Chapter 16

Development of the visual system

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The purpose of vision is to obtain information about the surrounding environment so that we may plan appropriate actions. Consider, for example, the view through the windshield when driving (Fig. 16.1). The driver must detect and react to the road and any possible obstacles, accommodating changes of direction and avoiding objects in the path; thus visual information helps guide decisions about where to steer and when to accelerate or brake. To remain safe, therefore, the driver must know what the risks are, and this invariably involves knowing what objects there are in the visual scene. The importance of accurate perception of our surroundings is attested by the allotment of cortical tissue devoted to vision: By some estimates, over 50% of the cortex of the macaque monkey (a phylogenetically close cousin to *Homo sapiens*) is involved in visual perception, and there are perhaps 30 distinct cortical areas that participate in visual or visuomotor processing (Felleman and Van Essen, 1991; Van Essen et al., 1992).

This chapter will review theory and data concerning development of the human visual system with an emphasis on object perception. As we will see, infants are prepared to see objects and understand many of their properties (e.g., permanence, coherence) well in advance of locomotion, so that by the time infants begin to crawl and walk, they have a good sense of what and where obstacles might be, even if the hazards these objects pose remain unknown.

There is much else for infants to learn. Visual scenes, for example, tend to be very complex: a multitude of overlapping and adjacent surfaces with distinct shapes, colors, textures, and depths relative to the observer. Yet our visual experience as adults is not one of incomplete fragments of surfaces, but instead one of *objects*, most of which have a shape that can be inferred from partial views and incomplete information. Is the infant's visual system sufficiently functional and organized to make sense of the world from the onset of visual experience at birth, able to bind shapes, colors, and textures into coherent forms, and to perceive objects as regular and predictable and complete across space and time? Or does the infant's visual system require a period of maturation and experience within which to observe and learn about the world?

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FIGURE 16.1 Incoming visual information helps us guide our actions.

These “nature versus nurture” questions begin to lose their force when the details of visual development are examined and explained, because visual development stems from growth, maturation, and experience from learning and action; all happen simultaneously and all influence one another. Infants free of disability or developmental delay are born with a functional visual system that is prepared to contribute in important ways to learning, but incapable of perceiving objects in an adultlike fashion. Developmental processes that lead to mature perception and interpretation of the visual world as coherent, stable, and predictable constitute an area of active investigation and are beginning to be understood.

16.1 Classic theoretical accounts

Discussions of the nature versus nurture of cognitive development are entrenched and persistent. Such discussions are particularly vigorous when concerning infant cognition, and have tended to be long on rhetoric but short on evidence, in part because the evidence has been, until recently, relatively sparse. Research on visual development, in contrast, has tended to focus on developmental changes in neural mechanisms, with much of the evidence coming from animal models (Kiorpes and Movshon, 2004; Teller and Movhson, 1986). Research on human infants’ visual development has often been motivated by two theoretical accounts, each of which considers seriously both the starting point for postnatal development and the mechanisms of change that yield stable, mature object perception: Piagetian theory and Gestalt theory.

16.1.1 Piagetian theory

The first systematic study of infants’ perception and knowledge of objects was conducted by Jean Piaget in the 1920s and 1930s (Piaget, 1952/1936, 1954/1937). According to Piaget, knowledge of objects and space developed in parallel, and were interdependent: one cannot perceive or act on objects accurately without awareness of their position in space relative to other objects and to the observer. Knowledge of the self and of external objects as distinct, coherent, and permanent entities grew from *active manual search*, initiated by the child. When the child experiences her own movements, she comes to understand them as movements of objects through space, and induces the same knowledge to movements of other objects.

Initially, prior to any manual action experience, infants understand the world as a "sensory tableaux" in which images shift unpredictably and lack permanence or substance; in an important sense, the world of objects that we take for granted does not yet exist. Active search behavior emerges only after 4 months, and marks the beginnings of "true" object knowledge. 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 desired object from under a cover when it had been seen previously. Later in infancy infants are able to search accurately for objects even when there are multiple potential hiding places, marking the advent of full "object permanence."

Piaget placed more emphasis on manual search than visual skills as holding an important role for developmental changes in object perception, yet the lessons from his theory for questions of development of the visual system could not be more relevant. Upon the infant's first exposure to patterned visual input, he does not inhabit a world of objects, but rather a world of disconnected images devoid of depth, coherence, and permanence. Building coherent things from these disconnected images comes from action and experience with objects over time.

16.1.2 Gestalt theory

Piagetian theory can be contrasted with a coeval, competing account. The Gestalt psychologists, unlike Piaget, were not strictly developmentalists, but they did have much to say about how visual experience might be structured in the immature visual system. They suggested that subjective experience corresponds to the simplest and most regular interpretation of a particular visual array in accord with a general "minimum principle," or *Prägnanz* (Koffka, 1935). The relatively basic shapes of most objects are more coherent, regular, and simple than disconnected and disorganized forms. The minimum principle and Prägnanz were thought to be rooted in the tendency of neural activity toward minimum work and energy, which impel the visual system toward simplicity (Koffka, 1935).

The minimum principle is a predisposition inherent in the visual system, and so it follows that young infants should experience the visual environment as do adults. 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), implying that one's perceptual experience is never one of disorganized chaos, no matter what one's position in the lifespan. Hebb (1949) noted, in addition, that the newborn infant's electroencephalogram (i.e., recording of continuous brain activity) was organized and somewhat predictable, perhaps reflecting organized sensory systems at birth and serving as a stable foundation for subsequent perceptual development. Gibson (1950) suggested that visual experience begins with "embryonic meanings," a position echoed by Zuckerman and Rock (1957), who argued that an organized world could not arise from experience in the form of memory for previously encountered scenes and objects, because experience cannot operate in an organized fashion over inherently disorganized inputs. 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), but the starting point for visual experience is necessarily quite different on the two accounts. On the Gestalt view, perceptual organization precedes object knowledge; on the Piagetian view, object knowledge and perceptual organization develop in tandem.

Piagetian and Gestalt accounts each specify a starting point for postnatal development, and each has particular views about how development of the infant's visual world might proceed. Neither account is wholly on one side of the nature-nurture issue, and both accounts have offered testable predictions that have guided subsequent research; and as we will see later in this chapter, both accounts have influenced important research on object perception in infants. Yet neither can be taken as complete, in part because neither took a sufficiently comprehensive approach to vision. A quote from Gibson (1979) helps explain why this is: the visual system comprises "the eyes in the head on a body supported by the ground, the brain being only the central organ of a complete visual system. When no constraints are put on the visual system, we look around, walk up to something interesting, and move around it so as to see it from all sides, and go from one vista to another" (p. 1). Vision is not passive, even in infancy; at no point in development are infants simply inactive recipients of visual stimulation. Instead, they are active perceivers, and active participants in their own development, even from before birth (von Hofsten, 2004). Young infants do not have all the action systems implied by Gibson's quote at their disposal, but eye movements are a notable exception, and as we will see in later sections, there are strong reasons to suspect a critical role for oculomotor behavior as a means of cognitive development.

16.2 Prenatal development of the visual system

The mammalian visual system, like other sensory and cortical systems, begins to take shape early in prenatal development. For example, in humans the retina starts to form around 40 days postconception and is thought to have a relatively complete set of cells by 160 days, though the growth of individual cells and their latticelike organization characteristic of mature structure continue to mature well past birth (Finlay et al., 2003). The distinction between foveal and extrafoveal regions (viz., what will become thalamus and cortex) is present early; like the retina, the topology and patterning of receptors and neurons continue to change throughout prenatal development and the first year after birth. Foveal receptors are overrepresented in the cortical visual system, and detailed information about different parts of the scene is enabled by moving the eyes to different points (see Section 16.4.3). 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).

Many developmental mechanisms are common across mammalian species, including humans, though the timing of developmental events varies (Clancy et al., 2000; Finlay and Darlington, 1995). Data from humans are sparse, but the few cases where deceased embryos and fetuses are available demonstrate that many major structures (neurons, areas, and layers) in visual cortical and subcortical areas are in place by the end of the second trimester in utero (e.g., Zilles et al., 1986). Later developments consist of the physical growth of neurons and the proliferation and pruning of synapses, which is, in part, activity-dependent (Greenough et al., 1987; Huttenlocher et al., 1986).

16.2.1 Development of structure in the visual system

The visual system consists of a richly interconnected yet functionally segregated network of areas, specializing in processing different aspects of visual scenes and visually guided behavior: contours, motion, luminance, color, objects, faces, approach versus avoidance, and so forth. 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. Spontaneous prenatal activity in visual pathways contributes to retinotopic mapping, the preservation of sensory structure (Sperry, 1963). Spontaneous activity begins in the retina and extends 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). Waves travel across the retinal surface and are then systematically propagated through to the higher areas. This might be one way by which correlated inputs remain coupled and dissimilar inputs become dissociated, prior exposure to light.

As soon as neurons are formed, find their place in cortex, and grow, they begin to connect to other neurons. There is a surge in synaptogenesis in visual areas around the time of birth and then a more protracted period in which synapses are eliminated, reaching adultlike levels at puberty (Bourgeois et al., 2000). This process is activity-dependent: synapses are preserved in active cortical circuits and lost in inactive circuits. Auditory cortex, in contrast, experiences a synaptogenesis surge several months earlier, which corresponds to its earlier functionality relative to visual cortex (viz., prenatally). Here, too, pruning of synapses extends across the next several years. (In other cortical areas, such as frontal cortex, there is a more gradual accrual of synapses without extensive pruning.) For the visual system, the addition and elimination of synapses, the onset of which coincides with the start of visual experience, provides an important mechanism by which the cortex tunes itself to environmental demands and the structure of sensory input.

16.2.2 Prenatal visual function

The visual system is sufficiently mature by the last trimester of pregnancy to produce responses to light introduced into the womb, typically by flashing a bright light adjacent to the mother's abdomen. Fetal brain responses, for example, can be recorded with functional magnetoencephalography (fMEG), which measures the magnetic fields generated by neuronal activity in the brain of the fetus, or with functional magnetic resonance imaging (fMRI), which measures changes in blood flow in the brain resulting from cortical activity. Both fMEG and fMRI have shown that the fetal visual system detects light (Dunn et al., 2015). Moreover, cortical and subcortical structures that control eye and head movements begin to develop prior to birth. One of the most important structures is the superior colliculus (SC), a midbrain structure that supports processing of visual, auditory, and somatosensory inputs and coordinates them with topographically ordered somatic and cortical representations, to orient the observer toward stimuli. The SC begins functioning in the third trimester, and its spatial layout and layered structure (Fig. 16.2) have been proposed to orient the neonate (and perhaps the fetus) preferentially to facelike stimuli (Pitti et al., 2013). (This topic is discussed in greater detail in Sections 16.3.3 and 16.4.8). This proposal was tested recently by placing a triangular, three-diode light source against the abdomens of pregnant women late in the term, while taking care to place the lights either in an upright or inverted orientation (Fig. 16.3) relative to the fetus's viewpoint, which was assessed simultaneously with ultrasound imaging (Reid et al., 2017). As seen in Fig. 16.3, fetuses tended to move their heads toward the more facelike configuration, evidence that fetuses can control their behavior based on visual inputs.

