Development of visual perception

Scott P. Johnson*

Processes of visual development that yield a view of the world as coherent and stable begin well before birth and extend over the first several years after the onset of visual experience. Infants are born capable of seeing and with specific preferences that guide the point of gaze to relevant portions of the visual scene to support learning about objects and faces. Visual development after birth is characterized by critical periods in many notable visual functions, and by extensive learning from experience and increasing control over eye movement systems.

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INTRODUCTION

When we encounter a visual scene, we quickly form an impression of its contents and we make moment-to-moment, context-appropriate decisions about our actions. Consider, for example, the street scene in Figure 1, taken on 6th Avenue in New York City. The scene is cluttered with numerous objects: vehicles, buildings, signs, trees, and so forth. In contrast, the beach scene in Figure 1, taken in Sarasota, Florida, contains few sizable objects and more open space. We seem to form these assessments effortlessly and instantly, and we can swiftly plan our actions if the need arises. In the case of the beach, we can move toward the water at a leisurely pace, but in the case of 6th Avenue, we need to move toward the sidewalk without delay lest we be run over by oncoming traffic!

Despite the apparent ease with which these determinations are made, there are characteristics of visual scenes that might be expected to pose a significant challenge to their interpretation. Many scenes, for example, are extraordinarily complex: a myriad of shapes, colors, and textures at various distances from the observer. A second potential challenge is occlusion of farther objects by nearer ones. In the New York scene the vehicles in the distance are only partly visible, blocked by other cars, and the many buildings hide others from view. Yet adults do not experience a world composed solely of shapes, colors, and textures, or of incomplete fragments of surfaces. Instead, we see objects, laid out in depth, many of which have a regular shape that can be inferred or predicted even with partial views and intricate surface appearance.

Infants inhabit the same world as do adults and encounter similar visual scenes—a visual environment furnished with objects that overlap and occluded one another. How do they meet the challenges of seeing and interpreting scenes just described? Is the infant's visual system sufficiently functional and organized to make sense of the world, 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, to coordinate visual and manual skills, to recognize and utilize individual visual cues, and to integrate auditory, haptic, and visual information?

The reader may recognize echoes of the nature-nurture debate in these questions: the extent to which an individual's physical and behavioral characteristics are innate or learned, independent of experience or its consequence. The nature-nurture argument begins to break down when examining in detail the mechanisms of visual cognitive development, because visual cognitive development is a function of growth, maturation, and experience from learning and from action; all happen at the same time and all influence one another. Research on critical periods, for example, some of which is reviewed subsequently, makes it clear that normal visual function cannot develop in the absence of visual experience.

Much of the motivation for research on visual development comes from experiments that reveal neural mechanisms in animal models,[1,2] and by extensive observations of human infants. A quote from Gibson[3] provides some perspective: The visual system comprises 'the eyes in the head on a body

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*Correspondence to: scott.johnson@ucla.edu

Department of Psychology, UCLA, Los Angeles, CA, USA

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FIGURE 1 | Two visual scenes.

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, from the beginning of postnatal life.[4] 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 there are strong reasons to suspect a critical role for oculomotor behavior as a means of cognitive development.

PRENATAL VISUAL DEVELOPMENT

The visual system, like other sensory and cortical systems, begins to take shape early in prenatal development. The retina (rods, cones, amacrine and ganglion cells, and so forth), for example, starts to form around 40 days postconception and is thought to have a full complement of cells by 160 days,[5] although it continues to mature after the first year after birth. It originates from the same structures that give rise to the rest of the nervous system, the ventricular zone in the embryonic neural tube. The distinctive division of fovea from extrafoveal regions is present early, though this particular topology, and the general shape of the eye, continue to change throughout prenatal development and the first year after birth. The process by which the length of the eyeball grows in proportion to changes in the cornea to keep input focused on the retina is known as *emmetropization*. These processes support high-acuity vision, the lens of the eye focusing incoming light onto the area of the retina (the fovea) with the highest concentration of photoreceptors. Relative to the retinal periphery, foveal receptors are overrepresented by greater 'territory' in the cortical visual system, and thus detailed information about different parts of the world is made possible by moving the eyes to different points in the visual scene (more on this later). 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.[6,7] (These cortical structures continue to develop after birth as well.)

A model timetable for development of subcortical and cortical visual structures in humans was described by Finlay and Darlington[8] based on the comparative literature on brain development. Many developmental mechanisms are conserved across mammalian species, permitting hypotheses about comparable developmental events in humans.[9] The timetable includes the timing and duration of maturation of individual visual processing streams and areas. Data from human embryos and fetuses are sparse, but in the few cases where they are available, they are largely consistent with Finlay and colleagues' model. Besides retinal development, most major structures (neurons, areas, and layers) in visual cortical and subcortical areas are in place by the end of the second trimester, which coincidentally is also about the time that the eyes first open *in utero*. Developments after this time consist of the growth of individual neurons, the proliferation and pruning of synapses (the connections between neurons), and the fine-tuning of visual areas.

