CHAPTER

15

The Development of Visuospatial Processing

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Visual input is a critical source of knowledge about the organization and structure of the spatial world. It provides information about everything from the structure of objects and scenes to their location or movement in space. Visuospatial processing encompasses a wide variety of neurocognitive abilities ranging from the basic ability to analyze how parts or features of an object combine to form an organized whole, to the dynamic and interactive spatial processes required to track moving objects, to visualize displacement, and to localize, attend, or reach for objects or visual targets in a spatial array. These varied processes work in concert to provide a seamless and immediate perception of the intricacies of the visual world. This perception provides an essential basis for precise and effective action in the world as well as a rich source of input for cognitive functions across many domains.

A complex neural architecture involving dozens of interrelated visual areas in the posterior cortices supports visuospatial processing (Van Essen et al., 1992). Ungerleider and Mishkin (1982) first proposed a model for understanding the organization of this complex set of cortical areas and functions in the early 1980s (Ungerleider, 1995). In their model, the cortical visual system is anatomically and functionally subdivided into the ventral and dorsal processing pathways or streams (see Figure 15.1). The ventral stream is dominant for processing information about patterns and objects, while the dorsal stream mediates spatial processing associated with attention to movement and location. Subsequent models describe dorsal stream functions as specialized for supporting visual processing related to action (e.g., Andersen et al., 1997; Goodale and Milner, 1992; Goodale and Westwood, 2004; Rizzolatti and Matelli, 2003).

This chapter begins with a summary of the neuroarchitecture of the ventral and dorsal visual streams. The summary focuses on the flow of visual information beginning, for both streams, in the primary visual cortex and then extending to the temporal and parietal lobes for the ventral and dorsal streams, respectively. Connections between the two major visual pathways as well as connections with the frontal lobes are also considered.
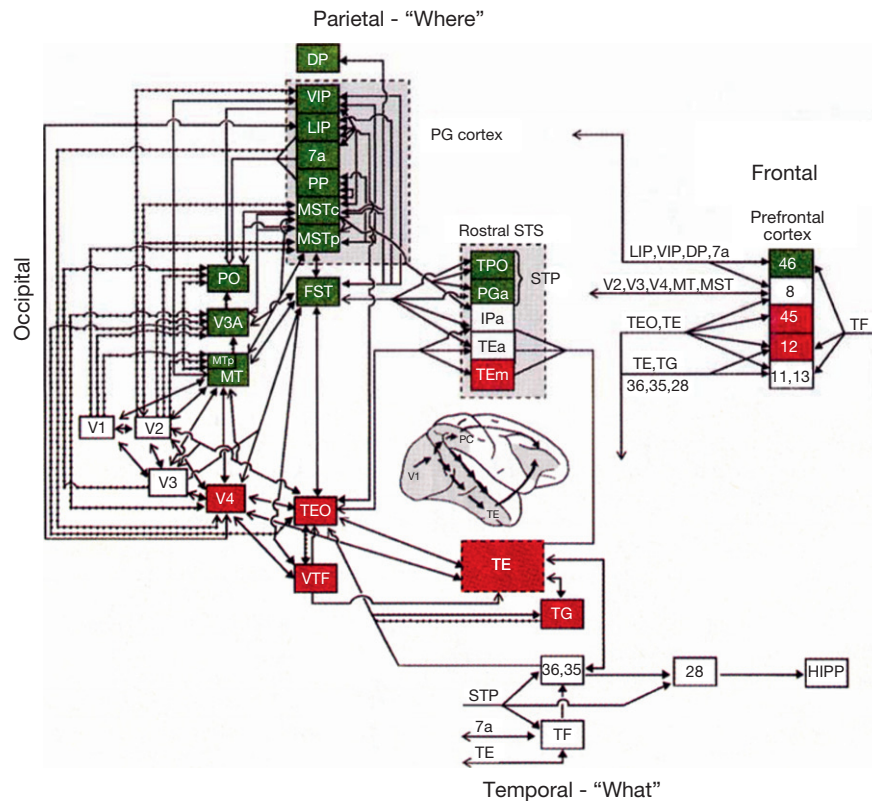
FIGURE 15.1   Dorsal and ventral visual-processing pathways in monkey. Solid lines indicate connections arising from both central and peripheral visual field representations; dotted lines indicate connections restricted to peripheral field representations. Red boxes indicate ventral stream areas related primarily to object vision; green boxes indicate dorsal stream areas related primarily to spatial vision; and white boxes indicate areas not clearly allied with either stream. Shaded region on the lateral view of the brain represents the extent of the cortex included in the diagram. Abbreviations: DP, dorsal prelunate area; FST, fundus of superior temporal area; HIPP, hippocampus; LIP, lateral intraparietal area; MSTc, medial superior temporal area, central visual field representation; MSTp, medial superior temporal area, peripheral visual field representation; MT, middle temporal area; MTp, middle temporal area, peripheral visual field representation; PO, parietal–occipital area; PP, posterior parietal sulcal zone; STP, superior temporal polysensory area; V1, primary visual cortex; V2, visual area 2; V3, visual area 3; V3A, visual area 3, part A; V4, visual area 4; and VIP, ventral intraparietal area. Inferior parietal area 7a; prefrontal areas 8, 11–13, 45, and 46, perirhinal areas 35 and 36; and entorhinal area 28 are from Brodmann (1909). Inferior temporal areas TEO and TE, parahippocampal area TF, temporal pole area TG, and inferior parietal area PG are from Von Bonin and Bailey (1947). Rostral superior temporal sulcal (STS) areas are from Seltzer and Pandya (1978), and VTF is the visually responsive portion of area TF (Boussaoud et al., 1991). *Reproduced from Ungerleider LG (1995) Functional brain imaging studies of cortical mechanisms for memory.* Science 270(5237): 769–775, with permission.

The next two sections consider the development of cognitive processes associated with the two principal brain visual systems. The section on ventral stream processing examines the development of visual pattern processing from infancy through adolescence focusing on changes in the perception of visual patterns and faces, and in the ability to construct spatial arrays. The section on dorsal stream processing examines the development of spatial attention, location processing, and mental rotation. The final section of the chapter turns the focus to neurodevelopmental disorders where visuospatial processing is a primary feature. It examines both the effects of frank neural insult on the development of spatial processes and the effects of specific genetic abnormalities on the development of the neural systems that underlie the development of spatial processes. The original descriptions of ventral and dorsal stream organization came from studies

of adults with injury to various subsystems within the cortical visual pathways. Data from children with neurodevelopmental disorders provide insight into the emergence of visual system organization following early pathology, and can address questions about how specific neural compromise and neural plasticity interact to affect the developmental trajectories of basic visuospatial functions and the neural systems that mediate them.

15.1 ANATOMICAL ORGANIZATION OF THE PRIMARY VISUAL SYSTEMS

The organization of the primary visual pathways has been most fully described for rhesus macaque monkeys; thus, the description presented here uses the nomenclature typically used for nonhuman primates.

However, the basic pathways in humans and monkeys appear to be largely homologous (Brewer et al., 2002; Orban et al., 2004). The ventral visual pathway begins at the retina and projects via the lateral geniculate nucleus (LGN) of the thalamus to the primary visual cortex, area V1. From there, the pathway proceeds to extrastriate visual areas V2 and V4, and then projects ventrally to the posterior (PIT) and anterior (AIT) regions of the inferior temporal lobe. Input to the ventral pathway is derived principally, though not exclusively, from P-type retinal ganglion cells that project to the parvocellular layers of the LGN and then to layer 4C beta of V1. Parvocellular input to V1 organizes into distinct areas called the blob and interblob regions (Kaas and Collins, 2004; Livingstone and Hubel, 1984; Wong-Riley, 1979). Cells in the blob regions are maximally sensitive to form, while cells in the interblob regions respond principally to color. The ventral stream processes information about visual properties of objects and patterns, and has been described as the 'what' pathway.

The dorsal visual pathway also begins at the retina and projects via the LGN to area V1. From there, the pathway proceeds to extrastriate areas V2 and V3, then projects dorsally to the medial (MT/V5) and medial superior (MST) regions of the temporal lobe, and then to the ventral inferior parietal (IP) lobe. Input to the dorsal pathway is derived principally, though not exclusively, from the large M-type retinal ganglion cells that project to the magnocellular layers of LGN and then to layer 4C alpha of V1. Cells in this pathway are maximally sensitive to movement and direction and are less responsive to color or form. The original functions identified for the dorsal stream involved processing of information about spatial location, optic flow, and motion, and allocation and maintenance of spatial attention. It was thus described as the 'where' pathway. More recently, work examining the dorsal stream's role in visually guided movements suggests that the pathway is and also involved in the integration of visual and motor functions. It has thus been called the 'how' system (e.g., Andersen et al., 1997; Goodale, 2011; Goodale and Milner, 1992; Rizzolatti and Matelli, 2003).

The dorsal and ventral pathways project rostrally to common and distinct, albeit adjacent, areas of the prefrontal cortex. Imaging studies suggest that these prefrontal networks are involved in a variety of dorsal and ventral stream functions (Farivar, 2009). For example, spatial working memory and attention rely on networks connecting the dorsolateral prefrontal cortex (DLPFC) and posterior parietal cortex (Awh and Jonides, 2001; Corbetta et al., 2002; Curtis, 2006), whereas object memory relies on systems connecting the prefrontal cortex with inferior temporal areas (Ranganath, 2006; Ranganath and D'Esposito, 2005; Ranganath et al., 2004). At least three principal projection pathways from the parietal lobe have been described: a parietal–prefrontal pathway mediating eye movement and spatial working memory, a parietal premotor pathway mediating visually guided movement (eye movement, reach, and grasp), and a parietal medial temporal pathway that processes complex spatial information for navigation (Kravitz et al., 2011). There is substantial evidence that the dorsal and ventral pathways are richly interconnected and at least partially overlapping in the mature (e.g., Dobkins and Albright, 1994, 1995, 1998; Marangolo et al., 1998; Merigan and Maunsell, 1993; Rosa et al., 2009; Sincich and Horton, 2005; Thiele et al., 2001; Zanon et al., 2010) and the developing (Dobkins and Anderson, 2002; Dobkins and Teller, 1996a,b) visual system. The dissociation of function across the two pathways may be less complete than originally thought. Subregions within each system may respond to functions typically associated with the other pathway (Husain and Nachev, 2007; Kawasaki et al., 2008; Konen and Kastner, 2008; Lehky and Sereno, 2007). For example, regions in the parietal lobe may respond to color and shape features (Kawasaki et al., 2008), and area MT/V5 in extrastriate visual cortex may show object-selective responses (Konen and Kastner, 2008).