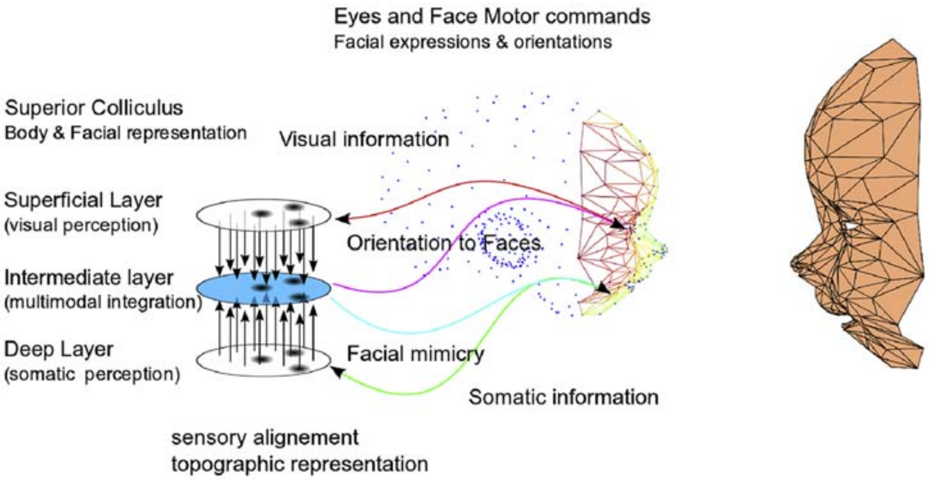


FIGURE 16.2 A model of fetal visual function in the superior colliculus (SC), a midbrain structure with connections to visual and somatic maps. If the spatial distribution of the neurons in the somatotopic map is preserved across layers, multimodal neurons in the SC may respond most strongly to visual patterns with a spatial configuration like eyes and mouth. This prediction was subsequently confirmed (Fig. 16.3). *Reproduced from Pitti, A., Kuniyoshi, Y., Quoy, M., Gaussier, P., 2013. Modeling the minimal newborn's intersubjective mind: The visuotopic-somatotopic alignment hypothesis in the superior colliculus. PLoS One 8, e69474.*

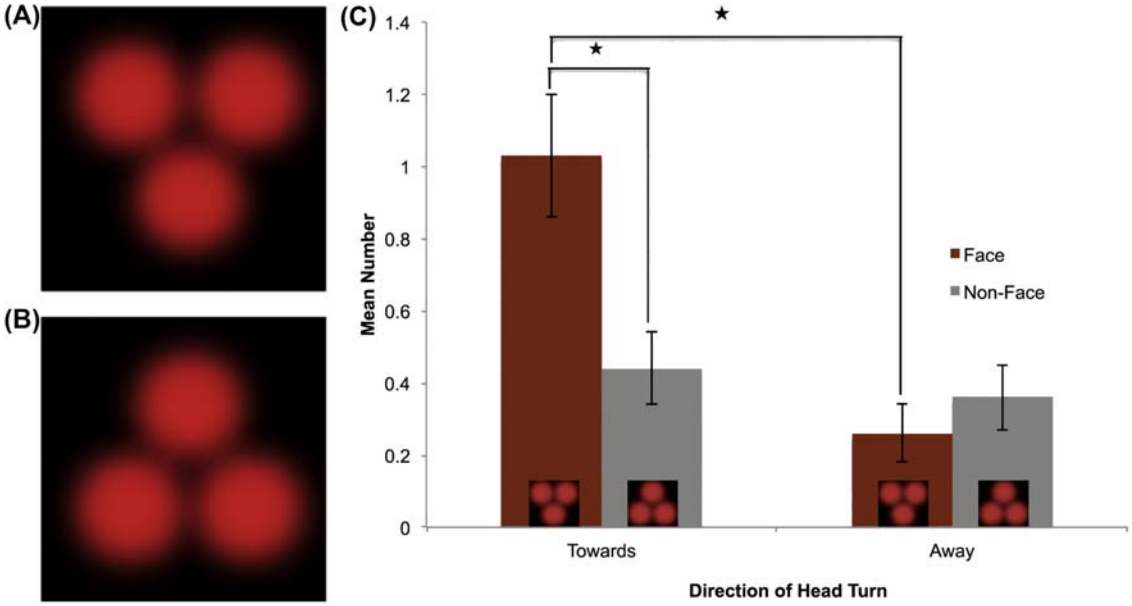


FIGURE 16.3 *Left*: Fetuses were presented with three-dot configurations that were either upright or inverted schematic faces. *Right*: Fetuses tended to turn their heads more frequently to the dots when they formed an upright schematic face. *Reproduced from Reid, V.M., Dunn, K., Young, R.J., Amu, J., Donovan, T., Reeissland, N., 2017. The human fetus preferentially engages with facelike visual stimuli. Curr. Biol. 27, 1825–1828.*

16.3 Visual perception in the newborn

Human infants are born with a functional visual system. The eye of the newborn is sensitive to light, and if motivated (i.e., awake and alert) the baby may react to visual stimulation with head and eye movements. Vision is relatively poor, however: acuity (detection of fine detail), contrast sensitivity (detection of different shades of luminance), color sensitivity, and sensitivity to direction of motion all undergo improvements after birth (Banks and Salapatek, 1983). The field of view is also relatively small, so that newborns often fail to detect targets too far distant or too far in the periphery. In addition, as far as we know neonates lack stereopsis, which is the perception of depth from binocular disparity (differences in the input to the two eyes). Maturation of the eye and cortical structures (see previous section) support developments in these visual functions, and learning plays an important role as well, discussed in greater detail in Section 16.5.

16.3.1 Visual organization at birth

Testing newborn infants is not for the faint of heart. Success is entirely dependent on the baby's mood; this is at its most capricious early in postnatal life, and there is no predicting neonate behavior. Having said this, a number of patient scientists have conducted careful experiments with neonates; these experiments have revealed that despite relatively poor vision, neonates actively scan the visual environment. Early studies, summarized by Haith (1980), revealed systematic oculomotor behaviors that provided clear evidence of visual organization at birth. Newborns, for example, will search for patterned visual stimulation, tending to scan broadly until encountering an edge, at which point scanning narrows so that the edge can be explored. Such behaviors are clearly adaptive for investigating and learning about the visual world.

In addition, newborn infants show consistent visual preferences. Fantz (1961) presented newborns with pairs of pictures and other two-dimensional patterns and recorded the member of the pair which attracted the infant's visual attention, which he scored as proportion of fixation times per exposure. Infants typically looked longer at one member of the pair: bull's eye versus stripes, or checkerboards versus solid forms, for example. Visual preferences have served as a method of choice ever since, in older infants as well as neonates. Slater (1995) described a number of newborns' preferences: patterned versus unpatterned stimuli, curvature versus rectilinear patterns, moving versus static patterns, three-dimensional versus two-dimensional forms, and high versus low-contrast patterns, among others. In addition, perhaps due to the relatively poor visual acuity of the newborn visual system there is a preference for "global" form versus "local" detail in newborns (Macchi Cassia et al., 2002).

16.3.2 Visual behaviors at birth

Fantz (1964) reported that repeated exposure to a single stimulus led to a decline of visual attention, and increased attention to a new stimulus, in 2- to 6-month-olds. A substantial number of subsequent investigations examined infants' preferences for familiar and novel stimuli as a function of increasing exposure, and these in turn led to standardized methods for testing infant perception and cognition, such as habituation paradigms (Cohen, 1976), as well as a deeper understanding of infants' information processing (Aslin, 2007; Hunter and Ames, 1989; Sirois and Mareschal, 2002).

Neonates (and older infants) will habituate to repeated presentations of a single stimulus; habituation is operationalized as a decrement of visual attention across multiple exposures according to a predetermined criterion. Following habituation, infants generally show preferences for novel versus familiar stimuli, implying both discrimination of novel and familiar stimuli and memory for the stimulus shown during habituation. Neonates and older infants also recognize visual constancies or *invariants*, the identification of common features of a stimulus across some transformation, for instance shape, size, slant, and form (Slater et al., 1983). Recognition of invariants forms the basis for categorization.

16.3.3 Faces and objects

Newborns prefer faces and facelike forms relative to other visual stimuli, and are thus well prepared to begin engaging in social interactions with conspecifics. Some have speculated that there is an innate representation for facial structure (Morton and Johnson, 1991); others have suggested that the preference stems from general-purpose visual biases that guide attention toward stimuli of a particular spatial frequency, with a prevalence of stimulus elements in the top portion, as seen in Fig. 16.4 (Turati et al., 2002; Valenza et al., 1996). As noted previously, fetuses, like newborns, also appear to orient preferentially to facelike patterns (Reid et al., 2017).

Newborns' object perception is not so precocious. Neonates perceive segregation of figure and ground (i.e., seeing objects as distinct from backgrounds), but there are limits in the ability to perceive *object occlusion*, as seen in Fig. 16.5A. Adults and older infants perceive this display as consisting of two objects, one moving back and forth behind the other (Kellman and Spelke, 1983). Neonates, however, seem to perceive this display as consisting of three disconnected parts (Slater et al., 1990). In these experiments, infants were habituated with the partly occluded rod display, followed by two test displays. One test display (Fig. 16.5B) consisted of the whole rod (no occluder), and the other consisted of two rod parts, separated by a gap in the space where the occluder was seen, corresponding to the visible rod portions in the habituation stimulus (Fig. 16.5C). For 4-month-olds, looking longer at the broken rod is taken as evidence that they perceived unity of the rod parts as unified behind the box, but for neonates looking longer at the complete rod implies perception of disjoint surfaces in similar displays. The developmental processes underlying this shift in perceptual abilities are discussed in Section 16.5.1.

