

John E. Richards

*Department of Psychology
University of South Carolina
Columbia, SC 29208*

Sharon K. Hunter

*Department of Psychiatry
University of Colorado Health
Sciences Center
Denver, CO 80262*

Testing Neural Models of the Development of Infant Visual Attention

Received 21 February 2001; Accepted 6 November 2001

ABSTRACT: *Several models of the development of infant visual attention have used information about neural development. Most of these models have been based on nonhuman animal studies and have relied on indirect measures of neural development in human infants. This article discusses methods for studying a “neurodevelopmental” model of infant visual attention using indirect and direct measures of cortical activity. We concentrate on the effect of attention on eye movement control and show how animal-based models, indirect measurement in human infants, and direct measurement of brain activity inform this model.* © 2002 Wiley Periodicals, Inc. *Dev Psychobiol* 40: 226–236, 2002. DOI 10.1002/dev.10029

Keywords: *infant visual attention; visual behavior; neural development; reflexive saccades; voluntary saccades*

Several theoretical models have related age-linked brain development to the development of visual attention in young infants. These models have a basic assumption that visual attention is closely related to activity in specific brain areas. These “neurodevelopmental” models posit that changes in these brain areas form the basis for the age-linked changes found in visual behavior.

The first model of this type was the “two visual systems” of Bronson (1974, 1997). This model postulated the existence of two visual systems in the brain that controlled visual behavior, the “primary” and “secondary” visual systems. The secondary system was hypothesized to be responsive to stimulus location and to movement and relatively mature at birth. Thus, visual behavior in the newborn and in the

very young infant (up to 3–4 months) was suggested to be dominated by behaviors sensitive to stimulus location or movement. The primary visual system was hypothesized to be responsible for fine-pattern visual analysis. It was thought to be relatively immature at birth in the human and to show important developments in the first 3 to 6 months. Thus, visual behavior based upon this system would emerge and develop after about 3 months. The development of visual behavior and attention then would be controlled by the development of the neural systems underlying these behaviors.

Other models of infant visual attention development have used Bronson’s model, and/or have relied upon more contemporary knowledge about visual neuroscience. Models such as those by Karmel and Maisel (1975), Maurer and Lewis (1979, 1991, 1998), Salapatek (1975), Johnson (1990, 1995; Johnson, Gilmore, & Csibra, 1998; Johnson, Mareschal, & Csibra, 2001; Johnson, Posner, & Rothbart, 1991), and Atkinson and Braddick (Atkinson & Braddick, 2002; Hood, Atkinson, & Braddick, 1998) have used several concepts in visual neuroscience to model

Correspondence to: J. E. Richards
Contract grant sponsor: NICHD
Contract grant number: R01-HD18942
Contract grant sponsor: NSF
Contract grant number: BCS-9977198

the development of visual attention in young human infants. Johnson, for example, took an established model of eye movement control (Schiller, 1985, 1998) and knowledge of the development of the primary visual area and presented a model that showed how infant visual behavior was governed by changes in neural systems. We also have presented a neurodevelopmental model that concerned the effect of arousal on visual behavior in young infants (Richards, 2001d, 2002b; Richards & Casey, 1992; Richards & Hunter, 1998). This model was based primarily on knowledge concerning the effects of a general neural arousal system on attention (Heilman, Watson, Valenstein, & Goldberg, 1987; Mesulam, 1983; Robbins & Everitt, 1995). These neurodevelopmental models explain developmental changes in a wide variety of behaviors and have been influential in generating research on infant visual attention.

These models have a common weakness. Most get information about neural development and function from nonhuman animal work. The information about human neural development often is based upon autopsy evidence (e.g., autopsy series of Conel, 1939–1967) or static measurements of human neurophysiological function (e.g., Huttenlocher, 1990). There are few, if any, direct measures of brain activity in human infants. Neuroimaging techniques used in cognitive neuroscience (Posner & DiGirolamo, 2000; see chapters in Gazzaniga, 1995, or Nelson & Luciana, 2001) have not been applied routinely to human infants in the study of visual attention development. The link between infant visual *behavior* and the underlying *neural systems* has been speculative rather than directly examined.

The goal of the present article is to examine methods for measuring the “neuro” in neurodevelopmental models of visual attention in infants. We will examine some of our recent studies of infant visual attention in light of a theoretical model of eye movement control. This will be done with the goal of illustrating methods that measure neural activity for use in research examining neurodevelopmental models of visual attention.

DEVELOPMENT OF TWO EYE MOVEMENT SYSTEMS: THE “NEURODEVELOPMENTAL” MODEL

The “neurodevelopmental” model that stimulated several of our recent studies is based on the existence of separate brain systems that control saccadic eye movements (see presentations of the model in Richards, 2001a, 2001d; Richards & Hunter, 1998).

This has been presented recently in Richards (2001a) and will be briefly reviewed here. Two brain systems control saccadic eye movements (Schiller, 1985, 1998). Work on the nonhuman primate visual system has found a neural system that controls reflexive saccades to sudden onset peripheral stimuli as well as voluntary (planned) saccades to targets anywhere in the visual field. Distinct brain pathways control these two systems: a reflexive pathway that passes through early visual sensory apparatus, then through the superior colliculus, and a voluntary pathway that involves several areas of the cortex (visual areas 1, 2, 4, parietal cortex area PG, frontal eye fields). Ultimately, the frontal eye fields or the superior colliculus controls brainstem areas that program the brainstem motoneurons that cause the ocular muscles to move the eye in its orbit. These brainstem areas control saccade velocity and other saccade characteristics.

