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Attention and Eye Movement in Young Infants: Neural Control and Development

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Attention has two characteristics: selectivity and intensity (Berg & Richards, in press; Berlyne, 1970; Ruff & Rothbart, 1996). Selectivity refers to the focusing of activity on the object to which attention is directed, whereas, intensity refers to the depth of processing that occurs concomitant with attention. For visual attention, selectivity often refers more specifically to the control of the direction of visual regard. This involves the general direction of gaze, as well as the control of eye movements during attentive tasks. Spatial selectivity is implemented in the visual domain as the active control of fixation in the direction to which attention is directed and the inhibition of eye movements in directions that would interfere with the current task. Thus, an important part of the study of visual attention's selectivity is an understanding of eye-movement control during attention.

There are many changes in the eye movements of infants across the first few months. These include changes in the characteristics of the eye movements themselves, as well as changes in how psychological variables affect eye movement. The thesis of this chapter is that many of these changes occur because of changes in the underlying neural systems controlling eye movement. Even further, there is an interaction of the eye-movement systems and changes in central nervous systems controlling attention. Development of eye movements is, therefore, considered to be a joint product of neural system development and developmental changes in attention. Thus, attention's "selectivity" characteristic in infant development may be physically implemented in eye-movement control systems that show development during the early part of infancy.

This chapter discusses three eye-movement systems that are involved in the development of infant fixation and attention. These are a short-latency reflexive eye-movement system, a longer-latency attentive saccadic system, and smooth-pursuit eye movements. Developmental changes in the neural areas controlling these eye movements, and the relation of these eye movements to early infant behavior, are presented.

THREE NEURAL SYSTEMS CONTROLLING EYE MOVEMENTS

In the earlier chapter concerning the neural control of visually guided eye movements, Schiller (this volume) discussed neural pathways and structures involved in the generation of eye movements. He presented two systems, posterior and anterior, consisting of several pathways responsible for various eye movements. There are three eye-movement systems that may be abstracted from this model. These three systems control reflexive saccades, target-directed saccades, and smooth-pursuit eye movements.

The system controlling reflexive saccades is the simplest of the systems. This system involves the "posterior" eye-movement control pathways (Schiller, this volume). The parasol cells in the retina are the primary input cell for this pathway. These cells have large visual fields, transient on- or off-responses, are predominantly located in the peripheral retina, and respond to broadband stimuli. Thus, they are optimized for responding to transient or moving stimuli in the peripheral visual field. They project to magnocellular layers in the lateral geniculate nucleus, and then to specific layers of the primary visual cortex. These layers of the primary visual cortex connect to the superior colliculus directly, or via the parietal cortex (Schiller, this volume), or via other areas of the cortex (e.g., suprasylvian cortex, Stein, 1988). Layers 5 and 6 of the visual cortex send, via corticotectal pathway, information to both the superficial and deep layers of superior colliculus, thus ensuring the functional integrity of the retinal image analysis (superficial superior colliculus layers) and the motor-visual properties of the deep layers of the superior colliculus, and reflexive saccade movements.

There are several characteristics of the "reflexive" saccadic system that are important for this chapter. First, it is the deeper (middle and deep) layers of the superior colliculus that are involved in this pathway (Schiller, this volume). The retinal input directly to the superior colliculus (primarily "W-cells"), however, is primarily restricted to the superficial layers. Second, there is little evidence for connectivity from the superficial to the deeper layers of the superior colliculus, so retinal-driven motor activity in the superior colliculus must be mediated by cortical pathways. Also, the super-

ficial layers, unlike the deeper layers, do not show the receptive field enhancement that is contingent on eye movement (Mohler & Wurtz, 1976, 1977; Wurtz & Mohler, 1976). Cortical visual systems, therefore, must mediate the retinal driving of the deeper layers of the superior colliculus. Third, cortex ablations, or microstimulation, show that the visual cortex, including areas 17, 18, 19, and lateral suprasylvian areas, mediate the parasol cells driving for at least 75% of the colliculus deeper layer activity (Berson, 1988). Additionally, in light of the scarcity of corticotectal pathways from V1 to deeper superior colliculus layer (Carpenter, 1976; Cusick, 1988; Sparks, 1986; Sparks & Groh, 1995; Stein, 1988), the cortical influence might involve other cortical areas (e.g., suprasylvian cortex, Stein, 1988). Finally, cortical ablation eliminates both intentional and reflexive saccades, whereas spontaneous saccades and quick phases remain (Tusa, Zee, & Herdman, 1986). Ablation of the primary visual cortex does not affect the visual responsiveness of the cells in the superficial superior colliculus. Visual cortex ablation does, however, remove the visual responsiveness of the deep layers (Schiller, this volume).

The second neural system controls target-directed saccades, and attention-influenced saccades. This system involves both the "anterior" and "posterior" eye-movement control pathways (Schiller, this volume). The midjet cells are the primary input cell for this pathway. These cells have small visual fields, sustained on- or off-responses, are predominantly located in the focal retina, and have color-opponent properties. Thus they are optimized for detailed pattern and color analysis. They project to the parvocellular layers in the LGN and then to specific layers of the primary visual cortex. Their major projections are then to parts of the cortical system involved in object identification (e.g., V4, inferotemporal cortex, "IT"; Schiller, this volume). At the same time, aspects of both the midjet and parasol systems are integrated at the level of V1, MT, and the parietal lobe. The former pathway (V4 and IT), involving the "what" processing stream, is necessary for identifying a specific target. The latter pathway (MT, parietal), involving the "where" system, may identify spatial location. These two systems must then be integrated to identify both the location and the type of object for target-directed saccades. Finally, the anterior system bypasses the superior colliculus in its connection to the brainstem and primarily uses the frontal eye fields or dorsal-motor frontal cortex to control eye movements.

There are several characteristics of this *target-directed* eye-movement system that are important for this chapter. First, this is a longer latency system. It involves processing of stimulus information and location, and thus must take longer than the reflexive system. Second, this system involves several areas of the cortex that are known to be affected by attention. For example, the posterior parietal cortex and V4 have cells that are selectively enhanced

in attention-demanding tasks, and nontargets are selective attenuated. This system ultimately controlling the target-directed eye-movement systems has been labeled the "posterior attention system" by Posner (Posner, 1995; Posner & Petersen, 1990). Third, this target-detection system is intimately involved in "selectivity" aspects of attention. Stimuli that are identified as targets are selectively enhanced in this system, particularly in the posterior parietal cortex and in V4. At the same time, in these cortical areas nontarget stimuli are attenuated. This system then has inhibitory influence over the superior colliculus (via frontal eye fields, and perhaps temporal lobe) to inhibit reflexive saccades to nontarget stimuli. Attention's selectivity is implemented as the active control of fixation toward targeted stimuli and the inhibition of eye movements that would interfere with the target task.

The third neural system of interest here is the one controlling smooth-pursuit eye movement. As part of a longer latency system, this pathway controls smooth-pursuit eye movements and is involved in motion detection and pursuit. This pathway involves the parasol cells in the retina, magnocellular layers of the LGN, and several higher cortical areas, such as V1, middle temporal, middle superior temporal, and parietal lobe areas. Cells in V1 respond to "retinal slip" when moving stimuli cross the visual field. Cells in the superficial layer of the superior colliculus may be primarily involved in the analysis of retinal image slip, particularly for computing retinal movement (e.g., vestibuloocular reflex and smooth pursuit). Motion-sensitive cells in V1 become active as a result of this retinal slip, and affect cells in the middle temporal (MT) and medial superior temporal (MST) cortex. MT and MST respond to such motion by initiating eye movements. It appears that MT responds primarily to the retinal slip information, and provides information to the smooth-pursuit system about the motion of potential pursuit targets. MST initiates motor commands necessary for the execution (maintenance) of smooth-pursuit eye movements, such as target velocity. Cells in MT and MST have direct connections to pontine or brainstem areas that control eye muscles. Once smooth-pursuit eye movements begin, the systems controlling the vestibuloocular reflex and optokinetic nystagmus (see Schiller, this volume, Fig. 1.24) participate in the control of eye movements during targeted smooth pursuit.