16.4 Postnatal visual development

As noted in Section 16.2, visual development begins prenatally; in this section I describe some of the ways it continues after birth. Both infants and adults scan visual scenes actively—on the order of two to four eye movements per second in

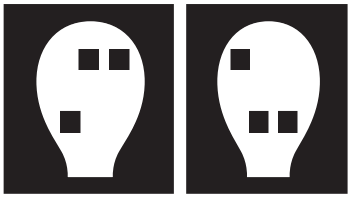
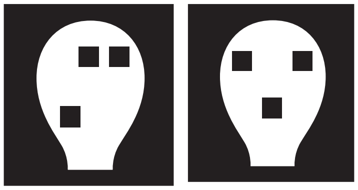
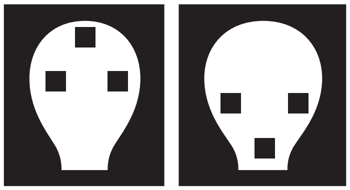
STIMULI	Total fixation time	Number of discrete looks
	53.86 s vs 37.62 s $p < 0.03$	10 vs 8.09 $p < 0.05$
	34.70 s vs 41.08 s $p > 0.20$	7.6 vs 8.3 $p > 0.30$
	44.15 s vs 22.89 s $p < 0.003$	10.43 vs 6.5 $p < 0.01$

FIGURE 16.4 Facelike stimuli from experiments on neonates' preferences. *Reproduced from Turati, C., Simion, F., Milani, I., Umiltà, C., 2002. Newborns' preference for faces: What is crucial? Dev. Psychol. 38, 875–882.*

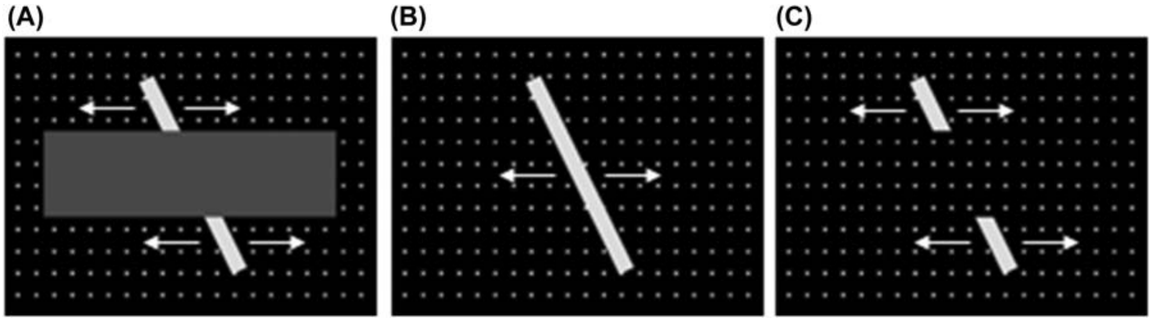


FIGURE 16.5 Rod-and-box displays from experiments on infants' perception of partly occluded objects. (A) habituation stimulus. (B) and (C) test stimuli.

general (Johnson et al., 2004; Melcher and Kowler, 2001; van Renswoude et al., 2019)—but visual function is relatively poor at birth in terms of processing and analyzing visual information. Functional visual development has been explained in terms of maturation of visual pathways in the brain and peripheral systems, such as the eyeball (Atkinson, 2000; Johnson, 1990, 2005). Acuity, for example, improves in infancy with a number of developments, all taking place in parallel: migration of receptor cells in the retina toward the center of the eye, elongation of the receptors to catch more incoming light, growth of the eyeball to augment the resolving power of the lens, myelination of the optic nerve and cortical neurons, and synaptogenesis and pruning.

16.4.1 Visual physiology

The visual system, like the rest of the brain, is organized modularly and hierarchically. Incoming light is transduced into neural signals by the retina, which passes information to the lateral geniculate nucleus (LGN, part of the thalamus), and then to primary visual area (V1) in cortex and higher visual areas. Successively higher visual areas code for visual attributes in larger portions of visual field and participate in more complex visual functions (see Fig. 16.6). For example, visual pathways extending from V5 (also known as area MT) through parietal cortex are largely responsible for coding motion. Infants younger than 2 months appear unable to discriminate different directions of motion until maturation of pathways extending to and originating in V5 (Johnson, 1990). For motion processing, therefore, development centers on a limited number of visual areas and a relatively small number of mechanisms (e.g., myelination, synaptic growth, and pruning). Object perception, in contrast, is far more complex, involving many areas, each of which is responsible for processing one or more of the many visual attributes that defines edges, surfaces, and objects.

16.4.2 Critical periods

A *critical period* refers to a time in an individual's ontogeny when some function or ability must be stimulated or it will be lost permanently (see Daw, 1995). This notion can be contrasted with a *sensitive period*, similar in concept but generally referring to scenarios in which effects of deprivation are not so severe. The formal study of critical periods was initiated by Wiesel and Hubel (1963), who covered or sutured one eye in kittens from birth for a period of 1—4 months and examined effects of visual deprivation by patching the unaffected eye and observing visual function of the affected eye alone. The deprived eye was effectively blind, as revealed by both behavioral and neural effects. Behavioral effects included an inability to navigate visually or respond to objects introduced by the experimenters, though the animals behaved normally under these circumstances when permitted to use the unaffected eye. Neural effects were examined by recording from single cells in visual cortex; in general, few cortical cells could be driven by the deprived eye in cortical regions normally responsive to input from both eyes, such as postlateral gyrus. Wiesel and Hubel also reported effects of eye closure in animals that were allowed some visual experience prior to deprivation, highlighting the distinction between critical and sensitive periods. The unaffected eye dominated activity of cells in visual cortex, but depended on both the extent of visual experience prior to deprivation and the duration of deprivation.

Stereopsis, the detection of distance differences in near space (e.g., threading a needle), seems to emerge during a critical period. Stereopsis relies on slight differences in the inputs to the two eyes when they are directed to the same point,

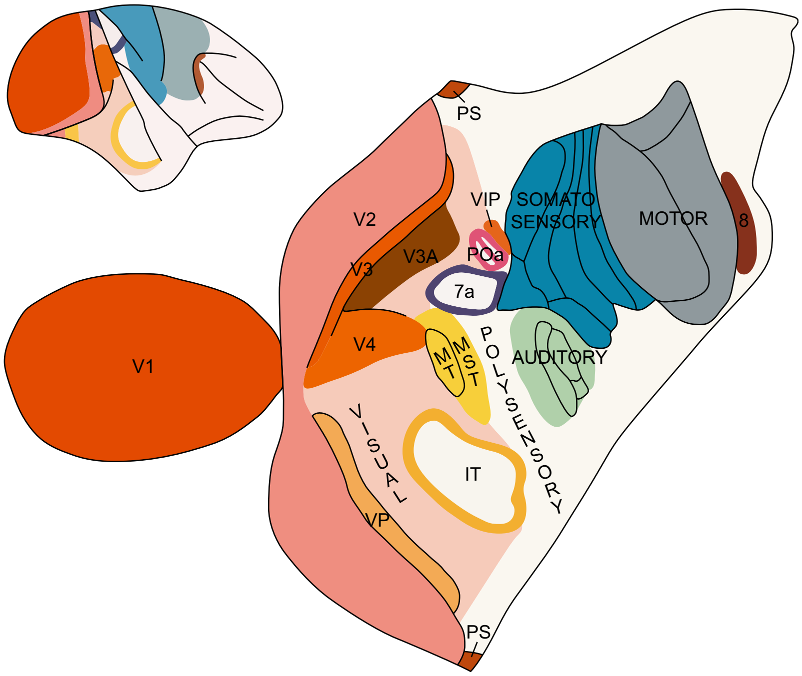


FIGURE 16.6 Cortical areas in the macaque monkey showing an outer view of the left hemisphere (upper left) and a flattened representation of sensory and motor regions. Visual areas are depicted in red, orange, and yellow. *Reproduced from Van Essen, D.C., Maunsell, J.H.R., 1983. Hierarchical organization and the functional streams in the visual cortex. Trends Neurosci. 6, 370—375.*

also known as disparity. Cells in primary visual cortex are organized into "ocular dominance" columns that receive inputs from the two eyes and register the amount of disparity between them. These require binocular function early in life—the two eyes must be directed consistently at the same points and focus on them. This can be disrupted by amblyopia (poor vision in one eye) or strabismus (misalignment of the eyes). Normally, mature visual cortex contains cells responsive to both eyes, and a few to only one eye. Abnormal visual experience can produce a preponderance of cells responsive to only one or the other eye, but not to both. In typically developing infants, stereopsis emerges at about 4 months, as inputs from the two eyes into the ocular dominance columns become segregated (Held, 1985). (Prior to this time the inputs are more likely to be superimposed, which may result in frequent diplopia, or double vision, early in life.) The critical period in humans for development of stereopsis in humans is estimated to be 1–3 years (Banks et al., 1975).

16.4.3 Development of visual attention

Visual attention—eye movements—is a combination of *saccades* and *fixations*. During a saccade, the point of gaze sweeps rapidly across the scene, and during a fixation, the point of gaze is stationary. Analysis of the scene is performed during fixations. Eye movements can also be smooth rather than saccadic, as when the head translates or rotates as the point of gaze remains stabilized on a single point in space (the eyes move to compensate for head movement), or when following a moving target.

Visual attention in infancy has attracted a great deal of interest, because it is a behavior that is relatively mature, even at birth, and because it is relatively easy to observe (Johnson, 2005; Richards, 1998). Oculomotor behaviors that have been examined include detection of targets in the periphery, saccade planning, oculomotor anticipations, sustained versus transient attention, effects of spatial cuing, and eye/head movement integration; other tasks have examined *inhibition* of eye movements, such as disengagement of attention, inhibition of return, and spatial negative priming. Bronson (1990, 1994) examined scanning patterns as infants viewed simple geometric forms, and reported changes with development in attention to distributed visual features, including a greater tendency to scan between features, to direct saccades with greater accuracy, and in general to engage in more "volitional" scanning, starting at 2–3 months.

There are important developments also in viewing complex scenes. In my lab, we recorded eye movements of infants and adults as they watched segments of an animated cartoon (*A Charlie Brown Christmas*) that was rich in social content (Frank et al., 2009). Three-month-olds' attention was captured most by low-level image salience (variations in color, luminance, and motion) and by 9 months there was a stronger focusing of attention on faces. There were no reliable differences between age groups in measures such as mean saccade distance and fixation duration. One interpretation of these results is a developmental transition toward attentional capture by semantic content—the "meaning" inherent in social stimuli. In addition, developing control over visual attention facilitates infants' ability to fixate stimuli of interest (Frank et al., 2014). Studies of real-world scene perception showed a similar trend: younger infants (3–4 months) tend to fixate the most visually salient regions of photographs, followed by a progression toward looking more at faces (Amso et al., 2014) and at objects in the scenes that were most often fixated by adults, presumably from semantic content (van Renswoude et al., 2019).