The “developmental” in this neurodevelopmental model has been postulated by several to explain age-related changes in behavior in young infants, particularly models by Johnson (Johnson, 1990, 1995; Johnson et al., 1998; Johnson et al., 2001; Johnson et al., 1991), Hood, Atkinson, and Braddick (Atkinson & Braddick, 2002; Hood, 1995; Hood et al., 1998), and Richards (Richards, 2001a; Richards & Casey, 1992; Richards & Hunter, 1998). The brain pathway controlling reflexive saccades is relatively mature at birth. Therefore, infants at early ages should show a predominance of these reflexive saccades. In particular, the pathways from the retina to the superior colliculus (via primary visual area) are functional at birth as is the brainstem apparatus that controls oculomotor nerves and ocular muscles. The pathway controlling voluntary saccades uses layers of the primary visual cortex that are immature at birth. These layers show rapid development over the first 6 postnatal months. Thus, attention-directed voluntary saccades have a more protracted developmental trajectory than reflexive saccades.

DEVELOPMENT OF THE MAIN SEQUENCE IN EYE MOVEMENTS: “MARKER TASKS”

A common method for examining neurodevelopmental models is the use of “marker tasks” (Johnson, 1997). Marker tasks are behavioral measures that have been used in nonhuman animals at any age or invasive or neuropsychological populations in humans at older ages (usually adults). The marker task is one in which the neural control of behavior in the task is well specified. For example, several aspects of the covert

orienting of attention in the spatial cueing task are mediated by the superior colliculus and the parietal cortex. This has been shown in adults with diseases of the superior colliculus or with lesions to the parietal cortex brought about by strokes or illness (e.g., Rafal, 1998). Johnson (1997) proposes that such tasks may be used with infants and that developmental changes in the behavior may be used to infer developmental changes in the brain area upon which this behavior is based. The marker task approach is used widely to study the neurodevelopmental models of infant visual attention.

Examples of how we have used the marker task approach to infer neural changes can be seen in studies we have done on the development of the “main sequence” relation in eye movements in young infants (Hunter, 2001; Hunter & Richards, 2000, in press; Richards & Hunter, 1997; McKinney, Lewis, Wills, & Richards, 2002). The main sequence is a relation between maximum saccade velocity and saccade amplitude (Bahill, Clark, & Stark, 1975) and is the direct result of the firing rate and firing duration of the brainstem motor neurons that control ocular muscles (Moschovakis & Highstein, 1994). According to the “neuro” part of the neurodevelopmental model, the main sequence should be controlled by brain systems involved in the final transmission of neural activity to effector muscles and, therefore, are common to the reflexive and voluntary saccade systems. The main sequence in this case is a marker task (marker behavior) indicating the functioning of the brainstem neural systems affecting muscle movement in the eyes. According to the “developmental” part of the model we presented earlier, these structures are thought to be well developed at birth. Therefore, changes in the main sequence relation across age would not be expected.

When we began examining the main sequence relation in young infants, we expected little change in the main sequence relation in the first 6 months of infancy. To our great surprise, we now have several studies that have shown that changes occur in the main sequence across age. For example, Richards and Hunter (1997) recorded eye movements using the electrooculogram (EOG). The existence of the main sequence was easily found in the EOG recordings—including linear, quadratic, and cubic polynomial regression relations between maximum saccade velocity and saccade amplitude. We tested 14-, 20-, and 26-week-old infants in that study. There was no difference across these three testing ages in the main sequence relation. So, in line with the neurodevelopmental model, this system was functional (probably from birth?) and did not develop. We did find

developmental changes under conditions of attention. When attention was engaged with a central stimulus and an eye movement was made to a peripheral stimulus, the 20- and 26-week-old infants had a slower peak velocity per saccade amplitude than the young infants. Thus, this “brainstem” system did change over this age range!

This was totally unexpected. We had been convinced that such low-level brain systems were fully functional at birth and should not show developmental changes. Perhaps “attention” was developing rather than the main sequence itself. This implied that the top-down control of the brainstem system by the voluntary saccadic system was different than the top-down control of the brainstem system by the reflexive saccadic system. This interpretation would be consistent with the idea that developmental changes in these two eye-movement systems occurred primarily in the voluntary and not the reflexive system.

Thus, we followed up this study with even more unexpected results. We were attempting to study a related question about the prevalence of “hypometric” saccades (Aslin & Salapatek, 1975) in very young infants and so extended the age range to include young infants (5-, 8-, and 11-week-olds). One of us (Hunter, 2001) was interested in looking at similar eye movement control issues in older children. Therefore, we also tested children ranging in age from 1 to 7 years. In a series of studies (i.e., Hunter, 2001; Hunter & Richards, 2000, in press), we examined the main sequence of eye movements in participants ranging in age from 5 weeks to 7 years. To our surprise (again, though not so great this time), we found age changes of several types in the main sequence. First, there was a decrease in the linear relation between maximum saccade velocity and saccade amplitude from about 5 to 11 weeks, and then this linear relation did not change from 14 to 26 weeks (Hunter, 2001; Hunter & Richards, 2000, in press). Figure 1 shows plots of the velocity/amplitude relation for infants from 5 to 26 weeks of age. The decreasing slope of the linear component of the main sequence may be seen to decrease from 5 to 14 weeks of age. It did not change for the 20- and 26-week-old infants. This implies that the low-level system involving the brainstem eye movement control areas, motoneurons, and ocular muscles did show postnatal age changes. It may have been “relatively mature” at birth, but it did show significant changes through about 3 months of age. This age change was independent of any changes in attention that may have been occurring over this age range since it occurred regardless of whether attention was engaged with