Development of the Topography of the Visual System

The visual system is composed of a richly interconnected yet functionally segregated network of areas, many of which specialize in processing different kinds of input or output: motion, color, objects, faces, visually guided action, and so forth. How do these areas arise? The basic areal patterns are laid down in the first trimester but the final forms of some areas are incomplete until well after birth. There are many developmental mechanisms: incipient connections from sensory organs, connections received and sent to other areas, the neurochemical environment, overproduction and subsequent elimination of unused pathways, integration with other sensory systems (directly or indirectly via subcortical structures), and others. An interesting fact about prenatal visual development prior to the onset of patterned visual input is that there is spontaneous yet organized activity in visual pathways from early on, activity that contributes to retinotopic 'mapping'.[10] Mapping refers to the preservation of sensory structure, for example the relative positions of neighboring points of visual space, from retina through the thalamus, primary visual cortex, and higher visual areas. One way in which mapping occurs is by 'waves' of coordinated, spontaneous firing of receptors in the retina, prior to eye opening, observed in some nonhuman species such as chicks and ferrets.[11] Waves of activity are propagated across the retinal surface at a point in development after connections to higher visual areas have formed; the wave patterns 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, even in the absence of exposure to light. In this respect mapping is a self-organizing process, neither learned nor genetically predetermined, one way in which activity inherent to the system can help to organize developmental events.

Prenatal Refinement of the Visual System

By the third trimester, the visual system is remarkably well developed, but several important developmental phenomena remain. 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 adult-like levels at puberty.[12] 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 may correspond to the fact that it begins to receive input earlier than 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, provide an important mechanism by which the cortex tunes itself to environmental demands and the structure of sensory input.

NEONATAL VISUAL PERCEPTION

Human infants are born with a functional visual system. The neonate's eye takes in light and passes it on to higher brain areas, and if awake and alert the baby typically reacts to different patterns of visual stimulation with head and eye movements. Vision is poor relative to adults, however, in terms of acuity (the ability to resolve fine detail), contrast sensitivity (the ability to resolve differences in shades of luminance), color sensitivity, and sensitivity to different directions of motion.[13] Neonates' field of view is also smaller, meaning that they appear not to attend to visual information too far distant or too far in the periphery, and they lack stereopsis, the perception of depth in near space from binocular disparity (differences in the input to the two eyes). Thus, neonates' vision is a somewhat blurry, hazy, and sluggish version of mature vision. Improvements in these visual skills stem by and large from maturation of the eye and cortical structures. Learning plays an important role as well, and these kinds of development will be discussed in greater detail in subsequent sections.

Visual Organization at Birth

Testing newborn infants can pose a significant challenge, as illustrated in Figure 2. Fortunately, a number of brave and persistent 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 in an exemplary volume by Haith,[14] revealed systematic oculomotor behaviors or 'rules' that provided unambiguous evidence of visual organization at birth. The rules include: (1) in the absence of patterned stimulation initiate a controlled search, (2) scan broadly until encountering an edge, and (3) stay in the vicinity of the edge. Such behaviors are clearly adaptive for purposes of exploring and learning about the visual world.

Neonates' vision is organized in a second way: Newborn infants exhibit consistent preferences for some stimuli relative to others. This was first reported by Fantz, who presented newborns with pairs of patterns and recorded which attracted the infant's visual attention, operationalized as

FIGURE 2 | A newborn infant tested for perception of object unity. The infant is held by an experienced research assistant and positioned in view of the stimulus display, seen at right. In this case the infant is not entirely cooperative. Photo courtesy of Alan Slater.

proportion of fixation times per exposure, typically 30 seconds. Often, the infants showed systematically longer looking at one member of the pair: bull's-eyes versus stripes, or checkerboard versus solid forms.[15] This *visual preference* method was used to great effect in subsequent experiments to examine more closely the kinds of visual discrimination neonates and older infants can perform and the kinds of spontaneous preferences they show. Slater[16] has described a number of these 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, there is a processing advantage for 'global' form versus 'local' detail in newborns, commensurate with the global precedence effect in adults,[17] most likely due to the poor spatial resolution characteristic of the newborn visual system.[18] At the same time, however, there appears to be a difficulty in seeing links or connections between local stimulus elements, which has led to the suggestion that infants' vision is 'fragmented' at birth.[19]

Looking Behaviors in the Neonate

Fantz[20] observed that repeated exposure to a single stimulus led to a decrement of visual attention, and increased attention to a new stimulus, in 2- to 6-month olds. His observation led to a number of empirical investigations examining the conditions under which infants' preferences for novel stimuli could be elicited, and these investigations led in turn to refined, standardized methods for testing infant perception and cognition, such as habituation paradigms,[21] as well as a deeper understanding of infants' information processing.[22–24]