15.2 VENTRAL STREAM PROCESSES

A major function of the ventral visual stream is the analysis of pattern information. Here, findings from three specific functions within the ventral stream are summarized: global–local processing, face processing, and spatial construction. Behaviorally, visuospatial analysis is defined as the ability to specify the parts and the overall configuration of a visually presented pattern, and to understand how the parts are related to form an organized whole (e.g., Delis et al., 1986, 1988; Palmer, 1977, 1980; Palmer and Bucher, 1981; Robertson and Delis, 1986; Smith and Kemler, 1977; Vurpillot, 1976). Thus, it involves the ability to segment a pattern into a set of constituent parts (referred to as featural or local-level processing), and integrate those parts into a coherent whole (referred to as configural or global-level processing). Different approaches to the study of spatial analysis have focused on level of processing and type of input. Perceptual processing studies focus largely on issues of global versus local or configural versus featural processing. Much of the data on perceptual processing of global and local aspects of objects and patterns come from hierarchical form-processing tasks (e.g., see Figure 15.2). Perceptual processing of faces is a related but generally distinct line of study. Faces constitute a critically important class of social stimuli for which most individuals acquire considerable processing expertise. Because of the importance of the information faces provide to typical social interaction and communication, faces may be
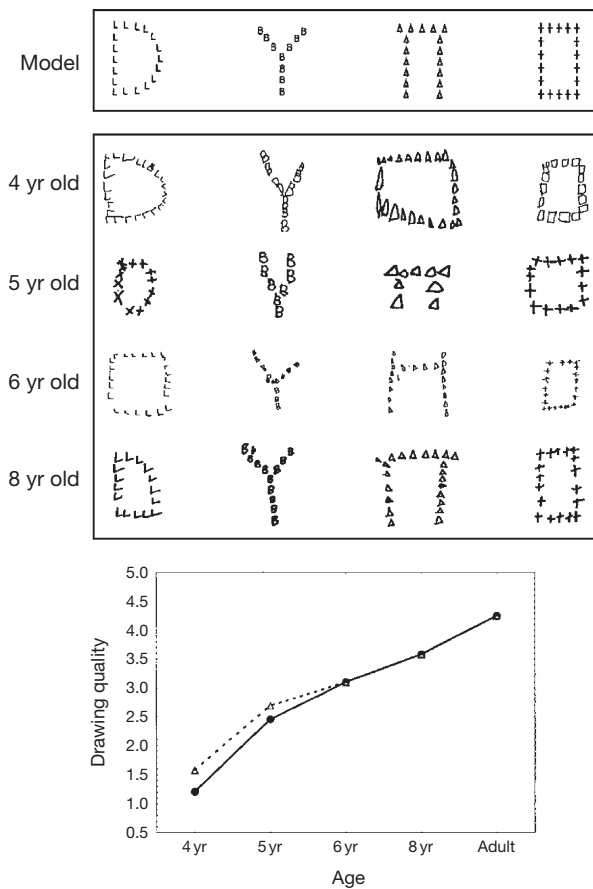
FIGURE 15.2 The model forms (top) provide examples of hierarchical form stimuli. Hierarchical form stimuli have two levels of organization: a large global/configural level comprised of appropriately arranged smaller forms constituting the local/featural level. A series of hierarchical form stimuli (the models) were presented one at a time and children were given 10 s to study the form. After a 30 s delay, they were asked to reproduce the forms from memory. The graph illustrates that systematic improvement in the accuracy of reproductions was observed among typically developing 4–8-year-old children, and also that there are no differences at any age in the relative accuracy of reproducing the global and local levels of the forms. At each age, children are equally accurate in their reproduction of global and local pattern information. *Reproduced from Dukette D and Stiles J (2001) The effects of stimulus density on children's analysis of hierarchical patterns.* Developmental Science *4(2): 233–251, with permission.*

processed differently compared to other classes of visual objects. Construction tasks provide a window to children's conceptual organization of spatial arrays. The processes and strategies children use to recreate spatial scenes can provide insight into their understanding of their spatial world.

15.2.1 Perception of the Global and Local Levels of Visual Pattern Structure

Differential laterality for global and local processing is well documented for adults with right hemisphere (RH) dominance for global and left hemisphere (LH)

dominance for local processing (e.g., Han et al., 2002; Martin, 1979; Martinez et al., 1997; Sergent, 1982; Volberg and Hubner, 2004; Yovel et al., 2001). Sergent (1982) suggested that these differences arise from preferential processing of lower spatial frequencies in the RH and higher spatial frequencies in the LH. Several experiments have presented sinusoidal gratings containing a single spatial frequency presented to the right visual field (RVF) or left visual field (LVF) to evaluate this hypothesis with generally positive results. Low spatial frequencies elicit faster responses when presented to the LVF-RH than the RVF-LH, while high spatial frequencies elicit the opposite pattern (Kitterle and Selig, 1991; Kitterle et al., 1990, 1992). Event-related potential (ERP) and other functional imaging studies have supported these basic patterns of lateralization (e.g., Fink et al., 1997; Heinze et al., 1998; Martinez et al., 1997).

In addition to the evidence for the laterality of global- and local-level processing, there is also strong evidence of a global–local processing asymmetry. Specifically, inconsistent or competing information at the global level interferes with local processing, but inconsistent local information does not affect global processing. These two findings led to the postulation of a global precedence effect in visual pattern processing, which states that global-level information is processed prior to local-level information (Navon, 1977). Although many factors may mitigate the global precedence effect in adults, it remains a robust finding within the standard task (Ivry and Robertson, 1998; Kimchi, 1992; Navon, 2003; Robertson and Delis, 1986; Robertson and Lamb, 1991; Robertson et al., 1993).

The ability to analyze spatial patterns begins to emerge in the first year of life. Newborns exhibit configural preferences and rudimentary part–whole processing (Cassia et al., 2002; Farroni et al., 2000; Quinn et al., 1993; Slater et al., 1991). There are dramatic changes in the complexity of visual pattern processing reflecting a systematic improvement in the infant's ability to process global- and local-level pattern information across the first year of life (Cohen and Younger, 1984). These patterns of change appear to reflect early hemispheric differences in processing. Infants as young as 4 months exhibit lateralized processing differences on global and local-processing tasks similar to those observed in adult neuroimaging studies (Deruelle and de Schonen, 1991, 1998).

Studies using the standard hierarchical form stimuli (see Figure 15.2) have also consistently documented a protracted period of developmental change in global–local processing that extends well into adolescence (Dukette and Stiles, 1996, 2001; Harrison and Stiles, 2009; Mondloch et al., 2003; Moses et al., 2002; Porporino et al., 2004; Vinter et al., 2010). The classic global precedence effect emerges slowly over the course

of development. Although some studies of children report a global processing bias (Cassia et al., 2002; Mondloch et al., 2003; Moses et al., 2002; Porporino et al., 2004), others report only modest effects that are modulated by altering task and stimulus demands. For example, increased task demands (Harrison and Stiles, 2009) and selective degradation of the global-level stimulus induce a shift in processing bias from the global to the local level that is much more pronounced in children than in adults (Dukette and Stiles, 1996). The combined data from studies of hierarchical form processing show that children are clearly able to engage in global- and local-level processing from a very early age. However, stable and mature levels of visuospatial processing emerge slowly over a protracted period of development. Variations in stimulus and task demands play an important role in modulating the dominant level of processing. Thus, the functional role of a global or local-processing bias or advantage may be different during development than it is later in life, and may reflect growing expertise and facility in processing complex visuospatial patterns.

Imaging studies of typical children confirm the behavioral findings and suggest that the neural systems associated with spatial analytic processing undergo a protracted period of development. Moses et al. (2002) tested children between 11 and 15 years of age using a hemifield reaction time (RT) task and functional magnetic resonance imaging (fMRI) protocols identical to those used by Martinez et al. (1997) with adult subjects. The pattern of RT data obtained from children across this age range differed from that of adults. Similar to the findings from the Mondloch et al. (2003) study, children were faster with global than with local targets and did not manifest the kinds of hemifield RT differences observed among adults. Importantly, children's profiles of activation in the fMRI study differed from those of the adults. For the global and local tasks, children showed statistically greater activation in the RH than in the LH. Overall activation among children was greater than among adults, and children showed considerably more bilateral activation particularly on the local-processing tasks than adults. Thus, at least for these perceptually demanding tasks, children showed a global processing advantage and overall RH dominance.

Anatomical changes are shown to be associated with the shift from local to global processing biases in children. In one study, 6-year-old children were assigned to one of two groups depending on performance on a behavioral global–local processing task (Poirel et al., 2011). One group of children exhibited the mature profile of global-level bias, and the other the more immature local-level bias profile. The investigators used voxel-based morphology to assess group gray matter density differences in brain regions implicated in global processing, specifically the calcarine

sulcus, the inferior occipital gyrus, the RH occipital lingual gyrus, the right parietal precuneus, and the precentral gyrus. The group of children exhibiting the behaviorally more mature 'global bias' showed reduced gray matter density in all of the brain regions associated with global-level processing. These findings suggest a link between brain maturation and performance on this important spatial-processing task.

15.2.2 Perception of Faces

The ability to recognize a face is essential for everyday social exchange. Although such recognition depends on the discrimination of subtle differences among faces, the task of identifying a face is effortless for adults, suggesting considerable expertise with this important class of stimuli (see also Chapter 18 for a more extended discussion of the development of face processing). Face processing is thought to rely disproportionately on configural cues such as the spacing between features. For example, unlike other objects, face recognition is significantly impaired when the stimuli are turned upside down (Rossion and Gauthier, 2002). It has been suggested that face inversion selectively disrupts facial configural information processing (Yin, 1969). Consistent with this interpretation, neuroimaging studies with adults find a strong RH bias for face activation within what has been described as the core brain network for face processing (Epstein et al., 2006; Gauthier et al., 2005; Grill-Spector et al., 2004; Kanwisher et al., 1997, 1999; Mazard et al., 2006; Rhodes et al., 2004; Wojciulik et al., 1998; Xu, 2005; Yovel and Kanwisher, 2004, 2005). The core face network is a ventral–occipital–temporal (VOT) system that includes the middle aspects of the lateral fusiform gyrus, often referred to as the fusiform face area (FFA), the inferior occipital gyrus in Brodmann's area 18, often referred to as the occipital face area (OFA), and the posterior superior temporal sulcus (Haxby et al., 2000a).