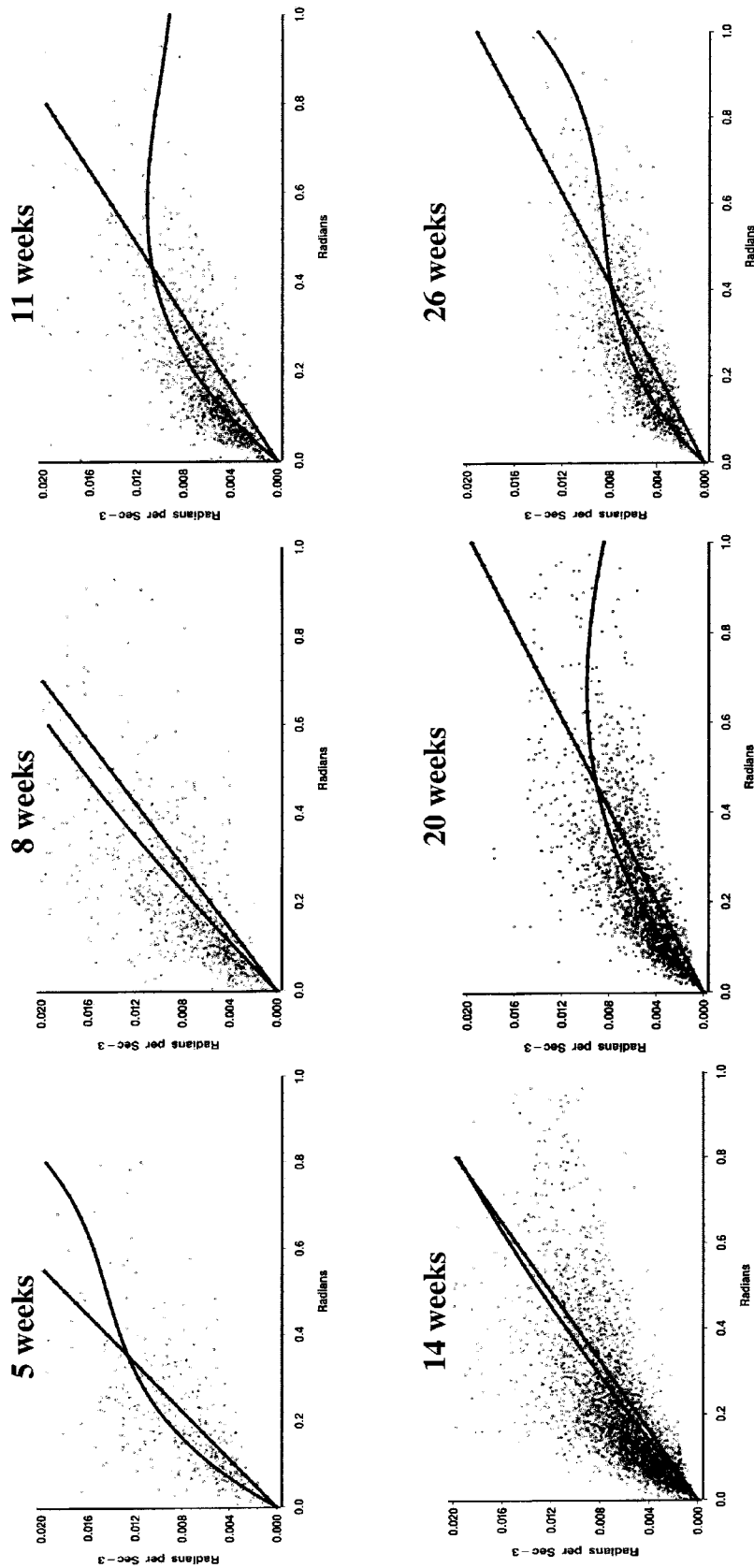


FIGURE 1 The main sequence relation between maximum saccade velocity and saccade amplitude for infants from 5 to 26 weeks of age. The lines are the best-fitting linear and quadratic regression lines. From "Developmental Changes in the 'Main Sequence' Relation in Infant Saccades," by S. K. Hunter & J. E. Richards, 2000. Paper presented at the meeting of the International Society for Infancy Studies, Brighton, England.

the central stimulus. We also found such an age change when infants moved their eyes around within a single varied stimulus (Hunter, 2001; Hunter & Richards, 2000) rather than just from a central to a peripheral stimulus (Hunter & Richards, *in press*; Richards & Hunter, 1997).

Additionally, age changes were found in the main sequence in older children (Hunter, 2001). There was an overall trend toward decreasing main sequence slopes with age that continued through the first 3 years of life. Perhaps more interesting is the pattern of changes in the main sequence relations. The slopes for the eye movements to peripheral stimuli showed a decline from 8 weeks to 14 weeks and were lower than those for the varied stimulus until around 20 weeks. The decline in the slopes for the varied stimulus began around 11 weeks and continued until around 23 weeks, and was relatively stable until age 1. From age 1 to age 7, the slopes for the single varied stimulus were generally greater, though there was less difference between the slopes for the two presentation types beginning around age 2.

There are two points to take from this. First, performance on the trials in which a peripheral stimulus was used required the reflexive saccade system. As in previous studies, this system showed changes over the first 14 weeks of life as indicated by the decreasing slopes. Once again, we replicated developmental changes over the first 3 months of life. Second, we believe the eye movements generated during the varied stimulus presentation are the result of the voluntary system. These eye movements showed developmental changes over roughly the first 6 months of life, again as indicated by the decreasing main sequence slopes. We believe changes in these slopes are the result of continued development of top-down control mechanisms.