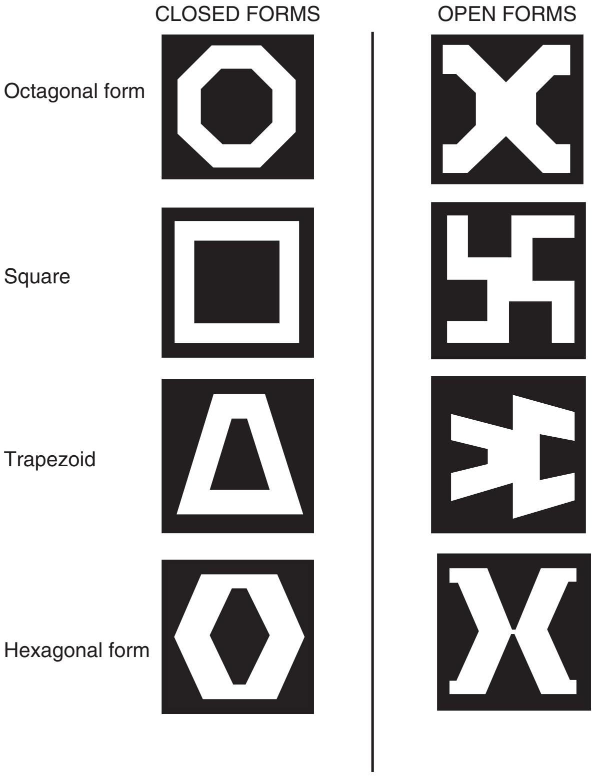


FIGURE 3 | Open versus closed forms from experiments on neonates' categorization. (Reprinted with permission from Ref 26. Copyright 2003 Lawrence Erlbaum Associates, Inc.)

These methodological advances also led to insights concerning infant memory, including memory capacities at birth.[16] Neonates 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, neonates will often show a visual preference for a novel versus a familiar stimulus. This implies not only discrimination of the familiar and novel stimuli, but also memory for the stimulus shown during habituation. Neonates' vision has also been shown to be organized around 'visual constancies', or *invariants* to use Gibson's[3] term, meaning they recognize common features of a stimulus across some detectable but irrelevant transformation, such as transformations across shape, size, slant, and form.[25] For example, newborns formed a 'perceptual category' for the forms in the left row of Figure 3, and a second category for the forms on the right, perhaps on the basis of closure.[26] In both cases the two classes included new instances of the same type (open vs closed) and excluded instances of the opposite type.

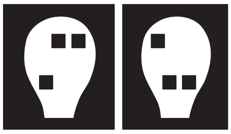
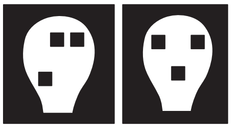
STIMULI	Total fixation time	Number of discrete looks
	53.86 s vs 37.62 s $p < 0.03$	10 vs 8.09 $p < 0.05$
	34.70 s vs 41.08 s $p > 0.20$	7.6 vs 8.3 $p > 0.30$
	44.15 s vs 22.89 s $p < 0.003$	10.43 vs 6.5 $p < 0.01$

FIGURE 4 | Face-like stimuli from experiments on neonates' preferences. (Reprinted with permission from Ref 28. Copyright 2002, American Psychological Association, Inc.)

Faces and Objects

The neonate's visual system is prepared to perceive faces and objects, principal elements of the visual world that often have semantic content, or meaning, for adults. Newborns prefer to look at faces and face-like forms relative to other visual stimuli, a fact that has motivated a large number of experiments attempting to pin down the precise nature of the preference. Explanations for the face preference have ranged from an inborn 'template' specifically for faces—a representation for facial structure that guides visual attention,[27] to its polar opposite, an inborn set of general-purpose visual biases that guide attention toward stimuli of a particular spatial frequency, with a prevalence of stimulus elements in the top portion.[28,29] Faces happen to match these characteristics but are not uniquely preferred over other stimuli that also match them, as illustrated in Figure 4. The issue of specific versus general predispositions is central to understanding the infant's developing responses to and interpretation of the visual world, and I will return to this issue later in the article. The issue also arises when considering newborn's object perception, which I turn to next.

Research on object perception at birth reveals that newborns perceive different surfaces as distinct and separate from one another and from the background (i.e., figure-ground segregation). Yet these studies also reveal a striking limitation in the ability to perceive object occlusion. Much of this research has addressed the question of newborns' perception of partly occluded objects, as seen in Figure 5. Adults and 4-month-old infants construe this display as consisting of two parts, a rod or bar moving back and forth behind an occluding rectangle.[30] Neonates, in contrast, construe this display as consisting of three separate parts: two disjoint rod parts and box.[31] These conclusions arise from experiments in which infants are habituated with the partly occluded rod display, followed by two test displays. One test display consists of the whole rod (no occluder), and the other consists 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. Given that infants generally show a novelty preference following habituation, it is reasonable to conclude that longer looking toward one test display ('complete' versus 'broken' rod parts) means that the preferred test stimulus is unfamiliar relative to the occlusion stimulus seen during habituation. Thus for 4-month olds, longer looking at the broken rod is taken as evidence that they perceived the rod parts as unified behind the box during habituation.[30] For neonates, however, longer looking at the complete rod[31] leads to the conclusion that they perceived the rod parts as disjoint during habituation, not unified. This has led to the more general conclusion that neonates are unable to perceive occlusion, and that occlusion perception emerges over the first several postnatal months.[19] Interestingly, all of these effects in infants depend on the occluded stimulus moving behind the occluder,[32] unlike adults who can perceive occlusion even with static images.

