Attention in Young Infants: A Developmental Psychophysiological Perspective

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Short Title: Attention in Young Infants

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TO DO

Review the Levitt and Stanwood chapter for the arousal section.

Review Csibra chapter for the EEG analysis and source analysis sections.

Review the structural MRI and brain chapter for source analysis

Review Johnson chapter for visual model.

Review Dannemiller chapter for specific aspects of visual system development.

ABSTRACT

This chapter reviews the development of attention in young infants, emphasizing heart rate changes in psychophysiological experiments as a measure of an arousal brain system. The neural systems affecting attention that may be indexed by psychophysiological measures are briefly reviewed. Heart rate, electroencephalogram (EEG), event-related potentials (ERP), and other physiological measures are reviewed that have been used for the study of attention development in young infants. The developmental changes in infant attention are related to changes occurring in the neural systems underlying attention. Several studies are reviewed that show how heart rate may be used as a measure of a general arousal system in young infants.

INTRODUCTION

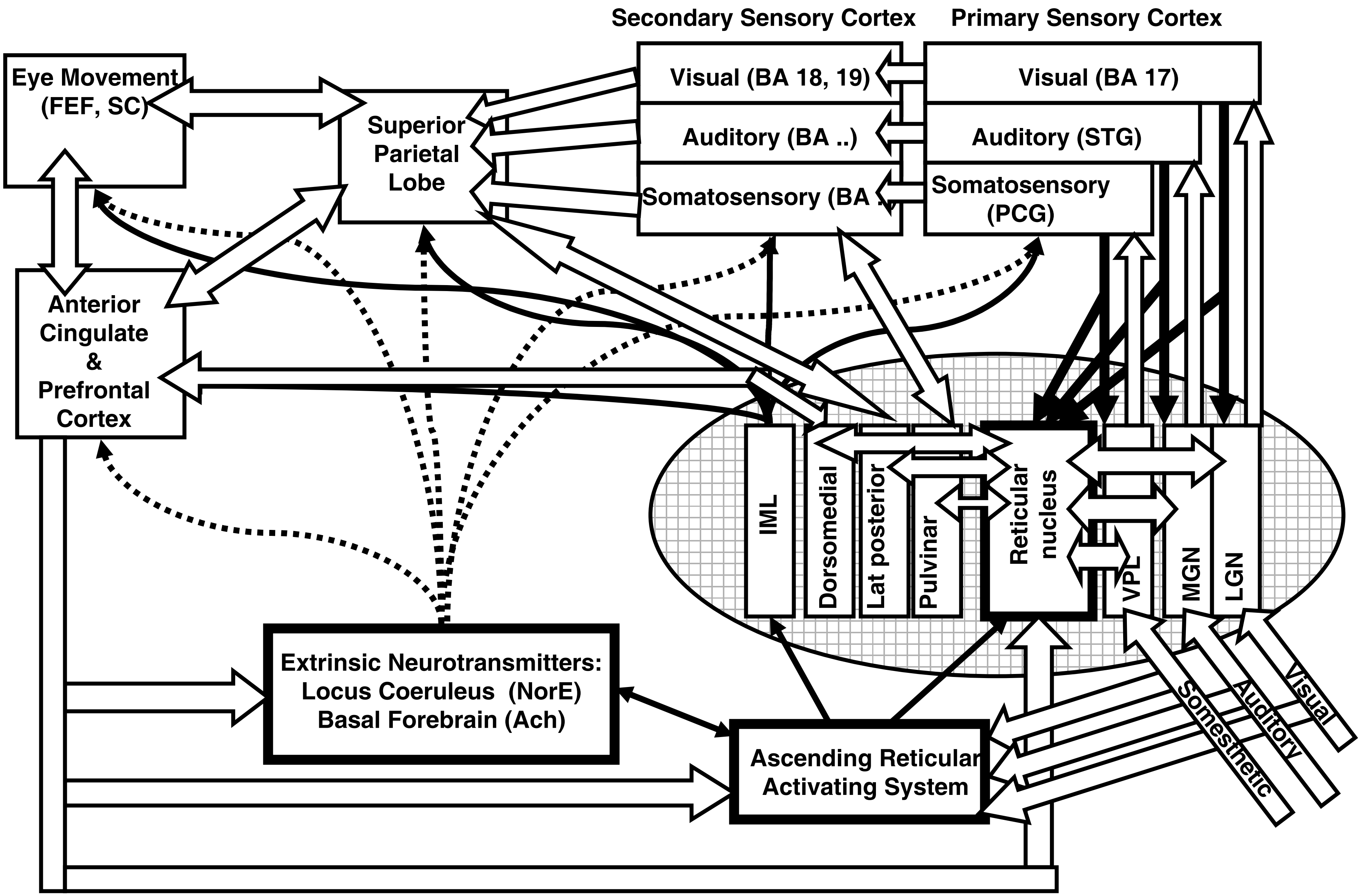
Attention, generally defined, shows dramatic development over the period of infancy. At birth infants attend primarily to salient physical characteristics of their environment or attend with nonspecific orienting (Berg & Richards, 1997). Between birth and two years the development of alert, vigilant sustained attention occurs. At the end of the first two years infants' executive attention system is beginning to function (Ruff & Rothbart, 1996; Rothbart & Posner, 2001). These dramatic changes in infants are commonly thought to be based predominantly on age-related changes in brain structures responsible for attention control.

The present chapter will attempt to accomplish three objectives. First, brain systems that may be involved in attention and which show development in infancy will be reviewed. These systems include a general arousal system that affects many cognitive functions as well as specific attention systems that are limited in their effect on cognition and attention. Second, psychophysiological measures that have been useful in the study of brain-attention relations in infants will be presented. The use of heart rate as a measure of the general arousal system will be emphasized. Finally, several studies will be examined that used these psychophysiological methods to study the development of infant attention. This review will emphasize the use of heart rate as an index of the development of sustained attention, which is a general arousal system affecting a wide number of behavioral and cognitive functions controlled by the brain. These experiments will be related to changes occurring in the neural systems underlying attention.

BRAIN SYSTEMS INVOLVED IN ATTENTION

Arousal attention system. One emphasis in the cognitive neuroscience of attention has been on the arousal associated with energized cognitive activity (Posner, 1995). The arousal emphasis has focused upon the increased behavioral performance that occurs when attention is engaged. This increased behavioral performance is associated with shortening of reaction times in detection tasks, increased focus of performance on specific tasks, and the sustaining of performance over extended periods of time. The arousal emphasis is non-specific, affecting multiple modalities, cognitive systems, and cognitive processes. This arousal emphasis characterizes attention’s energizing effect on cognitive and behavioral performance. Attention also may have a selective effect on specific cognitive processes or behavior without arousal properties (next subsection). In fact, selective attention may serve in some situations to inhibit behavior if such inhibition is appropriate for the goal of the task.

Specific locations or systems in the brain control the arousal aspect of attention. The brain systems underlying the arousal aspect of attention have been detailed in the theoretical and empirical research literature for a number of years. An example of this arousal emphasis is a model of neuroanatomical connections between the mesencephalic reticular activating system and the cortex (Heilman, Watson, Valenstein, & Goldberg, 1987; Mesulam, 1983). Figure 1 presents a diagram showing this system. This model presumes that information comes into the brain from visual, auditory, somesthetic, and other efferent pathways. These pathways have ascending connections through the thalamus to the cortex and descending connections to midbrain areas. The mesencephalic ascending reticular activating system influences parts of the thalamus that enhance sensory flow and at the same time stimulates extrinsic neurotransmitters. These effects directly or indirectly influence the limbic system, such as the basolateral nucleus of the amygdala and the subicular portion of the hippocampus, the cingulate cortex, prefrontal areas, and association areas (e.g., parietal area PG). This neuroanatomical system acts in synchrony to "energize" primary sensory areas in the cortex and increase the efficiency of

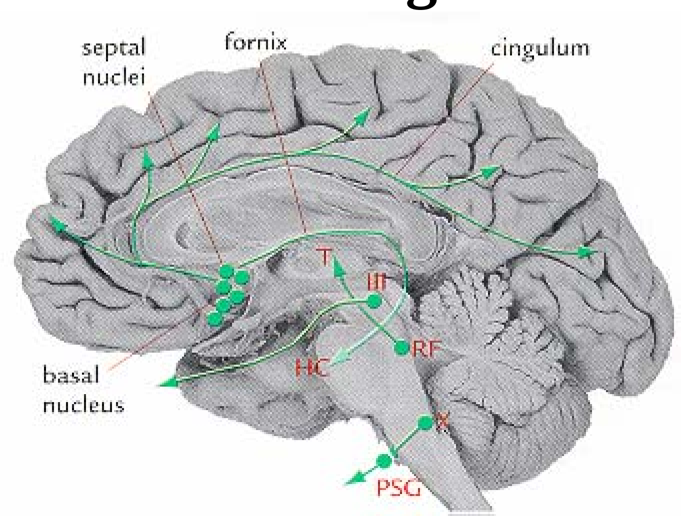


Secondary Sensory Cortex
Primary Sensory Cortex
Eye Movement (FEF, SC)
Superior Parietal Lobe
Visual (BA 18, 19)
Auditory (BA ..)
Somatosensory (BA ..
Visual (BA 17)
Auditory (STG)
Somatosensory (PCG)
Anterior Cingulate & Prefrontal Cortex
IML
Dorsomedial
Lat posterior
Pulvinar
Reticular nucleus
VPL
MGN
LGN
Extrinsic Neurotransmitters: Locus Coeruleus (NorE) Basal Forebrain (Ach)
Ascending Reticular Activating System
Somesthetic
Auditory
Visual

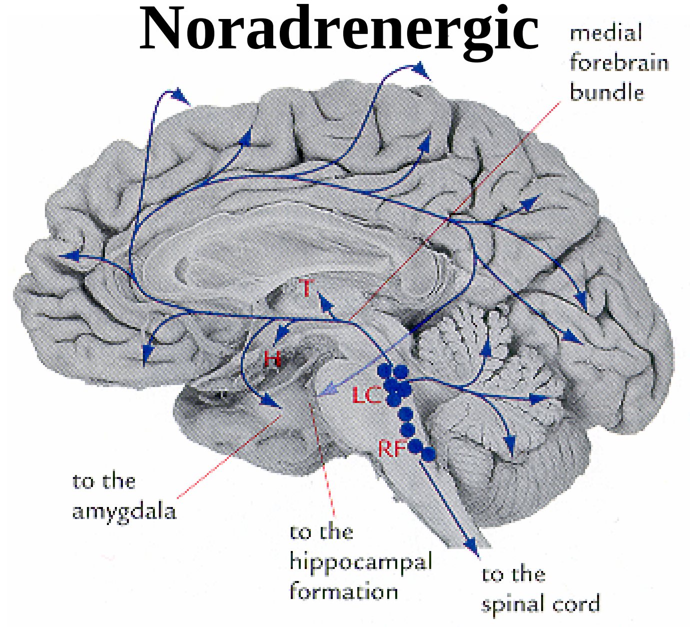
responding in those areas. This system also influences association areas and other attention systems, such as the posterior attention system described by Posner (Posner, 1995; Posner & Petersen, 1990). The non-specificity of this system is implied by its interconnections with multiple areas that influence cognitive processing. This arousal system "invigorates" or "energizes" cognitive processes leading to increased processing efficiency, shorter reaction times, better detection, and sustaining of cognitive performance for extended periods of time.