16.4.4 Cortical maturation and oculomotor development

Gaze control in mature primates is accomplished with a coordinated system of both subcortical and cortical brain areas, as seen in Fig. 16.7. Control of eye movements originates in areas with outputs that are connected to the brainstem (including SC, discussed previously), which sends signals to the oculomotor musculature. Development of visual attention has often been interpreted as revealing development of cortical systems that control it. Visual attention has been suggested to be largely under subcortical control until the first few months after birth, after which there is increasing cortical control (Atkinson, 1984; Colombo, 2001; Johnson, 1990).

For example, oculomotor smooth pursuit and perception of motion direction have been proposed to rely on a common cortical region, area V5, and the development of these visual functions in infancy has been tied to maturation of V5, as noted previously (Johnson, 1990). Smooth pursuit is maintenance of gaze on a moving target with nonsaccadic eye movements; motion direction perception is often tested with random dot displays, to control for the possibility that motion following is not simply a detection of change in position. Perceiving motion, and performing the computations involved in programming eye movements to follow motion, is thought to be founded on the same cortical structures (Thier and Ilg, 2005). This suggestion was tested empirically by Johnson et al. (2008), who observed infants between 58 and 97 days of age in both a smooth pursuit (Fig. 16.8, top panel) and a motion direction discrimination task (Fig. 16.8, center panel). Individual differences in performance on the two tasks were strongly correlated, and were also positively correlated with

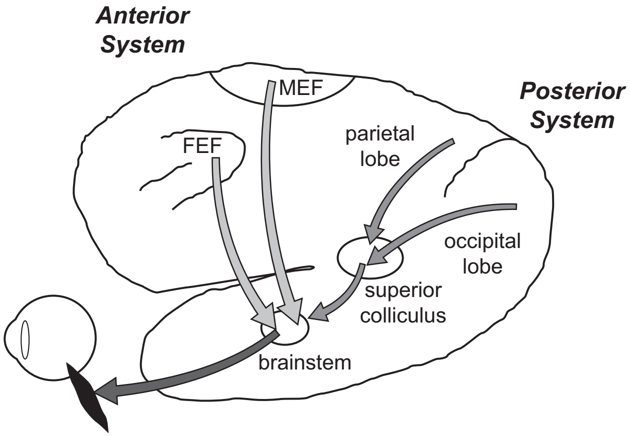


FIGURE 16.7 Subcortical and cortical structures involved in oculomotor control. *FEF*, frontal eye fields, *MEF*, medial eye fields. *Reproduced from Schiller, P.H, Tehovnik, E.J., 2001. Look and see: How the brain moves your eyes about. Prog. Brain Res. 134, 127–142.*

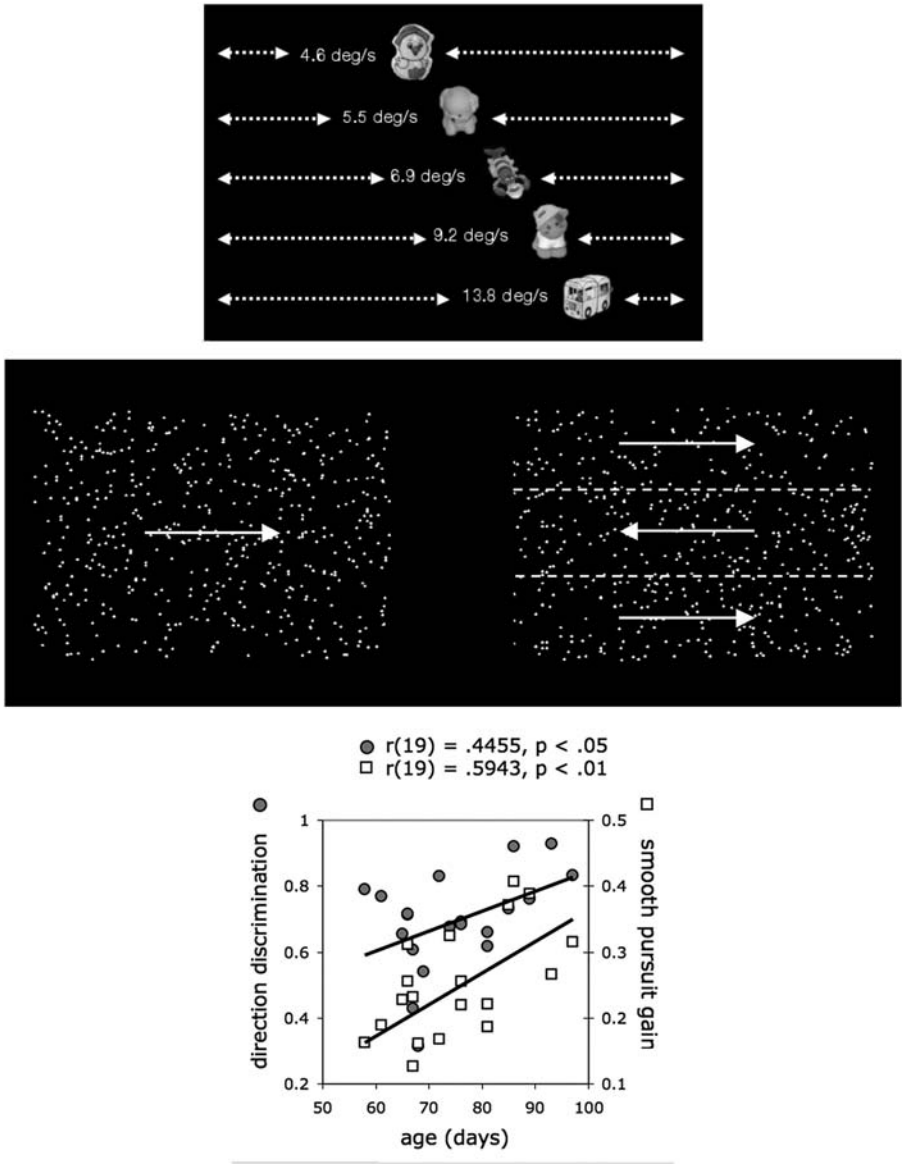


FIGURE 16.8 *Top*: Schematic depiction of stimuli used to examine smooth pursuit in young infants. A toy moved laterally at one of five speeds in one of five vertical positions on the screen. Only one toy was shown at a time. *Center*: Random-dot kinematograms used to examine motion direction discrimination in young infants. Dotted lines and dots, shown here to demarcate regions of motion, were not present in the stimulus. *Bottom*: Individual infant's performance in smooth pursuit and direction discrimination tasks were correlated with age. *Adapted from Johnson, S.P., Davidow, J., Hall-Haro, C., Frank, M.C., 2008. Development of perceptual completion originates in information acquisition. Dev. Psychol. 44, 1214–1224.*

age (Fig. 16.8, bottom panel), consistent with the maturation theory. Other visual functions in infancy that have been linked to cortical maturation include development of form and motion perception, stemming from maturation of parvocellular and magnocellular processing streams, respectively (Atkinson, 2000), and development of visual memory for object features and object locations, stemming from maturation of ventral and dorsal processing streams (Mareschal and Johnson, 2003).

16.4.5 Development of visual memory

Memory for events, object features, and locations improves over the first several postnatal months (Rose et al., 2004). As noted previously, newborns will habituate to repeated presentations of a visual stimulus and recover interest to a novel one, clear evidence for a functional short-term visual memory store available at birth. Visual short-term memory in older infants has been examined with a "change-detection" task in which infants viewed a pair of displays side by side, each of which contained one or more shapes. On one side the object or objects underwent color changes every 250 ms (Ross-Sheehy et al., 2003). When there was one object per side, 4-month-olds looked longer toward the side with color changes, implying a short-term store of the color information across the 250 ms temporal gap. Visual short-term memory develops rapidly: Ten-month-olds retained color information across a set size of four different colors (Ross-Sheehy et al., 2003), and 7.5-month-olds retained information about color-location combinations (set size of three) across a 300 ms delay (Oakes et al., 2006).

Studies of infant memory employing operant conditioning paradigms, in which infants are trained to kick their legs to move a mobile, have demonstrated long-term visual recognition stores that are available from at least 2 months under some conditions; the memories formed can last for several days or even weeks given sufficient training with the mobile and reminders (Rovee-Collier, 1999). Infants at 6 months can imitate observed behaviors after 24 h, and the retention interval is considerably longer in older infants (Barr et al., 1996). Developments in visual memory, like many other visual functions, have been proposed to stem from cortical development, in particular areas of the medial temporal lobe such as hippocampus, perirhinal and entorhinal cortices, and amygdala (Bauer, 2004; Nelson, 1995; Rose et al., 2004).

16.4.6 Development of visual stability

Our gaze moves frequently from point to point in the visual scene, and our bodies move from place to place. Despite these continual disruptions and interruptions in visual input, we experience the visual world as an inherently stable place. Consider, for example, the difference in your visual experience when you read this text while shaking your head back and forth (as if you wanted to signify "no" to someone). Reading is not much compromised. Now, if possible, shake the text back and forth while holding your head steady. You will discover reading to be more difficult, yet the spatial relation between your head and the text in the two situations is similar. When you rotate your head, compensatory eye movements known as the *vestibulo-ocular response*, or VOR, allow the point of gaze to remain fixed or to continue moving volitionally as desired (as when reading). When the text moves, there is no such compensatory mechanism.

Evidence from three paradigms suggests that visual stability emerges gradually across the first year after birth. First, young infants have difficulty discriminating *optic flow* patterns that simulate different directions of self-motion (Gilmore et al., 2004). Infants viewed a pair of random-dot displays in which the dots repeatedly expanded and contracted around a central point to simulate the effect of moving forward and backward under real-world conditions. On one side, the location of this point shifted periodically, which for adults specifies a change in heading direction; the location on the other side remained stationary. Under these circumstances adults detected a shift simulating a 5 degrees change in heading, but infants were insensitive to all shifts below 22 degrees, and sensitivity was unchanged between 3 and 6 months. Gilmore et al. speculated that optic flow sensitivity may be improved by self-produced locomotion after 6 months of age, or by maturation of the ventral visual stream.