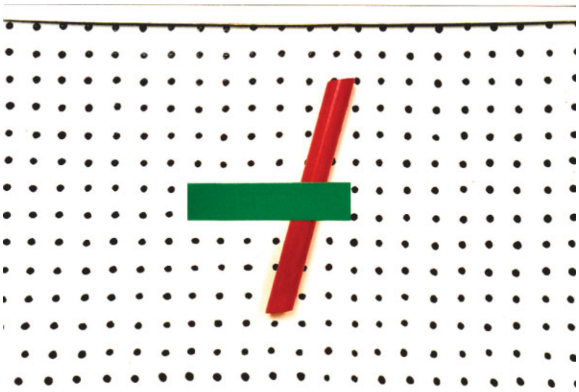


FIGURE 5 | A rod-and-box display from experiments on neonates' perception of object unity. Photo courtesy of Alan Slater.

POSTNATAL VISUAL DEVELOPMENT

Visual development begins prenatally in humans and extends for months and even years after birth for many

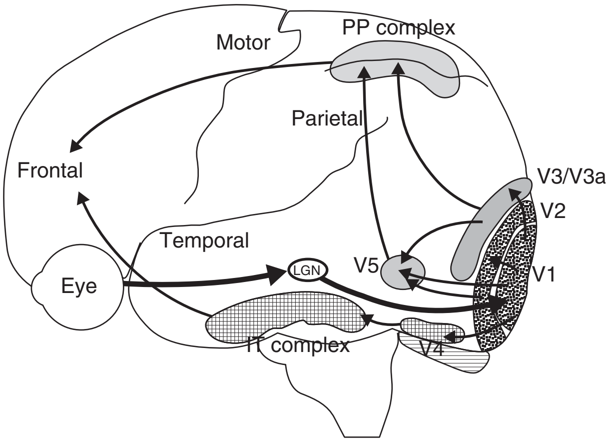


FIGURE 6 | Midbrain (LGN, the lateral geniculate nucleus) and cortical structures involved in visual processing, and the flow of visual input between structures. PP = posterior parietal, IT = inferior temporal. (Reprinted with permission from Ref 39. Copyright 2000 Oxford University Press.)

visual functions (e.g., spatial integration[33]). With perhaps one exception, all aspects of visual function undergo development postnatally. (The exception is the number of eye movements produced per unit of time when scanning a visual scene, about 2–4 per second both in young infants and in adults.[34,35]) Many kinds of functional visual development can be explained in terms of visual maturation,[36] by which I mean physical growth of neural and associated structures. 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 synapse formation and reduction, to name a few. Color vision, likewise, improves as retinal cones lengthen and cortical mechanisms to resolve chromatic contrasts become more finely tuned. Color vision also develops as contrast sensitivity improves, and infants become able to distinguish colored from achromatic regions.[37]

Visual Physiology and Visual Development

Figure 6 shows the modular organization of those portions of the mature brain that are devoted to the processing of visual input. 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. In general, successively higher visual areas are responsible for larger parts of the visual field and participate in more complex visual functions. Motion processing, for example, takes place in circuits originating in V1, projecting to V5, and extending from V5 through parietal cortex. Infants younger than 2 months appear unable to discriminate different directions of motion, and this may stem from immaturity in pathways extending to and originating in V5, also known as area MT.[38] For motion processing, therefore, the developmental story centers on a limited number of visual areas, relatively low in the visual 'hierarchy', and development might be limited to a relatively small number of mechanisms (e.g., myelination, synaptic growth, and pruning). Object perception, in contrast, is far more complex, involving a number of steps: perceptual completion; recognition; perception of shape, color, and depth; object-directed action, and so forth. Here, the developmental story necessarily involves many areas, each of which is responsible for one or more of the steps and each of which may develop according to a different timetable and set of mechanisms.

The formal study of the physiology of visual development has its roots in seminal observations by Wiesel and Hubel,[40] who reported results of unilateral eye closure in kittens. One eye was either covered or sutured shut from birth for a period of 1–4 months. The effects of visual deprivation were subsequently assessed 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. The cat was unable to navigate visually, bumping into obstacles and walking off the edge of a table into the air, showing no response to objects introduced by the experimenters. When the patch was removed, permitting use of the unaffected eye, the animal behaved normally. Neural effects were examined by recording from single cells in visual cortex. Few cortical cells could be driven by the deprived eye. In one set of recordings, for example, 20 of 25 cells were driven exclusively by the unaffected eye, and none by the affected eye. In normally developing animals, this particular region of cortex, the postlateral gyrus, is driven by input from either eye. Effects of deprivation in this example are especially striking given that this region receives most of its input from the contralateral side, which in this case was the deprived eye.

Wiesel and Hubel[40] also reported effects of eye closure in animals that were allowed some visual experience prior to deprivation. Again, the unaffected eye dominated activity of individual cells in visual cortex, but the effects were not so consistently dramatic, depending to an extent on both the amount of visual experience received prior to deprivation and the duration of deprivation itself. These observations, and others reported in Wiesel and Hubel's early work, yielded a number of important demonstrations: the skeletal outlines of mature form and function in the immature visual cortex, the necessity of normal visual experience for optimal developmental outcomes, a clear link between development of behavior and physiological development, and many others.[2] For our purposes the central lessons to be drawn from Wiesel and Hubel's work concern the importance of visual experience early in development to visual function later on, and this will be discussed next.