HEART-RATE DEFINED ATTENTION PHASES AFFECT EYE MOVEMENT CONTROL: INDIRECT MEASURES

The marker task approach to the study of neurodevelopmental models of infant visual attention has been useful. Another approach that may prove useful is to obtain an “indirect” measure of brain activity. Our idea of indirect measures are measures that are “directly connected” to neural activity and brain control, but involve systems removed at least one step from neural activity. Most psychophysiological measures—heart rate, electroencephalogram (EEG), and event-related-potentials (ERP)—are indirect measures. Heart rate, for example, is controlled directly

by innervation from the sympathetic and parasympathetic peripheral nervous systems. Changes in heart rate reflect an immediate assessment of this nervous system activity. As with behavioral marker tasks, the relation between the neural system governing arousal/attention (Heilman et al., 1987; Mesulam, 1983) and heart rate control are well known. In this respect, heart rate is a “behavioral marker task” similar to eye movements, reaction time, novelty preference, or habituation. Scalp measures of EEG and “event-related-potentials” (ERP) when concentrating on “ERP components” are such indirect measures. In the case of EEG and ERP, changes in these scalp electrical potentials are directly caused by underlying neural activity. However, ERP components (P300, P1, and N1) are indirect assessments of neural activity with a similar measurement status to behavioral marker tasks.

Heart rate used as an index of attention status has a long history in developmental psychophysiology (e.g., Berg & Berg, 1987; Berg & Richards, 1997; Richards, 2001d; Richards & Casey, 1992). We have used heart rate changes with infants to measure “sustained attention” (i.e., a long-duration engagement of active attention processes) (Richards, 2001d; Richards & Casey, 1992; Richards & Hunter, 1998). Given its relation to the arousal system of the brain (Richards, 2001d), we may think of the development of heart rate in psychological and behavioral tasks as contributing to neurodevelopmental models of infant visual attention. We will give a specific example of the use of heart rate in this regard in the context of the neurodevelopmental model of eye movement control presented earlier.

As an example of the use of heart rate as an indirect measure of neural activity, we turn back to the study of eye movements during attention. As previously mentioned, our first study of eye movements during attention found that the main sequence was affected by an attention and age interaction (Richards & Hunter, 1997). We presented infants with interesting central visual stimuli and waited until heart rate decelerated below prestimulus levels. This deceleration is a marker of “sustained attention” in young infants (Richards & Casey, 1992). When infants were attentive to the central stimulus, we presented a peripheral stimulus to which an eye movement may be made. Figure 2 shows one result from that study. This figure shows velocity/amplitude plots for 14-, 20-, and 26-week-old infants during attention. The 20- and 26-week-old infants had a slower peak velocity per saccade amplitude than the younger infants. This age difference did not exist if the heart rate had not yet decelerated (attention not

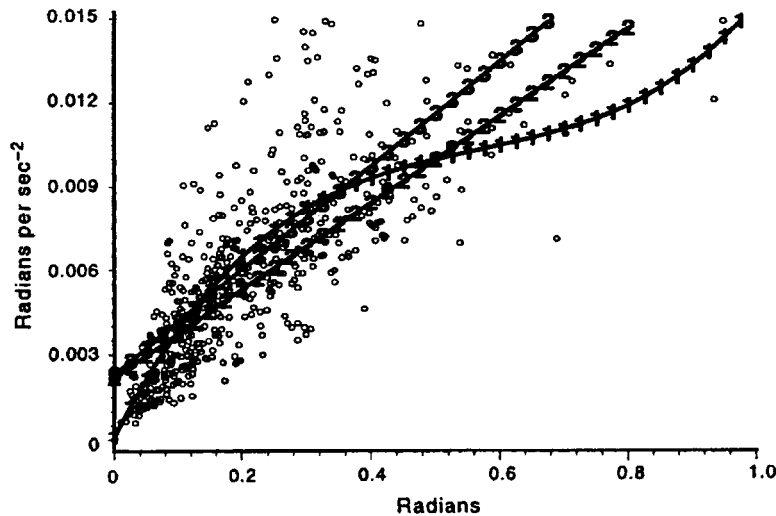


FIGURE 2 The main sequence relation during attention for 14- (“1”), 20- (“2”), and 26-week-old (“3”) infants. From “Peripheral Stimulus Localization by Infants with Eye and Head Movements During Visual Attention,” by J. E. Richards & S. K. Hunter, 1997, *Vision Research*, 37, 3021–3035. Copyright 1997 by Elsevier Science Ltd.

yet engaged) or if heart rate had returned to prestimulus levels (attention now unengaged). This implies that changes that occur at the oldest testing ages are related to developmental changes in attention rather than to eye movement changes, per se. This relation between the main sequence, age, and attention has been confirmed in several studies (Hunter, 2001; Hunter & Richards, 2000, in press; McKinney et al., 2002).

Our interpretation of the changes in the main sequence during attention in older infants involves an understanding of the neural model of eye movement control. Both the superior colliculus and the frontal eye fields control the brainstem eye movement area and oculomotor neurons. The amplitude of an eye movement is determined by information in the superior colliculus or frontal eye fields, and the brain stem areas move the eyes by stimulating burst neurons for durations related to the size of the saccade. The reflexive saccade pathway involves the superior colliculus (among other structures) whereas the voluntary saccade pathway involves the frontal eye fields, the superior colliculus, or both. The effect of attention (measured indirectly by heart rate changes) on the main sequence may be due to an increasing top-down influence of the frontal eye fields (and other cortical systems) on the brainstem eye movement areas from the ages of 3 through 6 months of life. Attention develops across this age range, and therefore differences may be seen in the attention-linked main sequence and the inattention-linked main sequence in older infants.

CORTICAL SOURCES OF ERP DURING SPATIAL CUEING: DIRECT MEASUREMENTS

The marker task and the indirect measurement of brain activity have been useful in the study of neurodevelopmental models. These approaches may be complemented by direct measures of brain function. Direct measures of brain function are measures that directly tap brain activity in a manner relevant to the underlying generation of that activity. In adults and older children, functional magnetic resonance imaging (MRI) may be used to directly measure the hemodynamic changes occurring in the brain and localize brain activity associated with cognitive processes. This methodology is described in a parallel special issue of *Developmental Science* (Casey, Davidson, & Rosen, 2002). Practical and ethical constraints limit the use of many of these techniques with human infants. Other more invasive techniques (i.e., single cell recording) are likewise out of bounds.