Second, young infants' saccade patterns tend to be *retinocentric*, rather than body-centered, in a "double-step" tracking paradigm (Gilmore and Johnson, 1997). Retinocentric saccades are programmed without taking into account previous eye movements. Body-centered eye movements, in contrast, are programmed while updating the spatial frame of reference or coordinate system in which the behaviors occur. Infants first viewed a fixation point that then disappeared, followed in succession by the appearance and extinguishing of two targets on either side of the display. The fixation point was located at the top center of the display, and targets were located below it at the extreme left and right sides. As the infant viewed the fixation point and targets in sequence, there was an age-related transition in saccade patterns. Three-month-olds tended to direct their gaze *downward* from the first target, as if directed toward a target below the current point of gaze. In reality the second target was below the first location—the original fixation point—not the current point of gaze. Seven-month-old infants, in contrast, were more likely to direct gaze directly toward the second target. These findings imply that the young infants' visual-spatial coordinate system, necessary to support perception of a stable visual world, may be insensitive to extraretinal information, such as eye and head position, in planning eye movements.

Third, there are limits in the ability of infants younger than 2 months to switch attention flexibly and volitionally to consistently maintain a stable gaze. Movement of one's body through the visual environment can produce an optic flow pattern, as can head movement while stationary (recall the head-shaking example). The two scenarios may produce similar visual inputs from optic flow, yet we readily distinguish between them. In addition, adult observers can generally direct attention to either moving or stationary targets, nearby or in the background, as desired. These are key features of visual stability, and four eye movement systems work in concert to produce it. *Optokinetic nystagmus*, or OKN, stabilizes the visual field on the retina as the observer moves through the environment. OKN is triggered by a large moving field, as when gazing out the window of a train: The eyes catch a feature, follow it with a smooth movement, and saccade in the opposite direction to catch another feature, repeating the cycle. The VOR, described previously, helps maintain a stable gaze to compensate for head movement. (OKN and the VOR are present and functional at birth, largely reflexive or obligatory, and are likely mediated by subcortical pathways; Atkinson and Braddick, 1981; Preston and Finocchio, 1983). The others are the saccadic eye movement system and smooth pursuit, to compensate for or cancel the VOR or OKN as appropriate. Aslin and Johnson (1994) observed suppression (cancellation) of the VOR to fixate a small moving target in 2- and 4-month-olds, but not 1-month-olds, and Aslin and Johnson (1996) observed suppression of OKN to fixate a stationary target in 2-month-olds, but not in a younger group.

16.4.7 Object perception

As noted previously in Section 16.3.3, "piecemeal" or fragmented perception of the visual environment appears to extend from birth through the first several months afterward, implying a fundamental shift in the infant's perceptual experience. Because neonates and 4-month-olds appear to construe dynamic rod-and-box displays differently—as disjoint surfaces and as occluded objects, respectively—an important step in understanding development of perceptual completion is investigations of performance in 2-month-olds. In an initial investigation, 2-month-olds were found to show an "intermediate" pattern of performance (no reliable posthabituation preference), consistent with the possibility that spatial completion is developing at this point but not yet in final form (Johnson and Náñez, 1995). A followup study examined the hypothesis that 2-month-olds may perceive unity if given additional perceptual support. We simply increased the amount of visible rod surface revealed behind the occluder by reducing box height and by adding gaps in it, and under these conditions 2-month-olds provided evidence of unity perception (Johnson and Aslin, 1995). Adopting this approach with newborns, however, failed to reveal similar evidence: Even in "enhanced" displays, newborns seemed to perceive disjoint rather than unified rod parts (Slater et al., 1996; Slater et al., 1994). However, when newborns were tested with rod-and-box displays in which the rod parts appeared to "jump" from one location to the next—that is, apparent motion rather than smooth motion—the infants appeared to perceive the rod parts as unified (Valenza and Bulf, 2011). These authors suggested that the smooth motion of rod parts (as tested by Slater et al., 1994, 1996) might be difficult to detect at birth, yet this explanation begs the question why newborns would construe rod parts undergoing smooth motion as disjoint surfaces. This question awaits further study.

A number of studies have shown that young infants can maintain representations of the solidity and location of fully hidden objects across brief delays (e.g., Aguiar and Baillargeon, 1999; Spelke et al., 1992). Yet newborns provide little evidence of perceiving partly occluded objects, leading to the question of how perception of *complete* occlusion, or existence constancy, emerges during the first few months after birth. To address this question, experiments have examined infants' responses to objects that move forward on a trajectory, disappear behind an occluder, reappear on the far side, and reverse direction, repeating the cycle (Fig. 16.9A). Following habituation to this display, infants viewed test displays consisting of continuous and discontinuous trajectories (Fig. 16.9B,C), analogous to the broken and complete test stimuli described previously. Four-month-olds appeared to treat the ball-and-box display depicted in Fig. 16.9A as consisting of

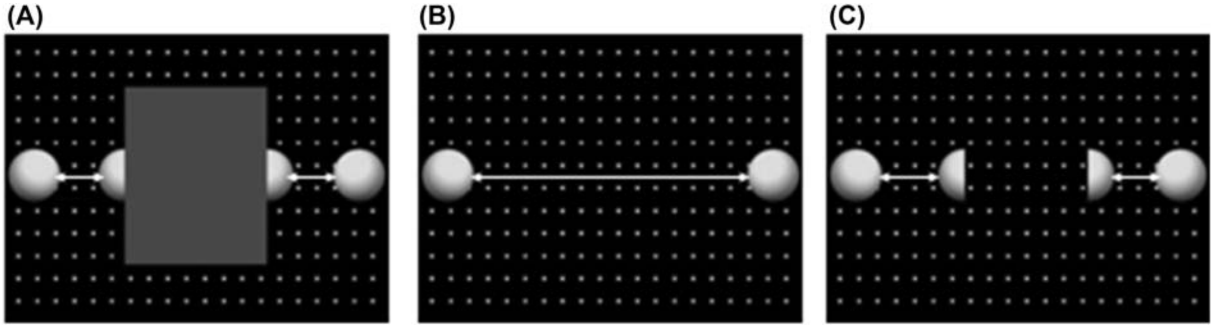


FIGURE 16.9 Ball-and-box displays from experiments on infants' perception of existence constancy. (A) habituation stimulus. (B) and (C) test stimuli.

two disconnected trajectories, rather than a single, partly hidden path (Johnson et al., 2003a,b), but by 6 months, infants perceived this trajectory as unitary. When occluder size was reduced, however, 4-month-olds' posthabituation preferences (and thus, by inference, their percepts of spatiotemporal completion) were shifted, partway by an intermediate width, and fully by a narrow width, so narrow as to be only slightly larger than the ball itself. Reducing the spatial gap, therefore, supported perception of a complete trajectory in 4-month-olds. In 2-month-olds this manipulation appeared to have no effect, implying a lower age limit for trajectory completion (i.e., existence constancy) in infants, just as there may be for spatial completion. To account for these and related findings, Bremner et al. (2015) proposed a model in which younger infants' perception of object persistence is subject to greater perceptual constraints compared with infants a few months older, and in which young infants require a combination of cues to perceive object persistence across occlusion.

16.4.8 Face perception

As noted in Section 16.3.3, infants are better prepared to perceive faces than objects at birth, showing preferences for faces and facelike structures. Research on face perception in infants provides additional insights on mechanisms of recognition. In adults, face recognition is near ceiling when faces are upright, but when faces were inverted, performance is relatively poor—the *inversion effect* (Yin, 1969). This appears to be specific to faces; other visual configurations normally seen upright, such as houses, and are not vulnerable to the effect. These findings are thought to reflect a difference in implicit processing "strategies" when viewing upright versus inverted faces. When faces are upright, they are processed in terms of both the individual features and the spatial relations among features (viz., both piecemeal and holistic processing), but when inverted, these relations are more difficult to access, forcing greater reliance on only a single source of information for recognition—the features—and thus impairing performance.

Carey and Diamond (1977) reported that children younger than 10 years of age do not show the inversion effect. This led to the suggestion that young children process faces according to features only, and that piecemeal to holistic processing develops during childhood, perhaps from experience viewing faces or maturation of the right cerebral hemisphere, implicated in complex visual-spatial tasks. Consistent with these findings, children's discrimination of faces was impaired more by a mismatch in the spacing of features than by a mismatch in the features themselves (eyes, nose, and mouth) or faces' outer contours, as seen in Fig. 16.10 (Mondloch et al., 2002), and there were dramatic improvements in performance from 6 years through adulthood to match identity of faces across changes of facial expression, orientation, and "lip reading" (mouthing different vowels), all of which require sensitivity to spatial relations among features (Mondloch et al., 2003).

Other reports, however, provide evidence for a much earlier piecemeal-to-holistic shift in processing faces. First, Younger (1992) found that 10-month-old infants were sensitive to correlations among facial attributes in a face discrimination task; 7-month-olds provided evidence of discrimination from featural variations only. Second, evidence from a "switch" paradigm showed that 7-month-olds processed configurations of facial features that were disrupted by inversion (Cohen and Cashon, 2001). In the switch design, infants are habituated to a pair of distinct stimuli (in this case, faces); at test, selected features are switched from one to the other and infants are observed for recovery of interest to the new configuration. Another study using this design found a developmental progression toward processing configurations between 4 and 10 months (Schwarzer et al., 2007). Third, the inversion effect was found in face recognition tasks with 5-, 7-, and 9-month-olds, but when outer contours and inner facial features were inverted in separate experiments, only the older two age groups showed impairment from inversion, suggesting a greater flexibility in their processing—utilizing either internal or external features to recognize the faces (Rose et al., 2008).

16.4.9 Critical period for development of holistic perception

Evidence for a critical period for holistic face perception comes from a study of individuals born with cataracts who underwent surgery to correct the problem (Le Grand et al., 2001). Each individual had at least 9 years of visual experience after surgery. The individuals were tested with face recognition tasks as described in the previous section, including tests of inversion effects, using some of the stimuli shown in Fig. 16.10. There was a specific deficit in recognition from configurational information—the spacing of features—but not from featural information, where performance was not reliably different than controls. A particularly striking characteristic of these findings concerns the timing of cataract replacement, which for every patient was less than 7 months of age—and in a few cases, as little as 2—3 months. The critical period for development of holistic processing, therefore, appears to be exceedingly brief. Interestingly, infants at 2—3 months show no signs of the inversion effect (Cashon and Cohen, 2003) and sensitivity to some kinds of holistic information in faces is not adultlike until several years after this time, as noted previously.