Smooth pursuit is the phylogenetically youngest of the eye movements. It is unique to frontal-eyed, foveate animals. The cortical aspects of this system have developed relatively late in evolution, but uses several systems known to be established in several species (e.g., vestibuloocular reflex, optokinetic nystagmus). The smooth-pursuit system therefore has a phylogenetically recent system that originates eye movements (middle temporal and medial superior temporal areas), and uses the phylogenetically primitive system to preserve accurate targeting.

DEVELOPMENT OF NEURAL SYSTEMS CONTROLLING EYE MOVEMENTS

The three neural systems controlling eye movements show different developmental changes over the course of early infancy. These developmental changes are hypothesized to underlie behavioral development in the young infant. These developmental changes, and models describing the relation between the neural and behavioral changes, are presented.

Theories of Development

"Neurodevelopmental" models of infant vision posit different developmental courses for these eye-movement systems (Bronson, 1974; Johnson, 1990, 1995; Johnson, Posner, & Rothbart, 1991; Maurer & Lewis, 1979; Richards, 1990; Richards & Casey, 1992). The most well-known of these is the "two visual systems" model of Bronson (1974). Bronson's model consists of a primary and secondary visual system. The primary visual system has excellent visual acuity, overrepresents the fovea, and is devoted to fine pattern visual analysis. The secondary system, on the other hand, has poor visual acuity, represents the fovea and periphery, responds to stimulus location and movement much more than pattern, and is devoted to the detection and localization of targets in the peripheral field and saccades to those targets. Bronson proposed that the secondary system is phylogenetically older, mature at birth, and, therefore, responsible for the newborn infant's visual behavior. The primary system, however, does not begin to play a role until 1 or 2 months of age. Other theories of developmental changes in eye-movement control are similar to that of Bronson's (1974; Karmel & Maisel, 1975; Maurer & Lewis, 1979; cf. Salapatek, 1975) in that they postulate two parallel systems that show different developmental rates.

More recent models by Johnson (1990, 1995; Johnson et al., 1991) and by Richards (1990) and Richards and Casey (1992) are based on recent neurophysiological models of eye-movement control and, therefore, have a much more complicated picture. Although some details about the neural systems underlying eye-movement behavior differ in these models, they are very similar.

Johnson (1990, 1995; Johnson et al., 1991), based on Schiller's model (Schiller, 1985; this volume), uses four pathways to explain eye-movement development. Three correspond to those discussed earlier, that is, a short-latency system involving the retina and superior colliculus, a smooth-pursuit pathway based on the middle temporal cortex, and a frontal eye field-directed pathway. A fourth pathway included in Johnson's model is an inhibitory pathway from the substantia nigra to the superior colliculus. In his model, Johnson traces the developmental changes in eye movements

and the parallel developmental changes in the underlying neural pathways. The differential development of the neural systems is then used to explain how the behavioral development may occur.

The models by Johnson (1990, 1995; Johnson et al., 1991) and others (Richards, Bronson) make concrete predictions and explanations of developmental changes. The reflexive saccade system, probably controlled by visual field information via the retina and superior colliculus and motor information via the short-latency pathway discussed earlier, is the first to develop and is functioning at a high level of maturity at birth or shortly thereafter. The second system to develop is the inhibitory pathway from the basal ganglia to the superior colliculus and probably systems in the cortex that control this inhibitory pathway. This pathway inhibits peripheral stimulus orienting in the presence of focal stimuli and may result in some types of "unusual" fixation-holding in 1- to 2-month-old infants, that is, "sticky fixation" (see chapters by Hood, Atkinson, & Braddick and Maurer & Lewis, this volume). The target-directed saccadic system involving the midget and parasol pathways from the retina, through the lateral geniculate nucleus, layers 4, 5, and 6 of V1, and the middle temporal area, is the third system to develop. This system is undeveloped at birth because the cortical systems do not have the functional maturity needed to operate. Based on the changes in the functioning and structure of the cortical systems, it has been speculated that this system shows rapid development from 2 to 6 months (Johnson, 1990, 1995; Johnson et al., 1991). The fourth system is involved in smooth-pursuit control and has the longest development course. The maturation of layers 2 and 3 of V1 allows for functioning of the frontal eye fields, and as with the predictive saccadic system, its functional onset seems to be in the 1 to 2 month period for the human infant. Many of the structures involved show some rapid development in the first few months following birth; however, the magnocellular pathways themselves have an extended developmental course. Thus, one would expect that this system is far from mature at 6 months and may even show development through the first 2 years.

Figure 4.1 shows a hypothesized developmental course for the reflexive saccades, targeted-saccades, and smooth-pursuit movements in the first year. Presumably, the short-latency saccadic system involved in tracking should not be affected by attention and should show little developmental change from 2 to 6 months. The longer-latency target-saccadic system should show the effects of attention and have a rapid developmental increase from 2 to 6 months. Finally, the longer-latency smooth-pursuit system should show the effects of attention but should have a more gradual development over this age range and not be at its full strength at 6 months.

Development of Eye Movement Systems

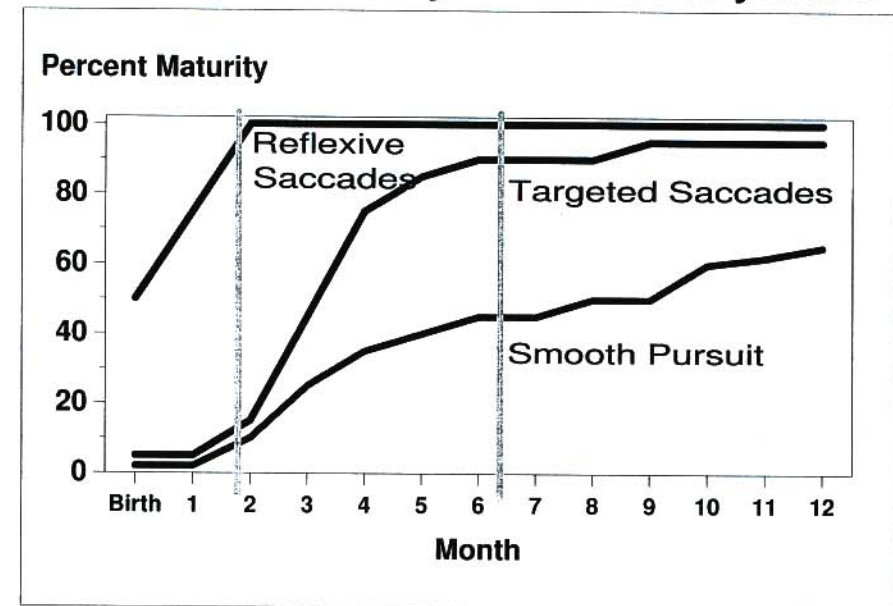


FIG. 4.1. Development of three visual systems involved in visual tracking. The "percent maturity" shown as a function of months, from birth through 12 months. There are three lines, corresponding to the reflexive saccades, targeted saccades, and smooth-pursuit systems.

Development of Neural Structures Involved in Eye Movements

The major development of the mammalian visual system, particularly that of primates, primarily occurs prenatally. This includes initial generation of neurons, synapse connection, and so forth. Postnatal development in primates consists primarily of maturation of the laminar nature of the visual cortex, completion of immature myelinization, and developmental changes in connectivity. Other species that have been widely studied (e.g., rodent or cat) have a more extensive postnatal development that corresponds to the prenatal primate visual development (see Maurer & Lewis, chap. 2, this volume, for a more detailed discussion).

Many postnatal changes in the primate visual system, in perspective to the total development of the primate visual system, seem more like fine tuning or modification of a nearly complete system. This corresponds as well to developmental changes in eye movements. Many of the systems

exist at birth but, with development, become more extensive, fine tuned, able to respond to a wide array of conditions, and subject to voluntary control. For example, the differential development of the early-developing parvocellular and late-developing magnocellular pathways parallels development of behaviors based on these systems.

Developmental changes relying on the magnocellular pathways are seen in smooth pursuit. The incorporation of the middle temporal area into the visual system is relatively late, being based on the higher cortical use of the broadband system. Visual cortex changes in layers 4 and 5 of V1 become mature near 2 to 3 months of age, and these pathways are sufficient for visual pathways to the middle temporal area. Thus, smooth-pursuit eye movements show extensive developmental changes beginning near 6 to 8 weeks, changes across the period from 3 to 6 months, and continues adjustments beyond that period (past 1 year).