According to the model presented in Figure 1, the arousal aspect of attention works through two mechanisms. The first mechanism involves the thalamus. The thalamus is the major sensory connection area between efferent activity and the cortex. The reticular nucleus and internal medullary lamina (Figure 1, IML) play a role in this effect. The reticular nucleus is enhanced both by the ascending reticular activity and by feedback mechanisms from primary sensory cortex. In turn its increased activity positively affects the activation of several lamina of the thalamus and thus enhances incoming sensory information. The IML acts as a connection area between midbrain reticular activity and other cortical areas. The second mechanism through which the arousal aspect of attention works is extrinsic neurochemical systems. Robbins and Everitt (1995; Levitt & Stanwood, this volume) distinguish four neurochemical systems that form the basis for the arousal functions of attention: noradrenergic, cholinergic, dopaminergic, and serotoninergic. Figure 2 shows the projections from midbrain nuclei for these four brain systems. The nuclei that give rise to these four neurochemical systems are located in brain regions adjacent to the mesencephalic reticular activating system. Robbins and Everitt (1995) review the evidence linking these neurochemical projection systems to attention and arousal. The noradrenergic and cholinergic systems are thought to be the neurochemical systems that are most closely involved in cortical arousal as it is related to attention. The dopaminergic system affects

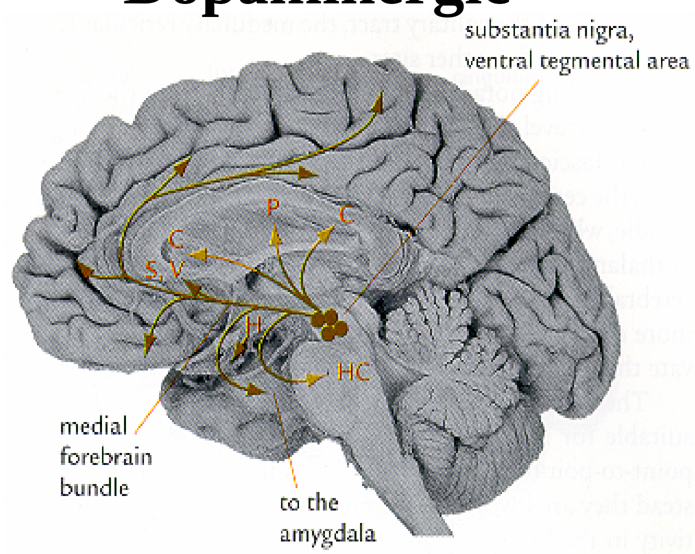
Cholinergic



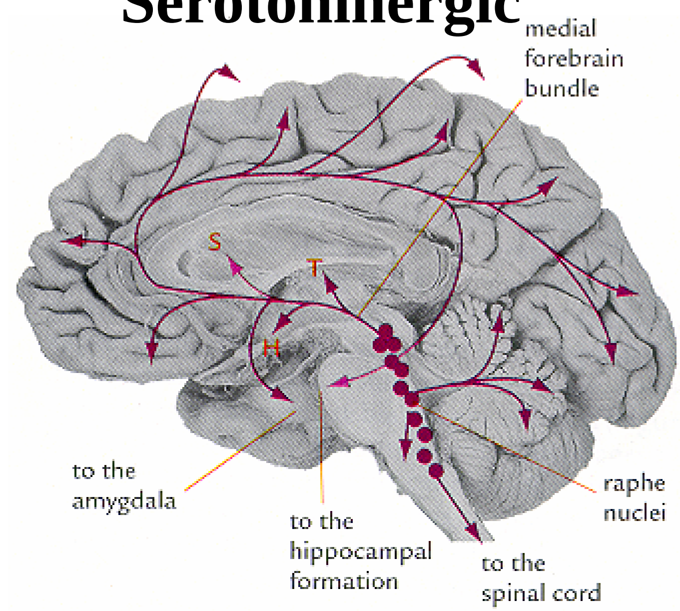
Noradrenergic



Dopaminergic



Serotoninergic



the motivational and energetic aspects of cognitive processing and the serotonin system affects the overall control of state. These four neurochemical systems are closely linked so that more than one is likely to be operating during an aroused state. These four neurochemical systems also show changes over infancy that imply that the arousal controlled by these systems develops in that time period (Levitt & Stanwood, this volume).

Specific attention systems. The second manner in which the brain affects the development of attention in infants are brain systems specific to selected functions. These brain areas show enhanced functioning under attention but affect only a single (or few) cognitive functions. Therefore, these systems have only a narrow impact on attention-based cognitive functioning.

Two of these are worth mentioning in this respect. First, the enhancement of visual receptive fields during attention to visual stimuli has been widely studied in invasive preparations (Desimone, & Duncan, 1995; Maunsell & Ferrera, 1995). This type of attention is selective for particular objects, particular spatial locations, or particular tasks. For example, the responses of visual receptive fields are enhanced in tasks requiring focused allocation of attention to that specific visual field or to objects occurring in that visual field. Objects occurring outside of that receptive field have unaffected responses when the field is irrelevant to the task, or may have attenuated responses if the object occurring in that location interferes with task performance in the specific visual field. For neurons (or neural areas) that respond in this manner, this type of attentional modulation is specific to a limited number of cognitive aspects (e.g., a specific stimulus, or modality, or task) and typically occurs in a very restricted portion of the brain (e.g., individual neurons or restricted brain areas). (Is this covered in the Dannemiller chapter?).

Second, a specific attention system of interest to the development of attention is the "posterior attention system" described by Posner (Posner, 1995; Posner & Petersen, 1990; Posner & Rothbart, 2000) involves the parietal cortex, pulvinar, superior colliculus, and perhaps, the frontal eye fields. This attentional network has a specific purpose, that of moving attention (visual attention?) around in space and localizing receptors (eyes?) to targets at specific locations. This attention system is not sensitive to specific targets, is unrelated to attention in stimulus modalities or cognitive functions that do not involve spatial localization, and does not enhance or attenuate other cognitive systems when it operates. The individual brain components of the posterior attention system show changed in infancy that affect the infant's eye movements during attention or inattention. This system also is involved in "covert orienting", or "covert attention", which shows changes in young infants.

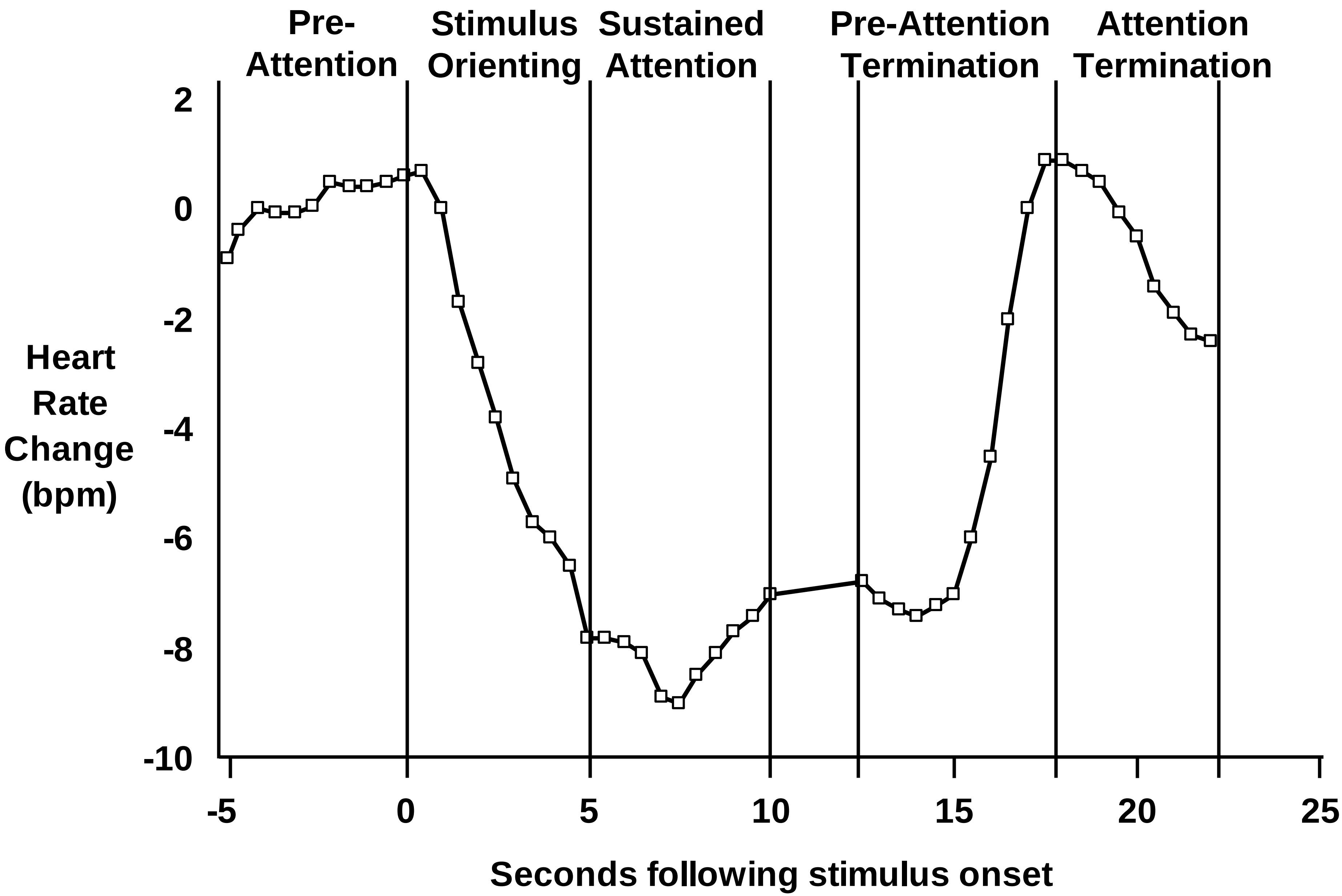
These specific brains systems show development in the period of infancy and are related to behavioral indices of infant attention that show development in the same time period. Such considerations may be found in the chapters by Johnson in this volume, by Dannemiller, and in other sources (e.g., see eye movement-attention model of Johnson, in Johnson, 1990, 1995a, this volume; Johnson, Gilmore, & Csibra, 1998; Johnson, Posner, & Rothbart, 1991). These specific attention systems will be covered insofar as they are affected by the arousal form of attention. (Does the Levitt & Stanwood chapter have relevant information?).