FIGURE 16.10 Stimuli used to test recognition of faces in which the spacing of features is varied (*top row*), the features (but not their spacing) are varied (*center row*), or the outer contours (but not features or spacing) are varied (*bottom row*). The faces in the leftmost positions of each row are identical; other faces in each row are variations of it. *Reproduced from Mondloch, C.J., Le Grand, R., Maurer, D., 2002. Configural face processing develops more slowly than featural face processing. Perception 31, 553–566.*

Some kinds of holistic object perception appear to be comprised by visual deprivation, but the evidence is complex. On the one hand, patients treated for cataracts showed no deficits, relative to controls, in identifying pictures of houses on the basis of both featural and configurational information, in contrast to face recognition (Robbins et al., 2008). And a case study of SRD, a woman who had cataracts removed at age 12, revealed few obvious deficits in object perception when tested 22 years later on shape matching, visual memory, and image segmentation tasks (Ostrovsky et al., 2006). Her performance at face recognition was impaired relative to controls, as expected from the Le Grand et al. (2001) study, but she was not tested explicitly for holistic object perception.

On the other hand, a case study of MM, a man who lost his vision at 3.5 years and had cataract replacement nearly 40 years later, revealed marked deficits in object perception skills (Fine et al., 2003). Five months after surgery, MM was unable to detect transparency in overlapping forms, to see depth from perspective in a Necker cube, or to identify a shape defined by illusory contours (a Kanizsa square)—the latter a paradigmatic instance of holistic processing, the binding of visual features across a spatial gap. Everyday objects were mostly unrecognizable, and he experienced difficulty discriminating faces and identifying emotional expression, reporting to rely on individual features rather than a “Gestalt” for these purposes. Cortical areas that give strong responses in normally sighted observers when viewing faces and objects (lingual and fusiform gyri) were largely inactive in MM. (Other visual functions were well preserved, such as contrast sensitivity, color perception, and motion perception, implying that they may have been more established and consequently robust to deprivation by the time MM was blinded in childhood).

A study of illusory contour perception in cataract-replacement patients provides additional evidence for severe compromise in feature binding from early visual deprivation (Putzar et al., 2007). Patients were divided into two groups, one with cataract replacement prior to 6 months and the second after this time, and their performance was compared to controls. The patient group treated after 6 months showed elevated reaction times and greater miss rates when searching for illusory shapes among distracters, relative to real shapes; the other groups showed reliably less of a difference on these measures. Interviews conducted after testing revealed that the post-6-month patient group did not perceive the illusory figures at all, but rather adopted a strategy of finding regions in the scenes where the inducing elements pointed inward. Consistent with experiments on face perception described previously, these results point to the first several months after birth as a critical period for spatial integration of visual information.

Notably, however, early visual deprivation does not impair all higher-level visual functions. Recent studies have shown that deprivation has little effect on susceptibility to the Ponzo and Müller-Lyer illusions, which are visual illusions involving geometric relations (Gandhi et al., 2015). In addition, effects of deprivation on categorizing faces versus nonface foils become attenuated during the first several months after cataract surgery—that is, patients' face categorization skills approach those of control participants with typical vision (Gandhi et al., 2017).

16.5 How infants learn about objects

16.5.1 Learning from targeted visual exploration

Infants in the transition toward spatial completion in rod-and-box displays—2 to 3 months of age—have been observed for evidence that scanning patterns are associated with unity perception. These links are clear. Amso and Johnson (2006) and Johnson et al. (2004) observed 3-month-old infants in a perceptual completion task using the habituation paradigm described previously (Fig. 16.5). Infants' eye movements were recorded with a corneal reflection eye tracker during the habituation phase of the experiment. We found systematic differences in scanning patterns between infants whose post-habituation test display preferences indicated unity perception and infants who provided evidence of perception of disjoint surfaces: "Perceivers" tended to scan more in the vicinity of the two visible rod segments, and to scan back and forth between them. In a younger sample (58−97 days), Johnson et al. (2008) found a reliable correlation between post-habituation preference (viz., our index of spatial completion) and *targeted visual exploration*, operationalized as the proportion of saccadic eye movements directed toward the moving rod parts, obviously the most relevant aspect of the stimulus for perception of completion. Spatial completion was not predicted by other measures of oculomotor performance, including mean number of fixations per second, mean saccade distance (to assess overall scanning activity), mean vertical position of each infant's fixations (to assess a bias for the upper portion of the stimulus), and mean dispersion of visual attention (to assess the scanning of limited portions of the stimulus vs. scanning more broadly). Nor was spatial completion associated with another measure of oculomotor control, smooth pursuit. Rather, spatial completion was best predicted by saccades directed toward the vicinity of the moving rod parts. This can be a challenge for a developing oculomotor system, attested by the fact that targeted scans almost always followed the rod as it moved, rarely anticipating its position.

Targeted visual exploration develops with time, stems from increasing endogenous control of oculomotor behavior, and consists of both *selection* of desired visual targets and *inhibition* of everything else in the visual scene. Evidence for development of selection comes from studies of orienting, discussed previously in Section 16.4.3. Evidence for development of its complement, inhibition, is relatively scarce. Newborns exhibit inhibition of return of the point of gaze to recently visited locations (Valenza et al., 1994), but inhibition of eye movements to covertly attended locations develops more slowly across the first year (Amso and Johnson, 2005, 2008). How selection and inhibition work together to maximize effective uptake of visual information is not yet known, but the experiments on spatial completion and eye movements begin to provide important insights. Very young infants' ability to perceive occlusion may be precluded by insufficient access to visual information for unity: alignment, common motion, and other Gestalt cues such as similarity and interposition. An alternate view stressing developmental mechanisms that are independent of learning and experience might posit that emergence of spatial completion stems exclusively from maturation of neural structures responsible for object perception, and, as infants begin to perceive occlusion, their eye movement patterns support or confirm this percept. Amso and Johnson (2006) found that both spatial completion and scanning patterns were strongly related to performance in an independent visual search task in which targets were selected among distracters. This finding is inconsistent with the possibility that scanning patterns were tailored specifically to perceptual completion, and instead suggests that a general facility with targeted visual behavior leads to improvements across multiple tasks—precisely the pattern of performance we observed. Scanning patterns during infants' natural scene viewing were also found to be modulated by developments in selection and inhibiton (van Renswoude et al., 2019).

How might developing object perception systems benefit from targeted scans? Eye movements may serve as a vital binding mechanism due to the relatively restricted visual field and poor acuity characteristic of infant vision. Visual information in the periphery is more difficult to access with a single glance, increasing the need to scan between features to ascertain their relations to one another. The developmental timing of targeted visual exploration in infants seems just right for another reason: the critical period for development of holistic object processing. It may be that motor feedback from scanning eye movements serves as a trigger for consolidation of neural circuits in areas that represent the stimulus, enabling association of the separate parts of an object seen on sequential fixations (Rodman, 2003). As an observer views salient object features, the point of gaze falls in rapid succession on components that will later be perceived as part of a coherent whole. Motor feedback signaling a series of sequential fixations within the central visual field could thus be a powerful cue to bind features together, a possibility consistent with close relations in adults between scan paths and pattern recognition (Noton and Stark, 1971; Rizzo et al., 1987) and scene perception (Henderson, 2003).

16.5.2 Learning from associations between visible and occluded objects

By 6 months, infants' short-term representations of unseen objects are sufficiently robust to guide reaching and oculomotor systems prospectively to intercept objects on hidden trajectories (Clifton et al., 1991; Johnson et al., 2003a; von Hofsten et al., 1998). At 4 months, prospective behavior—anticipations from eye and head movements to the place of reappearance of an object seen to move behind an occluder—is adapted to variations in occluder width and object speed, implying that under some conditions, infants may track with their "mind's eye" (von Hofsten et al., 2007). Yet under other circumstances, 4-month-olds process partly occluded trajectories in terms of visible components only, not complete paths (Fig. 16.9). Representations of occluded objects in 4-month-olds, therefore, appear to be rather fragile and not completely established.

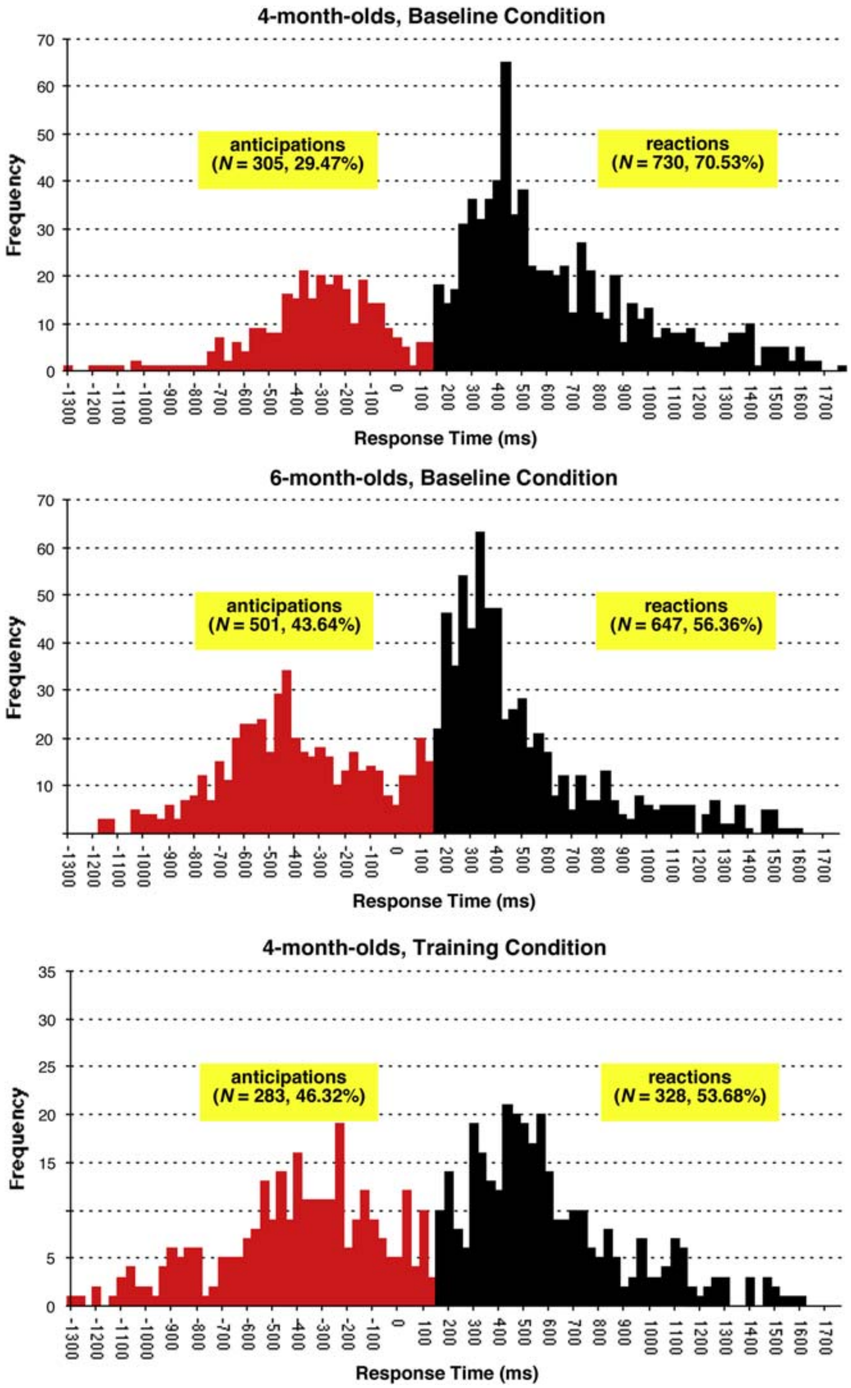
To examine the possibility that learning can facilitate spatiotemporal completion, my colleagues and I presented ball-and-box displays to 4- and 6-month-olds as we recorded their eye movements (Johnson et al., 2003a). We reasoned that a representation of the object and its trajectory under occlusion would be reflected in a consistent pattern of anticipatory eye movements toward the place of reemergence, before the object's appearance. The stimulus was identical to the displays used by Johnson et al. (2003b) to investigate spatiotemporal completion (Fig. 16.9A). Because 6-month-olds provided evidence of spatiotemporal completion in these displays when tested with a habituation paradigm, we predicted that oculomotor anticipations would be more frequent in the older age group. This prediction was supported. A higher proportion of 6-month-olds' object-directed eye movements was classified as anticipatory (i.e., initiated prior to the ball's emergence from behind the occluder, Fig. 16.11, top panel) relative to 4-month-olds (Fig. 16.11, center panel), corroborating the likelihood that spatiotemporal completion strengthens between 4 and 6 months.