An example of a system with strong input from the parvocellular, narrowband discrimination pathways is target saccades controlled by the frontal eye fields. The parvocellular layers in the lateral geniculate nucleus show very rapid development between 3 and 6 months of age, and reach adult size and functional characteristics early (6 months). Narrowband pathways through the visual cortex are well developed by 6 months. Thus, frontal eye fields-driven saccades, which depend on fine visual discrimination pathways, should show rapid change from 3 to 6 months, but finish developmental changes by around 6 months of age.

Postnatal changes also occur in the layered nature of the visual cortex. The layered aspect of the visual cortex exists at birth; however, while layers 5 and 6 are more developed at birth, layers 1–4 show more development after birth. Layers 5 and 6 of V1 project to the superior colliculus (and lateral geniculate nucleus) and are responsible for retinal image analysis and are perhaps involved in reflexive saccades. The other layers (2, 3, and particularly level 4) participate in more sophisticated visual analysis (movement, stereopsis, form, pattern, color). These areas show rapid increases in size, complexity, and interconnections from birth through 8 to 9 months of age in the human.

Because layers 2, 3, and 4 are less developed at 1 to 2 months than layers 5 and 6, it might be expected that components of visual behavior that rely on their use (e.g., V4, inferior temporal cortex, middle temporal cortex, frontal eye fields) are relatively unused at this age. By 3 months of age layer 4 is capable of supporting activity. Between 3 and 6 months the highest layers (2 and 3) are becoming capable of supporting neural activity, although they continue to show development for several months (Banks & Salapatek, 1983; Conel, 1939–1963).

Many of the more complex eye movements are governed by higher cortical centers. This is particularly true of voluntary, intentional eye

movements, such as targeted saccades (i.e., frontal eye fields and parietal cortex area PG). However, the actual developmental progression of these areas is much less well-known than that of the visual cortex or subcortical visual systems.

It is likely that these systems show two types of developmental changes. First, they undoubtedly have intrinsic changes in structure, function, synaptic connections, size, and so forth. These changes are very likely to occur later than those in the primary and secondary visual areas. For example, development in frontal areas occurs over several years of postnatal life, and development is not restricted to the first 6 months, or even through the first year. Second, their connectivity to other cortical or subcortical systems changes. For example, the layers of the visual cortex have pathways differentially distributed to the higher cortical centers. The functionality of these higher centers would, therefore, have to wait for the development of the primitive systems. The middle temporal lobes' control of smooth eye movements, for example, must wait for the development of broadband connections in layers 4 and 5 of the visual cortex, and in the columns of V2. Given the need for stimulus input for development, several of these higher centers' development may not begin until they receive input from the lower centers.

DEVELOPMENTAL CHANGES IN EYE MOVEMENTS

There are several reviews of eye movements in young infants (e.g., Hainline, 1988; Hainline & Abramov, 1985, 1992). Some include a discussion of the issues involved in measuring eye movements in infants (Aslin, 1985; Shupert & Fuchs, 1988); others, concerning infant visual perception, or visual capacity, also include sections about eye movements (e.g., Banks & Salapatek, 1983). The following sections summarize the developmental changes in eye movements.

Reflexive Saccades

By all theoretical and empirical accounts, the most mature eye-movement system at birth involves short-latency, reflexive superior colliculus saccades. Some theorists assume (e.g., Bronson, 1974; Johnson, 1990, 1995; Johnson et al., 1991) that the retinotectal pathway (retina to superior colliculus) is responsible for these short-latency, reflexive saccades in the newborn and very young infant. However, it is unlikely that retinal input to the superior colliculus directly affects superior colliculus-driven eye movements for two reasons. First, the cells likely involved in this reflexive saccadic eye movement are the parasol cells. These cells do not form a major input from

the retina to the superior colliculus directly, but involve cortical pathways. Second, direct retinal-superior colliculus connections are primarily in the superficial layers of the superior colliculus. This layer is involved in retinal image slip and other receptive functions, but does not have the motor cells as do the deeper layers of the superior colliculus. Again, these deeper layers, involving both receptive and motor fields, receive input from the retina indirectly via the cortex (see Schiller, this volume).

There are two implications of the early existence of these reflexive saccades. First, and perhaps most obvious, the first eye movements that infants make postnatally are reflexive and saccadic in nature. Both Bronson (1974) and Johnson (1990, 1995; Johnson et al., 1991) affirm this. The second implication of the existence of these early eye movements is that the neural pathways serving them must exist at birth. This system involves the magnocellular, broadband pathways and connections between VI (layers 5 and 6), secondary visual areas, and corticotectal connections. Thus, a minimal broadband pathway must exist between these structures in order for this reflexive pathway to function at birth.

Saccades made by infants have some distinct characteristics. These saccades usually are of fixed length, and, in some cases, the infant may approach a target with several small, equal-sized saccades. For example, Aslin and Salapatek (1975) reported that 1- and 2-month-olds localized 10° targets with single or double saccades while targets at 20, 30, or 40° were localized with a series of equally spaced, small saccades (hypometric). The magnitudes of saccades across these target distances were not equal; infants' saccades increased in magnitude as target distance increased. Salapatek, Aslin, Simonson, and Pulos (1980) suggested that the series of hypometric saccades may be due to an initial computation of target position, which is accurate, but which uses several small saccades. With increasing age the ability of the infant to localize a target depends on the increasing use of higher cortical areas implicated in spatial attention for accurate single saccade localization (e.g., parietal cortex area PG/frontal eye fields system). Other studies have demonstrated a developmental progression in the ability to localize targets with single saccades. For example Roucoux, Culee, and Roucoux (1982, 1983) found that at 8 weeks, infants could localize targets at 15° with a single saccade; 30° at 12 weeks; and 45° at 16 weeks.

Hypometric saccades have not been reported in all studies of infant eye movements, such as those found when infants scan an interesting visual stimulus (Hainline & Abramov, 1985; Hainline, Turkel, Abramov, Lemerise, & Harris, 1984). In this case, infants were scanning an interesting visual stimulus in the focal visual field. These hypometric and step-like saccades have not been reported in studies of adult saccades to peripheral targets. A typical sequence for multiple eye movements in adults involves a large saccade that traverses the majority of the eccentricity, and then one or two

small "corrective" saccades for final localization of the target (Becker, 1976; Prablanc & Jennerod, 1975; Prablanc, Mase, & Echallier, 1978).

So, why the apparently conflicting data? One difference between these studies may be the type of stimulus used. The stimuli used by Hainline et al. were complicated textured patterns or simple patterns that filled the viewing area. The stimuli of the former studies were small targets, filling only a small portion of the visual field. They also were in the peripheral visual field. Studies using small targets require that the infant execute a saccade to a specific spatial location. In the full stimulus presentation the infant may choose a large variety of locations at different eccentricities. Thus, moving (Roucoux et al., 1982, 1983) or peripheral stimuli may result in hypometric saccades, whereas the static stimulus filling the visual field do not.

There are only a few studies in which other saccade characteristics have been systematically investigated. One study conducted by Ashmead (1984) showed that each of the small saccades was a well-formed main sequence saccade. Main sequence refers to the relation between the saccade's velocity and amplitude (or duration and amplitude). That the main sequence was intact suggests that part of the infant's immaturity is in the use of spatial location to foveate objects, implicating the immaturity of the systems involved in spatial attention. Thus, early saccades may be more "reflexive," subcortical, in nature.

Attention may play a role in saccadic eye movement in infants. A report by Hainline et al. (1984) suggests that attention enhances the main sequence relation for infants, but that during inattention it is irregular. Saccades by 14 to 151 day-old infants (1–4.5 months) to complex (interesting) targets showed the same main sequence relation (Bahill, Clark, & Stark, 1975) as with adults. That is, the velocity–amplitude relation was the same across different degrees of targets. However, with relatively simple (uninteresting) stimuli, the slope of the velocity–amplitude function was much lower for infants. The main sequence for adults is unaffected by attention manipulations.

Head movements may occur with saccadic eye movements in order to localize targets, and these head movements may also be hypometric (Regal, Ashmead, & Salapatek, 1983; Regal & Salapatek, 1982). In adults, saccades to target eccentricities less than about 20° occur without head movements, whereas target localizations to larger eccentricities usually involve head movements (Tomlinson & Bahra, 1986a, 1986b). It is unknown whether target eccentricity has a similar effect in infants.