Critical Periods for Visual Function

The notion of a *critical period* in development, the time in an individual's ontogeny when some function or ability must be stimulated or it will be lost, has been examined extensively in the visual system. Daw[41] described a number of examples. Stereopsis is perhaps the best known and will be considered in some detail subsequently; others include motion (direction) sensitivity, acuity, and contrast sensitivity. Each has a characteristic developmental time course and is affected by deprivation and experience in a different way. Cells at all levels of the cortical visual system can be affected by deprivation. In general, critical periods in visual development begin with the onset of visual experience, and extend for several years in many cases; this is the time in which normal visual experience must occur or else vision is compromised. More severe deprivations (longer, earlier) have more disruptive effects on visual function. Higher visual areas tend to develop later and are more plastic—susceptible to deprivation, and recovery.

Development of stereopsis in humans occurs during a critical period. Stereopsis is detection of depth from disparity, meaning that the inputs to the two eyes vary even when they are directed to the same point in visual space. This is due to the difference in horizontal positions of the two eyes in the head. Disparity contributes to depth perception only in near or 'action' space, because the inputs to the eyes are highly correlated beyond this distance.[42] Stereopsis is made possible by specialized cells in primary visual cortex grouped into 'ocular dominance' columns that receive inputs from the two eyes and register the amount of disparity between them. These disparity detectors require binocular function early in life; that is, 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). Under normal conditions mature visual cortex contains a number of cells responsive to both eyes, and fewer to only one eye. Abnormal visual experience can yield a pattern in which cells respond to only one or the other eye, but not to both. The precise critical period in humans for development of stereopsis likely varies between individuals; one estimate puts it at 1–3 years.[43] This estimate was derived from performance on an interocular transfer task in adults who had surgery to correct strabismus. Those who had surgery prior to age 3 had better outcomes than those after this time. In typically developing infants, stereopsis is thought to emerge at about 4 months, through a process of segregation of inputs from the two eyes into the ocular dominance columns mentioned previously.[44] The segregation process is activity dependent: Disparity detectors cannot operate without coordinated input from both eyes, which compete for representation in cortical territory early in postnatal development. In general, the timing of the critical period depends on the nature of the perturbation to normal visual input and when it is corrected.

Development of Visual Attention

'Attention' can refer to a general level of 'alertness' or a specific kind of behavior, such as eye movements.[45] I use the term here to refer to patterns of eye movements, which presumably reflect some kind of decision made somewhere in the visual system to foveate locations in the visual scene for inspection.

Foveation is an ingenious mechanism to balance the need to derive detailed visual information from the world and the need to reduce as much as possible the metabolic demands of a large brain necessary to process the information. As noted previously, the fovea has the highest concentration of photoreceptors, and these are preferentially mapped onto visual cortical tissue. Acuity is best at the point of gaze and drops off abruptly with increasing visual eccentricity into a low-resolution visual surround. This is mirrored by the distribution of photoreceptors on the retina, as seen in Figure 7.[46] Detailed representation of a visual scene, therefore, which entails extensive processing by visual cortex, takes place only for a region within about 2° visual angle of the viewed scene (approximately the size of a thumbnail at arm's length). To avoid the need to build the large brain that would be needed to process detail about the entire scene, the visual system compromises by periodically shifting the point of gaze with saccadic eye movements, and thus reorienting the specific location in the scene that is best represented and processed. Although the fovea undergoes much postnatal development,[47] very young infants scan visual scenes actively and appear to be attracted

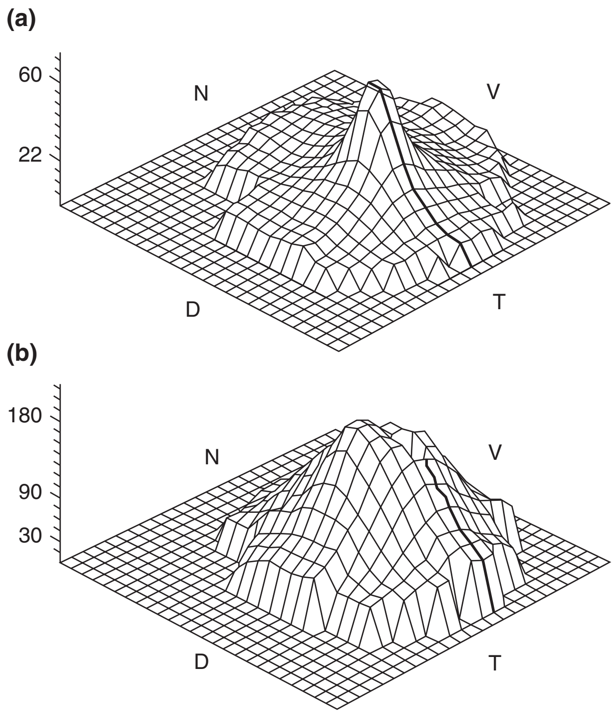


FIGURE 7 | Distribution of photoreceptors in the retina, corresponding to the dropoff in acuity with greater eccentricity (distance from the fovea). (a) Cone density; (b) rod density. N = nasal, T = temporal, D = dorsal, V = ventral. (Reprinted with permission from Ref 46. Copyright 1990, Wiley.)

to regions of high visual salience, as discussed subsequently.