Evidence for learning as an important contributor to this developmental change came from a new group of 4-month-olds in a "training" condition. These infants were first presented with an unoccluded, fully visible ball trajectory (no occluder) for 2 min followed by the ball-and-box display as per other conditions, and their eye movements were recorded. Here, the proportion of anticipations was reliably greater than that observed in the "baseline" conditions with untrained 4-month-olds, but not reliably different than that of untrained 6-month-olds (Fig. 16.11, bottom panel). In other words, 2 min of exposure led to behaviors characteristic of infants who are 2 months older. This rapid learning may stem from the ability to form associations between fully visible to partly or fully hidden objects.

In the real world, infants are exposed to many different objects moving in different ways, presenting multiple opportunities for learning. For associative learning about occlusion to be a viable means of dealing with real-world events, associations between visible and partly occluded paths must be committed to memory. How long does such rapidly acquired associations last? To address this question, we replicated the Johnson et al. (2003a) methods with new groups of 4-month-olds, and observed a nearly identical pattern of anticipatory behaviors in baseline and training conditions (Johnson and Shuwairi, 2009). A third group received a half hour break between training and test, and performance reverted to baseline, implying that memory for the association was lost during the delay. But a fourth group, provided with a single "reminder" trial after an identical delay, showed a recovery of oculomotor anticipations equivalent to the no-delay training condition. (A fifth group, provided only a single training trial, showed no benefit in the form of anticipatory looking.) These findings suggest that accumulated exposure to occlusion events may be an important means by which existence constancy arises in infancy.

16.5.3 Learning from visual-manual exploration

Spatial and spatiotemporal completion involve occlusion of far objects by nearer ones. Solid objects also occlude parts of themselves, meaning we cannot see the opposite surfaces from our present vantage point. Perceiving objects as solid in three-dimensional space constitutes 3D object completion, and we recently asked whether young infants perceive objects in this way (Soska and Johnson, 2008). Four- and 6-month-olds were habituated to a wedge rotating through 15 degrees around the vertical axis such that the far sides were never revealed (Fig. 16.10). Following habituation infants viewed two test displays in alternation, one an incomplete, hollow version of the wedge, and the other a complete, whole version, both undergoing a full 360 degree rotation revealing the entirety of the object shape. Four-month-olds showed no consistent posthabituation preference, but 6-month-olds looked longer at the hollow stimulus, indicating perception of the wedge during habituation as a solid, volumetric object in 3D space. When tested with a more complex object (an L shape), however, 3D object completion was observed in 6-month-old boys, but not girls (Soska and Johnson, 2013). This is consistent with the possibility of a male advantage in imagining how an object looks from another viewpoint, a process known as *mental rotation* (Shepard and Metzler, 1971). Mental rotation in infants is discussed in more detail subsequently.


4-month-olds, Baseline Condition

6-month-olds, Baseline Condition

4-month-olds, Training Condition

FIGURE 16.11 Histograms showing oculomotor anticipations (*gray bars*) versus reactions (*black bars*) as infants view ball-and-box displays. Each eye movement is coded for latency with respect to the emergence of the ball from behind the box, time 0. Eye movements initiated prior to this time are anticipations, and eye movements initiated after this time are reactions. *Top panel*: 4-month-olds. *Center panel*: 6-month-olds. *Bottom panel*: 4-month-olds after "training" with a fully visible trajectory. *Adapted from Johnson, S.P., Amso, D., Slemmer, J.A., 2003. Development of object concepts in infancy: Evidence for early learning in an eye tracking paradigm. Proc. Natl. Acad. Sci. U.S.A. 100, 10568–10573.*

How does 3D object completion arise? One possibility is that developmental changes in infants' motor skills might underlie the ability to perceive the unseen parts of objects. Two types of motor skills, self-sitting and coordinated visual-manual object exploration, seem particularly important, because independent sitting frees the hands for play and promotes gaze stabilization during manual actions (Rochat and Goubet, 1995). Thus, self-sitting might spur improvements in coordinating object manipulation (e.g., rotating and transferring hand-to-hand) with visual inspection, providing infants

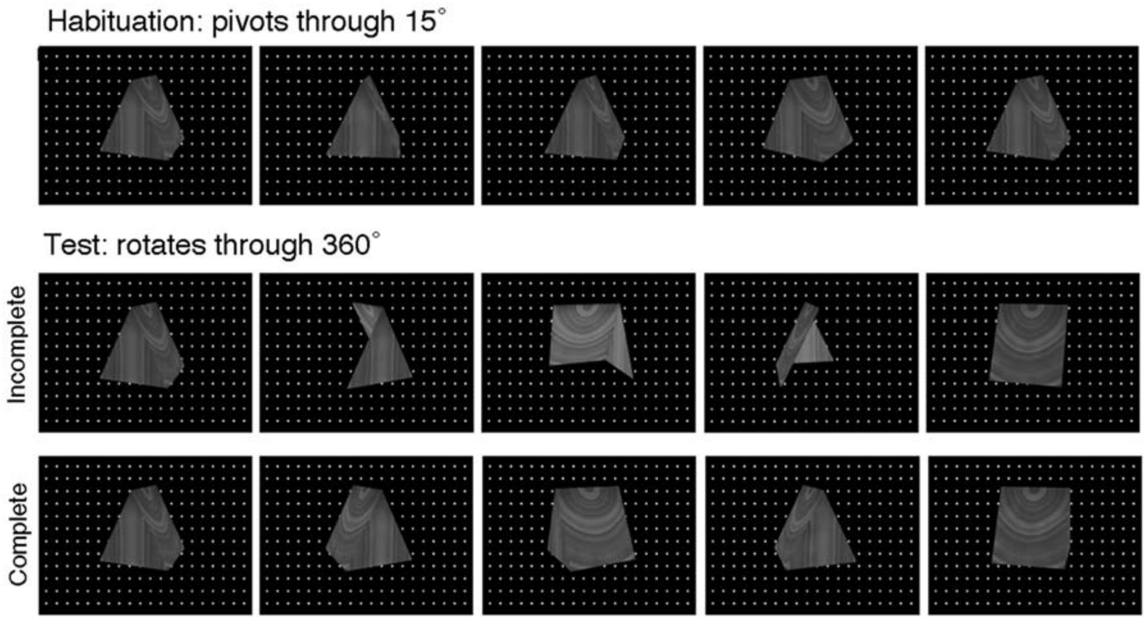


FIGURE 16.12 Rotating object displays from experiments on infants' perception of three-dimensional object completion. *Top panel*: habituation stimulus. *Center and bottom panels*: test stimuli. *Adapted from Soska, K.C., Johnson, S.P., 2008. Development of 3D object completion in infancy. Child Dev. 79, 1230–1236.*

with multiple views of objects. We tested these hypotheses in a group of 4.5- to 7.5-month-olds by replicating the Soska and Johnson (2008) methods and evaluating the infants' motor skills (self-sitting and manipulation of different objects) on the same day (Soska et al., 2010). We found strong and significant relations between both self-sitting and visual-manual coordination (from the motor skills assessment) and our measure of 3D object completion (from the habituation paradigm). (Other motor skills we recorded, such as holding skill and manual exploration without visual attention to the objects, did not predict 3D object completion (Fig. 16.12). These results provide evidence for a cascade of developmental events following the advent of visual-motor coordination, including learning from self-produced experiences.

Evidence from spatial completion experiments reveals that newborns perceive surface segregation even under conditions in which older infants and adults see the identical surfaces as unified (Slater et al., 1990), yet under other circumstances, say when stationary surfaces are directly adjacent, their connectivity or segregation may be ambiguous (Needham, 1997). This was demonstrated by Needham and Baillargeon (1998) for 4.5-month-olds' interpretation of stimulus displays containing two dissimilar but adjacent, stationary objects (Fig. 16.11). After viewing these objects during a familiarization trial, infants were presented with test events in which a hand pulled the cylinder; the box either remained stationary or moved with the cylinder. The authors reasoned that infants would look longer at the event that was unexpected (e.g., the "move-apart" event if the objects were perceived as connected), a result found with 8-month-olds (Needham and Baillargeon, 1997), but the 4.5-month-old infants looked about equally at the two test events, providing no evidence for either interpretation on the infants' part.

Needham and Baillargeon (1998) asked whether 4.5-month-olds would learn from a brief prior exposure to either object in isolation and subsequently perceive the two as segregated. Their hypothesis was confirmed: either a 5-s exposure to the box or a 15-s exposure to the cylinder alone supported segregation of the adjacent cylinder-and-box display into two separate units when infants were tested immediately afterward. Some effects of such training last as long as 72 h (Dueker et al., 2003). This learning effect has been extended in a number of important ways. For example, the effect generalizes from exposure to objects in different orientations (Needham, 2001) (Fig. 16.13), but not to objects with distinct features, unless infants are introduced to the different objects in a variety of settings or contexts prior to testing, prompting formation of a perceptual category for the objects (Dueker and Needham, 2005). Categorization is facilitated as well by increasing the number or variety of exemplars during the learning phase of the experiment (Needham et al., 2005).