PSYCHOPHYSIOLOGICAL MEASURES OF INFANT ATTENTION

Psychophysiological measures are useful in the study of infant attention and infant brain development. Psychophysiology studies psychological processes using physiological measures and is focused on the psychological processes themselves as well as their relation to the processes affecting the physiological measures (Andreassi, 1989). The physiological measures used in psychophysiology are noninvasive and so may be used with human participants such as infants. Additionally, most of these physiological measures are also practical in psychological experiments. Recording equipment and sensors are non-intrusive and the sensors do not disrupt the infant’s normal behavior patterns. The use of heart rate and EEG/ERP as psychophysiological measures of attention will be reviewed briefly as exemplars of this approach.

Heart rate. The most common measure used by psychophysiologists studying young infants is heart rate (Reynolds & Richards, in press). The electrocardiogram (ECG) is measured with surface electrodes placed on the infant's chest, back, arms, or legs. Heart rate is derived from the ECG by measuring the interval between two "R-waves" of the ECG and is defined as the "inter-beat interval" (IBI; "R-R Interval"), or as the inverse of the IBI, heart rate (beats-per-minute, "BPM"). The infant's heart rate may be measured in response to psychological manipulations as a measure of attention .The infant's heart rate also may form the basis for determining if the infant is attending to a stimulus and psychological manipulations are then made on the basis of the heart rate change (e.g., Richards, 1987). Heart rate may be used to distinguish general and specific forms of attention.

The author in several places (Berg & Richards, 1997; Reynolds & Richards, in press; Richards, 1995, 2001, 2004a; Richards & Casey, 1992; Richards & Hunter, 1998) has presented a model where infants’ heart rate changes during stimulus presentation are used to distinguish four attention phases. These phases are the automatic interrupt, the orienting response, sustained attention, and attention termination. Heart rate and attention level vary during these phases. Figure 3 schematically depicts the heart rate changes occurring during these phases of attention. This figure represents heart rate changes of infants from 3 to 6 months of age presented with a



Pre-Attention
Stimulus Orienting
Sustained Attention
Pre-Attention Termination
Attention Termination
Heart Rate Change (bpm)
2
0
-2
-4
-6
-8
-10
-5
0
5
10
15
20
25
Seconds following stimulus onset

visual stimulus (Richards & Casey, 1991). The figure also has labeled a "pre-attention" and "pre-attention termination" phase. These periods are simply the period of time before the presentation of the stimulus (pre-attention) and before heart rate returns to its prestimulus level but after sustained attention has occurred (pre-attention termination).

Sustained attention and attention termination affect a wide range of cognitive functions in infants. The heart rate slows down and remains below prestimulus levels during sustained attention. Cognitively, this phase of attention involves subject-controlled processing of stimulus information. Sustained attention is accompanied behaviorally by maintaining fixation on a focal stimulus in the presence of a peripheral distracting stimulus (Hicks & Richards, 1998; Hunter & Richards, 1997; Lansink & Richards, 1997; Richards, 1987, 1997a), acquiring stimulus information (Richards, 1997b) and exhibiting recognition memory (Reynolds & Richards, 2005; Richards, 2003a; Richards & Casey, 1990), and enhancement of responses in a selected stimulus modality and inhibition of responses in a non-selected stimulus modality (Richards, 1998, 2000a). Alternatively, at the end of sustained attention the heart rate returns to its prestimulus level and the phase of attention termination occurs. Attention termination is accompanied by inattentiveness toward the stimulus in the presence of continued fixation on the stimulus, i.e., heightened levels of distractibility, lack of acquisition of stimulus information, and lack of selective modality effects.

The phases of sustained attention and attention termination are markers of the nonspecific arousal system of the brain (Reynolds & Richards, in press; Richards & Casey, 1992; Richards & Hunter, 1998; Richards, 2001, 2004a). The neural control of this heart rate change originates from cardioinhibitory centers in the orbitofrontal cortex via the “vagus nerve” (10^{th} cranial nerve). This area has reciprocal connections with the limbic system and through these connections is involved in modulating activity within the mesencephalic reticular formation arousal system (Heilman et al., 1987; Mesulam, 1983) and probably the dopaminergic and cholinergic neurotransmitter systems (Robbins & Everitt, 1995; Levitt & Stanwood, this volume). The cardioinhibitory centers act through the parasympathetic nervous system to slow heart rate when the arousal system is engaged. The heart rate changes occurring during sustained attention (sustained heart rate slowing) index the onset and continuing presence of this arousal. The heart rate changes during attention termination (return of heart rate to its prestimulus level) index the lack of activation of this arousal system. These two phases of attention therefore reflect the nonspecific arousal that may affect a number of sensory and brain systems. Incidentally, these phases and the "automatic interrupt" and "stimulus orienting" attention phases also may be used to measure specific attentional systems in the young infant (e.g., Berg & Richards, 1997; Balaban, 1996; Richards, 1998, 2000a).

Other psychophysiological measures. There are other psychophysiological measures that have been used in the study of infant attention and its development. Two in particular are worth mentioning: the electroencephalogram (EEG) and scalp-recorded event-related-potentials (ERP). These are reviewed extensively in another chapter in this volume (Csibra, this volume) and will not be reviewed in detail here. Spontaneous electrical activity of very small magnitude may be recorded from the human scalp. However, EEG activity has been used in adults and infants as a measure of nonspecific arousal (e.g., Ray, 1990; Bell, 1998). This measure is interesting because it is a more direct measure of neural activity than is heart rate and possibly could be used as a noninvasive measure of neural activity level enhanced by arousal. This chapter will not review the developmental changes occurring in EEG, but the reader should refer to other sources (e.g., Bell, 1998, 1999; Bell & Fox, 1992, 1994; Bell & Wolfe, in press; Berg & Berg, 1987).

Scalp-recorded event-related-potentials (ERP) are derived from the EEG recording. The ERP is thought to reflect specific cognitive processes and therefore may provide a noninvasive and direct measure of functioning within specific brain areas (e.g., see Hillyard et al., 1995). For example, specific components of the ERP change in response to familiar and unfamiliar visual stimuli (Nelson & Collins, 1991, 1992). These authors (Nelson and Collins, 1991, 1992) demonstrated changes in the amplitudes and latencies of specific ERP components in response to visually-presented novel stimuli. Likewise, the ERP also may be used to index specific attentional responses. One such measure is the Nc component (Nc is “Negative” “central”; Courchesne, 1977, 1978) that is thought to represent a relatively automatic alerting response to the presence of a visual stimulus, especially a novel stimulus (cf., heart-rate-defined “stimulus orienting”, Richards & Casey, 1992; Reynolds & Richards, 2005; Richards, 2003a). The ERP has been used in the study of covert orienting (e.g., Richards, 2000b, 2000c, 2004b, 2005) and thus might be used in the study of some specific aspects of attention. The ERP has been used extensively in infant participants and many reviews of this measure are available (e.g., Berg & Berg, 1987; de Haan, in press; Nelson, 1994; Nelson & Dukette, 1998, Csibra, Johnson, and others in this book).

Psychophysiological measures as "Marker Tasks". Some comments should be made on the nature of the psychophysiological measures as direct or indirect measures of brain activity. Many psychophysiological measures are indirect measures of brain activity. Heart rate as an index of a general arousal system in the brain should be considered an indirect measure. The connections between the mesencephalic reticular activating system, its associated attention-arousal system (Heilman et al., 1987; Mesulam, 1983), and heart rate control are well known. Also, the connection between the neurochemical arousal systems (Robins & Everett, 1995; Levitt

& Starwood, this volume) and cardiac control are known. But, the measurement of such brain systems only is indirect when using heart rate as a psychophysiological measure of infant attention.

The indirect measure of brain activity with heart rate is similar to the “marker task” concept detailed by Johnson (1997; see Richards & Hunter, 2002). Marker tasks are behavioral tasks that have been studied in animal or invasive preparations and are controlled by specific brain areas or systems. Johnson (1996) proposes that such tasks may be used in infants and children with the understanding that developmental changes in these tasks should reflect developmental changes in the brain areas that control their functioning. In the case of behavioral marker tasks or psychophysiological measures, a solid theoretical or empirical basis for relating the measure to a brain system or controlling brain functions is necessary. The study of attention further requires that these brain systems be related to common attention functions (arousal, selection). Finally, heart rate or behavioral tasks should be used in experimental situations in which relevant psychological processes affect the physiological system (or behavioral marker task). The marker tasks allow inferences to be made about brain development and help to inform a developmental cognitive neuroscience approach to attention.

Some psychophysiological indices reflect brain activity more directly (Richards & Hunter, 2002). The EEG and ERP in some contexts are direct measures of brain function. Both are generated by neural activity occurring in cell bodies or extracellular space. They are closely related in time to this neural activity and are generated in specific areas of the brain related to cognitive activity. The identification of the brain area generating the electrical activity cannot be done with the scalp-recorded electrical activity alone. But, cortical ERP measures using high-density EEG recording (Johnson, de Haan, Oliver, Smith, Hatzakis, Tucker, & Csibra, 2001;

Tucker, 1993; Tucker, Liotti, Potts, Russell, & Posner, 1994) may be used to hypothesize cortical sources of the electrical activity and thus identify specific brain regions involved in cognitive tasks (Michel, Murray, Lantz, Gonzalez, Spinelli, Grave de Peralta, 2004; Nunez, 1990; Scherg, 1990; Scherg & Picton, 1991; recent cortical source chapter). Functioning of the cortical areas may be inferred from these cortical source localization procedures in a direct fashion. The use of the ERP and cortical source localization procedures as a direct measure in the study of attention is beginning with infant participants (Johnson, Griffin, Csibra, Halit, Farroni, de Haan, Baron-Cohen, & Richards, 2005; Reynolds & Richards, 2005; Richards, 2005, 2006). Such use of the EEG and ERP should lead to a higher quality of information about the relation between the brain and attention in infant psychological development.