Visual attention is a combination of saccades and fixations. During a saccade, the point of gaze for both eyes sweeps rapidly across the scene, and during a fixation, the point of gaze is relatively stationary. Information about the scene is acquired during the fixations. Analysis of the scene cannot be performed during a saccade, whose purpose is to direct attention to a different part of the scene for subsequent processing. 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.

Research on development of eye movements has often been viewed as an indirect means to examine cortical development, on the assumption that oculomotor behaviors can serve as 'markers' to specific brain systems.[38] This notion is discussed more fully in the next section when I describe development of *smooth pursuit*, nonsaccadic eye movements produced in response to a small moving target. In the present section, I will describe some of the types of saccadic eye movements that have been studied and note that a presumed brain–behavior connection has guided many of the choices of particular eye movements to be investigated.

Many studies of infant saccades have examined *orienting*—engagement of visual attention—as infants are presented with a limited number of small static or moving targets.[48] Bronson[49,50] explored developmental changes in scanning patterns as infants viewed simple geometric forms. The youngest infants tested (2 weeks) were reported to attend primarily to a single prominent feature, whereas older infants (3 months) were more likely to scan between features, and to direct saccades with greater accuracy, perhaps reflecting a transition from reflexive to 'volitional' scanning.

These experiments have yielded a rich knowledge base about saccade development in infancy under the controlled conditions typical of laboratory experiments. Less is known about scanning patterns when infants view complex scenes. In one recent study from my own laboratory, we recorded eye movements of 3-, 6-, and 9-month-old infants and adults under 'free viewing' conditions: watching an animated cartoon, *A Charlie Brown Christmas*.[51] Our goal was to better understand the determinants of fixation patterns across the first year after birth, and we reasoned that faces, in particular, would be highly salient and attract the infants' attention. Our results were inconsistent with this intuition, however: Three-month-olds' fixations were best predicted by low-level image salience—variations in color, luminance, and motion—rather than the locations of faces. Between 3 and 9 months we observed a gradual focusing of infants' attention on faces: There were not obvious differences between age groups in such measures as mean saccade distance or fixation duration that seemed related to attentional focus. Instead, the results are perhaps best interpreted as a transition from attentional capture by low-level salience toward attentional capture by semantic content—the 'meaning' inherent in faces. Alternatively, infant performance might have been increasingly influenced by the linguistic content of the cartoon as infants gain exposure to speech across the first year, or by an increasing sensitivity to intermodal content—the match between the talking faces and their voices.

Cortical Maturation and Oculomotor Development

Gaze control in adults is accomplished with a coordinated system comprising both subcortical and cortical components, as seen in Figure 8. Six muscles are connected to the eyeball, each under direct control by brainstem. Eye movements are executed by signals

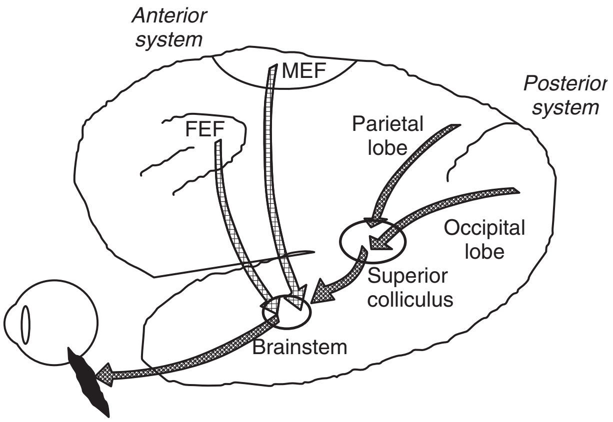


FIGURE 8 | Subcortical and cortical structures involved in oculomotor control. The posterior system makes decisions about target selection and fixation duration, and the anterior system helps guide the eye movements accurately. Both are part of the secondary system discussed in the text. FEF = frontal eye fields, MEF = medial eye fields. (Reprinted with permission from Ref 52. Copyright 2001, Elsevier.)

that originate in cortical areas with outputs that innervate brainstem, such as the frontal eye fields in cortex, or superior colliculus, a subcortical area that receives inputs from several cortical regions.[53] Development of smooth and saccadic eye movements in infants has often been interpreted as revealing development of distinct cortical systems that control them. An early and influential proposal held that there are *two* discrete visual systems, a relatively primitive and phylogenetically older 'secondary' system, and a relatively sophisticated 'primary' system that is more recent to humans in evolutionary time.[54] In the neonate, visual behavior was held to be guided principally by the secondary system, which is characterized by poor foveal vision. The secondary system is restricted to reflexive or reactive eye movements to peripheral stimuli, and does not participate in analysis of complex visual patterns. The primary system was thought to develop across the first several postnatal months, accompanies improvements in acuity and contrast sensitivity, and is responsible for the emergence of endogenous or internal control of saccades so as to support inspection of visual scenes.[55] More recent interpretations of the two-systems model have suggested that visual attention is solely or largely under subcortical control until the first few months after birth, after which there is increasing cortical control.[36,38,45,48]