Preference for face stimuli has been documented from the first hours of life (Johnson et al., 1991). Infants as young as 2–3 months show selective cortical responses to faces (Halit et al., 2004; Tzourio-Mazoyer et al., 2002). Some studies suggest that infants show an RH bias for faces (de Schonen and Deruelle, 1991; de Schonen and Mathivet, 1990; De Schonen et al., 1996). Despite these early competences, there is overwhelming evidence for developmental change in face processing that extends at least through the school-age period (Chung and Thomson, 1995; Taylor et al., 2001). Early studies suggested that changes in face processing might reflect a shift from a more feature-based to a more configural or analytic strategy (Carey and Diamond, 1977; Diamond and Carey, 1986; Tanaka and Farah, 1993). However, accumulating evidence supports a pattern of

slower, quantitative age-related change (Itier and Taylor, 2004; Taylor et al., 1999) and increasingly more effective use of the same types of cues used by adults (Baenninger, 1994; Freire and Lee, 2001). These kinds of change may be associated with the acquisition of greater expertise in processing faces and other visual objects (Carey, 1996; Diamond and Carey, 1986; Gauthier and Nelson, 2001).

Recent developmental fMRI studies of face processing suggest that the core brain network for face processing undergoes a protracted change that extends through the school-age period into adolescence (Aylward et al., 2005; Gathers et al., 2004; Golarai et al., 2007; Grill-Spector et al., 2008; Passarotti et al., 2003). Most developmental studies have focused on individual components within the core VOT network, particularly the FFA. The preponderance of evidence indicates that school-age children may produce reliable FFA activation, but the patterns of activation within the fusiform gyrus region vary considerably from those observed among adults. Systematic increases in fMRI blood oxygen level dependent (BOLD) signal activation both in terms of the extent (Brambati et al., 2010; Golarai et al., 2007; Peelen and Kastner, 2009) and intensity of activation (Brambati et al., 2010; Cohen Kadosh et al., 2011; Golarai et al., 2007; Joseph et al., 2011) have been reported from the early school-age period through adulthood. These developmental activation changes correlate with improvement in recognition memory for faces (Golarai et al., 2007, 2010) and with task demand (Scherf et al., 2011). A small number of studies have looked at changes in the organization of brain networks for face processing, and report that young children appear to nonselectively recruit much more extensive networks. With age and growing expertise, these networks become more focused and task specific (Joseph et al., 2011).

15.2.3 Spatial Construction

Spatial construction tasks such as drawing or block assembly provide insight into an individual's conceptualization of the organization of spatial arrays. They can reveal how the participant construes both the parts of an array and the relations among parts that combine to form the overall configuration. Studies of adults with unilateral brain injury use construction tasks extensively. These studies consistently report lateralized differences in the kinds of construction errors produced. Specifically, adults with injury to right posterior brain regions are able to identify, or segment, the parts of spatial forms but have difficulty organizing these parts into integrated spatial configurations. In contrast, adults with injury to left posterior brain regions are able to reproduce the overall pattern configuration, but fail to

incorporate pattern detail and tend to simplify the spatial arrays (Akshoomoff et al., 1989; Delis et al., 1986, 1988; Piercy et al., 1960b; Shorr et al., 1992).

Studies of children's spatial construction activities suggest that before 12 months children engage in very little systematic organization of objects (Forman, 1982; Gesell, 1925; Guanella, 1934; Langer, 1980). In block construction tasks, stacking begins at about 12 months, and by 18 months, children begin to arrange blocks in lines by placing the blocks next to one another (Bayley, 1969; Forman, 1982; Gesell, 1925; Stiles-Davis, 1988). It is not until 3–4 years that children regularly build both vertical and horizontal components within a single spatial construction (Guanella, 1934; Stiles-Davis, 1988). There is also systematic change in processes used to generate block constructions (Stiles and Stern, 2001; Stiles-Davis, 1988). At 24 months, children rely upon a simple repetitive process with a single relation (e.g., stacking). By 36 months, they can use more than one relation (e.g., including a stack and a line in the same construction), but they typically generate them in sequence (e.g., completing the stack, and then the line). By 48 months, children are able to produce multicomponent constructions, with multiple spatial relations, extending in multiple directions in space, and with multiple points of contact between components (e.g., shifting between the line and the stack while building; creating multicomponent construction such as a bridge and several roads). Similar changes are observed in studies of children's drawings. For example, Prather and Bacon (1986) showed that children can attend to either the parts or the whole of a spatial pattern, but their performance can be influenced by specific task and stimulus manipulations. Data from a large series of studies using different measures with children ranging in age from 3 to 12 years show that initially children segment out well-formed, independent parts and use simple combinatorial rules to integrate the parts into the overall configuration (Akshoomoff and Stiles, 1995a,b; Feeney and Stiles, 1996; Stiles and Stern, 2001; Tada and Stiles, 1996). Across the preschool and school-age period, change is observed in both the nature of the parts and the relations children use to organize the parts. Further, pattern complexity affects how children approach the problem of analysis. In a study using the Rey-Osterrieth Complex Figure and simplified variants (see Figure 15.3), it was shown that simplification of the pattern induced more advanced reproduction strategies (Akshoomoff and Stiles, 1995a,b).

15.3 DORSAL STREAM PROCESSES

A variety of spatial processes have been associated with dorsal visual stream processing. We consider three of these processes in this section: spatial localization, spatial

Rey-Osterreith complex form

Representative copies
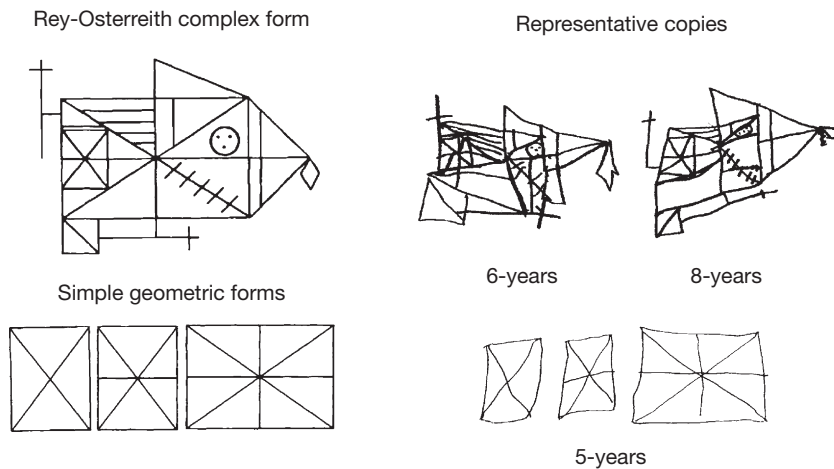
Simple geometric forms

6-years 8-years

5-years

FIGURE 15.3 Models of the Rey-Osterrieth Complex Figure (ROCF) and the three simple geometric forms are shown on the left. Children were given unlimited time to copy each model form. On the right side are examples from 6- and 8-year-old children's copies of the ROCF, and a representative example of a 5-year-old child's copies of the simple geometric forms. Although the simpler forms are contained within the ROCF, children are more accurate in reproducing them in isolation than in the context of the more complex form. *Reproduced from Akshoomoff NA and Stiles J (1995) Developmental trends in visuospatial analysis and planning: I. Copying a complex figure.* Neuropsychology 9(3): 364–377, with permission.

attention, and mental rotation. The characterization of these basic dorsal system processes as independent and distinct from those of the ventral stream is somewhat artificial in that, for example, localization of an object may also require a shift in spatial attention, and mental translation of an object must involve both localization and attention in space. Nonetheless, there is substantial evidence for functional and anatomical independence of key features of each process.

15.3.1 Spatial Localization

Evidence from human and animal studies shows that the dorsal stream plays a critical role in perceptual localization (Belger et al., 1998; Chiba et al., 2002). In a series of studies using positron emission tomography (PET) imaging, Haxby and colleagues examined profiles of posterior brain activation using tasks that required adults to compare the location of objects in two visually presented arrays (Haxby et al., 1991, 1994). In addition to activation in bilateral extrastriate cortex presumed to be involved in early visual processing, there was also robust activation of bilateral regions of parietal lobe, including posterior superior parietal areas extending rostrally to the intraparietal sulcus (Brodmann's area 7). These human brain activation findings on location processing are consistent with animal studies (Colby and Duhamel, 1996; Colby and Goldberg, 1999; Rizzolatti and Matelli, 2003), and have been largely replicated in subsequent fMRI, PET, and transcranial magnetic stimulation studies (Belger et al., 1998; Casey et al., 1998; Ellison and Cowey, 2006; Jonides et al., 1993; Nelson et al., 2000; Oliveri et al., 2001; Smith et al., 1995, 1996). Moreover, subsequent studies identified the IP lobe as important in perceptual processing of location (Colby and Duhamel, 1996; Courtney et al., 1996). A large number of functional neuroimaging studies have demonstrated the importance of frontal regions in spatial working memory for locations. Two regions that appear

to be particularly important for spatial working memory in humans include the superior frontal cortex (Courtney et al., 1998; Curtis, 2006; Haxby et al., 2000b; Sala et al., 2003) and DLPFC (Curtis, 2006; Postle et al., 2000).

The task of looking or reaching to a spatial location involves a complex network of neural areas within the dorsal frontoparietal system (Colby and Duhamel, 1996; Colby and Goldberg, 1999; Johnson et al., 1996; Pierrot-Deseilligny et al., 2004; Rizzolatti and Matelli, 2003; Wise et al., 1997). Prefrontal motor areas mediate planning and preparation for motor action; activation of these areas typically precedes the actual motor event. There is considerable evidence for superior parietal input to dorsal premotor and motor cortices; activation in frontal and superior parietal areas is concordant, suggesting a network of spatial-motor control (Rizzolatti and Matelli, 2003; Rizzolatti and Sinigaglia, 2010). In addition, IP areas connect to frontal premotor areas and play an important modulatory role in spatial-motor activity (Andersen et al., 1997). Rizzolatti and Matelli (2003) have suggested that the dorsal system may comprise two separate but interrelated systems: an IP system dominated by visual perceptual inputs and a superior parietal system governed by somatosensory information that is used to guide action.

Location processing is postulated to rely on the computation of two distinct types of relations: categorical and coordinate (Kosslyn, 1987, 2006; Kosslyn et al., 1989, 1992). Categorical relations provide generalized abstract positional information about the relative location of two elements, such as above/below or right/left. Coordinate relations provide precise metric information about spatial relations. Neuroimaging studies have implicated posterior parietal regions for both categorical and coordinate relational processing (Kosslyn et al., 1989, 1995a, 1998; Trojano et al., 2002) but the laterality of the two processes appears to differ. Specifically, categorical processing is LH dominant, while coordinate processing is RH dominant (Kosslyn, 2006; Kosslyn et al., 1989, 1995a).