The rest of the chapter will review studies that show the developmental changes that occur in the arousal form of attention. The first section will review some studies that show the effect of the developing arousal system on eye movements that themselves show development over the first six months of infancy (Hunter & Richards, 2003, submitted; Holley & Richards, 1999). The next section of the reviews will present some studies that show developmental changes in sustained attention that are related to a “higher cognitive function”, infants' recognition of briefly presented visual stimuli (Frick & Richards, 2001; Reynolds & Richards, 2005; Richards, 1997b, 2003; Richards & Casey, 1990). These studies will show that familiarization of patterns presented for only a few seconds during sustained attention will result in recognition memory (Frick & Richards, 2001; Richards, 1997b). This section also will present some new data that show that during attentive states will recognize stimuli very quickly and will show appropriate EEG and ERP changes associated with recognition memory. These studies identify with cortical source analysis the brain origins of this activity (Reynolds & Richards, 2005; Richards, 2003a). These studies should be considered examples of how developmental psychophysiology may contribute to developmental cognitive neuroscience of attention.

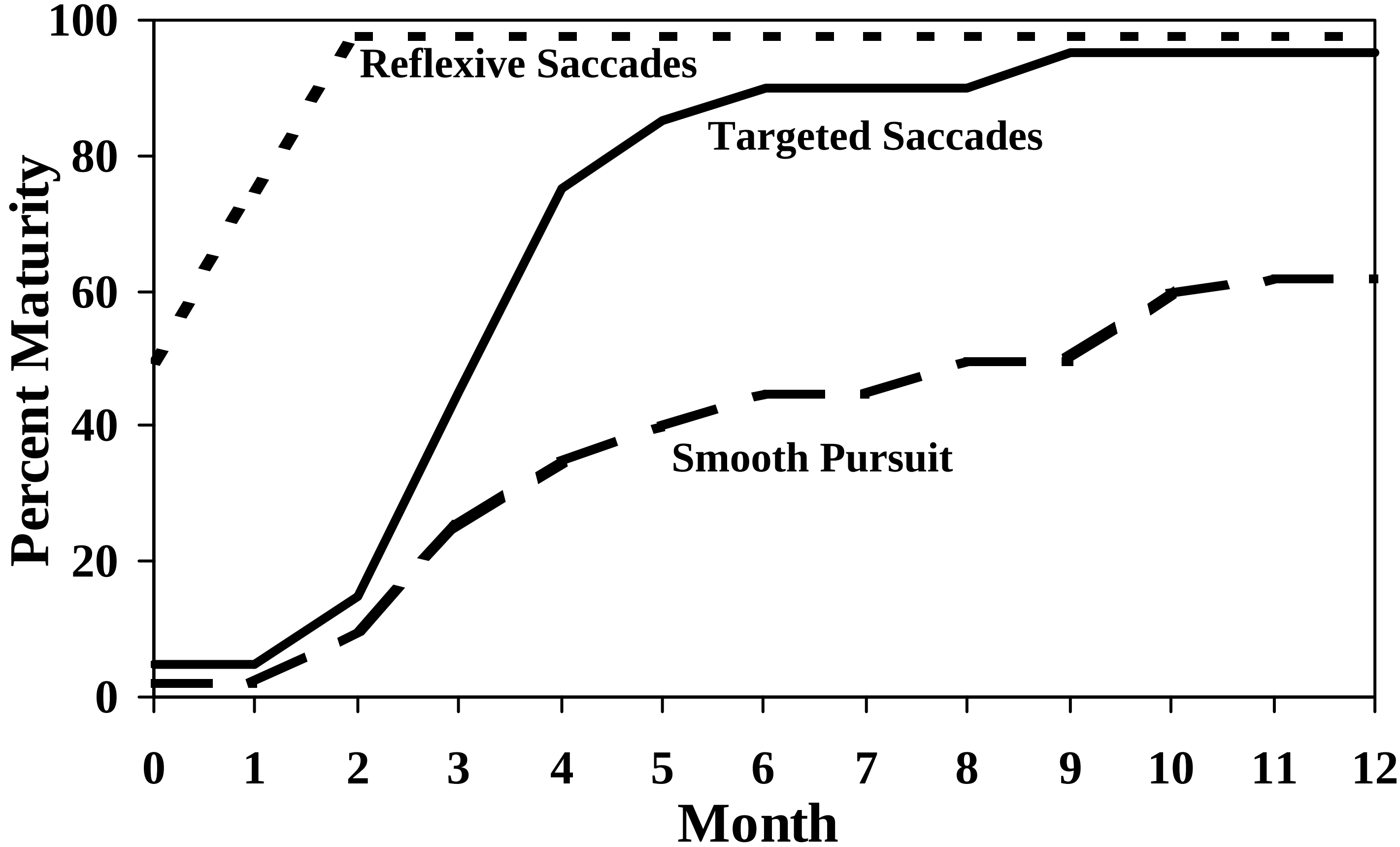
EYE MOVEMENTS AND ATTENTION

This section will review the relation between the development of the arousal attention system in young infants and three eye movement control systems that show development in the same period of time. There are three types of eye movements that may be made when tracking visual stimuli. Each eye movement type is controlled by separate areas of the brain. "Reflexive saccadic" eye movements occur in response to the sudden onset of a peripheral stimulus. These eye movements are controlled by a brain pathway involving the retina, lateral geniculate nucleus, superior colliculus, and perhaps, the primary visual area (Schiller, 1985, 1998). "Voluntary saccadic" eye movements occur under voluntary or planned control. These eye movements often involve attention-directed targeted eye movements. The voluntary saccadic eye movements are controlled by a brain pathway involving several parts of the cortex, visual areas 1, 2 and 4, the parietal cortex area PG, and the frontal eye fields (Schiller, 1985, 1998). The third type of eye movements used in tracking visual stimuli are "smooth pursuit" eye movements. These eye movements occur only in the presence of smoothly moving visual stimuli, and smoothly track visual stimuli over a wide range of visual space. Smooth pursuit eye movements also are controlled by brain pathways involving the cortex, including area MT (medial temporal), areas MST (middle superior temporal), and perhaps the parietal cortex (Schiller, 1985, 1998). The voluntary saccadic and smooth pursuit eye movements are affected by attention whereas reflexive saccadic eye movements are relatively independent of attention control.

The brain areas involved in the control of these three eye movement systems undergo developmental changes in the first six months (included in Dannemiller, this volume?). There have been several models of the brain changes affecting eye movement development, including models by Bronson (1974, 1997), Maurer and Lewis (1979, 1991, 1998), Johnson and colleagues (Johnson, 1990, 1995a, this volume; Johnson et al., 1991, 1998), Hood (Hood, 1995; Hood, Atkinson, & Braddick, 1998), and Richards (Richards & Casey, 1992; Richards & Hunter, 1998). A model of Johnson (1990, 1995a, this volume; Johnson et al., 1991, 1998) describes the developmental changes in these three eye movement systems. This model hypothesizes that layers of the primary visual area develop at different rates and become mature at different ages. The primary visual area layers containing brain pathways that control reflexive eye movement are relatively mature at birth and therefore reflexive saccadic eye movements dominate the infant's behavior in the first 2 postnatal months. The primary visual area layers that contain brain pathways that control voluntary saccadic eye movements develop rapidly from the first to the sixth postnatal months. In conjunction with this development, attention-directed voluntary saccades show developmental changes over the first six months. Finally the primary visual area layers that contain brain pathways that control smooth pursuit eye movements develop more slowly than the other layers. Several parts of the brain pathways that control smooth pursuit eye movements show protracted developmental changes over the first two years (Richards & Hunter, 1998). Thus, smooth pursuit eye movements are the latest to begin development and show changes over a longer period than just the first six months of infancy. Figure 4 (from Richards & Hunter, 1998) shows a hypothetical developmental trend for these three eye movement systems.

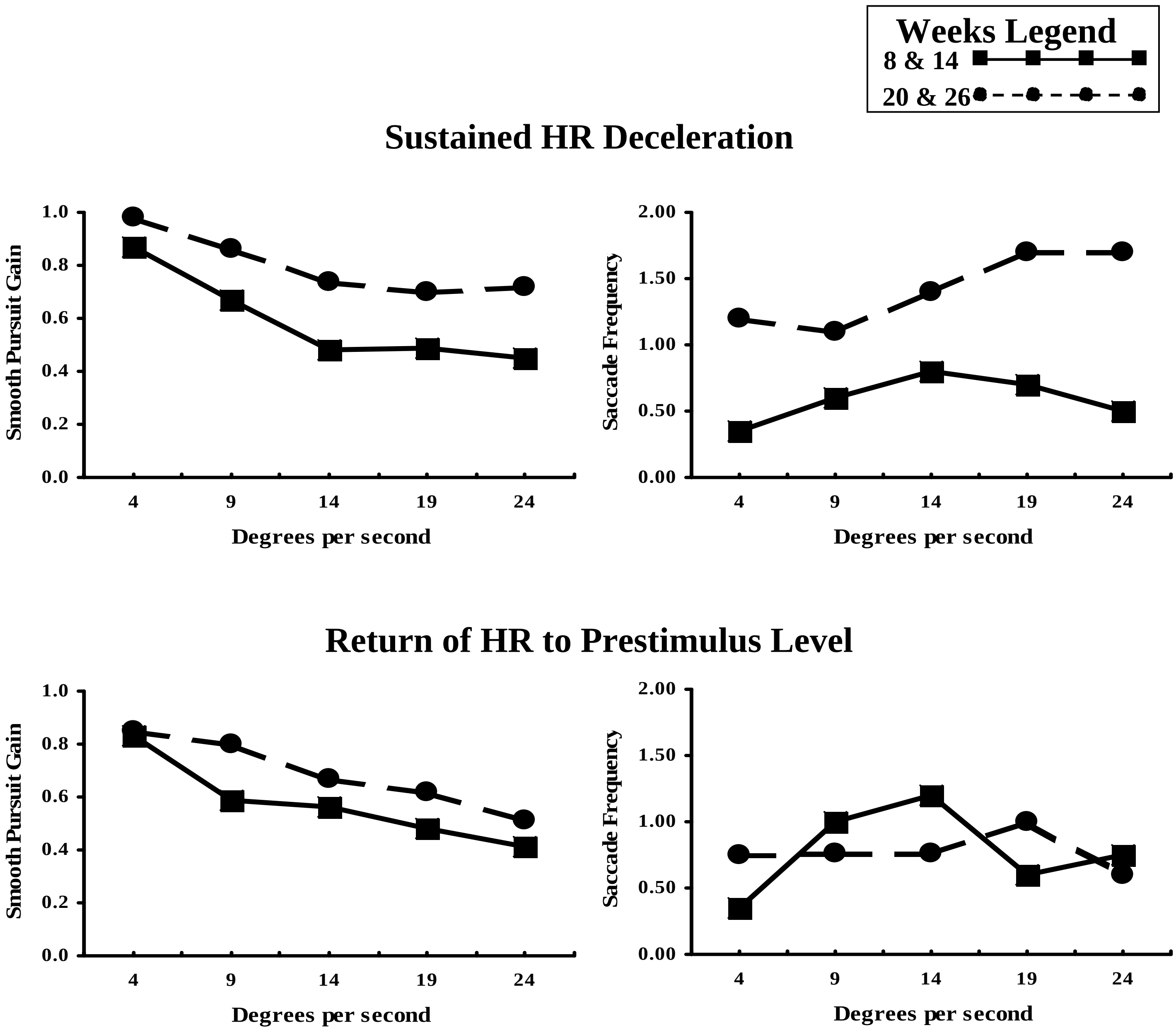
One study (Richards & Holley, 1999) examined the effect of attention on all three eye movement types. In this study infants tracking behavior over this age range under conditions of attention and inattention. This study shows how the development of the general arousal system affects the exhibition of eye movements in the first six months of infancy. Infants at 8, 14, 20,