An example of how oculomotor control may emanate from cortical development is found in Johnson.[38] There are striking improvements between 6 and 10 weeks in smooth pursuit, assessed by showing the infant a small moving target against a featureless background, and in motion direction discrimination, generally assessed with oscillating random dot patterns.[56,57] Smooth pursuit is operationalized as the ability to maintain gaze on the target with smooth, rather than saccadic, eye movements; the dependent variable is gain, the ratio of the velocity of the point of gaze to target velocity (Figure 9(a)). Motion direction discrimination is operationalized as the ability to detect differences in motion patterns within the random dot displays; the dependent variable is preferential attention to a particular region with a motion difference relative to the remainder of the stimulus (Figure 9(b)). Johnson[38] suggested that a common developmental path underlies emergence of both smooth pursuit and motion sensitivity: maturation of pathways to and from visual area V5 or MT. Perceiving motion and performing the computations involved in programming eye movements to follow motion, therefore, are thought to be subserved by the same cortical structures.[58] This suggestion was recently tested empirically in my lab.[59] We observed infants between 58 and 97 days of age in both a smooth pursuit and a motion direction discrimination task. Individual differences in performance on the two tasks were strongly correlated, and were also positively correlated with age (Figure 9(c)), consistent with a maturational model (though not necessarily uniquely predicted by it).

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,[39] which are less distinct in infants,[60] and development of visual memory for object features and object locations, stemming from maturation of ventral and dorsal processing streams.[61] There have been marked recent advances in the sophistication of theoretical views on brain maturation and cognitive development, such as the notion of 'neuroconstructivism'.[62] This view stresses the embodiment of neural structures and the context in which behavior is observed, across multiple cortical regions and timescales of development, leading to the progressive elaboration of increasingly complex neural and behavioral structure.

Difficulties Establishing Brain–Behavior Links

Despite these advances, our understanding of the neural-maturational components of infants' developing visual perception remains fragmentary, and observed behavior can be difficult to reconcile with theory. Consider newborns' behavior in light of the