Smooth Pursuit

Perhaps the second major postnatal developmental change in human eye movement is in smooth-pursuit motor movements. Smooth pursuit involves retinal image slip, processing of broadband information through the visual

cortex, origination of smooth pursuit by the middle temporal and medial superior temporal areas, and cerebellar adjustment of eye movements.

The systems for retinal image slip exist at birth. By 2 months of age, the layers of primary visual cortex sending efferents to the higher CNS levels mature. These include projections to both the secondary visual area and the middle temporal area. Smooth-pursuit origination, therefore, is possible by this age, and as demonstrated in behavioral studies, begins.

In behavioral studies, smooth pursuit shows developmental changes at least through 12 months of age, and probably beyond. This may be due to at least three developmental reasons. First, the slowly maturing broadband magnocellular pathways probably change for 1 to 2 years, suggesting continuing changes in smooth-pursuit functioning. The areas of smooth pursuit origination (middle temporal and medial superior temporal areas) may also show developmental changes over an extended period. These developmental changes may be internal or involve connections with other brain areas. A second reason is that attention-based smooth-pursuit movements involve the parietal cortex area PG. This higher cortical level may also show developmental changes.

Smooth pursuit, therefore, is immature in human infants at birth and develops slowly over the next 2 to 3 months. Behaviorally, newborn infants show little sustained smooth-pursuit tracking, although some periods of smooth pursuit exist to slow velocity objects (e.g., 15% of approximate 370 ms duration to velocities of less than 19° per sec; Kremenitzer, Vaughan, Kurtzberg, & Dowling, 1979). Most newborn tracking is based on saccadic eye movements. Five-week-olds use head and eye movements to track objects moving at 11° per sec, but saccades and poorer smooth pursuit occurred at 23° per sec. Eight-week-old infants track 13° per sec stimuli primarily with smooth pursuit, but 39° per sec or 45° per sec with a combination of smooth pursuit and saccades (Roucoux et al., 1982, 1983). By 12 months of age, infants track stimuli at 45° per sec well, although still not as well as adults (Roucoux et al., 1982, 1983).

Figure 4.2 shows data from Aslin (1981), which displays tracking behavior of 6- and 10-week-old infants, and adults. As you can see, infants younger than 6 weeks of age show little smooth pursuit. Instead, they track the object with a series of saccades. Between ages 6 and 8 weeks, segments of smooth pursuit are interspersed with saccadic interruptions. Infants continue to use saccades to track the object, and, in the 6-week-old, often seem to be corrective of inaccurate smooth-pursuit direction. By 10 to 12 weeks of age, the smooth pursuit becomes nearly as accurate as that of adults. At this age, saccadic interruptions rarely occur (Aslin, 1981, 1985; see Shea & Aslin, 1984). Like adults (e.g., Barnes, 1979), infants often do smooth-pursuit target tracking with a combination of smooth-pursuit eye movements and localizing head movements (Roucoux et al., 1982, 1983).

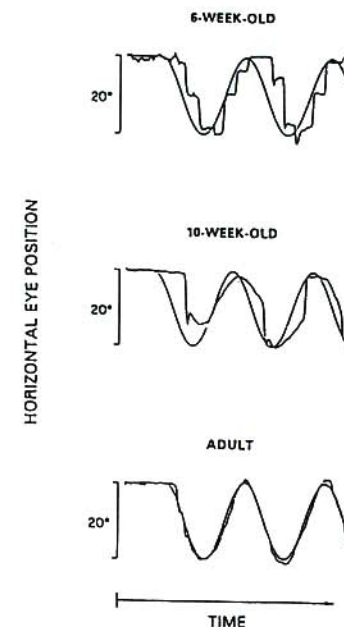


FIG. 4.2. Smooth-pursuit eye-movement development.

Some research has indicated that smooth-pursuit functioning might occur earlier with velocity and stimulus manipulations. Adults track objects with smooth-pursuit eye movements up to 72° per sec. Newborn infants track targets with velocities as slow as 9° per sec with few (<15%) smooth-pursuit eye movements, although they do exist (Kremenitzer et al., 1979). Therefore, newborn infants may be able to track very low target velocities (10° per sec or less), with very large targets (12°), although with poor pursuit latencies and gain (Hainline, 1988; Hainline & Abramov, 1985, 1992). These results suggest that parts of the system for smooth pursuit may be in place very early, but functions poorly or under severely restricted conditions.

It may be, for example, that the slow tracking velocities are required because of the retinal image slip information, or the connections through the visual system, are slow due to inadequate or immature myelination. Also, part of the smooth-pursuit system controlling gain (accuracy), such as the cerebellum connections, may not exist at all. With increasing age, the maximum velocity for which smooth pursuit is predominant and accurate increases.

Localizing saccades that result in head movements may indirectly cause the slow eye-movement systems (e.g., smooth pursuit, vestibuloocular reflex) to participate in target localization. As discussed earlier, head movements following saccades are accompanied by "compensatory ocular responses" that move the eye in the direction opposite to the initial saccade

and head movement in order to preserve target localization. In adults and older children, compensatory ocular responses are primarily vestibuloocular responses (Barnes, 1979; Funk & Anderson, 1977; Pelisson, Prablanc, & Urquizar, 1988; Uemura, Arai, & Shimazaki, 1980; Zangemeister & Stark, 1982). This is probably true for infants as well (Finocchio, Preston, & Fuchs, 1987; Regal et al., 1983). The vestibuloocular reflex exists in function similar to adult function at least by 1 to 2 months (Regal et al., 1983; Reisman & Anderson, 1989). The neural components of the human vestibular system are well-established and functional at birth. However, parameters of the vestibuloocular response change to some degree with age, such as a decrease in the gain of the response (Ornitz, Kaplan, & Westlake, 1985; Reisman & Anderson, 1989).

Frontal Eye Fields Saccades

Third in the developmental progression of eye movements are those movements controlled by the frontal eye fields pathways. Beginning at age 2 to 3 months, there is rapid development in the primary visual cortex in layers 2, 3, and 4 and a corresponding rapid development in the narrowband, color-opponent form discrimination pathways of the visual system. These probably include connections to V2, V3, and inferior temporal cortex. These lower level systems are antecedent to the mature functioning of the frontal eye fields-parietal cortex area PG control of attentional eye movements.

These areas seem to mature rather quickly, reaching adult levels by 6 to 9 months of age. So, although they start their rapid development later than the smooth-pursuit systems, their development is rapid. However, similar to smooth-pursuit eye-movement control, not much is known about development of the higher CNS structures that control attention-directed eye movements (e.g., frontal eye fields, parietal area PG).

DEVELOPMENTAL CHANGES IN INFANT ATTENTION—SUSTAINED ATTENTION DEVELOPMENT

The three eye-movement systems that have been presented show behavioral developmental patterns that parallel the development of the underlying neural systems. This suggests that development of these neural systems is responsible for developmental patterns seen in behavioral changes. However, another important development is occurring in infant behavior in a similar age range. This is the development of "sustained attention." Developmental changes in attention also may play a role in the behavioral

development seen in these eye-movement systems. Specifically, the targeted-saccadic system and the smooth-pursuit system likely are strongly influenced by attention, whereas the reflexive saccadic system is not directly enhanced by attention. We now take a diversion to show some changes in attention that occur over the early period of infancy that may be related to these eye-movement systems.

Many studies by the first author have shown that heart rate (HR) in young adults is an index of different attention types. In the young infant HR has been shown to index at least four visual information-processing phases (Graham, 1979; Graham, Anthony, & Zeigler, 1983; Porges, 1980; Richards, 1988; Richards & Casey, 1992). These phases include the automatic interrupt, the orienting response, sustained attention, and attention termination.

Heart rate and cognitive activity differ during these attention phases. The automatic interrupt is characterized by a brief biphasic deceleration-acceleration, or small deceleration in HR, and behaviorally reflects the initial detection of stimulus change. Stimulus orienting is characterized by a marked deceleration in HR and involves the evaluation of stimulus novelty. Heart rate remains below prestimulus levels during sustained attention. This phase involves subject-controlled processing of stimulus information. During the final phase, attention termination, HR returns to prestimulus levels and the infant continues to fixate on the stimulus. Since the infant may be easily distracted during this time (Casey & Richards, 1988; Richards, 1987) or looks away voluntarily from the stimulus, it is assumed that the infant is no longer processing information in the stimulus.