Hypothesized Development of Three Eye Movement Systems



and 26 weeks of age were presented with stimuli that moved at varying speeds (8 to 24 deg per s) on a television monitor. The infants' heart rate was recorded and periods of visual tracking were separated into attentive and inattentive states using the heart-rate-defined attention phases described earlier. The infants' eye movements were recorded with the "electrooculogram" (EOG) by recording electrical potential changes due to shifts in the eyes. The eye movements were separated into smooth pursuit and saccadic eye movements and related to the attentiveness of the infant.

There were two important findings from that study. First, there was an increast in tracking ability over this age. This increase in tracking occurred in both the infants use of smooth pursuit eye movements and in saccades. Figure 5 shows smooth pursuit and saccadic eye movement results under conditions of attention and inattention. The lower right part of Figure 5 shows the saccade frequency occuring during the inattentive periods. These would be most similar to the reflexive saccadic eye movements. The younger and older infants show approximately equal numbers of these eye movements. The upper panels of Figure 5 show saccade frequency and smooth pursuit gain during sustained attention, corresponding to voluntary saccadic and smooth pursuit eye movements. Both showed improvement from the youngest to the oldest ages. These findings show the expected age changes for these three eye movement systems as might be predicted from Figure 4. The second important finding is related to the speed of the stimulus. The tracking stimulus was presented at speeds ranging from "very slow" to "very fast" for the capabilities of infants' smooth pursuit (Richards & Holley, 1999). The reflexive saccadic eye movements were unresponsive to the stimulus speed (Figure 5, lower right panel), whereas smooth pursuit tracking and saccadic tracking during attention were responsive to stimulus speed (Figure 5, upper panels). When the stimulus became to fast for


Weeks Legend
8 & 14
20 & 26
Sustained HR Deceleration
Smooth Pursuit Gain
1.0
0.8
0.6
0.4
0.2
0.0
4
9
14
19
24
Degrees per second
Saccade Frequency
2.00
1.50
1.00
0.50
0.00
4
9
14
19
24
Degrees per second
Return of HR to Prestimulus Level
Smooth Pursuit Gain
1.0
0.8
0.6
0.4
0.2
0.0
4
9
14
19
24
Degrees per second
Saccade Frequency
2.00
1.50
1.00
0.50
0.00
4
9
14
19
24
Degrees per second

smooth pursuit eye movements to follow, the infants shifted from smooth pursuit tracking to saccadic tracking (Figure 5, cf. left and right panels). Thus the oldest infants during aroused attentive states used the smooth pursuit and voluntary saccadic eye movements to track the visual stimulus and adjusted the parameters of the eye movements according to the speed of the tracking stimulus.

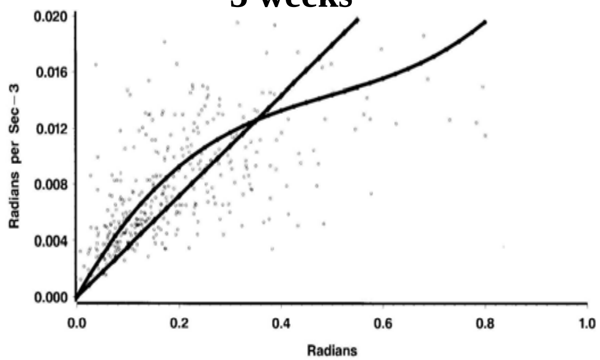
The results from this study suggest at least two roles that sustained attention may play in behavior. First, the arousal system of the brain acts to energize specific brain systems involved in cognitive activities. In this study the general level of increased performance during sustained attention reflects this arousal. The simultaneous development of the eye movement systems (smooth pursuit, voluntary saccadic) and arousal system (sustained attention) resulted in a synchrony between attention and eye movement control. Second, sustained attention does more than just energize involved systems. Tracking behavior during sustained attention was preserved over increases in tracking speeds by shifting from smooth pursuit tracking to saccadic tracking when smooth tracking failed. The attention-arousal system also acts to select the appropriate behavior given the feedback being received from the stimulus display and whatever goals the infant has in the situation.

A second way in which the relation between eye movements and attention has been examined has been by examining the physiological characteristics of saccades. One characteristic of eye movements is that the maximum velocity of the saccade and the total saccade amplitude are related, i.e., the “main sequence” in eye movements (Bahill, Clark, & Stark, 1975). The main sequence is the direct result of the firing rate and firing duration of the brainstem motor neurons that control ocular muscles (Moschovakis & Highstein, 1994). This area of the brain is hypothesized to be relatively well-developed at birth and therefore should not show many changes. According to the neurodevelopmental models cited above, one might expect that since these structures are well-developed that the main sequence should be relatively fixed at very early ages for infants.

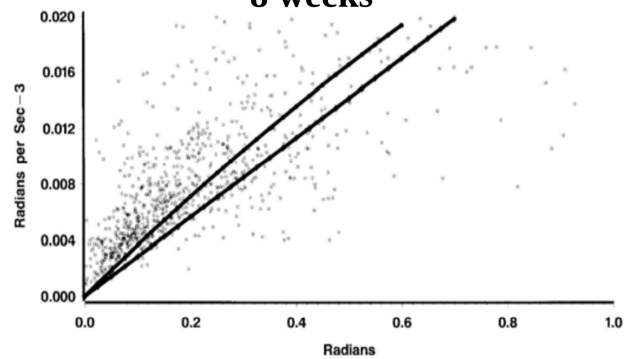
In several studies the main sequence development has been studied (Hunter & Richards, 2003, submitted; Richards & Hunter, 1997). Richards and Hunter (1997) recorded eye movements using the electrooculogram (EOG). Infants at 14-, 20-, and 26 weeks of age were presented with visual stimuli in the periphery to which a saccade was made. The main sequence was easily seen in the EOG recording and did not differ across these ages. So, in accord with the neurodevelopmental model, this system seemed to be functioning at similar levels in infants. However, more recently we examined the eye movements of younger infants during “free viewing” of interesting audiovideo stimuli (Hunter & Richards, submitted). In this study in the youngest infants we found a decrease in the linear relation between maximum saccade velocity and saccade amplitude, the main sequence, from 5 to 14 weeks of age, but no difference from 14 to 26 weeks of age. Figure 6 shows plots of the velocity / amplitude relation for infants from 5 to 26 weeks of age. The 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.

The effect of attention on the main sequence relation also has been studied (Hunter & Richards, submitted; Richards & Hunter, 1997). The times at which the infant made an eye movement to the peripheral stimulus (Richards & Hunter, 1997) or during the free viewing of an interesting audiovisual stimulus (Hunter & Richards, submitted) were separated into those trials where sustained attention was occurring, or the infant was inattentive (i.e., attention termination).

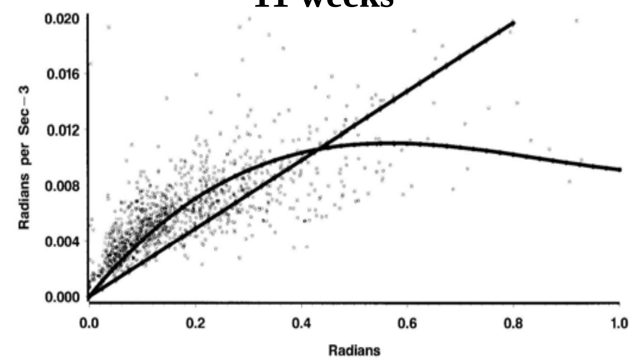
5 weeks



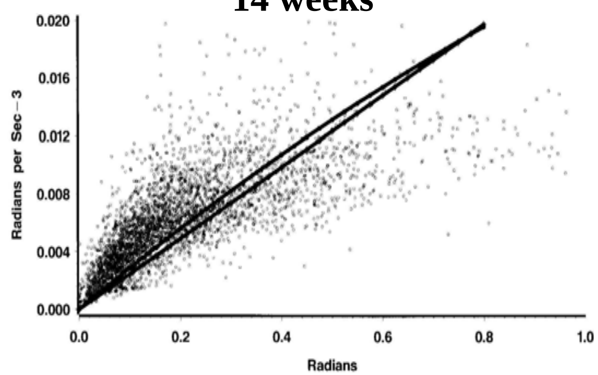
8 weeks



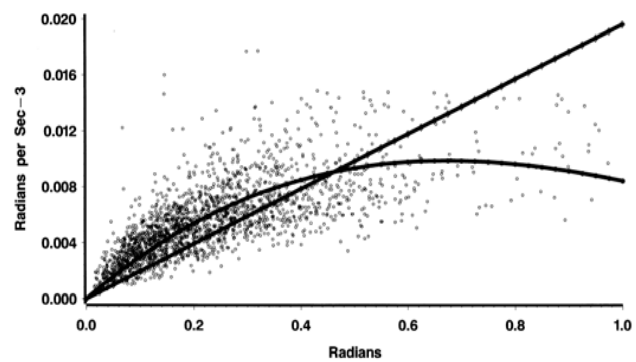
11 weeks



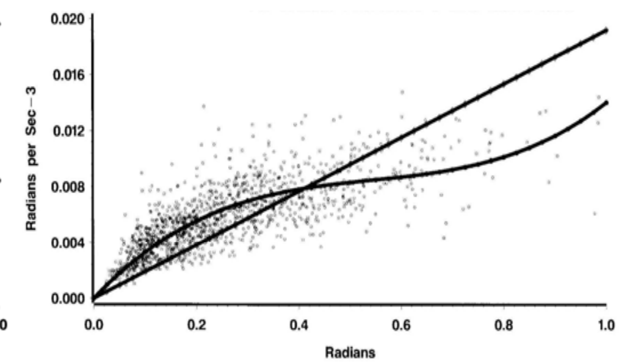
14 weeks



20 weeks



26 weeks



When attention was engaged, either to a specific stimulus or generally to the visual display, the older infants in these studies had a slower peak velocity per saccade amplitude than the young infants. These age changes also have been studied in infants and older children (Hunter, 2001). There seemed to be an increase in the amount of depression of the main sequence relation from 26 weeks to 1 year and from 1 year to about 7 years of age. However, after 2 years of age the difference between the main sequence between attention and inattention were not as great.