One of the largest bodies of data on the early development of visuospatial processing comes from a simple, spatial hiding task, originally introduced by Piaget (1952). Infants watch as a toy is hidden under one of two screens (A or B) and are then encouraged to retrieve it. Eight-month-olds easily retrieve the object hidden under A (but also see Smith et al., 1999), but when the object is then hidden under B, they continue to search at A committing what has been termed the A not B error (AB error). This error has been widely conceptualized as an index of object permanence, that is, of the infant's knowledge that objects exist independently over space and time. A wide range of factors have been shown to affect the likelihood of making the AB error. For example, the beginning of self-locomotion reduces the likelihood of AB error (Bertenthal and Campos, 1990; Horobin and Acredolo, 1986; Kermoian and Campos, 1988). In addition, healthy preterm infants are more advanced on the AB search task compared to full-term peers matched for gestational age, suggesting that extra experience in the world offers the healthy preterm infants a developmental advantage (Matthews et al., 1996). Altering task demands effects AB task performance. Some factors, such as the use of salient landmarks, distinctive screens, or increased distance between the screens, improve performance (Butterworth et al., 1982; Wellman et al., 1987). By contrast, increasing task demands by increasing the delay between hiding and search negatively impacts performance. Introduction of a delay between hiding and retrieval increases error frequency among children as old as 12 months (Diamond, 1985; Spencer et al., 2001).

Although neuropsychological data on AB task performance are limited, several studies implicate the DLPFC. In adult rhesus monkeys, bilateral lesions of the DLPFC disrupt AB search task performance (Diamond, 1991; Diamond et al., 1994). Studies using near-infrared spectroscopy to measure localized brain activation in infants provide converging evidence for the association between frontal lobe development and successful search performance (Baird et al., 2002). Electroencephalography (EEG) data have been used to examine potential markers of object representation. Gamma-band activity has been associated with maintenance of mental representations of objects among adults (Tallon-Baudry et al., 1998). Studies measuring gamma-band activity in the EEG of 6-month-old infants during object processing and object occlusion tasks suggest that the neural signature of object representation can be detected by the middle of the first year of life (Csibra et al., 2000; Kaufman et al., 2003, 2005). In summary, these data suggest that a complex network of neural systems emerge across the first year of life to support performance on this seemingly simple task. The data point to changes in both frontal and parietal regions within the dorsal stream, and suggest comparable changes within temporal and frontal regions of the ventral stream. As Johnson noted, changes within these neural regions are unlikely to be unitary events; rather, neural development likely reflects a more gradual 'coming online' of the different components of the complex neural system that progressively comes to support the range of behaviors involved in the visual search task (Johnson et al., 2001).

Although studies of location coding in toddlers suggest that they can make use of fine-grained distance information when searching for hidden objects, the tendency to subdivide space (hierarchical coding) to facilitate remembering an object's location does not emerge until approximately age 4 (Huttenlocher et al., 1994). Further, it is not until age 10 that children show reliable, adult-like spatial coding of fine-grained, multidimensional categorical information (Sandberg et al., 1996). This is consistent with other studies demonstrating improvements in location memory through mid to late childhood (Bell, 2002; Luciana et al., 2005; Orsini et al., 1987; Zald and Iacono, 1998). Increasing task demands by requiring that multiple spatial positions be recalled in a certain order extends the period of immature performance into early adolescence (Farrell Pagulayan et al., 2006; Gathercole et al., 2004; Luciana et al., 2005). Fine-tuning of location information encoded in memory is reported to extend through late adolescence (Luna et al., 2004).

Visual hemifield tasks are used to examine hemispheric specialization of categorical and coordinate image generation (Kosslyn et al., 1995b). In these studies, participants decide whether probe marks (X) presented on a blank grid (categorical task) or bracketed square (coordinate task) appeared on a previously studied letter (see Figure 15.4). Target grids or brackets are presented to either the right (RVF) or left visual hemifield (LVF). For adults, the grid task elicits an LH 'categorical' advantage, whereas the bracket task elicits an RH 'coordinate' advantage. This profile of lateralization appears to emerge gradually during middle childhood. Specifically, 8-year-olds show an RH advantage for both categorical and coordinate tasks, but 10-year-olds begin to show the profile of lateralized differences characteristic of adults (Reese and Stiles, 2005). It is notable that the overall performance of 8-year-olds is considerably poorer than that of 10-year-olds, and the RH advantage is evident primarily on less challenging trials when the probe appears in a salient location marked by global spatial cues (so-called early probes). The finding of a developmentally early RH advantage on these location-processing tasks is consistent with the finding of an RH-mediated, global-processing advantage for children on a global–local processing task discussed earlier (Moses and Stiles, 2002). It appears that the more detailed LH-mediated processing required for both local-level and coordinate spatial processing are later emerging aspects of neural specialization.

Categorical task

Study stimulus Test stimulus

f   f

Coordinate task
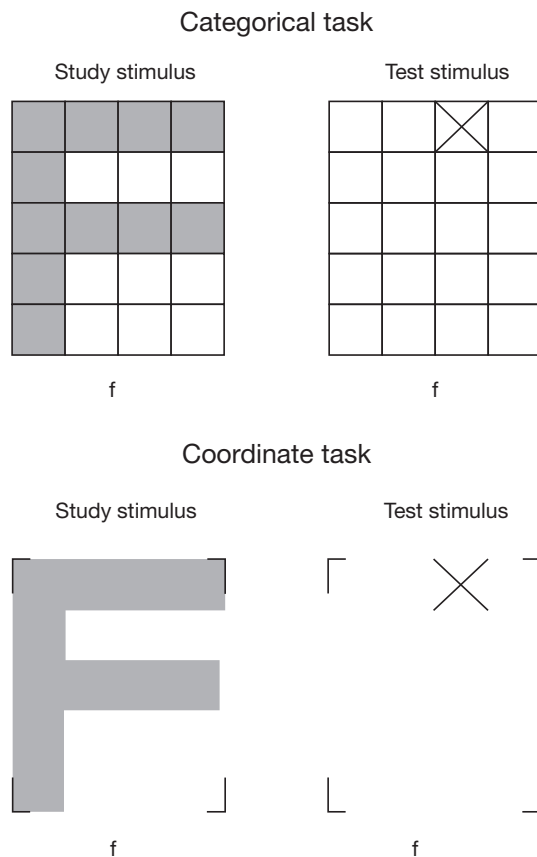
Study stimulus Test stimulus

f   f

FIGURE 15.4   Examples of the categorical (grids, above) and coordinate (brackets, below) stimuli (Kosslyn et al., 1995a). During the test phase, subjects were asked to read the lowercase letter beneath the stimulus and decide whether the corresponding block letter would cover the X mark in the grid (categorical task) or brackets (coordinate task) if it were present. *Reproduced from Kosslyn SM, Maljkovic V, Hamilton SE, Horwitz G, and Thompson WL (1995) Two types of image generation: Evidence for left and right hemisphere processes.* Neuropsychologia 33(11): 1485–1510, with permission.

15.3.2 Spatial Attention

A closely related line of investigation focuses on the neural systems associated with the ability to shift attention to different spatial locations. In contrast to work examining profiles of brain activity when subjects are required to directly perceive or remember the location of an object, spatial attention tasks investigate the brain systems engaged when attention must shift to a new location. There is considerable clinical and experimental evidence that the posterior parietal lobes play a crucial role in the ability to shift attention (Heilman and Valenstein, 1993; Hillyard and Anllo-Vento, 1998; Ivry and Robertson, 1998; Posner, 1980; Posner et al., 1984; Rafal and Robertson, 1995; Robertson, 1992). Posner's influential model of the attention system involves an interconnected network of structures that modulate and control different aspects of attention (Posner, 1980;

Posner and Petersen, 1990). The posterior parietal network plays an essential role in disengaging attention from one location and allowing a shift of attention to another location.

In the standard task used to test covert shifts of attention (Posner and Cohen, 1980), subjects are required to fixate on a point located centrally between two identical, flanking squares. After a fixed period, a visual cue is presented either centrally (e.g., an arrow) or peripherally (e.g., one box brightens), and soon after a target appears briefly in one box. The subject responds as soon as the target is detected. The critical variable is the validity of the cue. On most trials (75–80%), the cue is 'valid' and the target appears in the cued box. On the remaining trials, the cue is 'invalid,' and the target appears in the opposite box. If cueing serves to covertly shift attention, it should take less time to detect the target when the cue is valid than when it is invalid. One additional, well-established finding concerns response differences associated with the length of the interval between the valid cue and target, or stimulus onset asynchrony (SOA). With short SOAs (<200 ms), the classic facilitation of RT is observed. However, at longer SOAs (300–1300 ms), responses to the cued target are slowed (e.g., Posner et al., 1985). This phenomenon, which has been called inhibition of return (IOR), is thought to reflect the suppression of responses to an already attended location.

To examine patterns of brain activation associated with shifting attention, Corbetta used a variant of the attentional cueing task (Corbetta, 1998; Corbetta et al., 1993). The results of this study confirmed earlier reports from human and animal work on the role of the parietal lobes in shifting spatial attention. Significant foci of brain activation were observed in left and right superior parietal regions. However, the patterns of activation to stimuli presented to the RVF and LVF were not symmetrical across the hemispheres. Presentation of targets to the LVF produced significantly more activation in the RH than the LH, whereas presentation of targets to the RVF produced significant levels of activation in both the RH and LH. Furthermore, distinct activation sites for RVF and LVF targets were identified within the right superior parietal region, suggesting that different brain regions within the RH are responsible for processing information from the two sides of space.