Infant looking behavior differs dramatically during these phases. For example, looking back and forth between two interesting visual stimuli depends on the phase of attention and the type of stimulus. For two novel stimuli, the duration of individual looks to one of two stimuli is much longer during sustained attention than during attention termination. However, if one of the stimuli is novel and the other is familiar, infants will look at the novel stimuli longer than the familiar stimuli during sustained attention, but will look at both stimuli with equal duration during attention termination. Thus HR, indexing the level of arousal in attentional systems, covaries with infant fixation patterns (Richards & Casey, 1990).

Heart rate changes during sustained attention are also paralleled by behavioral indices of sustained attention. These include focusing on a central stimulus (e.g., Richards, 1987), exhibiting recognition memory (Richards & Casey, 1990), maintaining fixation on a central stimulus in the presence of a peripheral distracting stimulus (Hicks & Richards, submitted; Hunter & Richards, 1997; Lansink & Richards, 1997; Richards, 1987, 1997), and acquiring stimulus information (Richards, in press). The "selective" aspect of attention has been demonstrated in several studies to

be particularly true of sustained attention. Infants will not be distracted from viewing a central stimulus during sustained attention, and are poorer in localizing a peripheral stimulus if sustained attention to a central stimulus is in progress. Alternatively, the presence of a focal stimulus alone during "inattention" (attention termination phase) does not inhibit localization of peripheral stimuli. Thus, it is during sustained attention that the selective aspect of attention is manifested (Berg & Richards, *in press*).

There are important developmental changes occurring in infant attention, as defined by these heart rate defined attention phases. Specifically, a consistent pattern of developmental changes in sustained attention has emerged from several studies (Casey & Richards, 1988; Richards, 1987, 1989a, 1989b). The level of HR change during sustained attention, which is a reflection of cognitive processing intensity, increases from 14 to 26 weeks of age. This age change parallels the finding of an increasingly sustained HR response for the older age infants during the sustained period of attention (Richards, 1985). This change in HR during sustained attention parallels some of the behavioral manifestations of attention. This includes, for example, an increasing ability of infants to acquire familiarity with stimulus characteristics in a fixed length of time (Richards, *in press*). This occurs primarily during sustained attention, rather than the other attention phases. For younger ages (e.g., 8 weeks), behavioral and HR indices of attention are not as well-synchronized as they are at older ages (Hicks & Richards, *submitted*; Richards, 1989b).

Why are HR changes in infants during fixation indexing infant attention phases? The answer to this lies in an understanding of the neural systems affecting HR, and "arousal" attention systems. The neural control of this HR change likely originates from a "cardioinhibitory" center in the frontal cortex. This area has reciprocal connections with several areas, all of which are part of the limbic system, and thus involved in the mesencephalic reticular formation arousal system (Heilman, Watson, Valenstein, & Goldberg, 1987; Mesulam, 1983). The mesencephalic reticular formation and the limbic system (Heilman et al., 1987; Mesulam, 1983), as well as dopaminergic and cholinergic neurotransmitter systems (Robbins & Everitt, 1995) control this arousal form of attention. This arousal-sustained alertness system sustains attention and maintains an alert, vigilant state. This system subserves several component systems, including audition, visual-spatial attention, and form-color object discrimination (Posner, 1995; Posner & Petersen, 1990). Attention, then, may operate in a nonselective manner on visual areas, including enhancing form and color discrimination, motion detection and visual tracking, and eye movements.

Heart rate changes during attention in infants are an index of the arousal system. Therefore, they may indirectly index the sensitivity of the

visual system to external stimuli. Heart rate may reflect the arousal effects occurring in the nondifferentiated areas of V1 and V2. Heart rate changes during attention should be closely associated with the eye-movement changes found in higher cortical areas also, because these areas are closely associated with the cingulate's input to the parietal cortex area PG—superior colliculus—frontal eye fields attention network, and contribute to the arousal found in the selective attention networks. Arousal also contributes to the form discrimination network, represented by V4 and inferior temporal cortex. Arousal contributes to the selective attention properties of those areas by heightening the selective responsiveness of the visual fields in V4 and inferior temporal cortex. Thus HR changes should also occur when the processing of pattern or configuration information is the primary activity, and significant eye movements do not occur.

The changes in sustained attention that occur from 3 to 6 months of age may partially form the basis for changes in eye movements across this age range. As presented earlier, the targeted-saccadic system is controlled by several cortical areas that are influenced by attention. These areas show both selective enhancement of targets for attention, and attenuation of neural and behavioral responses to nontargeted stimuli during attention. The hypothesized developmental changes in the eye-movement systems (Johnson, 1990, 1995; Johnson et al., 1991; Richards, 1990; Richards & Casey, 1992) that control these systems is paralleled by HR and behavioral changes in sustained attention.

These changes in attention parallel the eye-movement systems. The early looking system of the infant is predominated by the reflexive saccade system that is relatively unaffected by attention. This is consistent with the finding that HR changes during fixation are relatively unsynchronized with peripheral stimulus localization in the 8-week-old infant (Hicks & Richards, *submitted*; Richards, 1989b). As sustained attention develops, and at the same time as the cortical areas controlling targeted saccades develop, the infant begins to focus fixation on attention-eliciting stimuli and withstand distraction by peripheral or nontargeted stimuli. Thus, changes in eye-movement behavior in the period from 14 to 26 weeks may be caused by parallel developmental changes in the neural systems underlying eye movements and developmental changes in sustained attention. The similar developmental changes in eye-movement systems and sustained attention suggest that they may be complementary perspectives of the same underlying phenomenon.

How does this fit together? What are the behavioral results of the interaction between developing neural structures, developing eye movements, and developing attention? The following are two examples of the interaction of attention and eye movements in infants.

EXAMPLE: EYE AND HEAD MOVEMENTS DURING ATTENTION

In the opening section of this chapter we briefly discussed the neural pathways indicated by Schiller (this volume) to be involved in eye-movement generation. Two of those pathways were said to control the generation of saccadic eye movements, while a third controls smooth-pursuit eye movements. One of the saccadic pathways is the short-latency system from the retina to the superior colliculus via primary visual cortex. The second pathway is a longer latency pathway involving the retina, primary visual cortex, V2, posterior parietal cortex, and frontal eye fields. It is this second, longer-latency saccadic pathway that is thought to be affected by attention.

Localizing head movements that accompany saccadic eye movements center the eye with respect to the head so that eye control muscles do not have to actively hold the orbit at large eccentricities. The relation between head movements and target eccentricity in infants has been informally reported in some studies (Regal & Salapatek, 1982; Regal et al., 1983; Roucoux et al., 1982, 1983), and the findings suggest an increase in the number of head movements accompanying peripheral stimulus localization with increases in eccentricity. In general, it has been found that eye movements usually precede head movements (Regal & Salapatek, 1982; Regal et al., 1983; Roucoux et al., 1982, 1983; Tronick & Clanton, 1971). However, head movement initiation probably occurs at the same time as that of eye movements, but the delay is a result of biomechanical lag (Zangemeister & Stark, 1982).

Peripheral stimulus localization is one method that has been used to study developing eye and head movements in infants. The study of eye movements in this paradigm has often been based on visual judgments of eye movements (e.g., Atkinson, Hood, Braddick, & Wattam-Bell, 1988; Atkinson, Hood, Wattam-Bell, & Braddick, 1992; de Schonen, McKenzie, Maury, & Bresson, 1978; Harris & MacFarlane, 1974; Hood & Atkinson, 1993; Richards, 1987, 1997). A few studies have investigated the characteristics of saccadic eye movements used for stimulus localization, but none have studied the velocity-amplitude relation for peripheral stimulus localization in infants.

As has been reported in many studies, the presence of a competing stimulus in the central or focal visual field results in a lower localization percentage of a peripheral stimulus. It is not, however, the presence of competing stimuli that inhibits peripheral stimulus localization. Rather, the lower localization percentage is due to the engagement of attention to the visual stimulus. Using the HR changes known to be associated with infant attention or inattention, it has been shown that the latency of looking toward a peripheral stimulus is longer in 3- to 6-month-olds when attention is engaged with the central stimulus than when the infant is fixating the central stimulus but attention is unengaged (Richards, 1987, in press).