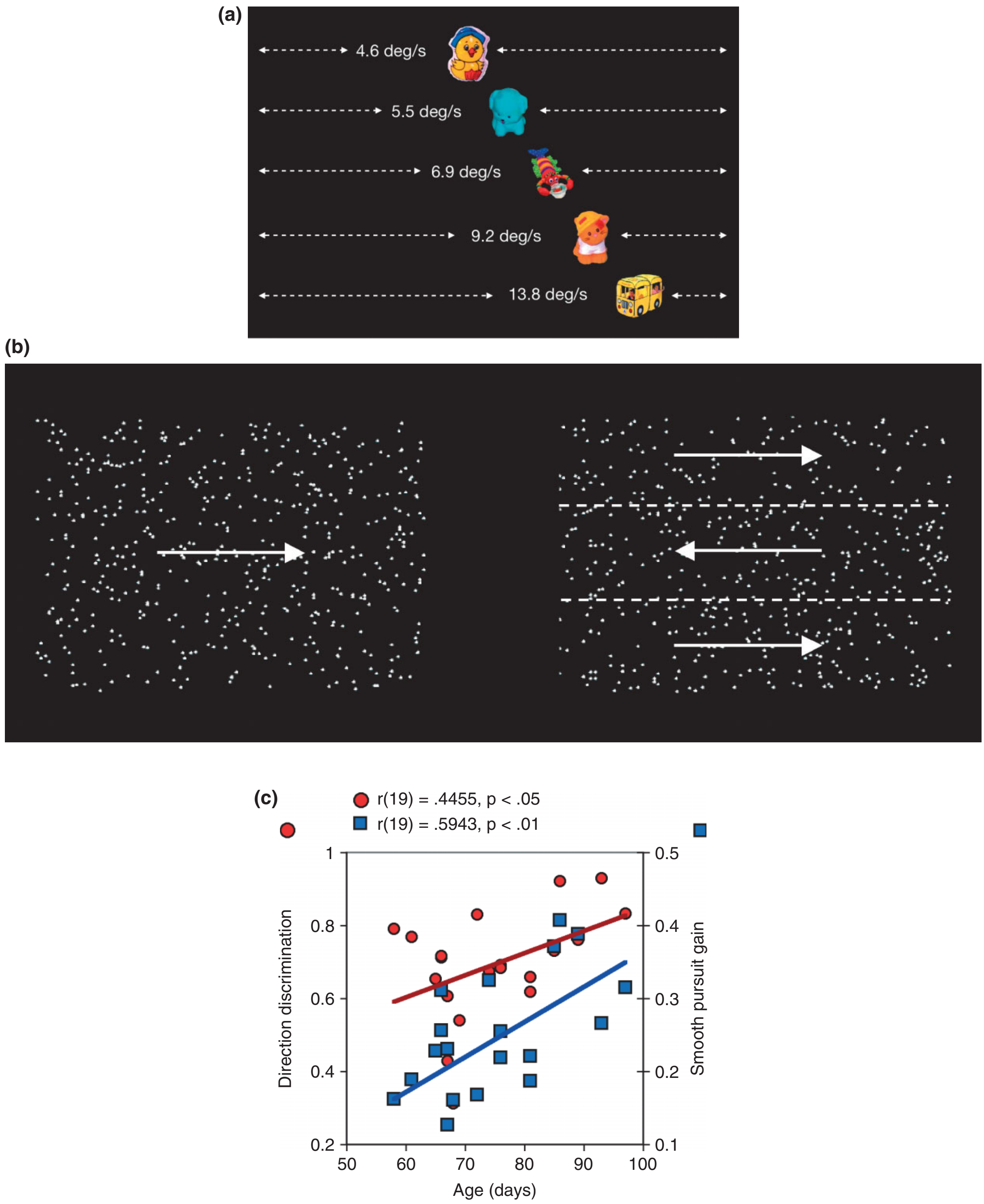


FIGURE 9 | (a) Schematic depiction of stimuli used to assess smooth pursuit in young infants. A toy moved laterally at one of five speeds in one of five vertical positions on the screen. Only one toy was shown at a time. (b) Random-dot kinematograms used to assess motion direction discrimination in young infants. Dotted lines and dots, shown here to demarcate regions of motion, were not present in the stimulus. (c) Individual infants' performance in smooth pursuit and direction discrimination were correlated with age. (Reprinted with permission from Ref 59. Copyright 2008, American Psychological Association, Inc.)

two-systems accounts discussed previously, which hold that oculomotor function is largely or entirely under subcortical control until several months after birth. Recall that neonates' visual attention wanes in response to repeated presentation of a single stimulus, and recovers in response to a novel stimulus. By patching alternate eyes between habituation and test, Slater and colleagues[63] demonstrated that habituation cannot be due to adaptation at the subcortical (e.g., retinal) level, and experiments showing orientation discrimination in neonates also imply some level of cortical function, because orientation-selective cells are found in visual cortex but not in structures lower in the visual hierarchy.[64] In addition, much of the neonate's visual activity, such as spontaneous exploration of patterned stimuli, seems more volitional than reflexive,[14] and thus presumably influenced by top-down control. It is also difficult to imagine that subcortical structures alone could support size and shape constancy, or retain information across a substantial delay as has been shown in studies of newborn's memory, without considerable input from cortex.[16]

Dannemiller[65] and Finlay[66] discussed additional challenges to discovery of specific, *causal* brain–behavior links. For example, discontinuities in behavior can arise from underlying developmental processes, including neural developmental processes, that are essentially continuous.[67] There is scant evidence, moreover, that any isolated part of the cortex 'switches on' postnatally. Rather, the cortex is electrophysiologically active even when it is initially constructed, prior to birth,[68] and cortical areas can be difficult to define in developing cortex, because areas represent assemblies of different features: neurogenesis, maturation of the input from thalamus and other areas, and maturation of the output, all in the greater context of the maturation of the entire organism.[69] Finally, functions ascribed to particular cortical areas and systems in adults may be handled by different areas and systems in infants. Face processing, for example, has been proposed to be mediated principally by superior colliculus in newborns[27] and, in adults, by the 'fusiform face area', part of secondary visual cortex[70] or by more widely distributed, multiple cortical loci.[71]

CONCLUSION

Prenatal development yields a visual system in the neonate that is richly structured and organized. All neurons are in place, and connections with other sensory systems are present and partly refined. Connections among the visual areas, including reciprocal pathways linking lower and higher areas in the visual stream hierarchy, are partly developed, and continue to undergo refinement with the onset of exposure to patterned visual input. Postnatal visual development begins from a foundation at birth consisting of an ability to direct gaze, preferences for specific kinds and classes of stimuli, and a functional visual memory. All aspects of vision improve: The infant's visual world becomes more clear and defined, objects appear in depth, motion is detected and tracked, and eye movement patterns become more refined as infants increasingly direct attention to meaningful stimuli in complex scenes. Many visual functions develop during a critical period during which normal visual experience takes place. Neural development is rapid at all levels of the visual system, and our knowledge of how neural development yields specific changes in visual perception and visual behavior continues to grow.

We do not yet know if the means by which infants construct their visual world are general to all objects, faces, and scenes, or, apart from the propensity to look at face-like patterns, if these diverse inputs are somehow processed in specific and specialized ways from the start. Mature cortical mechanisms for face and object processing are dissociable,[72,73] yet might arise from a common developmental foundation: fragmented-to-holistic processing, and the oculomotor behaviors that contribute to it. Also unclear are the direct contributions in individual infants of rapid neural developments that exist in all levels of the visual processing hierarchy, and, in turn, the shaping of these neural developments by the infant's own experience and behavior. Some of these and other questions may be best addressed for now by computational models of infant perceptual and cognitive development. Recent models of visual attention and object perception have identified important roles for two kinds of cortical development: recurrent (repetitive) loops of activation in simulated parietal cortex, to facilitate selection of relevant image fragments and inhibition of less important parts, and connections within early visual cortex, to compare and link these relevant parts of the scene.[74] The roles of other putative mechanisms, such as an increase in coherence of activity in coordinated neural assemblies and top-down connections, remain to be examined.

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