There is a small, but growing literature on infants' ability to shift attention in the visual field (also see Colombo, 2001). A number of studies have shown that by 6 months, infants show both facilitation and IOR (Clohessy et al., 1991; Harman et al., 1994; Hood, 1993; Johnson et al., 1994; Johnson and Tucker, 1996; Varga et al., 2010). Attempts to evoke these responses from younger infants have been mixed. However, control of factors such as SOA duration and cue/target eccentricity

appears to be critical for eliciting the responses. Using 200 and 700 SOAs, Johnson and Tucker (1996) demonstrated reliable facilitation and IOR among 4-month-olds, but not among 6-month-olds. However, when a 133 ms SOA was introduced, 6-month-olds showed strong facilitation. This finding suggests that while the basic attentional responses may be robust as early as 4 months, the timing parameters that elicit the response may change with development. Consistent with this, Varga et al. (2010) reported a developmental shift from facilitation to inhibition between 4.5 and 6 months with 300 ms SOAs. Similarly, Harman et al. (1994) found no IOR response among 3-month-old children when stimuli were presented at 30° eccentricity, but a strong response at 10°. Thus, distribution of attention across the visual field may also change with development. Few studies have examined facilitation and IOR in children under 2 months. Johnson and Tucker (1996) reported only weak facilitation effects and no IOR effects among 2-month-old infants. However, Valenza et al.'s (1994) study of newborns suggests that IOR may be present in the first days of life. Further, the child's prior experience in the world, as indexed by familiarity responses, has been shown to affect individual components of the EEG response. Specifically, a negative ERP component that is measured over frontal and central electrodes (the so-called negative central or Nc component) has been shown to increase in response to novelty. Reynolds and Richards (2005) reported a smaller Nc response to familiar compared with novel stimuli in children as young as 4.5 months, suggesting that memory may have a modulatory effect on attention from very early in life. Finally, social cues can direct covert shifts of attention in children as young as 4 months of age (Reid et al., 2004). Direction of eye gaze is a potent cue for shared attention. When infants observed an adult shift gaze toward (cued) or away (uncued) from a target object, ERP responses to subsequent presentations of the cued or uncued object differed in frontotemporal brain regions. These findings suggest that a social cue can induce covert shifts in the infants' attention.

The existing literature on the development of spatial attention in the school-age period is limited, and the findings somewhat inconsistent (Brodeur and Enns, 1997; Enns and Brodeur, 1989; Nougier et al., 1992; Pearson and Lane, 1990). Schul et al. (2003) studied a large sample of children ranging in age from 7 to 17 years on a classic covert orienting task. They reported systematic developmental improvement in aspects of visual attention, including orienting, disengaging, and attending an uncued location. Across the 10-year age window, there was a systematic linear decline in response time, coupled with a linear increase in accuracy (see Figure 15.5).
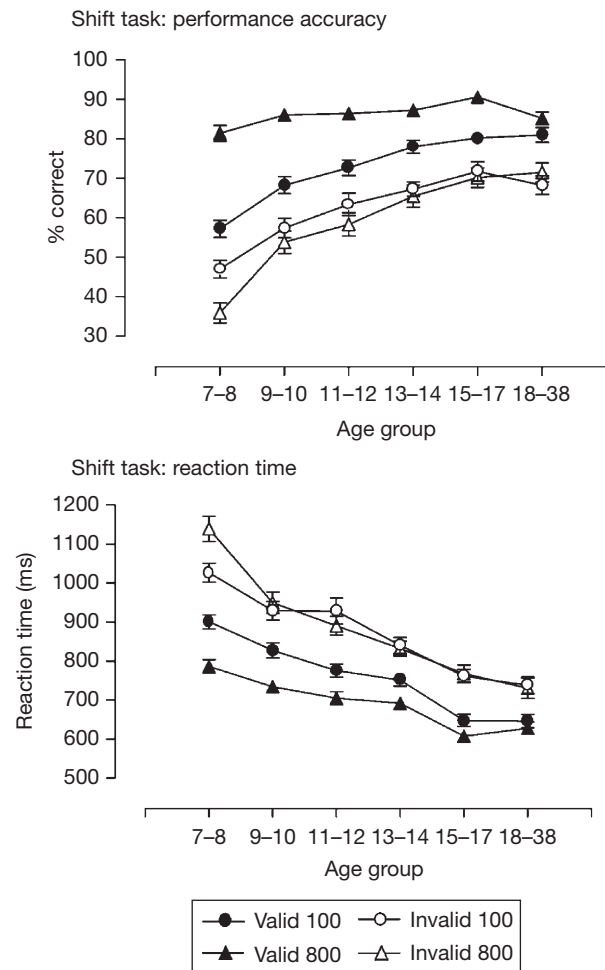

FIGURE 15.5   The accuracy and reaction time performance of typically developing 7–20-year-olds on a shift attention task show a regular pattern of improvement that emerges gradually through the school-age and adolescent periods. *Reproduced from Schul R, Townsend J, and Stiles J (2003) The development of attentional orienting during the school-age years.* Developmental Science 6(3): 262–272, with permission.

15.3.3 Mental Rotation

Mental rotation is an important spatial operation that involves the ability to mentally transpose the orientation of an object in space, thus allowing for the computation of a canonical mental representation of a noncanonically presented stimulus, for example, constructing a canonical side-view image of a dog or cat when presented a noncanonical view from behind. Mental rotation requires a host of visuospatial skills including visual pattern processing, visuospatial attention, and visuospatial working memory. A common method used to study mental rotation is to present two objects, one upright and one rotated off vertical, and ask participants if the objects are the same or mirror images. The robust result is that response times vary as a linear, monotonically increasing function of angular disparity between the

two objects. This linear response time has become the hallmark characteristic of mental rotation (see Shepard and Cooper, 1986). Over the past decade, a number of neuroimaging studies have documented a neural network associated with mental rotation that includes the right superior parietal lobe, higher-order visual areas (such as MT), and the premotor area (Richter et al., 1997; Riecansky, 2004).

Children as young as age 5 can perform mental rotation (Kosslyn et al., 1990; Marmor, 1975). In an early study, Marmor (1975) found that the RT regression slopes of 5-year-olds were similar to adults and concluded that children are able to perform mental spatial transformations. Subsequent studies have replicated this basic finding (Kosslyn et al., 1990) and confirmed through verbal reports that children use mental rotation to make judgments even under conditions where no explicit instructions to mentally rotate are given (Estes, 1998). Although young children can engage in mental rotation, developmental differences are observed in speed and efficiency of processing (Hale, 1990; Kail et al., 1980; Merriman et al., 1985; Snow, 1990). Further, a wide range of factors including IQ, gender, socioeconomic status, videogame playing, stimulus type employed, and practice on the mental rotation task all impact performance (Cai and Chen, 2000; De Lisi and Wolford, 2002; Okagaki and Frensch, 1994; Waber et al., 1982; Willis and Schaie, 1988). These data suggest that the observed developmental changes could reflect improvement of initially rudimentary mental rotation skills, or they reflect changing strategies for solving the matching problems presented within the context of the standard mental rotation tasks.

Only a few studies have reported data on the neural systems that underlie mental rotation during development. In general, children show patterns of parietal activation similar to adults, but their activation appears more diffuse (Booth et al., 1999, 2000; Roberts and Bell, 2002). The distinctive patterns of activation, including greater superior parietal activation, reported for adults compared to 9- to 10-year-olds may be an index of increasing functional specialization (Booth et al., 2000). Further, an ERP study of 8-year-old children reported bilateral, but asymmetrical parietal activation (right < left) that could reflect emerging hemispheric specialization for mental rotation (Roberts and Bell, 2002). More recently, Ark (Ark, 2005) tested 9–10-year-old children using behavioral and fMRI measures of mental rotation with challenging 3D stimuli. The activation data suggested differences between adults and children in two important brain areas related to mental rotation: the parietal area and MT. Consistent with earlier studies, children produced greater bilateral and widespread activation in the parietal lobe than adults. In addition,

adults produced greater activation in MT than the low-performing children, but not the high-performing children. MT is thought to play a role in imagining the movement of the figures in the mental rotation task. Based on the behavioral data, the low-performing children did not activate MT because they were not performing mental rotation efficiently.

15.4 TRAJECTORIES OF DORSAL AND VENTRAL STREAM DEVELOPMENT

Although many studies have examined the development of ventral or dorsal stream functions separately, work comparing the developmental trajectories of these two systems is limited. The available data present contradictory views of the relative rates of maturation of the two visual systems. One body of data that draws largely from studies of infants younger than a year suggests that dorsal stream functions involved in motion and location processing emerge earlier than ventral stream functions involved in feature processing. In contrast to these findings, studies of older children tend to support the view that the ventral stream matures earlier than dorsal stream.

Much of the evidence for the early maturation of the dorsal stream comes from infant studies of object individuation in which spatiotemporal cues involving motion and location processing are pitted against featural cues. The violation-of-expectation paradigm studies contrast infant responses when spatiotemporal or featural violations are introduced during the test. Infants under about 12 months of age (8 months with simplified tasks) recognize spatiotemporal violations, but fail to notice featural changes (Bonatti et al., 2002; Feigenson and Carey, 2003; Krojgaard, 2000, 2003, 2007; Van de Walle et al., 2000; Xu and Carey, 1996; Xu et al., 2004). This has led to the suggestion that the dorsal system develops earlier than the ventral stream. Other evidence indicates that ventral stream information, such as color, is incorporated into object processing only toward the end of the first year of life (Kaldy and Leslie, 2003; Leslie et al., 1998).

In contrast to the infant work, studies of older preschool and school children generally report that the development of dorsal stream lags behind the ventral stream. In their ERP studies, Neville and colleagues reported significant effects of response latency for the motion but not color stimuli that extended across the age span (Armstrong et al., 2002; Coch et al., 2005; Mitchell and Neville, 2004). However, visual evoked potential (VEP) studies contrasting spatial frequency (Gordon and McCulloch, 1999) and chromaticity (Madrid and Crognale, 2000) found evidence of a lag

in ventral stream functioning. Other studies testing thresholds for motion and form coherence reported that ventral stream-mediated form coherence matures significantly ahead of dorsal stream-mediated motion coherence (Atkinson et al., 2005; Braddick et al., 2003; Gunn et al., 2002). Behavioral studies of children using the dual-stream framework comparing 'what' versus 'how' (Milner and Goodale, 1995) are rare. Atkinson (1998) reported data from a small sample of 4–7-year-old children using Milner and Goodale's (1995) 'postbox' task, which requires manual posting of a letter into a slot at a particular angle (dorsal) or visual matching of the perceived angle of the slot (ventral). They reported a significantly better performance with the visual-matching task. A second study using the same task but focused on 3–4-year-old children suggested a ventral stream advantage based on a similar pattern of the results (Dilks et al., 2008).

The mixed and often contradictory results from studies comparing the relative rates of dorsal and ventral stream development have led a number of investigators to suggest that it may be misleading to treat the development of either visual system as a unitary event. Quinn and Bhatt (2006) have suggested that the global dichotomy likely overlooks subtler changes that occur within each stream across development. In addition, Johnson, Mareschal, and colleagues suggest that the inconsistency in the data may also arise from another factor related to the immaturity of the visual system (Johnson et al., 2001; Kaufman et al., 2003; Mareschal and Johnson, 2003). They note that while there is good evidence that both streams are functional from very early in development, there is little support indicating that information from the two streams is integrated until late in the first year. This lack of integration may account for some of the findings of the early dominance of spatiotemporal information in the infant literature.