Similarly, the probability of detecting a peripheral target of limited duration is lower if the infant is attending to a central visual stimulus than when inattentive fixation is occurring (Finlay & Ivinskis, 1984; Richards, 1997). When a central stimulus is present but attention is unengaged, peripheral stimulus localization occurs at latencies and with probabilities similar to the noncompeting situation when the central stimulus is absent (Finlay & Ivinskis, 1984; Richards, 1987, 1997). Recent work has suggested that the presence of a central stimulus and attention to that stimulus changes the infant's response bias such that a response is less likely during attention to the central stimulus than during inattention, or without a central stimulus (Hicks & Richards, submitted; Richards, 1997).

Richards and Hunter (1997) examined attentional effects on head and eye movements in infants. Specifically, the study looked at the probability of head movements accompanying localization and the affect attention to a focal stimulus had on them, and the study examined the characteristics of saccadic eye movements during attention and in relation to head movements.

Infants were tested at 14, 20, and 26 weeks of age (3, 4.5, and 6 months) in an interrupted stimulus paradigm (see Fig. 4.3). In this paradigm, a trial

Stimulus Presentation Protocol

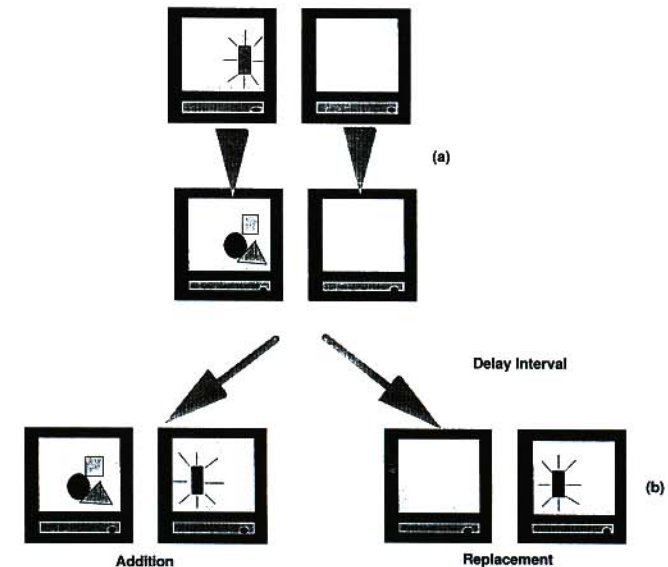


FIG. 4.3. Interrupted stimulus paradigm. (a) Infant's fixation is engaged on a stimulus in the central visual field. (b) Interrupting stimulus is presented in the periphery.

begins once the infant's fixation is engaged on a stimulus in the central visual field. Another stimulus is then presented at some distance in the periphery. The presentation of this peripheral stimulus either occurs immediately (concurrent with the central visual stimulus) or after some delay.

For this particular study, stimuli were placed at eccentricities of either 25, 35, or 45° in the periphery. The delay for presentation of the peripheral stimulus was manipulated to result in differing attention level; specifically: the peripheral stimulus was presented after focal localization of a simple blinking dot; the focal and peripheral stimulus were presented simultaneously; the peripheral stimulus was presented after a 2 sec delay; the peripheral stimulus was presented after a significant HR deceleration; or the peripheral stimulus was presented after HR returned to its prestimulus level after a significant deceleration. Also, on some trials the focal stimulus remained on, while in other trials it was removed upon presentation of the peripheral stimulus.

The results of this study showed a developing inhibition of saccadic localization of peripheral stimuli in 3- to 6-month-old infants. As you can see in Fig. 4.4, peripheral stimulus localization occurred less frequently near the beginning of fixation and when a significant HR deceleration had occurred (sustained attention) than when no focal stimulus was present or after HR had returned to prestimulus level (attention termination).

Localization and Eccentricity

Percent Localization

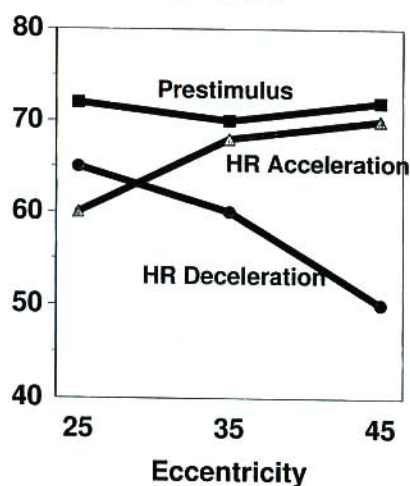


FIG. 4.4. Percentage of peripheral stimulus localizations as a function of peripheral stimulus eccentricity and attention conditions. Note the eccentricity effect occurred primarily during sustained attention (HR deceleration condition).

Localization of the peripheral stimulus was accompanied by head movements on more than two thirds of the trials, and the likelihood of head movements was positively associated with stimulus eccentricity (see Table 4.1). However, there were unusual localizing head movements in the attention conditions in the absence of localizing saccades or changes in fixation for the two older age groups. During attention conditions the 6-month-olds often made "localizing head movements" toward the peripheral stimulus while fixation remained on the focal stimulus. Because infant attention modulates eye movement, characteristics of infants' eye-head relations during infant attention may be different than during inattention.

There was a strong relation between peak velocity and amplitude of the localizing saccades during the prestimulus period with a simple nonpatterned stimulus array (Fig. 4.5A). There were no age changes in this main sequence relation, and it is assumed that adult-like relations characterize these velocity-amplitude relations. In contrast, in the two conditions under which focal stimulus attention is maximally engaged (2 sec and HR deceleration) unusual velocity-amplitude relations were found. This consisted of a faster peak velocity relative to saccade amplitude than during prestimulus periods. This effect occurred primarily in 20- and 26-week-old infants (Fig. 4.5B). These age differences were not found in any other condition, nor in the prestimulus period or the saccades to the blinking dot.

These findings suggest that there was an increasing inhibition of the reflexive peripheral saccades during sustained attention over the age range from 3 to 6 months. The distinction between sustained attention and attention termination became sharper with increasing age (14 to 26 weeks), both in distraction times and in the characteristics of reflexive peripheral localization. The emergence of attention-directed targeted saccades and fixation to the focal stimuli, controlled by the posterior attention system and the frontal eye fields, was accompanied by the suppression of reflexive peripheral saccades over this age range.

The interpretation of the effect of attention on the main sequence, and on peripheral stimulus localization generally, involves an understanding of the brain systems controlling eye movement during attention. Earlier

TABLE 4.1
Localizations With and Without Accompanying Head Movements on
Peripheral Stimulus Present Trials as a Function of Delay Conditions

	Prestim	Immediate	2-Sec	HR Dec	HR Acc	All Types
Number of PS Trials	144	200	184	165	141	824
PS Localization	78.3%	66.3%	83.3%	76.4%	80.9%	75.9%
Saccade Only	25.7%	38.5%	20.6%	48.5%	29.0%	32.7%
Saccade & Head Movement	74.3%	61.5%	79.4%	51.5%	71.1%	67.3%

Main Sequence

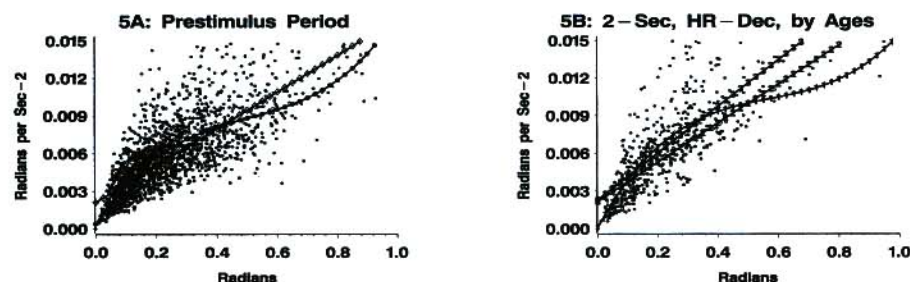


FIG. 4.5. Main sequence relation between maximum saccade velocity and total amplitude of saccade. 5A: Prestimulus saccades, with linear equation and best-fitting polynomial equation; 5B: Saccades to peripheral stimulus in 2-s and HR deceleration conditions, with separate regression lines for 14-, 20-, and 26-week-old infants. 5B: 1-14 week-olds, 2-20 week-olds, 3-26 week-olds.

in the chapter, we referred to the pathway from the lateral geniculate nucleus to the frontal eye fields for the control of targeted saccades during attention (Schiller, this volume). The HR changes during attention probably index a general arousal-alertness system (Heilman et al., 1987; Mesulam, 1983; Posner, 1995; Robbins & Everitt, 1995) that "invigorates" the posterior attention network (Richards & Casey, 1992). The saccades that manage to avoid this inhibition may be unusual. Perhaps saccade amplitude is programmed and then attention-based inhibitory systems affect saccade parameters.