The results from these studies of eye movement and attention are revealing about the development of the arousal system and how it affects behavior that is controlled by other brain systems. There may be age changes in the underlying brain areas that are modulated by attention. The saccade system showed development in these studies both in the duration of tracking (Richards & Holley, 1999) and in the main sequence relation (Hunter & Richards, submitted). The effect of attention on the main sequence may be due to an increasing top-down influence of the frontal eye fields (and other cortical systems) on the brain stem eye movement areas after the age of about 4 months. In another case, it appeared to act directly to energize the infant's behavior in the support of a goal such as tracking a smoothly moving object.

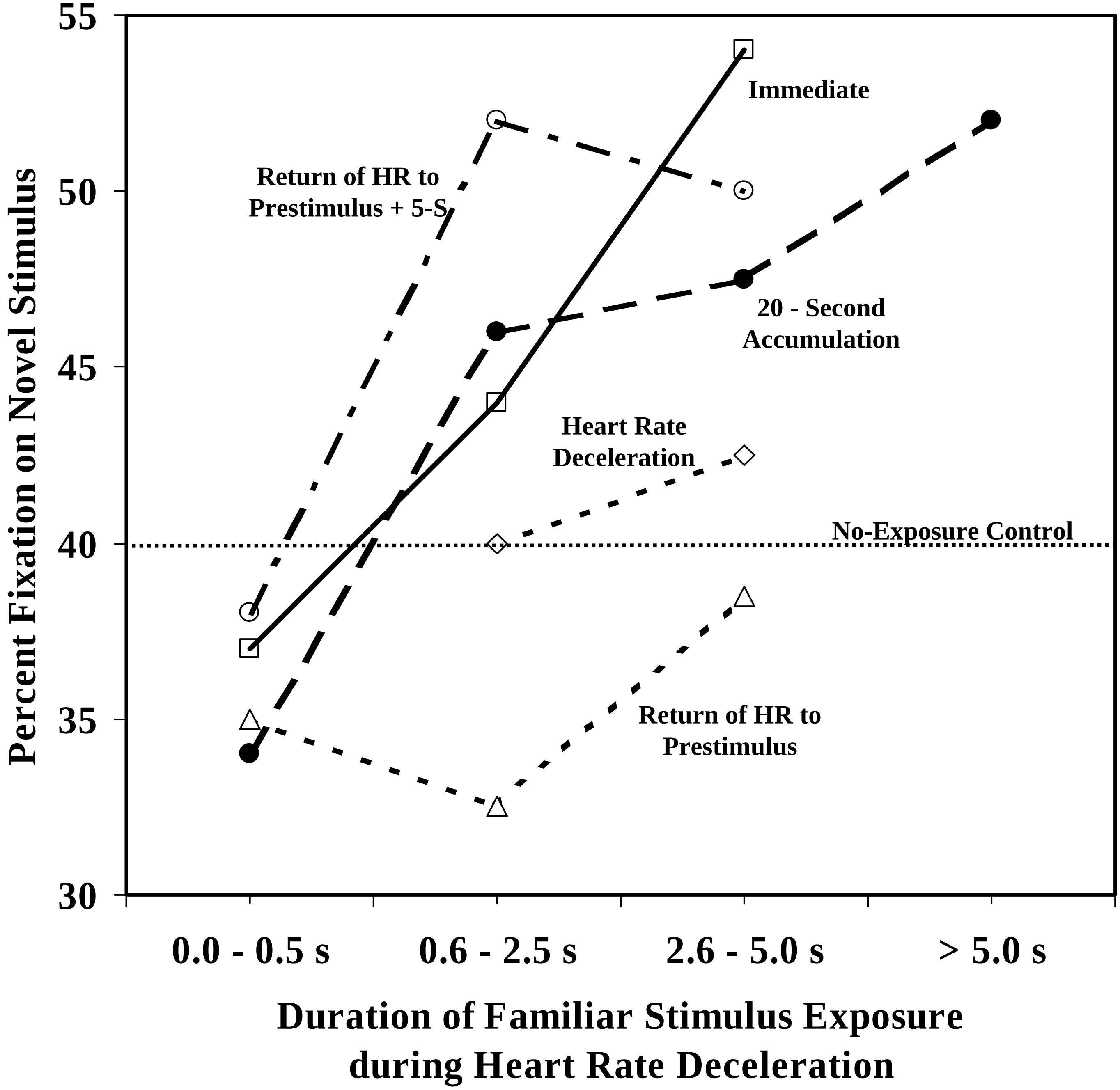
RECOGNITION OF BRIEFLY PRESENTED VISUAL STIMULI

This section will review studies showing the effect of sustained attention on infant recognition memory. Infant recognition memory often is studied with the paired-comparison procedure (Fagan, 1974). In this procedure infants are familiarized with a single stimulus ("familiar" stimulus) during a familiarization phase. Then, during the recognition memory test phase the familiar stimulus is paired with a stimulus not previous seen ("novel" stimulus). Recognition memory for the familiar stimulus is inferred if the infants show a novelty preference, i.e., look longer at the novel stimulus than the familiar stimulus during the paired-comparison test phase.

Two studies using heart-rate defined attention phases have shown that exposure to the familiar stimulus during sustained attention results in recognition memory for stimuli presented for only 5 or 6 seconds (Frick & Richards, 2001; Richards, 1997b). In these studies infants at 14, 20, or 26 weeks of age were presented with a “Sesame Street” movie, “Follow that Bird” on a television monitor. This movie is very interesting to young infants and reliably elicits the full range of heart rate changes that are related to the attention phases. On separate trials, at a delay defined by the deceleration of heart rate, a delay defined by the return of heart rate to its prestimulus level, or time-defined delays, a familiarization stimulus was presented for 5 or 6 s. One condition with the “Sesame Street” movie alone was provided (no familiarization stimulus, i.e., no-exposure control) and one condition with 20-s of exposure to the familiar stimulus was presented. Following each familiar stimulus presentation, a paired-comparison recogniton memory test was done. The infants’ duration of fixation on the novel and the familiar stimulus during the first 10 s of the test phase were recorded.

There were several results that showed that the infants recognized the familiar stimulus and preferred to look at the novel stimulus in the test phase, with only 5 s of familiar stimulus exposure. For example, when compared to the no-exposure control trial, infants looked longer at the novel stimulus than at the familiar stimulus.Furthermore,, infants looked at the novel stimulus in the test phase for the brief exposure trials (5 or 6 s) as long as they did during the traditional 20-s accumulated fixation exposure trial.

The most interesting result from these studies is illustrated in Figure 7 (from Richards, 1997b). This figure shows the duration of the exposure to the familiar stimulus during the



Percent Fixation on Novel Stimulus
55
50
45
40
35
30
Immediate
Return of HR to
Prestimulus + 5-S
20 - Second
Accumulation
Heart Rate
Deceleration
No-Exposure Control
Return of HR to
Prestimulus
0.0 - 0.5 s
0.6 - 2.5 s
2.6 - 5.0 s
> 5.0 s
Duration of Familiar Stimulus Exposure
during Heart Rate Deceleration

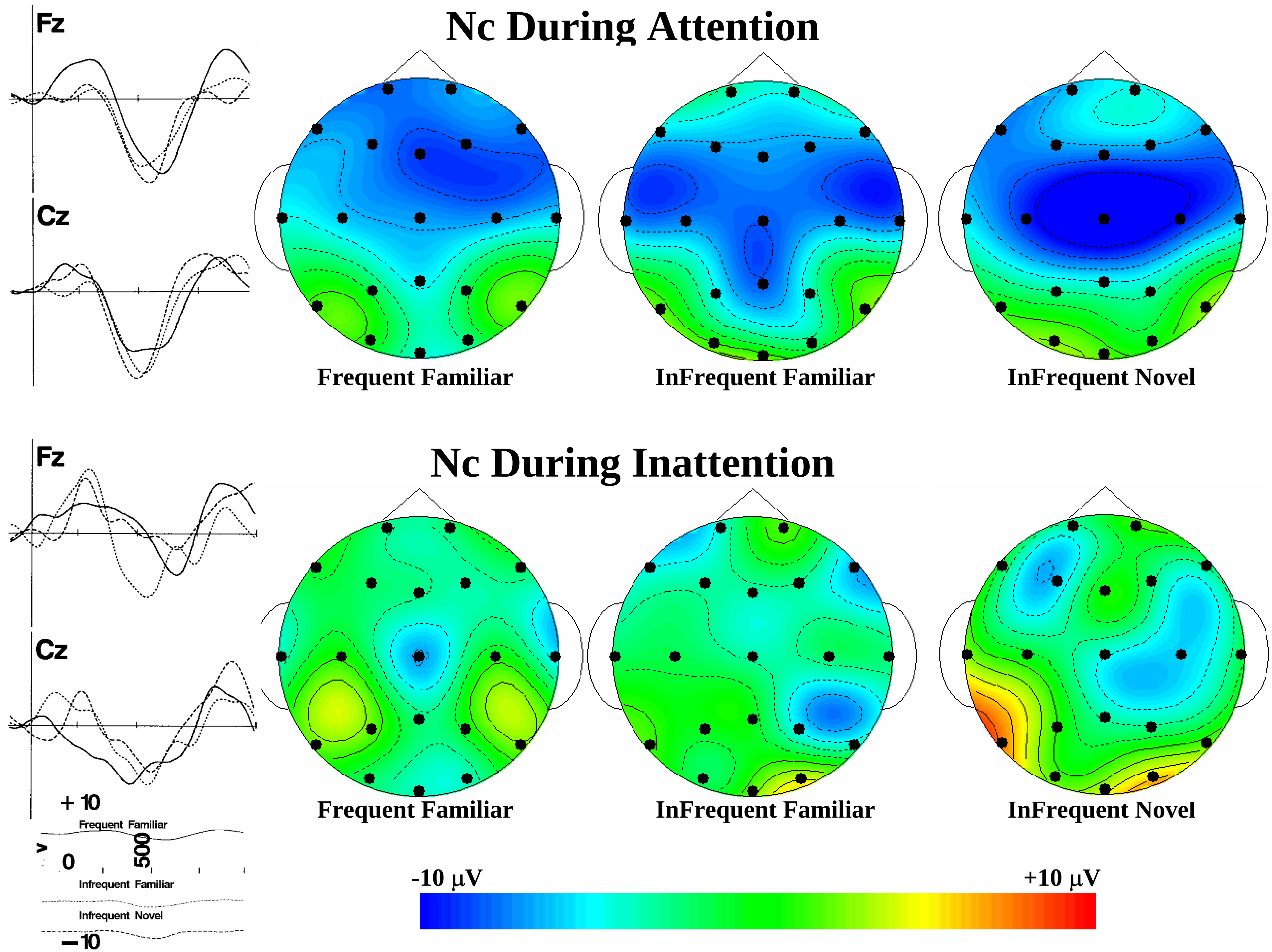
familiarization phase, but for different lengths of exposure during the sustained heart rate deceleration. That is, for some trials the infants' sustained attention overlapped the familiar stimulus exposure for only a brief period of time (e.g., < 1 s) and on other trials the overlap was much greater (e.g., > 5 s). This exposure is shown for different trials and the percent fixation on the novel stimulus in the recognition memory test phase is plotted. A very brief overlap of sustained attention and the familiar stimulus resulted in novelty preference scores at or below the no-exposure control condition. As the amount of familiar stimulus exposure during sustained attention increased, there was a corresponding increase in the novelty preference. This positive correlation between familiar exposure during sustained attention and later recognition memory level (novelty preference level) implies that incorporation of stimulus information is accompanished when the infant is in a highly aroused (aka attentive) state.