Recent neuroimaging studies of older children examining structural connectivity and functional networks provide relevant data for the developmental trajectory of the dorsal and ventral streams. In a cross-sectional study of development, Lebel et al. (2008) evaluated fractional anisotropy (FA) from diffusion tensor imaging (DTI) in multiple major white matter tracts in typically developing people aged 5–30 years. Figure 15.6 shows an example from their findings comparing FA measures from a major dorsal pathway, the superior longitudinal fasciculus, and a major ventral pathway, the inferior longitudinal fasciculus. While the inferior longitudinal fasciculus appears mature in the late childhood period, the superior longitudinal fasciculus does not reach full maturity until mid to late adolescence. An extended trajectory for dorsal stream processing was also evident in a study of functional network structure in a developmental study of face processing. Haist et al.
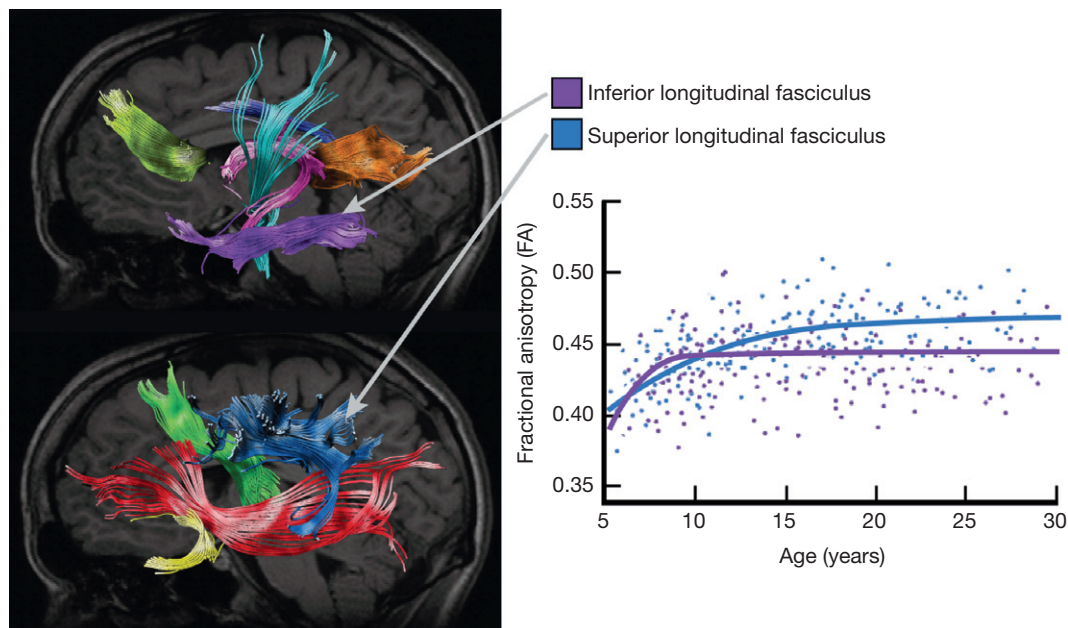

FIGURE 15.6   Evidence for developmental differences in dorsal and ventral stream white matter tracts from diffusion tensor imaging (DTI). Fractional anisotropy (FA) was measured in 202 healthy people ranging from 5 to 29 years in ten major white matter pathways. The tractography in these pathways from a representative adult participant is shown in the left panel. The right panel displays the FA findings across development in the superior longitudinal fasciculus (SLF; dorsal stream) and inferior longitudinal fasciculus (ILF; ventral stream), indicating an extended developmental trajectory for the dorsal stream relative to the ventral stream. Specifically, the SLF does not reach maturity until adolescence, whereas the ILF reaches maturity in late childhood. *Reproduced from Lebel C, Walker L, Leemans A, Phillips L, and Beaulieu C (2008) Microstructural maturation of the human brain from childhood to adulthood.* Neuroimage *40(3): 1044–1055, with permission.*

(2011) evaluated functional activation in children (ages 7–12), adolescents (ages 13–17), and adults (ages 18–40) during a simple face and object viewing task (i.e., no explicit memory or other cognitive task requirements). Adults produced a modestly greater extent of activation of the fusiform gyrus (FFA) relative to children but not adolescents, and there was a positive correlation with age and activation in the OFA. The striking finding was that children produced hyperactivation relative to adults in regions in the so-called extended face network (Haxby et al., 2000a), including regions in the ventral stream such as the anterior temporal pole (superior temporal gyrus) and amygdala, and dorsal stream such as the IP lobule and inferior frontal gyrus. Adolescents produced hyperactivation relative to adults only in the dorsal stream regions.

15.5 NEURODEVELOPMENTAL DISORDERS OF VISUOSPATIAL PROCESSING

Patient data have been an important source of information on the functional organization of the two major visual pathways. Studies of adult patients with frank injury to either the dorsal or ventral stream networks have been an important source of data on functional organization within the human brain. These studies rely on the logic of subtraction, looking for associations between site of lesion and specific functional loss. The study of developmental disorders requires a somewhat different perspective. Rather than simple associations, the central questions concern the multiple, alternative patterns of brain organization that can arise following early injury to the developing brain or disruption of molecular signaling pathways at critical points in early brain development. These studies thus address issues concerning neural plasticity and compromise, and their effects on the development of basic functions. This section reviews a few of the neurodevelopmental disorders that affect visuospatial functions. It examines both the effects of frank neural insult on the development of spatial processes and the effects of specific genetic abnormalities.

15.5.1 Perinatal Stroke

Perinatal stroke (PS) is a cerebrovascular event that occurs in the period just before birth or immediately after and is usually observed among infants born at term (Lynch and Nelson, 2001). The incidence rate of PS is estimated at 1 in 4000, but it is widely believed that the estimates are low reflecting only those cases that present with identifiable symptoms (Nelson and Lynch, 2004). PS most commonly involves the middle cerebral artery distribution, creating large lesions that

compromise much of one cerebral hemisphere. In adults, such lesions result in significant cognitive deficits, the specific patterns of which differ depending on the side and site of the injury. However, children with such large lesions often achieve considerably better functional outcomes. They typically have normal or corrected-to-normal sensory functions, and intellectual functioning that falls within the normal range on standardized IQ tests (Aram and Ekelman, 1986; Ballantyne et al., 1994; Bates, 1999; Levine et al., 2005; Nass et al., 1989; Stiles et al., 2012).

There is, however, evidence that different neural systems and functions may vary in their capacity for adaptive reorganization, even when injury is early. While basic sensory and motor systems are capable of considerable reorganization, the residual effects on function are often greater than for other domains (Himmelmann et al., 2006; Nelson and Ellenberg, 1982; Van Heest et al., 1993; Wu et al., 2006; Yekutiel et al., 1994). Within cognitive domains, level of function is consistently superior to that of adults with comparable injury, but varies by skill domain. Early developing functions such as those associated with visuospatial processing appear to be more vulnerable than later-developing functions such as language (Reilly et al., 2008; Stiles et al., 2009, 2012). Similarly, functions such as visuospatial processing that have a long evolutionary history and are closely linked to a specific sensory system exhibit somewhat less functional plasticity.

Studies of ventral stream processing among adults with unilateral injury have shown that different patterns of spatial deficit are associated with LH and RH injury (Arena and Gainotti, 1978; Gainotti and Tiacci, 1970; McFie and Zangwill, 1960; Piercy et al., 1960a; Ratcliff, 1982; Swindell et al., 1988; Warrington et al., 1966). Injury to LH brain regions results in disorders involving difficulty defining the parts of a spatial array. For example, patients with LH injury tend to oversimplify spatial patterns and omit details when drawing. On perceptual judgment tasks, they rely upon overall configural cues and ignore specific elements. In studies of global versus local processing, LH injury is associated with local-processing deficits. By contrast, patients with RH lesions have difficulty with the configural aspects of spatial analysis. In drawing, they include details, but fail to maintain a coherent organization among the elements. In perceptual judgment tasks, they focus on the parts of the pattern without attending to the overall form. In studies of global versus local processing, RH injury results in global-level deficits (Delis et al., 1986, 1988).

Data from children with PS suggest that the basic organization of the ventral stream is established early, but is capable of at least limited adaptive organization. Children with RH and LH injury show similar patterns of impairment as adults, but their deficits are milder and performance improves with development (Stiles et al., 2008, 2012). For example, reproduction accuracy for

the global-level forms, but not local-level forms, is significantly lower than controls in children with RH injury; the reverse pattern is observed in children with LH injury (see Figure 15.7(a)). Further, while accuracy improves in all groups with development, the pattern of deficit persists for both of the groups with PS (see Figure 15.7(b) for examples at two developmental time points for one child with LH and one with RH injury). These performance differences reflect alternative patterns of brain organization that can arise following early injury. In fMRI studies of global–local processing, adolescents with PS do not show a typical profile of right posterior activation for global- and left posterior activation for local-level processing (Moses et al., 2002). Rather, regardless of the side of lesion, activation for both tasks is confined to the ventral–temporal regions of the contralesional hemisphere. As shown in Figure 15.6(c), LH (left hemisphere lesion) shows

extensive activation on the right and little or no activation on the left on both the global- and local-processing tasks, while RH (right hemisphere lesion) shows extensive activation of the LH and very little activation of the RH. These findings suggest that an alternative, lateralized pattern of brain organization emerges in the wake of early injury. While functional, this alternative pattern of activation is not optimal as reflected in the behavioral performance profiles. Similar lateralized differences in global/configural versus local/featural deficits are observed across a range of tasks including block construction (Stiles et al., 1996; Vicari et al., 1998), copying and drawing (Akshoomoff and Stiles, 2003; Akshoomoff et al., 2002), and face perception (de Schonen et al., 2005; Mancini et al., 1994; Stiles et al., 2006).