The changes in the main sequence relation for the attention conditions in the two older age groups, and the unusual head movements toward the peripheral stimulus in the absence of localizing saccades, reflect the inhibition of the reflexive system by the attention system. These results are consistent with the *neurodevelopmental* model with which we began this chapter, hypothesizing a focal attention system that over this age range increasingly inhibits reflexive saccadic eye movements used to localize peripheral stimuli (Johnson, 1990, 1995; Richards, 1990; Richards & Casey, 1992).

There are two unanswered questions posed by this study. First, some characteristics of saccades (e.g., main sequence relations, "corrective" rather than "hypometric" saccades) were found to develop over the entire age range of the study. This suggests that the onset of these phenomena should occur at earlier ages, perhaps in the 8- to 11-week-old range. Second, differences affecting peripheral stimulus localization between sustained attention and attention termination were found in relatively "intact" levels at the earliest

age (14 weeks). Studies with 8-week-olds (Richards, 1989a, 1989b; Hicks & Richards, submitted) have suggested that the sustained attention-attention termination differential effect is much less pronounced.

EXAMPLE: DEVELOPMENT OF SMOOTH PURSUIT UNDER ATTENTION AND INATTENTION

The eye-movement systems presented by Schiller (1985; this volume) were shown in previous sections to show developmental changes in early infancy, both in the neural systems controlling the eye movement, and in behavioral studies of eye-movement characteristics. There were three systems that have been discussed in this chapter that were recently examined in two studies (Richards & Holley, submitted). These systems are: (a) a short-latency reflexive system involving the retina, LGN, primary visual cortex, and superior colliculus, (b) a longer-latency system involving the parvocellular retina and LGN cells, that involves several higher cortical areas (V1, V2, posterior parietal cortex, FEF, and SC), and (c) a longer-latency system involving the magnocellular retina and LGN cells, and several higher cortical areas (V1, V2, V4, MT, MST). These systems differ in the type of eye movements that are controlled, the involvement of attention in the eye movements, and developmental course. The first two systems control saccadic eye movements, with the short-latency pathway being involved in reflexive peripheral saccades and the second system involved in the control of attention-directed saccades. This system controls smooth-pursuit eye movements, and is heavily involved in motion detection and pursuit. Like the second system, it is strongly affected by attentive behavior.

The changes in these behaviors were recently studied (Richards & Holley, submitted). In this study infants at 8, 14, 20, and 26 weeks of age were presented with a small sinusoidal moving stimulus that ranged in speed from 4 to 24° per sec while EOG was used to record eye movements. We used EOG on the outer canthi of the eyes, which measures electrical activity in the eye relative to the head. The composite EOG was separated into saccadic and smooth-pursuit components. Attention phases were once again determined by the changes in HR previously noted. Sustained attention was defined as occurring following a significant HR deceleration; stimulus orienting any period prior to sustained attention; attention termination as the return of HR to its prestimulus level following sustained attention. The distinction between attention and inattention, and smooth pursuit and saccades, allowed us to examine the three eye-movement systems (reflexive-saccades; attentive-saccades; attentive-smooth pursuit).

Now to some results from the eye-movement data. Figure 4.6 shows the coherence between the composite EOG signal and the moving stimulus.

Stimulus Tracking Across Testing Age

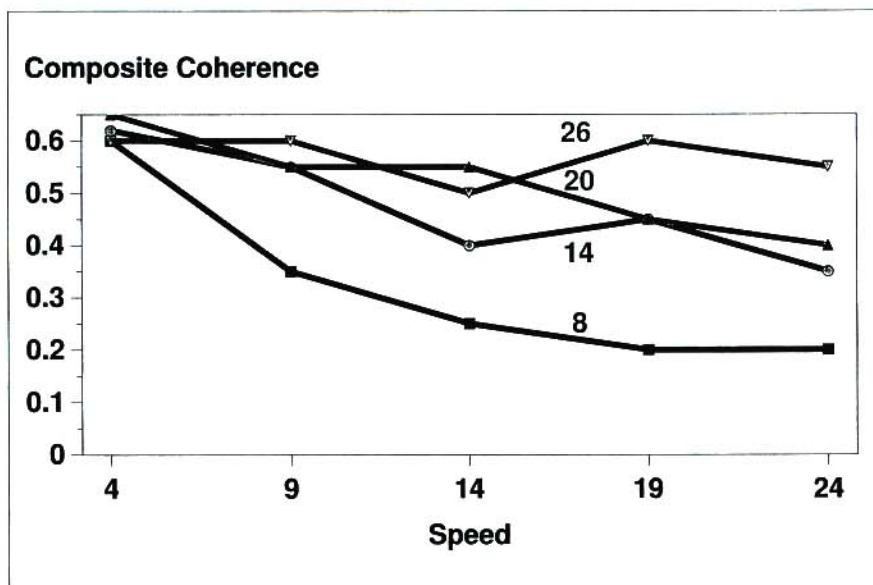


FIG. 4.6. The coherence between composite EOG and tracking stimulus, as a function of tracking speed, for the four age groups. An increase in coherence at the higher speeds occurs over this age range.

This represents how well the infant tracks the signal regardless of the nature of the eye movements. This is separated for the four age groups, plotted for the horizontal stimulus, and at the different tracking speeds. There is a large drop-off in the tracking of the 8-week-olds at very slow speeds, and a gradual increase over the next three ages in the level of tracking. This is shown by the increased sustaining of the coherence between the signal and the eye movements for the four ages over the increases in tracking speed. This generally shows an increase in visual stimulus tracking over this age range.

Figure 4.7 shows the number of saccades made during the tracking at the different ages. The graph on the left is when HR has significantly decelerated below prestimulus level. This represents sustained attention to the visual tracking stimulus. The graph on the right is when HR has returned to its prestimulus level, though the infant continues to fixate toward the TV stimulus. During the attention-HR change, there is an increase over age in the number of saccades toward the tracking stimulus as speed increases. This seems to peak for the 3-month-olds at about 14 degrees per sec, and then decline at the fastest speed. The 20- to 26-week-olds show increases in saccade

Saccade Tracking

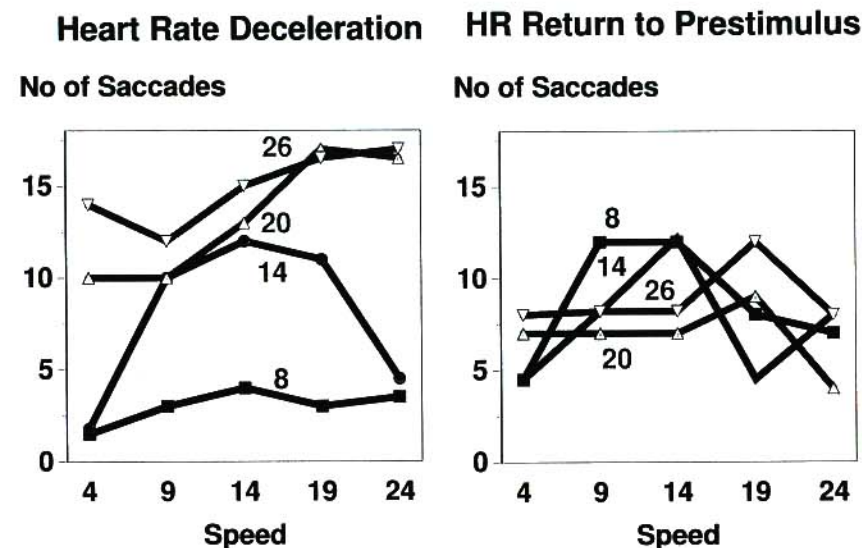


FIG. 4.7. Number of saccades, as a function of stimulus speed, for the four age groups. Left graph is HR deceleration, and right graph is return of HR to prestimulus level.

number over the faster speeds all the way until the fastest speed. Thus, although smooth-pursuit tracking is becoming poor, and saccadic system needs to be used, the visual pursuit continues. Saccadic tracking during attention represents a longer-latency system involving the parvocellular retina and LGN cells that involves several higher cortical areas (V1, V2, posterior parietal cortex, FEF, and SC). This shows a dramatic increase from 2 to 4.5 months, and not much change to 6 months.