Scalp-recorded electrical activity may provide an acceptable direct “neuroimaging” technique for use with infant participants. The EEG is electrical activity occurring on the scalp caused by action potentials summed over large numbers of neurons, synapses, neural pathways, and neural systems. ERPs are EEG activity that is time locked to experimental or cognitive events, and are even more useful than EEG in correlating observed cognitive processes with scalp electrical activity. Measurement of EEG and ERP is indirect as a measure of brain activity. However, the

ERP has varying positive and negative electrical waves that are referred to as “components” (Fabiani, Gratton, & Coles, 2000; Hillyard, Mangun, Woldroff, & Luck, 1995; Swick, Kutas, & Neville, 1994). These components are controlled by known neural areas and psychological processes. High-density EEG recording (Johnson et al., in press; Tucker, 1993; Tucker, Liotti, Potts, Russell, & Posner, 1994) and cortical source localization (Huizenga & Molenaar, 1994; Nunez, 1990; Scherg, 1990, 1992; Scherg & Picton, 1991) may be used with ERP to identify cortical areas involved in cognitive processes. Taylor and Baldeweg (2002) described methods for using ERPs in a parallel special issue of *Developmental Science* on imaging methods.

An example of the use of these methods with infant participants comes from studies of covert orienting (Richards, 2000a, 2000b, 2001a, 2001b, 2001c, 2002a). Several studies have shown that infant participants show “facilitation” and “inhibition of return” of localization of peripheral targets as a function of the presence of a cue indicating where the target should appear (Hood, 1993, 1995; Hood & Atkinson, 1991; Johnson, Posner, & Rothbart, 1994; Johnson & Tucker, 1996). That is, infants show decreased reaction time to move the eyes from a center location to a peripheral location when a cue indicates the target will appear in that location (“facilitation”). They also show an increase in reaction time if the cue- and target stimulus-onset asynchrony is long enough. This finding was replicated in several studies by Richards (2000a, 2000b, 2001b).

The behavioral measure, reaction time to move the eyes to the target, would be a marker task in this experiment (cf. Rafal, 1998, for adult studies). In addition to this marker behavior, ERPs were recorded at the onset of the target. The spatial relation between the cue and the target significantly affected the ERP to the onset of the target. There was a larger positive ERP component occurring at about 135 ms when the cue and target were in ipsilateral hemifields (valid trials) than when the cue and target were in contralateral hemifields (invalid trials) or when a cue did not precede the target (neutral trials). This validity effect was similar to the P1 validity effect found in adult studies in this task (Eimer, 1996, 1997; Hillyard, Luck, & Mangun, 1994; Hillyard et al., 1995; Hopfinger & Mangun, 1998; Martinez et al., 1999). This component, then, was an indirect assessment of brain activity modified by covert orienting to the peripheral stimulus when it was presented as a cue. The results from this study indicated that infants were shifting attention to the cued

location covertly and that this early sensory–perceptual gating occurs in infant attention as it does in adult attention.

The ERPs in these studies were an “indirect measure.” We are currently using a more direct measure of cortical activity during this task (Richards, 2001c, 2002a). The ERP in response to a target has been recorded in about 16 infants so far, in a spatial cueing task, using high-density EEG recording. A 128-channel EEG system (Johnson et al., in press; Tucker, 1993; Tucker et al., 1994) is being used to record EEG, and ERPs are segmented from the ongoing EEG around the onset of the target. The ERP segments for an individual infant are analyzed with spatial principal components analysis (Spencer, Dien, & Donchin, 1999; Richards, 2001). This results in a set of principal component loadings that may be interpreted as the spatially coordinated ERP activity in that infant. Similar components were clustered across infants, and equivalent current dipole solutions were calculated. Localization of activity can be determined from the principal component clusters and dipole analysis.

One example of the dipole analysis will be given. There was a principal component found in all 16 infants that was organized over the occipital scalp recording sites contralateral to the onset of the target. The time-related activation of the component indicated this was the “P1” ERP component, i.e., its activation was larger for the trials on which the location of the target was validly indicated by the preceding cue. Equivalent dipole analysis was done for the component loadings for each of the 16 infants. Figure 3 shows an MRI representation of the location of the dipoles from these infants. Some of the dipoles were located in the primary visual area of the occipital cortex (Brodmann area 17; Figure 3, “Primary Visual Area”). This area is the first cortical area that receives visual information. The activation of these principal components did not show the validity effect. Some of the dipoles were located in the fusiform gyrus (Brodmann area 19; Figure 3, “Fusiform Gyrus”). This area is one of the pathways from the primary visual area to the object identification areas in the temporal cortex (“ventral processing stream”). The principal components located in the fusiform gyrus were the ones whose activation showed the P1 validity effect.

At this point, only a preliminary interpretation of the results may be given. The results suggest that the role of attention to the cued location is not to enhance primary sensory areas in the infant cortex. The pathway from the primary cortex through the fusiform gyrus leads to the “ventral pathway” involved in