Consistent with data from ventral stream functioning, studies of children with PS report patterns of deficit for
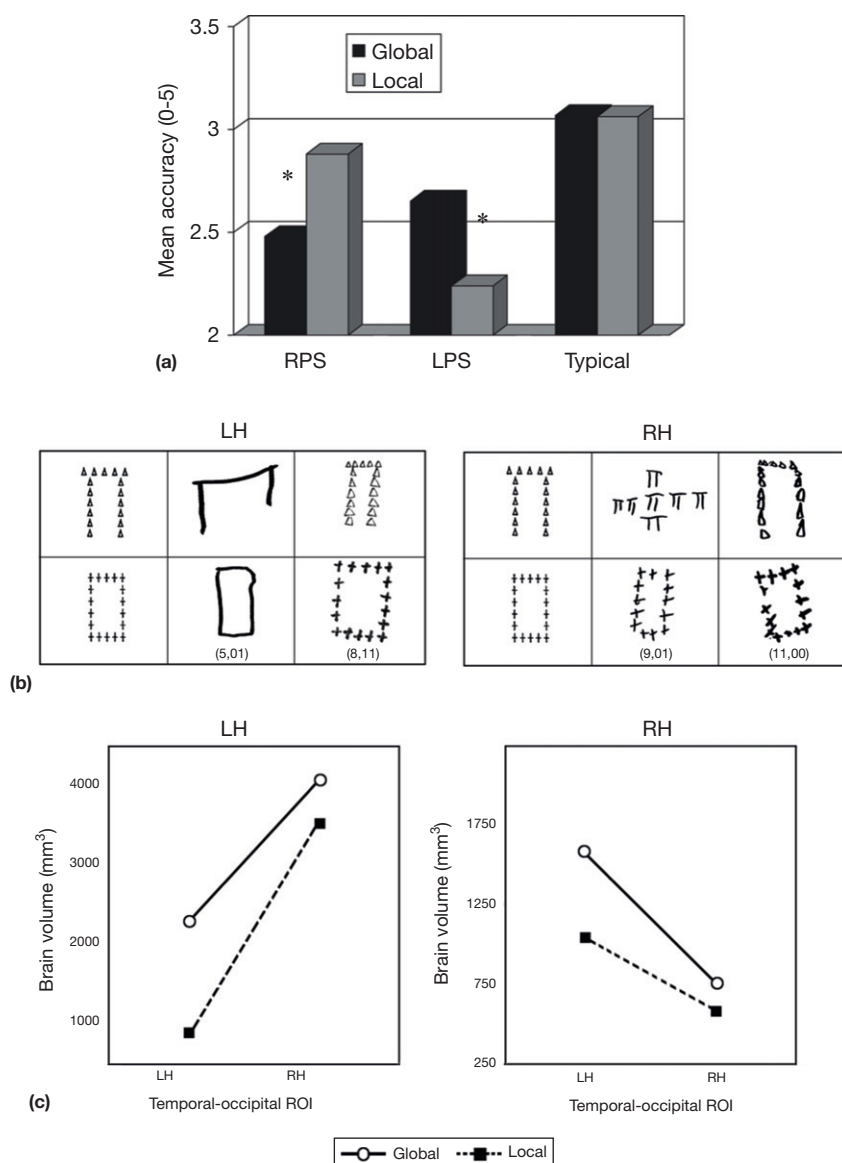

FIGURE 15.7 Behavioral and functional brain activation data from hierarchical form-processing tasks. (a) In contrast to age- and IQ-matched controls, who are equally accurate in reproducing the global and local pattern levels, 5–12-year-old children with RPS injury were more accurate in reproducing the local pattern level, and children with LPS injury were more accurate in reproducing the global pattern level. *Reproduced from Stiles J, Stern C, Appelbaum M, Nass R, Trauner D, and Hesselink J (2008) Effects of early focal brain injury on memory for visuospatial patterns: Selective deficits of global–local processing.* Neuropsychology 22(1): 61–73, with permission. (b) Examples of reproductions from two children, one with LH injury (left) and one with RH injury (right) at two developmental time points. While performance improves with age, subtle levels of specific deficits persist. (c) Brain activation to a perceptual hierarchical-form-processing task is lateralized to the contralesional hemisphere for both global and local processing. Activation is based on an ROI analysis in a region of the posterior lateral temporal–occipital lobe. *Activation data are from the same two children whose earlier drawings are shown in panel b. Reproduced from Stiles, J., Moses, P., Passarotti, A., Dick, F. and Buxton, R. 2003. Exploring developmental change in the neural bases of higher cognitive functions: The promise of functional magnetic resonance imaging.* Developmental Neuropsychology, 24(2&3), 641–668 with permission.

dorsal stream function that are consistent with those observed among adults, though the severity of deficit is less pronounced. Here again, there is clear evidence for performance improvements from the preschool to the late adolescent period, suggesting that children may be better able to compensate for their spatial-processing deficits than adults with comparable injury. Studies of adults suggest that LH injury interferes with categorical processing of spatial locations, while RH injury interferes with coordinate processing (Laeng, 1994; Palermo et al., 2008; Postma et al., 2008; van Asselen et al., 2008). Very similar patterns of results have been reported for children with PS. In an object-retrieval task, 3-year-olds with RH injury were impaired in their use of coordinate relations, performing below the level of typical 18-month-olds (Lourenco and Levine, 2009). Performance improved with development such that by age 5 children showed mastery of this task. However, evidence of persistent subtle deficit emerges among older children on more challenging tasks. Reese et al. (in preparation) tested 10–16-year-olds on Kosslyn's visual hemifield categorical and coordinate processing task (Kosslyn et al., 1995a). Similar to findings from adults with unilateral injury, children with RH injury showed subtle deficits in coordinate processing, and children with LH injury in categorical processing. These studies focused on dorsal stream processing are consistent with those focused on ventral stream processing in that they show evidence of developmental improvement in spatial processing against a backdrop of subtle, persistent lateralized deficit.

15.5.2 Spina Bifida

Spina bifida meningomyelocele is a major neurodevelopmental disorder caused by an open lesion in the spinal cord through which the meninges protrude into a fluid-filled sac (Fletcher and Dennis, 2009; Mitchell et al., 2004). It is usually associated with a malformation of the cerebellum and hindbrain (Chiari II malformation), which in turn causes hydrocephalus. Callosal dysgenesis is also common. Each of the primary CNS abnormalities associated with spina bifida can directly affect neurobehavioral outcomes. Eye movement disorders are common. The ability to perform visually guided hand and arm movements is often affected, particularly in children with higher spinal cord lesions (Fletcher et al., 2005). These are likely a result of insult to the midbrain and tectum as well as impact to the cerebellum.

In addition to hydrocephalus, spina bifida can also be characterized by hypoplasia of the corpus callosum, cortical thinning, and/or white matter loss. The secondary effects of these abnormalities can also impact neuropsychological functioning. Although outcomes are variable, children with spina bifida generally have a relatively stronger language performance and weaker perceptual and motor skills, particularly as demonstrated by comparing their verbal and performance IQ scores (Fletcher et al., 1992).

In order to examine the visual perceptual deficits found in children with spina bifida, Dennis et al. (2005) compared the results across a series of studies on measures emphasizing object-based perception or ventral processing and those emphasizing action-based or dorsal processing. Among children with IQs at or above 70, performance was relatively better on ventral stream tasks (face recognition and visual illusions) and poorer on dorsal stream tasks, particularly those requiring action-based movement (visual pursuit, drawing, route finding, and route planning). Poorest performance relative to control subjects was found on stereopsis and visual figure-ground tasks. Results from a study of object-based visual processing also provide further support for sparing of the ventral visual stream in spina bifida, despite damage to posterior brain regions (Vinter et al., 2010). Weaknesses in both visual–spatial ability and phonological processing are related to poor math performance in preschoolers with spina bifida (Barnes et al., 2011).

The early disruption of brain development associated with spina bifida appears to lead to relatively more disruption of functions associated with the dorsal visual stream. Spatial test performance is correlated with corpus callosum measures in children with hydrocephalus, including those with spina bifida (Fletcher et al., 1996). Recent MRI and DTI results indicate disruption of the white matter and reorganization of cortical regions, with the greatest impact on posterior regions (Hasan et al., 2008; Juranek et al., 2008). Direct comparisons between neuropsychological test performance and imaging results are needed to examine specific aspects of visuospatial processing in more detail.

15.5.3 Neurogenetic Syndromes

Three neurogenetic syndromes are associated with deficits in the development of visuospatial skills, particularly those skills associated with the dorsal visual stream. Neuroimaging data from patients with these syndromes also implicate greater neurodevelopmental abnormalities and perhaps greater early neurodevelopmental vulnerability within the dorsal visual stream.

15.5.3.1 Williams Syndrome

Williams syndrome (WS) is caused by a hemizygous microdeletion of approximately 25 genes on chromosome 7q11.23. Most individuals with WS have mild to moderate intellectual impairment (IQs range from the high 50s to the low 70s). There is an unusual cognitive

profile associated with WS, with relative sparing of language and relative impairment in visuospatial and visuomotor task performance (Bellugi et al., 2000; Mervis et al., 2000; Meyer-Lindenberg et al., 2006; Sarpal et al., 2008). Difficulties with visuospatial construction tasks, particularly drawing and block construction tasks, are hallmark deficits in WS. Deficits in location-processing tasks are also found. In contrast, face processing is an area of remarkable strength in WS. These results led to the suggestion of a clear deficit in the dorsal stream with relative sparing of the ventral stream in WS (Galaburda and Bellugi, 2001; Mills et al., 2000; Sarpal et al., 2008). However, task demand differences inherent in these tasks left open the possibility that there were other explanations for this phenomenon. This was examined directly in a study of face and place processing in children and adults with WS (Paul et al., 2002). The perceptual tasks were precisely matched. Individuals with WS did not differ significantly in performance from controls in the face-processing task but were significantly worse in the place (location)-processing task, providing further evidence of a dorsal stream deficit.

Deficits on construction tasks in individuals with WS are consistent across different ages, paradigms, and samples (Bellugi et al., 2001; Donnai and Karmiloff-Smith, 2000). These deficits may be related to the considerable motor demands of such tasks in contrast to tasks that tap other ventral stream skills, such as face processing, with minimal motor demands. However, the reliance on both ventral and dorsal stream processing is an alternative explanation for these discrepancies. In order to more closely examine the dorsal stream deficit hypothesis without the possible impact of intellectual impairment, a group of adults with WS with normal intelligence participated in a series of fMRI experiments (Meyer-Lindenberg et al., 2004). One task used identical stimuli in two conditions. The object-based condition required participants to indicate if two shapes match while the visuospatial decision condition required participants to indicate if two shapes could be constructed to make a square (motor). Both control and WS participants showed comparable activation in the ventral stream during these conditions. While control participants activated bilateral regions of the parietal portion of the dorsal stream in the match minus motor contrast, individuals with WS showed no significant activation. Similar results were found in the attention to object versus attention to location condition. The authors concluded that this hypoactivation reflects a persistent functional deficit in WS that becomes rate limiting when higher demands are placed on the dorsal stream during construction tasks. A subsequent fMRI study demonstrated dorsal stream deficits as well as results that suggest that the medial ventral stream is affected more than the lateral ventral stream (O'Hearn et al., 2011).

