Features

Infants are able to perceive global features of their language at a very early age. After only a few days, newborns can distinguish their mother's language from foreign languages, even when the speech is high-pass filtered, preserving only prosodic information such as fundamental frequency changes and rhythmic features (Mehler & Christophe, 2000). Rhythm may be of primary importance in early experiences of speech. The prenatal environment is somewhat acoustically deprived, but sound recordings

from within the womb indicate that at least rhythmic and some low-frequency information are available to fetuses, perhaps explaining newborns' sensitivity to rhythmic and prosodic information in speech. Some authors nevertheless maintain that infants may have a predisposition to pay attention to the rhythmic features of speech, which facilitate learning about prosodic features of one's native language (Sansavini, 1997).

Rhythm may provide critical information for early discrimination of native from nonnative speech. Languages have been divided up into three different rhythmic classes (Jusczyk, 2002): *stress-timed*, which alternate strong and weak syllables (e.g., English and German), *syllable-timed*, in which each syllable receives equal stress (e.g., Spanish and French), and *mora-timed*, in which rhythmic units are syllabic or subsyllabic (e.g., Japanese). Newborns and 2-month-olds can discriminate between sentences from different rhythmic classes, such as English and Japanese, but not sentences from the same rhythmic class, such as English and Dutch (Nazzi et al., 1998). By 5 months, infants can discriminate sentences of their own language (English) from sentences in foreign languages from the same rhythmic class (Dutch), and they can also tell the difference between American English and British English. They cannot, however, discriminate between foreign languages of the same rhythmic class even when it is in the same class as their native language, suggesting that these changes are specific to knowledge acquired about one's own language (Nazzi, Jusczyk, & Johnson, 2000). Interestingly, infants born to bilingual mothers (e.g., English and Tagalog, stress- and syllable-timed, respectively) show preferences for both languages, implying that infants' perception of global language structure starts with experience gained during prenatal exposure to the mother's speech (Byers-Heinlein, Burns, & Werker, 2010).

Speech Segmentation

Many researchers have noted the challenge of segmenting speech streams into words. Although words on the page have spaces between them, the acoustical information that comes to the ears from typical utterances does not. Yet infants appear sensitive to word boundaries. When 7-month-olds were presented with word pairs such as *feet* and *bike*, followed by speech streams either containing or not containing those words, infants showed a familiarity preference for speech containing the target words. Additionally, infants exhibited a familiarity preference for an isolated test presentation of target words after familiarization with speech passages that contained those words

(Jusczyk & Aslin, 1995). And, just as they use prosodic cues like rhythm and stress to discriminate native from nonnative speech, infants may also use prosodic cues to segment words from speech. For example, some time between 6 and 9 months, English-learning infants segment words according to the predominant stress patterns in English. In English, the initial syllable of a word is usually stressed, and it is only these words that 7.5-month-old infants are able to segment. These infants could correctly segment bisyllabic words with the predominant strong/weak accent pattern, such as "kingdom," but not words that began with unstressed syllables, like "guitar" (Jusczyk, Houston, & Newsome, 1999).

Infants also provide evidence of exploiting statistical probabilities of word boundaries to segment speech. For example, 8-month-old infants used the transitional probabilities (co-occurrence statistics) in a sample of artificial speech to discriminate three-syllable words from three-syllable part-words, after being familiarized with a continuous stream of unsegmented speech input (Saffran, Aslin, & Newport, 1996). By 9 months, infants can segment words using their knowledge of their native language's *phonotactic* constraints, which determine which sequences of sound are permissible within versus between words. For example, in English, certain combinations of successive consonants are more likely between words, such as "vt" and "ng," while others are more common within words, such as "ft" and "st." Infants exhibit a preference for speech streams in which nonsense words (defined by stress patterns and pauses) coincide with the phonotactic structure common to English (Mattys & Jusczyk, 2001). Incidentally, it is shortly after this time (8–9 months) that infants are able to segment words that begin with unstressed syllables (Jusczyk, 2002). This suggests that infants take advantage of a wide variety of perceptual cues to segment speech.

VISION

The purpose of the visual system is to transduce light reflected from surfaces in the environment into neural signals that are relayed to the brain for processing and action. Light is first transmitted through the cornea, the outer protective covering, and then the lens, which provides focus of near and far objects, and is finally intercepted by the retina, a thin film of tissue covering the back of the eyeball. The retina is composed of layers of photoreceptors as well as a rich network of connections and nonsensory neurons that provide initial processing of visual information. Different