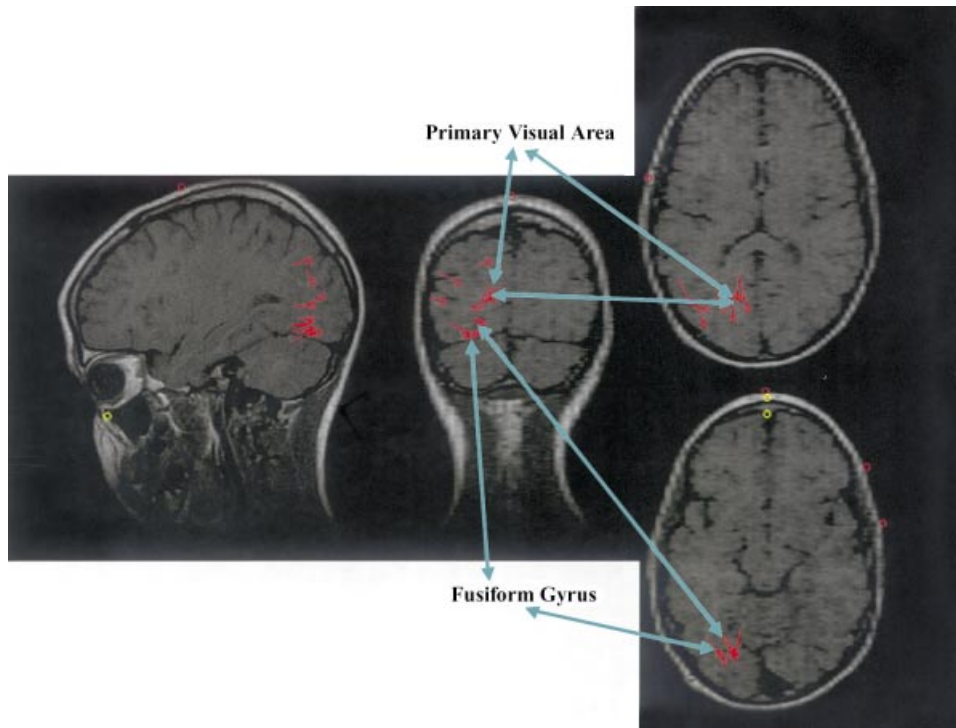


FIGURE 3 Equivalent current dipole locations for individual infants for a principal component reflecting the “P1 validity effect” in a spatial cueing task. The dipole locations are plotted on an MRI from a young child. From by “Cortical Sources of the P1/N1 Validity Effect in Spatial Cueing in Young Infants,” by J. E. Richards, 2002a. Paper presented at the International Conference on Infancy Studies, Toronto.

object identification and analysis. One interpretation of these findings is that the cueing and subsequent covert orienting acts to enhance the object’s properties of the target (“ventral pathway”) rather than to enhance the spatial location in which the target appears (“dorsal pathway”). If this interpretation is correct, then we may find that covert orienting to peripheral targets for young infants is based upon the characteristics of the object as much as the spatial location in which the object appears. The direct measurement of brain activity in this work provides some new hypotheses to be studied in future research.

SUMMARY

Our goal was to examine ways to test neural models of development in human infants. The paradigms used in our lab employed markers tasks such as main sequence, indirect measures such as heart rate, and direct measures such as ERP in an effort to illuminate development in the visual system of the human infant. These were merely examples of the research methods

being employed. Other marker tasks actively in use include inhibition of return tasks, visual expectation tasks, and smooth-pursuit tracking tasks, to name a few. Currently, there is an explosion in the use of ERP and other direct measures in developmental studies. Findings from all of these studies are leading to the refinement of existing models.

A further value in the usage of these marker tasks and indirect and direct measures lies in their ability to be used to identify developmental problems early on. For example, respiration and heart rate (both indirect measures) have been used to identify attentional differences in high-risk, preterm infants (Frick & Richards, 2001). Additionally, research studies are currently under way that use eye movement characteristics to better understand development in children at risk for psychotic illnesses (i.e., schizophrenia). The hypothesized relation between developmental disorders and brain development may be investigated with measures of brain activity such as those presented here. These techniques will be useful in mapping the brain–behavior–development relation assumed in neurodevelopmental models of visual attention and its disorders.