Gray matter volume reduction was found in the adjoining parietal–occipital and intraparietal sulcus in WS. Subsequent studies have reported smaller superior parietal lobe volumes in WS (Eckert et al., 2005) as well as DTI abnormalities that suggest that the underlying white matter tracts subserving the dorsal stream of visual processing may be aberrant in WS (Hoeft et al., 2007).

15.5.3.2 Fragile X Syndrome

Fragile X syndrome is a single-gene disorder caused by an expansion of CGG repeats in the promoter region upstream of the *FMR1* gene on the long arm of the X chromosome (Walter et al., 2009). It is the most common known cause of autism, with 15–30% of males with fragile X meeting DSM-IV criteria for autistic disorder and a higher percentage showing more autistic behaviors than expected based on their developmental level. The cognitive deficits can range from mild learning disabilities to severe intellectual disability, with males more likely to be severely affected than females (Schneider et al., 2009). In addition to difficulties in social abilities and executive functions, individuals with fragile X have impaired visuospatial skills (Kwon et al., 2001).

Males and females with fragile X have difficulty with mental manipulation of the spatial relationships between objects and visuomotor coordination, as well as construction tasks and visuospatial working memory (Reiss and Dant, 2003). Children with fragile X also have difficulty with arithmetic skills, with the appearance of poor math achievement scores in early childhood (Mazzocco, 2001). In a study of the relationship between visuospatial skills and math performance, girls with fragile X showed impairment on some aspects of 'where' spatial processing, but no apparent difficulty in identifying objects (Mazzocco et al., 2006). Specifically, girls had difficulty with processing global-level information during a memory for location task and integrating parts during the visual closure task. Significant correlations between math tasks and visual perception tasks were also found. These visuospatial deficits may be tied to the dorsal stream, which in turn implicates dysfunction in the posterior parietal cortex. Evidence from both structural and functional neuroimaging supports the dorsal stream deficit hypothesis in fragile X. As shown in Figure 15.8, DTI neuroimaging has shown that dorsal stream white matter tracts, including the frontal–striatal and parietal sensory–motor tracts, are altered in fragile X (Barnea-Goraly et al., 2003). Functional MRI indicates that fragile X is associated with decreased activation in the frontal–parietal areas during math computation and working memory tasks (Reiss and Dant, 2003).
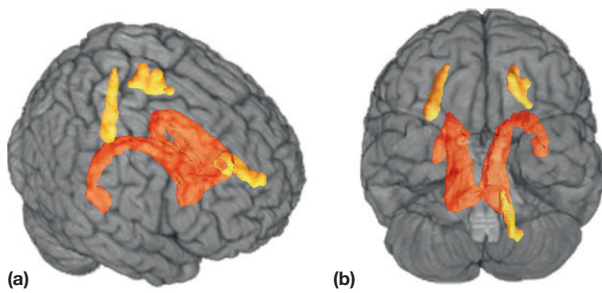
FIGURE 15.8 Example of neuroimaging evidence of a dorsal stream deficit in a neurogenetic disorder. Ten females with fragile X (mean age = 16.7 years) and ten typically developed females (age = 17.0) were examined using diffusion tensor imaging (DTI). The figure shows regions of reduced DTI fractional anisotropy (FA; colored in yellow), a measure of white matter integrity, in fragile X syndrome compared to the control participants. Specifically, abnormal FA was found in the frontal–parietal and parietal sensory–motor pathways. The caudate nucleus (colored in red) is shown for reference. Findings are shown in 3D perspective viewed from (a) superior lateral perspective of the right hemisphere and (b) inferior perspective viewed from under the frontal lobe. Rendered T1 images are shown representing the orientation of the viewing perspective. *Adapted from Barnea-Goraly N, Eliez S, Hedeus M, et al. (2003) White matter tract alterations in fragile X syndrome: Preliminary evidence from diffusion tensor imaging.* American Journal of Medical Genetics Part B: Neuropsychiatric Genetics *118B(1): 81–88, with permission.*

15.5.3.3 *Turner Syndrome*

Turner syndrome is caused by the partial or complete loss of one female X chromosome. Females with this condition typically have IQ scores in the average range, with performance IQ scores lower than verbal IQ scores, and specific difficulties on visuospatial and math tasks and visuomotor control (Mazzocco, 2001; Walter et al., 2009). There is decreased volume of the parietal and occipital cortices, particularly the superior parietal lobe and postcentral gyri, in Turner syndrome (Brown et al., 2004). Although full-scale IQ is correlated with volume of the postcentral gyri, the relationship between the volume of these posterior brain regions and visuospatial deficits has not been investigated.

Girls with Turner syndrome demonstrate a different pattern of performance across a battery of visuospatial tasks than females with fragile X syndrome (Mazzocco et al., 2006). Girls with Turner syndrome have difficulty with tests of both the 'what' and 'where' systems of visuospatial processing. Specifically, performance on a 'where' task was correlated with performance on a counting task, although it was not clear whether this reflected the visuospatial or the working memory demands of the enumeration task.

Reduced activation of the frontal–parietal network is associated with reduced performance on a visuospatial working memory task (Tamm et al., 2003). Reduced activation in the parietal–occipital regions of the cortex was found on a functional imaging version of the judgment of line orientation task (Kesler et al., 2004). DTI data also implicate abnormalities within the frontal–parietal network (Walter et al., 2009). There is additional evidence for abnormalities within the temporal lobe that may help to explain recent evidence of ventral stream visuospatial deficits in Turner syndrome (Kesler et al., 2003; Rae et al., 2004).

The data from these three distinct neurogenetic syndromes indicate relative deficits in visuospatial skills, particularly the skills associated with the dorsal stream or 'where' visual system. The results from available neuroimaging studies implicate greater involvement of posterior brain regions, but it is not clear how these generally similar behavioral and neurobiological findings result from such different genetic abnormalities. Walter et al. (2009) observed that disruption of the *FMR1* gene associated with fragile X and disruption of the LIMK1 gene associated with WS affect early dendritic morphology. This disruption may have a relatively greater impact on the dorsal visual stream due to its reliance on larger dendritic fields.

15.6 SUMMARY AND CONCLUSIONS

The ultimate product of typical visuospatial processing is a rich and fine-grained understanding of the visual world around us that provides the basis for efficient behavioral and cognitive interactions with the environment. This ability arises from the intricate coordinated activity of multiple brain regions organized into two generally construed neurofunctional brain systems architecturally defined as the ventral and dorsal visual-processing streams, and functionally distinguished for pattern and object processing (i.e., 'what') and spatial or action processing (i.e., 'where' or 'how'), respectively.

The basic neural systems mediating both of these aspects of spatial functioning appear to be specified in a rudimentary fashion early in development. Infants are able to track and retrieve hidden objects by the middle of the first year of life. Basic markers for control of spatial attention can be documented by 4 months and may be available earlier. Dissociable patterns of spatial analytic deficit can be documented in children with perinatal brain injury. All of these data are indicative of the early emergence of basic neural systems that are specified for processing certain types of information. However, early specification of a neural system does not imply full or optimal functioning early in development. There is ample evidence for protracted change extending throughout childhood, with some abilities not reaching maturity until adolescence. Therefore, the developmental perspective using both typical and atypical development is imperative to provide insights into the functional organization of visuospatial processing,

and to understand the plasticity and cognitive–behavioral consequences of early pathology.

Consideration of the dorsal and ventral processing systems as independent is widely believed to be too simplistic, as there is clear evidence for interaction or potential interaction between the systems at multiple points of anatomy and function. Nevertheless, the major developmental hypothesis regarding the trajectory posits that the dorsal system-dependent visuospatial processing matures after the ventral system pattern and object processing abilities. As summarized, this hypothesis is not entirely consistent with findings from infants, but is generally supported by findings in typically developing preschool to school-age children. This has profound implications in developmental disorders. Specifically, dorsal stream functions may be particularly vulnerable to insult at multiple points during development (Atkinson and Braddick, 2007). Findings from several developmental disorders, including frank neurological insult from perinatal stroke and spina bifida, and neurogenetic syndromes, including WS, fragile X syndrome, and Turner syndrome, were summarized that clearly demonstrate disproportionate deficits in dorsal-stream visuospatial functions relative to ventral stream functions. Together, the preponderance of evidence from developmental disorders converges to suggest that visuospatial dorsal-stream functions are specifically vulnerable and less capable of compensation.

There is considerable speculation regarding the neurofunctional basis for dorsal-stream vulnerability in development (Atkinson and Braddick, 2011; Grinter et al., 2010). From an anatomical perspective, evidence points to the possibility of greater vulnerability to insult in magnocellular pathways, the dominant visual cell type in the dorsal stream, relative to the parvocelluar pathway, the dominant visual cell type in the ventral stream. Thus, there is good reason to suspect that dorsal-stream vulnerability results from deficits originating from the earliest visual-processing stages and cascading to advanced spatial processing within the parietal cortex. From a neurocognitive systems perspective, there are additional reasons to suspect greater vulnerability within dorsal stream processing. As summarized, recent models consider the primary role for dorsal stream function to be in the service of behavioral and cognitive 'action,' and there is compelling evidence that typical visuospatial functions depend on the tightly integrated activity between the parietal and frontal cortex networks. Recent neuroimaging findings investigating structural (DTI) and functional connectivity (Fair et al., 2007, 2008, 2009) converge to suggest that the parietal–frontal networks have a protracted development period that does not reach maturity until adolescence. Thus, disruption of typical visual development that impacts parietal lobe-related visuospatial functions would be compounded later in childhood when advanced visuospatial abilities require the contributions from frontal lobe-dependent processes in addition to the posterior visuospatial abilities in the ventral occipital–temporal and parietal networks.

As this chapter suggests, the present state of the field requires a much greater emphasis on coordinated studies of the development of dorsal and ventral stream visual-processing networks. In the real world, there is no dissociation between these important processing systems; they work seamlessly and in concert to guide visual perception and action. Across development, it is likely that change in one system affects change in the other. The challenge is to better define the emergence in developmental time of each of these systems and to understand how their separate activities become coordinated. Studies of functional connectivity across development hold considerable promise for defining the emergence and integration of these systems at the neural level. At the behavioral level, studies designed to directly compare and contrast the developmental trajectories can inform our understanding. It is essential that studies link spatial perception and cognition to address the understudied problem of how spatial action systems emerge.

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