The right side of Fig. 4.7 is the number of saccades during the inattentive period when HR has returned to prestimulus levels. Note that tracking still occurs, though coherence between the visual stimulus and the EOG movements is lower. However, there is no age difference in this condition, and the tracking does not increase dramatically with visual stimulus speed. Saccadic tracking during inattentive periods was found to be the poorest, and did not change over the age ranges studied. Remember, saccades during "inattention" represent a short-latency system involving the retina, LGN, primary visual cortex, and superior colliculus. This system is thought to exist at or near birth (or at least by 1-2 months) and control saccadic eye movements to peripheral targets.

Changes in smooth-pursuit tracking are shown in Fig. 4.8. This shows the coherence between the smooth-pursuit eye movements, and the track-

Smooth Pursuit Tracking

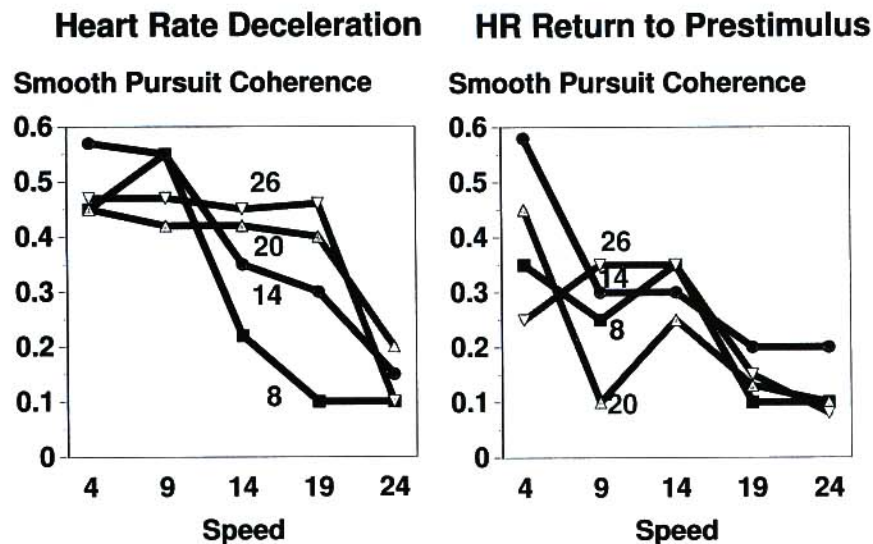


FIG. 4.8. Coherence between smooth-pursuit eye movements and visual stimulus, as a function of stimulus speed, separate for the four ages. Left graph shows HR deceleration, and right graph shows return of HR to prestimulus level.

ing stimulus, as a function of the stimulus speed, separately for the four age groups. Again, on the left is the data for the HR deceleration period, and the right shows the data for when HR has returned to its prestimulus level. The coherence decreases with the tracking speed for the four ages. However, in the graph at left, representing attention, there is a steady increase over the four ages in the coherence-speed function. Again, as with the saccadic tracking number, the smooth-pursuit coherence following the return of HR to its prestimulus level is not as good, and does not show the dramatic age differences as the attention-based tracking does.

There was a gradual increase in the level of smooth-pursuit tracking across these ages, particularly during attention. Smooth-pursuit tracking represents a longer-latency system involving the magnocellular retina and LGN cells, and several higher cortical areas (V1, V2, V4, MT, MST). This system shows development starting after 2 months, and has a very long developmental course (up through 18–24 months). Like the attentive-saccadic system, it is strongly affected by attentive behavior.

It is worth comparing the results in Fig. 4.7 and Fig. 4.8 with the hypothetical graph in Fig. 4.1. This hypothetical graph shows a rapid increase in saccadic tracking in the short-latency system. This is represented by

saccadic tracking that occurs in the infant during “inattentive” periods. Though not shown in the graphs, there is also some evidence that this type of age function (no age change in this age) is typical of the saccadic eye movements during stimulus orienting. Second, the “attention-directed” saccadic tracking system shows a rapid development over this age range. By 6 months, it is at peak maturity level, and doesn’t change much after that. Third, the smooth-pursuit system shows gradual development over this age range, and is closely related to attention as with the attention-directed saccadic system, but shows development in much later periods of infancy and perhaps into early childhood.

The “attentive-saccadic” system and the “attentive smooth-pursuit” system are involved in focal stimulus attention. These systems show changes over the entire period from 2 to 6 months. The “reflexive-saccadic” system, that exists at birth, is the system that controls peripheral stimulus localization and is inhibited during focal stimulus attention. The developmental changes in these systems needs to be studied in the time period before 14 weeks of age, with a systematic study of the effect of the newly emerging focal sustained attention systems on the reflexive-saccadic system.

Similarly, the changes in the eye-movement systems affected by attention occur over this entire age range and would likely be involved in the development of response inhibition and covert attention that would be studied in Experiment months of age. This tracking ability continues to change over the first year, and well into the second year, perhaps peaking by the end of that year.

SUMMARY AND CONCLUSIONS

The selectivity of attention is a vacuous notion that needs to be filled in with specific details. In the case of visual attention, selectivity often involves the *competition* between eye-movement systems. The systems controlling fixation enhance focal field processing, and those systems involving peripheral stimulus localization are inhibited. Alternatively, some saccadic eye-movement control may be enhanced during attention. The increasing development of the predictive system in the smooth-pursuit study is an example that not just fixation is enhanced, but eye-movement systems that aid in the task requirements are enhanced (either saccades or smooth pursuit).

This chapter has presented two main theses. First, we asserted that developmental changes in the neural systems controlling eye movement form the basis for changes in overt eye-movement behavior. The changes in these neural systems arise as individual systems begin to function, as individual systems reach maturity, and as the interaction between these

systems occurs. The "cognitive developmental neuroscience" models of eye-movement control predict specific patterns of development in overt behavioral systems.

Second, it has been asserted that developmental changes in sustained attention also occur over the same time period as these overt and neural changes. These changes in sustained attention may form the basis for much of the development of two eye-movement systems, targeted saccades and smooth-pursuit eye movements. The changes in sustained attention and in the neural systems act as complementary changes that show up in infants' overt eye-movement responses in psychological tasks. In the case of eye movements, overlapping developmental trajectories between the various eye-movement control systems, and development in sustained attention, results in unique patterns of developmental changes in the effect of attention on eye movements in young infants. These overt behavioral changes may be best understood as a confluence of the developmental changes in the underlying systems and the increasing coordination of those changes in the first few months of infancy.

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Summary and Commentary: Eye Movements, Attention and Development

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Many of the most important concepts in psychology have proved elusive to define and frustrating to study. The prime example is probably intelligence. Another is attention. The difficulties of finding comprehensive definitions of such constructs that map cleanly onto an agreed-upon, comprehensive sets of methods and measures are well illustrated by the decades of work on both topics. Yet in both cases, the obvious evidence of such psychological processes in everyday life is sufficient to maintain healthy research efforts and continuing attempts to harness the concepts theoretically. In 1890, William James said of attention that “everyone knows what [it] is”; for James, it implied withdrawing from something in order to deal effectively with others (James 1890/1950, p. 403). Since that time, researchers have used attention to mean, *inter alia*, selection, search, mental effort, concentration, and arousal, risking the possibility, as Eysenck and Keane (1990) remarked, that a concept “used to explain everything” might “turn out to explain nothing.” Still the interest in attention perseveres.

This volume reflects an ambitious attempt to approach the attention construct developmentally, focusing on visual attention from the perspective of neural development. The chapters in this section illustrate the multiple ways in which attention has been characterized in recent work. The authors appear to be in general agreement that attention involves the selective deployment of information-processing resources. They also manifest general agreement that visual attention can be both overt (i.e., manifested in external behaviors such as orienting eye movements) and covert (implicitly