REFERENCES

- Aslin, R. N., & Salapatek, P. (1975). Saccadic localization of visual targets by the very young infant. *Perception and Psychophysics*, 17, 293–302.
- Atkinson, J., & Braddick, O. (2002). Visual development. In M. de Haan & M. H. Johnson (Eds.), *The cognitive neuroscience of development*. Hove, Sussex, England: Psychology Press.
- Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence: A tool for studying human eye movements. *Mathematical Bioscience*, 24, 191–202.
- Berg, W. K., & Berg, K. M. (1987). Psychophysiological development in infancy: State, startle, and attention. In J. D. Osofsky (Ed.), *Handbook of infant development* (pp. 238–317). New York: Wiley.
- Berg, W. K., & Richards, J. E. (1997). Attention across time in infant development. In P. J. Lang, R. F. Simons, & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 347–368). Mahwah, NJ: Erlbaum.
- Bronson, G. W. (1974). The postnatal growth of visual capacity. *Child Development*, 45, 873–890.
- Bronson, G. W. (1997). The growth of visual capacity: Evidence from infant scanning patterns. In C. Rovee-Collier & L. P. Lipsitt (Eds.), *Advances in infancy research* (Vol. 11, pp. 109–141). Greenwich, CT: Ablex.
- Casey, B. J., Davidson, M., & Rosen, B. (2002). Basic principles and applications of fMRI in developmental science. *Developmental Science*, 5.
- Conel, J. L. (1939–1967). *The postnatal development of the human cerebral cortex*. Cambridge, MA: Harvard University Press.
- Eimer, M. (1996). ERP modulations indicate the selective processing of visual stimuli as a result of transient and sustained spatial attention. *Psychophysiology*, 33, 13–21.
- Eimer, M. (1997). Attentional selection and attentional gradients: An alternative method for studying transient visual–spatial attention. *Psychophysiology*, 34, 365–376.
- Fabiani, M., Gratton, G., & Coles, M. G. H. (2000). Event-related brain potentials: Methods, theory, and applications. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of psychophysiology* (pp. 53–84). New York: Cambridge.
- Frick, J. E., & Richards, J. E. (2001). Individual differences in infants' recognition of briefly presented visual stimuli. *Infancy*, 2, 331–352.
- Gazzaniga, M. S. (Ed.). (1995). *Cognitive neurosciences*. Cambridge, MA: MIT Press.
- Heilman, K. M., Watson, R. T., Valenstein, E., & Goldberg, M. E. (1987). Attention: Behavior and neural mechanisms. In V. B. Mountcastle, F. Plum, & S. R. Geiger (Eds.), *Handbook of physiology* (pp. 461–481). Bethesda, MD: American Physiological Society.
- Hillyard, S. A., Luck, S. J., & Mangun, G. R. (1994). The cueing of attention to visual field locations: Analysis with ERP recordings. In H. J. Heinze, T. F. Munte, & G. R. Mangun (Eds.), *Cognitive electrophysiology* (pp. 1–25). Boston: Birkhauser.
- Hillyard, S. A., Mangun, G. R., Woldroff, M. G., & Luck, S. J. (1995). Neural systems mediating selective attention. In M. S. Gazzaniga (Ed.), *Cognitive neurosciences* (pp. 665–682). Cambridge, MA: MIT Press.
- Hood, B. M. (1993). Inhibition of return produced by covert shifts of visual attention in 6-month-old infants. *Infant Behavior and Development*, 16, 245–254.
- Hood, B. M. (1995). Shifts of visual attention in the human infant: A neuroscientific approach. *Advances in Infancy Research*, 10, 163–216.
- Hood, B. M., & Atkinson, J. (1991, April). Shifting covert attention in infants. Paper presented at the meeting of the Society for Research in Child Development, Seattle, WA.
- Hood, B. M., Atkinson, J., & Braddick, O. J. (1998). Selection-for-action and the development of orienting and visual attention. In J. E. Richards (Ed.), *Cognitive neuroscience of attention: A developmental perspective* (pp. 219–250). Hillsdale, NJ: Erlbaum.
- Hopfinger, J. B., & Mangun, G. R. (1998). Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science*, 9, 441–446.
- Huizenga, H. M., & Molenaar, P. C. M. (1994). Estimating and testing the sources of evoked potentials in the brain. *Multivariate Behavioral Research*, 29, 237–262.
- Hunter, S. K. (2001). *Changes in saccadic eye movements: Attentional and developmental implications*. Unpublished doctoral dissertation, University of South Carolina.
- Hunter, S. K., & Richards, J. E. (July, 2000). Developmental changes in the “main sequence” relation in infant saccades. Paper presented at the International Society for Infancy Studies, Brighton, England.
- Hunter, S. K., & Richards, J. E. (in press). Peripheral stimulus localization by 5- to 14-week-old infants during attention. *Infancy*.
- Huttenlocher, P. R. (1990). Morphometric study of human cerebral cortex development. *Neuropsychologia*, 28, 517–527.
- Johnson, M. H. (1990). Cortical maturation and the development of visual attention in early infancy. *Journal of Cognitive Neuroscience*, 2, 81–95.
- Johnson, M. H. (1995). The development of visual attention: A cognitive neuroscience perspective. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 735–747). Cambridge, MA: MIT Press.
- Johnson, M. H. (1997). *Developmental cognitive neuroscience*. London: Blackwell.
- Johnson, M. H., de Haan, M., Oliver, A., Smith, W., Hatzakis, H., Tucker, L. A., & Csibra, G. (in press). Recording and analyzing high density ERPs with infants using the Geodesic Sensor Net. *Neuropsychology*.
- Johnson, M. H., Gilmore, R. O., & Csibra, G. (1998). Toward a computational model of the development of saccade planning. In J. E. Richards (Ed.), *Cognitive neuroscience of attention: A developmental perspective* (103–130). Hillsdale, NJ: Erlbaum.