16.5.4 Hormonal and environmental influences on object perception

As noted previously, mental rotation is the ability to imagine how an object that is seen from one perspective would look if it were rotated in space and viewed from a different perspective. There is a relatively strong sex difference in performance

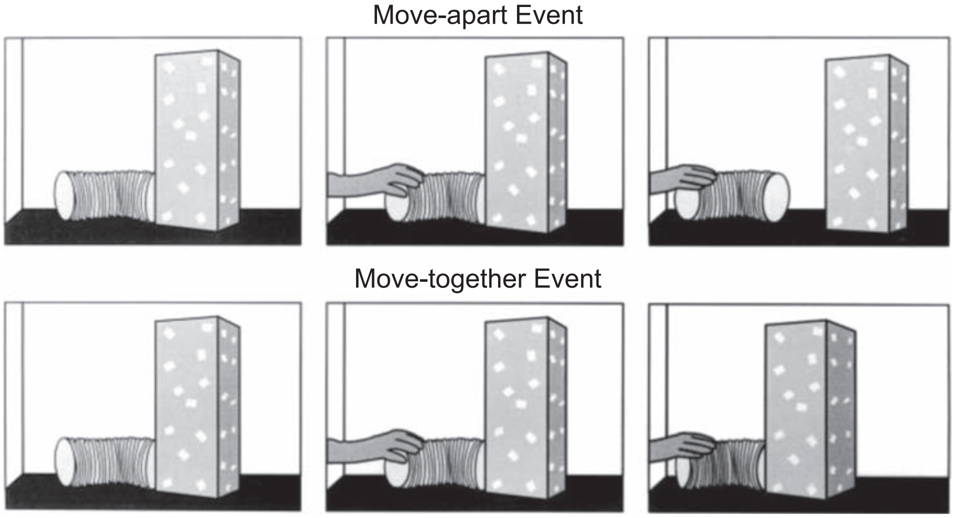


FIGURE 16.13 Schematic depictions of stimuli used to assess object segregation in infants. *Reproduced from Needham, A., 2001. Object recognition and object segregation in 4.5-month-old infants. J. Exp. Child Psychol. 78, 3–24.*

on mental rotation tasks—on average, male participants outperform female participants—in adults (Schöning et al., 2007; Voyer et al., 1995) and children (Linn and Petersen, 1985). Studies of mental rotation in infants have revealed a possible male advantage as young as 3–5 months (Moore and Johnson, 2008, 2011; Quinn and Liben, 2008, 2014), raising questions about the developmental origins of sex differences in perception of complex objects. Exposure to the hormone testosterone early in life, including prenatal exposure, is linked to a substantial number of sex differences, including features such as height, sexual orientation, and gender identity (Hines, 2010); testosterone exposure also influences mental rotation performance in adults (Pintzka et al., 2016) and children (Grimshaw et al., 1995), as well as children's gender-related playmate and toy preferences (Constantinescu and Hines, 2012).

To test for a possible role for testosterone exposure and mental rotation in infants, my colleagues and I used a visual habituation paradigm involving complex objects rotating in 3D space (Constantinescu et al., 2018). As seen in Fig. 16.14A, the object viewed during habituation was a *chiral* arrangement of cubes—that is, the object's configuration was nonsuperimposable on its mirror image (akin to human hands). The object rotated partially around the vertical axis. Post-habituation test displays depicted the same complex object, but now seen from a different perspective (Fig. 16.14B), alternating with a mirror-image object (Fig. 16.14C). We reasoned that recognizing the same object (i.e., habituation and test objects) across different viewpoints would yield a test display preference for the mirror-image display, and we observed this effect in 5-month-old boys, but not in girls (replicating the findings of Moore and Johnson, 2008). Saliva samples were obtained to measure testosterone when infants were 1–2.5 months of age, a time known as "mini-puberty" in infancy due to a surge in testosterone, particularly in males (Lamminmäki et al., 2012). As seen in Fig. 16.14D, there was a statistically reliable correlation between testosterone measured at 1–2.5 months and the visual novelty preference measured at 5 months, but only in boys (data for girls are not shown). Importantly, we also found that for girls, mental rotation performance at 5 months (i.e., the novelty preference) was correlated with parental attitudes concerning gender roles assessed with the Child Gender Socialization Scale (Blakemore and Hill, 2008), specifically disapproval of gender-atypical characteristics. Thus both hormones and the social environment modulated infants' mental rotation performance, but in different ways for girls and boys.

16.6 Summary and conclusions

From its prenatal origins to its postnatal refinement, learning to see is a mixture of developmental mechanisms, some of which operate outside of experience, and some of which are dependent on it. Although newborn infants can see fairly well upon their first exposure to patterned visual stimulation, as best we can tell the initial inputs are not bound into a stable, predictable, coherent visual world. The visual world as we adults know it emerges across the first year after birth. Developmental mechanisms are not limited only to cortical maturation or experience or learning, but instead comprise all of these and their interactions.

The theoretical views most relevant to questions of visual cognitive development described previously—the views of Piaget and the Gestalt theorists—forecasted some of the research I have described. As Piaget proposed, an infant's

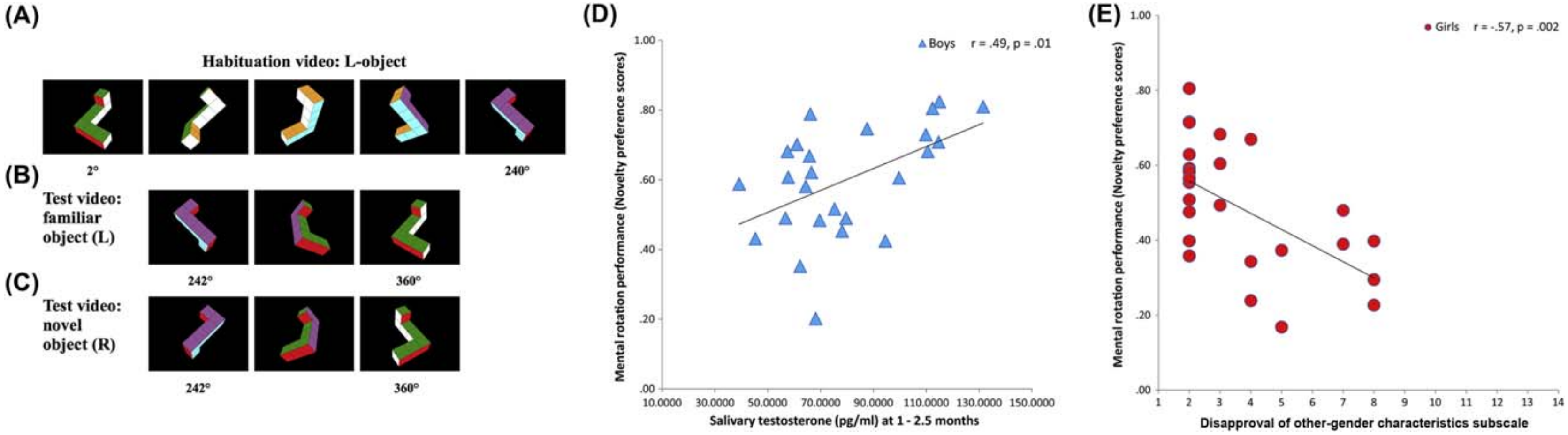


FIGURE 16.14 Stimuli and results from a study testing mental rotation in 5-month-old infants. A: habituation stimulus, rotating back and forth through 240 degrees around the vertical axis. B and C: identical or mirror image stimuli, seen from a different perspective. D: significant correlation between testosterone at 1−2.5 months and mental rotation performance at 5 months in boys (the correlation for girls was not statistically significant). E: significant correlation between parental disapproval of atypical gender norms and mental rotation performance at 5 months in girls (the correlation for boys was not statistically significant). *Reproduced from Constantinescu, M., Moore, D.S., Johnson, S.P., Hines, M., 2018. Early contributions to infants' mental rotation abilities. Dev. Sci. 21, e12613.*

experience of the visual world begins with a limited capacity to detect object boundaries, particularly under occlusion, and develops in part as a result of the infant's interactions with the environment. And as the Gestalt theorists proposed, visual perception is organized at birth and elaborated with experience; many of the organizational principles characteristic of adult vision appear to be operational in infants (if not at birth). These theories have proven prescient and have given direction to many investigations of infant perception and cognition, yet neither theory is fully adequate to explain the foundations of vision and its development.

Although our understanding of visual cognitive development continues to grow, the current state of knowledge is substantial and the outlines of a comprehensive account can now be summarized, as follows:

- To understand how infants come to experience a stable and predictable world of substantial, volumetric objects, overlapping and extending in depth—the visual world that we adults experience—we must look to experiments that elucidate visual development.
- Visual development begins well before birth. The visual system begins to develop within weeks after conception, and continues to develop rapidly prior to the onset of patterned visual stimulation. Visual responses to light introduced into the womb indicate that the visual system is at least partly functional before birth.
- Vision is partially organized at birth. Neonates show systematic scanning patterns and visual preferences, in particular preferences for areas of high contrast and motion. These preferences are well suited for directing attention to features of the visual world relevant to learning about objects. But neonates most likely do not perceive objects as do adults—as solid and substantial entities.
- Newborn's experience of the visual world is fragmented and unstable. Visual and motor systems that yield an experience of coherent objects and the position of the observer relative to a stable environment emerge across the first postnatal year.
- There is a critical period for development of face and object perception. Normal visual experience during this time is essential to their development, as are patterns of eye movements, and other action systems, in binding features into wholes.
- Developmental mechanisms include cortical maturation, visual experience, and learning, and the interplay between these developmental events.
- Developments in some visual functions have been linked directly to maturation of specific cortical regions and visual pathways. Development of smooth pursuit eye movements and motion direction discrimination is thought to stem from maturation of cortical area V5 (also known as MT), form and motion perception from parvocellular and magnocellular processing streams, respectively, and visual memory from structures in the medial temporal lobe. These developments occur between birth and 6 months of age.
- Infants have multiple means of learning at their disposal, and learning is an indispensable part of understanding the visual world. Infants learn from their own behavior as well as by observing relevant events in the environment.

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