We also have shown that the distributions of the fixations on the novel and familiar stimulus in the test phase of the paired-comparison recognition memory procedure are affected by the infants' attention state (Richards & Casey, 1990). In that study heart rate was recorded and the heart-rate-defined attention phases were evaluated during the test phase of the recognition memory procedure. The infants showed novelty preference, indicating recognition memory, primarily during sustained attention. For example, on the average in these 3 to 6 month old infants there was about 11.8 seconds of sustained attention on the recognition memory test phase. Of this, about 7.3 s were spent looking at the novel stimulus and 4.5 s were spent looking at the familiar stimulus. Alternatively, during attention termination (or inattentiveness) the infants spent equal amounts of time looking at the novel and familiar stimulus. And, on no-familiar-stimulus trials (no-exposure control) there were equal amounts of looking at the novel and familiar stimulus during each phase. These results show that the exhibiton of recognition memory generally takes place during sustained attention, when heart rate is below baseline. That is, the infants recognize the familiar stimulus and move fixation to the novel stimulus. This move to the novel stimulus most likely is to acquire new stimulus information. Thus the exhibition of recognition memory during this paired-comparison procedure, shown as novelty preference, is precisely the infant's attempt to acquire new information from the previously unseen stimulus during sustained attention!

Two recent studies show the effect of attention on individual cognitive processes that may occur in the brain after exposure to familiar and novel stimuli. Nelson and his colleagues (Nelson & Collins, 1991, 1992; Nelson & deRegnier, 1992; Nelson & Salapatek, 1986; also see reviews by Nelson, 1994, Nelson & Dukette, 1998, and de Haan, in press) and others (Karrer & Ackles, 1987, 1988; Karrer & Monti, 1997; Courchesne, 1977, 1978; Courchesne, Ganz, and Norcia, 1981) have examined infant recognition memory recording ERPs during stimulus presentations of very brief duration (~150 ms). These studies use the "oddball" paradigm in which one stimulus is presented relatively frequently and a second stimulus is presented infrequently. These studies report a large negative ERP component occurring about 400-800 ms after stimulus onset located primarily in the frontal and central EEG leads. This has been labeled the Nc component (Nc is "Negative" "central"; Courchesne, 1977, 1978). In most studies the Nc component is larger to the infrequently presented stimuli and is thought to represent a general attentive or alerting to the presence of a novel stimulus. If the frequently presented and infrequently presented stimuli are already familiar to the infant the Nc component does not differ (Nelson & Collins, 1991, 1992). This distinction does not occur in 4-month-old infants (e.g., Karrer & Ackles, 1987; Nelson & Collins, 1991, 1992) but occurs in 6-month-old and older infants.

Two recent studies examined these ERP measures of brain activity and their relation to attention. In both studies, attention was first elicited by showing a “Sesame Street” movie, “Follow that Bird”, that elicit the heart rate changes that define sustained attention and inattentiveness. Then, during sustained attention or attention termination brief visual stimuli were presented overlaid on (replacing) the attention-eliciting stimulus. The brief stimuli had been previously familiarized (frequent familiar, infrequent familiar) or were novel on each trial (infrequent novel). The ERP responses to these stimuli were recorded and separated into those that occurred when then infant was attending to the stimulus (sustained attention) or showing inattentive visual regard (attention termination). There was a close relation between the size of the Nc ERP component and the infant’s attentiveness. Figure 8 shows the Nc response occurring during attention and inattention for the three stimulus types. There was a larger Nc during sustained attention and this was true regardless of the familiarity (familiar, novel) or frequency (frequent, infrequent) of the stimulus. There also were age changes in the amplitude of the Nc from 20- to 26- to 32- weeks of age. These age changes occurred predominantly in sustained attention. The close association of the Nc with attention suggests that this component reflects a general attention orienting to the stimulus rather than a specific measure of recognition memory (c.f., Nelson, 1994; Nelson & Dukette, 1998; Nelson & Monk, 2001).

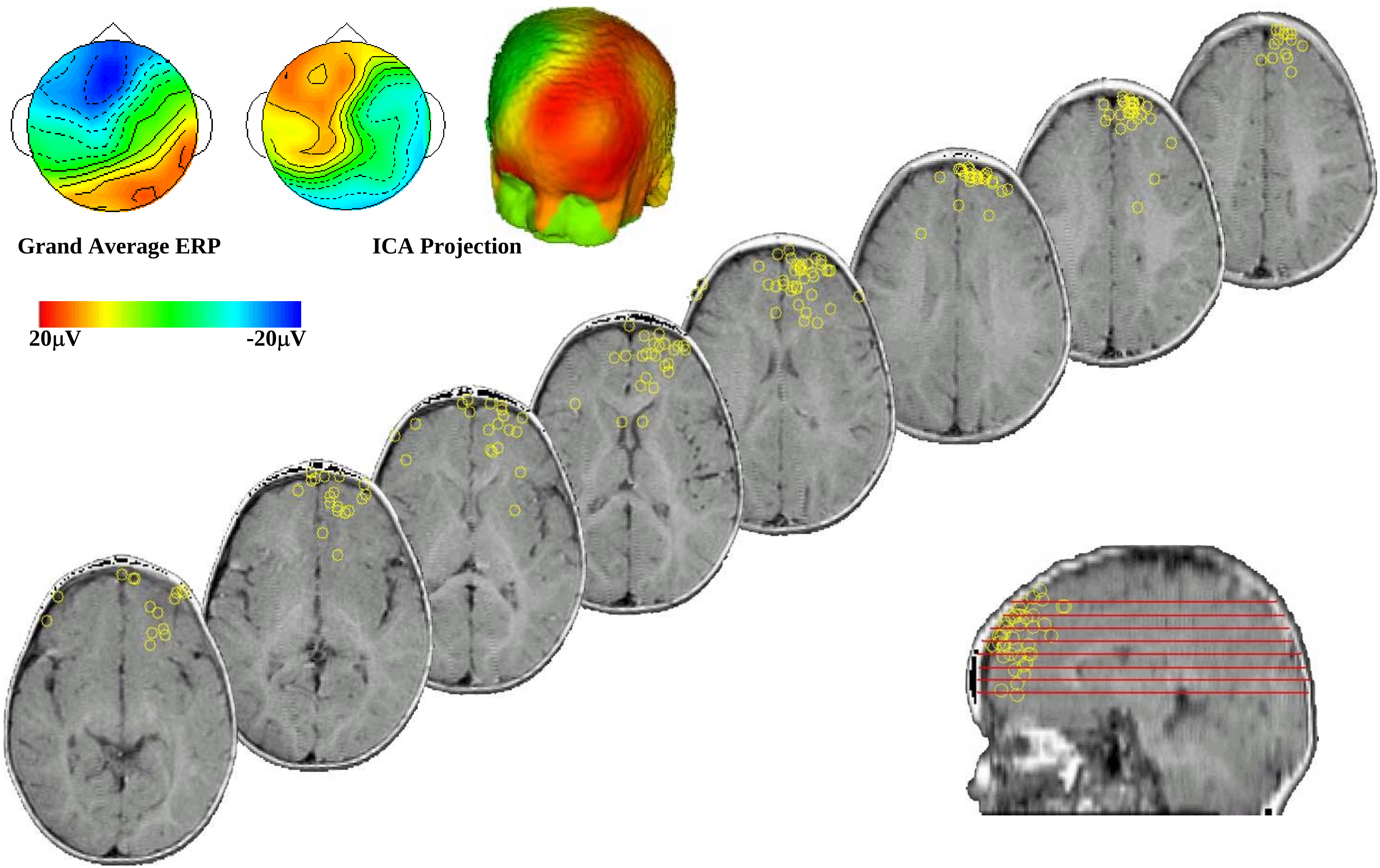
The second study used similar procedures and points to specific brain areas that may generate the Nc ERP component (Reynolds & Richards, 2005). In that study a high-density EEG recording (128 electrodes; Johnson, de Haan, Oliver, Smith, Hatzakis, Tucker, & Csibra, 2001; Tucker, 1993; Tucker, Liotti, Potts, Russell, & Posner, 1994) was used. A similar presentation procedure was used as in Richards (2003a), and again it was found that the Nc component was significantly affected by attention. Since the high-density recording was used, the ERP