- Johnson, M. H., Mareschal, D., & Csibra, G. (2001). The functional development and integration of the dorsal and ventral visual pathways: A neurocomputational approach. In C. A. Nelson & M. Luciana (Eds.), *Developmental cognitive neurosciences* (pp. 339–352). Cambridge, MA: MIT Press.
- Johnson, M. H., Posner, M. I., & Rothbart, M. K. (1991). Components of visual orienting in early infancy: Contingency learning, anticipatory looking, and disengaging. *Journal of Cognitive Neuroscience*, 3, 335–344.
- Johnson, M. H., Posner, M. I., & Rothbart, M. K. (1994). Facilitation of saccades toward a covertly attended location in early infancy. *Psychological Science*, 5, 90–93.
- Johnson, M. H., & Tucker, L. A. (1996). The development and temporal dynamics of spatial orienting in infants. *Journal of Experimental Child Psychology*, 63, 171–188.
- Karmel, B. Z., & Maisel, E. G. (1975). A neuronal activity model for infant visual attention. In L. B. Cohen & P. Salapatek (Eds.), *Infant perception: From sensation to cognition* (Vol. 1, pp. 77–131). New York: Academic Press.
- Martinez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., Wong, E. C., Hinrichs, H., Heinze, H. J., & Hillyard, S. A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, 2, 364–369.
- Maurer, D., & Lewis, T. L. (1979). A physiological explanation of infants' early visual development. *Canadian Journal of Psychology*, 33, 232–252.
- Maurer, D., & Lewis, T. L. (1991). The development of peripheral vision and its physiological underpinnings. In M. J. S. Weiss & P. R. Zelazo (Eds.), *Newborn attention: Biological constraints and the influence of experience* (pp. 218–255). Norwood, NJ: Ablex.
- Maurer, D., & Lewis, T. L. (1998). Overt orienting toward peripheral stimuli: Normal development and underlying mechanisms. In J. E. Richards (Ed.), *Cognitive neuroscience of attention: A developmental perspective* (pp. 51–102). Hillsdale, NJ: Erlbaum.
- McKinney, B., Lewis, E., Wills, V., & Richards, J. E. (2002, April). Developmental changes in the main sequence using interesting visual stimuli. Paper presented at the International Conference on Infancy Studies, Toronto, CA.
- Mesulam, M. M. (1983). The functional anatomy and hemispheric specialization for directed attention. *Trends in Neuroscience*, 6, 384–387.
- Moschovakis, A. K., & Highstein, S. M. (1994). The anatomy and physiology of primate neurons that control rapid eye movements. *Annual Review of Neuroscience*, 17, 465–488.
- Nelson, C. A., & Luciana, M. (Eds.). (2001). *Developmental cognitive neuroscience*. Cambridge, MA: MIT Press.
- Nunez, P. L. (1990). Localization of brain activity with electroencephalography. *Advances in Neurology*, 54, 39–65.
- Posner, M. I., & DiGirolamo, G. J. (2000). Cognitive neuroscience: Origins and promise. *Psychological Bulletin*, 126, 873–889.
- Rafal, R. D. (1998). The neurology of visual orienting: A pathological disintegration of development. In J. E. Richards (Ed.), *Cognitive neuroscience of attention: A developmental perspective* (pp. 181–218). Hillsdale, NJ: Erlbaum.
- Richards, J. E. (2000a). Localizing the development of covert attention in infants using scalp event-related-potentials. *Developmental Psychology*, 36, 91–108.
- Richards, J. E. (2000b, July). The development of covert attention to peripheral targets and its relation to attention to central visual stimuli. Paper presented at the International Conference for Infancy Studies, Brighton, England.
- Richards, J. E. (2001a). Cortical indices of saccade planning in infants. *Infancy*, 2, 123–133.
- Richards, J. E. (2001b). Cortical indices of saccade planning following covert orienting in 20-week-old infants. *Infancy*, 2, 135–157.
- Richards, J. E. (2001c, April). Using high-density EEG recording to localize cortical sources of infant attention. Paper presented at the Society for Research in Child Development, Minneapolis.
- Richards, J. E. (2001d). Attention in young infants: A developmental psychophysiological perspective. In C. A. Nelson & M. Luciana (Eds.), *Developmental cognitive neuroscience*. Cambridge, MA: MIT Press.
- Richards, J. E. (2002a, April). Cortical sources of the P1/N1 validity effect in spatial cueing in young infants. Paper presented at the International Conference on Infancy Studies, Toronto.
- Richards, J. E. (2002b). Development of attentional systems. In M. de Haan & M. H. Johnson (Eds.), *The cognitive neuroscience of development*. East Sussex, UK: Psychology Press.
- Richards, J. E. (2001). Cortical sources of event-related-potentials in the prosaccade and antisaccade task. Manuscript submitted for publication.
- Richards, J. E., & Casey, B. J. (1992). Development of sustained visual attention in the human infant. In B. A. Campbell, H. Hayne, & R. Richardson (Eds.), *Attention and information processing in infants and adults* (pp. 30–60). Mahwah, NJ: Erlbaum.
- Richards, J. E., & Hunter, S. K. (1997). Peripheral stimulus localization by infants with eye and head movements during visual attention. *Vision Research*, 37, 3021–3035.
- Richards, J. E., & Hunter, S. K. (1998). Attention and eye movement in young infants: Neural control and development. In J. E. Richards (Ed.), *Cognitive neuroscience of attention: A developmental perspective* (pp. 131–162). Mahwah, NJ: Erlbaum.
- Robbins, T. W., & Everitt, B. J. (1995). Arousal systems and attention. In M. S. Gazzaniga (Eds.), *Cognitive neurosciences* (pp. 703–720). Cambridge, MA: MIT Press.

- Salapatek, P. (1975). Pattern perception in early infancy. In L. Cohen and P. Salapatek (Eds.), *Infant Perception*. New York: Academic Press.
- Scherg, M. (1990). Fundamentals of dipole source potential analysis. In F. Grandon, M. Hoke, & G. L. Romani (Eds.), *Auditory evoked magnetic fields and potentials* (Vol. 6, pp. 40–69). Basel: Karger.
- Scherg, M. (1992). Functional imaging and localization of electromagnetic brain activity. *Brain Topography*, 5, 103–111.
- Scherg, M., & Picton, T. W. (1991). Separation and identification of event-related potential components by brain electrical source analysis. In C. H. M. Brunia, G. Mulder, & M. N. Verbaten (Eds.), *Event-related brain research* (pp. 24–37). Amsterdam: Elsevier.
- Schiller, P. H. (1985). A model for the generation of visually guided saccadic eye movements. In D. Rose & V. G. Dobson (Eds.), *Models of the visual cortex* (pp. 62–70). New York: Wiley.
- Schiller, P. H. (1998). The neural control of visually guided eye movements. In J. E. Richards (Ed.), *Cognitive neuroscience of attention: A developmental perspective* (pp. 3–50). Mahwah, NJ: Erlbaum.
- Spencer, K. M., Dien, J., & Donchin, E. (1999). A componential analysis of the ERP elicited by novel events using a dense electrode array. *Psychophysiology*, 36, 409–414.
- Swick, D., Kutas, M., & Neville, H. J. (1994). Localizing the neural generators of event-related brain potentials. In A. Kertesz (Ed.), *Localization and neuroimaging in neuropsychology. Foundations of neuropsychology* (pp. 73–121). San Diego: Academic Press.
- Taylor, M., & Baldeweg, T. (2002). Basic principles and applications of EEG, ERPs, and intracranial methods. *Developmental Science*, 5.
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, 87, 154–163.
- Tucker, D. M., Liotti, M., Potts, G. F., Russell, G. S., & Posner, M. I. (1994). Spatiotemporal analysis of brain electrical fields. *Human Brain Mapping*, 1, 134–152.