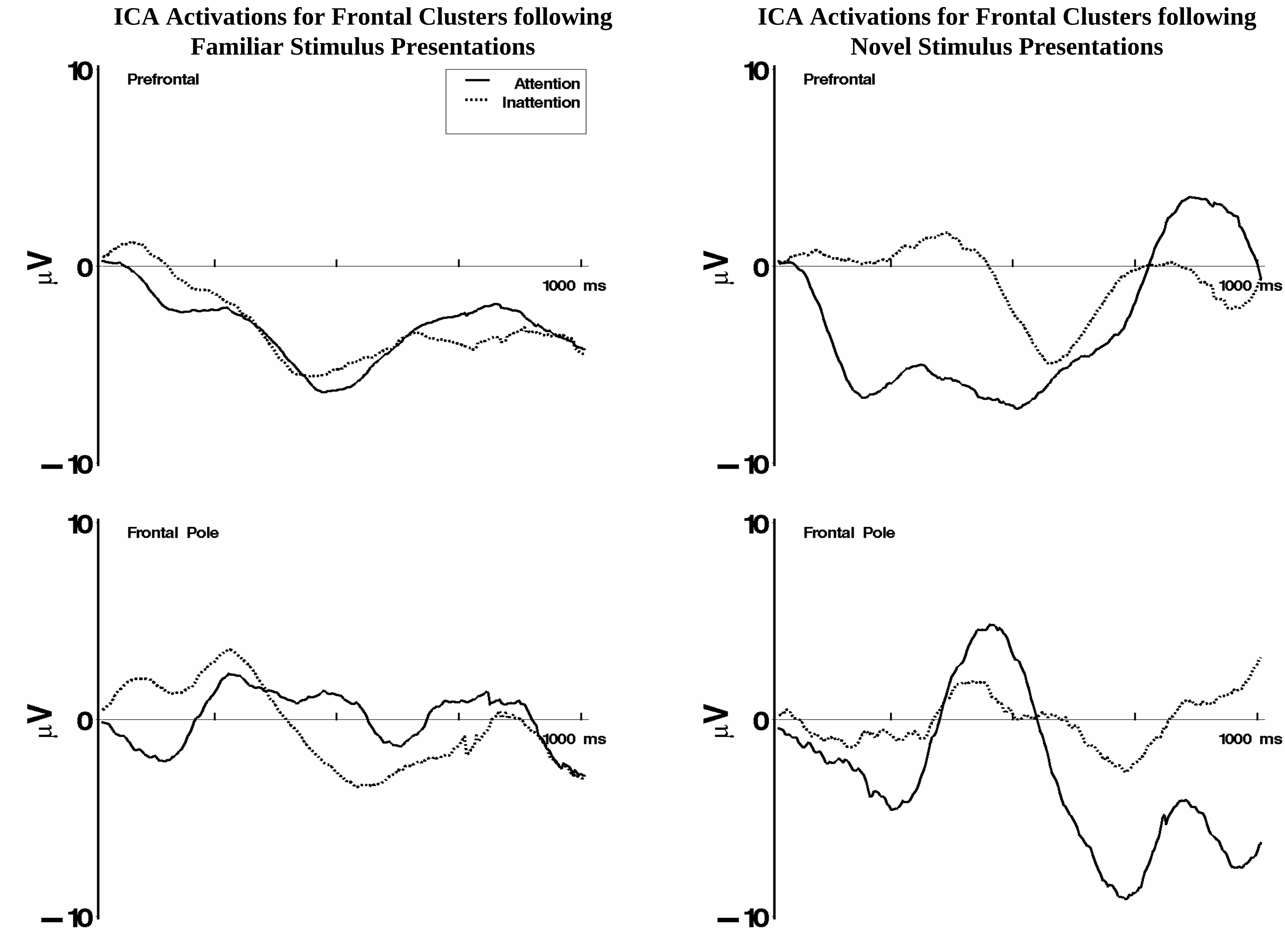

Fz
Cz
Nc During Attention
Frequent Familiar
InFrequent Familiar
InFrequent Novel
Fz
Cz
Nc During Inattention
Frequent Familiar
InFrequent Familiar
InFrequent Novel
+ 10
Frequent Familiar
0
500
Infrequent Familiar
Infrequent Novel
− 10
-10 μV
+10 μV

components could be analyzed with cortical source localization. Two cortical sources were found that are of interest. First, a cortical source was located with that had dipole locations primarily in the frontal pole of the brain. Second, a cortical source was located that had dipole locations scattered throughout several areas of the prefrontal cortex. Figure 9 shows the latter cortical locations. Figure 10 shows the activity of these cortical sources with respect to the experimental conditions. Both locations seem to be involved in the generation of the Nc ERP component, and both were affected by attention. The “prefrontal” source showed activity with its maximum occurring at about 500 ms following stimulus onset, which was the same time course as the Nc in that study. On novel stimulus presentations this activity occurred nearly immediately (upper right panel, solid line) and was sustained throughout the timecourse of the Nc. The “frontal pole” component showed activity later with respect to the stimulus, near the end of the Nc occurrence (Figure 10, bottom figures). However, this occurred primarily for the attention trials on the novel stimulus presentations. This second brain area might be involved in the latter phases of the Nc and in the upcoming slow waves occurring in this task.

The relation between sustained attention and infants recognition of briefly presented visual stimuli shows that the arousal form of attention is related to complex infant cognition. Recognition memory is accomplished by several brain areas and cognitive functions. It requires the acquisition of stimulus information and memory storage over some period of time. The measurement of recognition memory also requires performance on a task exhibiting the existance of the stored memory. The results of these studies show that the arousal aspect of attention may “invigorate” each of these cognitive processes. This enhances familiarization when information acquistion is occurring, may facilitate memory consolidation during the waiting period, and enhances the processes involved in the exhibition of recognition memory. The effect on

Prefrontal ICA Cluster: Medial Frontal Gyrus (25) , Inferior Frontal Gyrus (47), Anterior Cingulate Cortex (8)
(Talairach coordinates: 9.4, 42.9, 16.4)




ICA Activations for Frontal Clusters following Familiar Stimulus Presentations
ICA Activations for Frontal Clusters following Novel Stimulus Presentations
Prefrontal
Attention
Inattention
Frontal Pole
μV
10
0
−10
1000 ms

recognition memory is true for the overall responses to the stimulus in the paired-comparison recogntiion-memory test phase (Richards & Casey, 1990) and for the individual cognitive processes occurring for transient responses to the stimulus (Reynolds & Richards, 2005; Richards, 2003). The enhancement of the Nc ERP component during attention implies that the general arousal system represented by sustained attention affects specific memory or attention processes that have specified locations in the brain. The facilitative effect of attention on infant recognition memory (e.g., Richards, 1997; Frick & Richards, 2001) may occur because specific brain areas responsible for information acquisition or recognition are enhanced during attention (Reynolds & Richards, 2005; Richards, 2003a).

Some comments will be made about the use of the cortical source analysis in this study. If we assume that the activity of specific neurons or groups of neurons is responsible for the electrical activity recorded in the EEG and ERP, then this electrical activity might be considered a direct measure of brain activity. Analysis of the sources of this electrical activity provides an estimate of the location in the brain of the activity occurring on the scalp. For ERP this activity is coordinated with experimental events or cognitive activity, so the source analysis provides a measure of “event-related brain activity”. This is analogous to the functional neuroimaging provided by the BOLD response of the fMRI (Thomas, chapter in this volume) or the NIRS response (Pena & Mehler, chapter in this volume). The advantage of using ERP is that this provides a neuroimaging modality that is generated by neural activity rather than vascular activity and therefore has the same time-scale as neural responses.

The cortical sources inferred with this approach contain some unresolved issues for infant work. The models used in these studies (e.g., Johnson et al., 2005; Reynolds & Richards, 2005; Richards, 2005) are based on parameters derived from adult participants. These include impedance (resistance) values cortical matter, skull, and scalp of adult participants. Adult values of impedance are higher than those in infants. The use of adult impedance values with infant participants may have the effect of inferring the source of the current on infant participants as being deeper in the cortex than where it actually occurred. Second, the use of these models, even with adults, is preferable when structrual MRIs exist that can constrain the dipole locations to realisitic topographies derived for each participant (Richards, 2003b, submitted). These concerns are particularly relevant for infant participants where skull irregularities (unseamed sutures, thin skull) and head topography (scalp thickness, lobe location) may differ greatly from adults. Due to these limitations, it is appropriate to make these conclusions about the cortical sources of the Nc response with some tentativeness. Notwithstanding these problems, however, the localization of the cortical sources of these ERP components is a great advance in the study of the ERP components of infant recognition memory (Richards, 2006). In the first edition of this volume (Richards, 2001) I spectulated that the measurement of brain function with cortical source localization methods had a bright future for the study of infant attention. The work reviewed in the current chapter shows that this potential is being realized. This work is still in its "infancy", but the use of these techniques should be profitably applied to an understanding of the developmental changes in brain areas that are involved in the development of infant attention.

SUMMARY AND CONCLUSION

Attention shows dramatic development in the early period of infancy, from birth to 12 months. This chapter has emphasized an attention system that represents a general arousal of cognitive functions. The system in the brain controlling this arousal develops in the first few months of life and this brain development is responsible for the behavioral / attentional development seen in young infants. This chapter reviewed several studies that showed the effect of this arousal system, indexed by heart rate changes showing sustained attention. There were developmental changes in infant sustained attention that were reflected in developmental changes in specific attentional systems or that corresponded to developments occurring in other brain-based attention-directed infant behavior.

There are two ways in which future research and progress in the study of the development of attention-arousal in infants could progress. First, this review was limited to studies using heart rate as a measure of the general arousal system in the brain. There are other measures that may be useful in this regard. For example, continuous levels of EEG activity are thought to be influenced by general arousal mechanisms in the brain. Since the EEG represents the summed activity of large groups of neurons, one might expect that the brain areas controlling arousal or the neurochemical systems should have an influence on overall neural activity (extent, duration, and localization). Thus, measures of EEG such as spectral power and coherence may give information about arousal. Such measures also may show relatively localized CNS arousal.

A second area in which research on the development of the brain systems controlling arousal may benefit is direct measures of the brain. Such measures in animal models have included invasive chemical manipulations and measurement as well as destruction of the areas controlling arousal through lesions or neurochemical inhibitors. These measures cannot be applied in infant participants because of ethical considerations. However, noninvasive measurements from psychophysiological measures that are tuned to specific neurochemical systems might be found. Perhaps one type of quantitative activity in the EEG may be linked to a specific neurochemical system and another type linked to another system. The simple recording of EEG, ERP, or heart rate cannot be used to distinguish the four arousal systems detailed in Robins and Everitt (1995). The EEG and heart rate would be expected to respond to any manipulation of an underlying arousal system. Some type of quantitative activity in the EEG would have to be linked to the underlying neurochemical system in order to use psychophysiological measures for this direct evaluation of the brain systems controlling this arousal form of attention.

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FIGURES

Figure 1. The arousal system of the brain.

Figure 2. The neurochemical systems involved in attention and arousal. Abbreviations: III: oculomotor nucleus; T: thalamus; HC: hippocampal formation; RF: reticular formation; PSG: parasympathetic ganglion cell; X: dorsal motor nucleus of the vagus; H: hypothalamus; LC: locus ceruleus; C: caudate nucleus; P: putamen; S: septal nuclei; V: ventral striatum. (Copyright 1995, Mosby; Reprinted with permission of the publisher from Nolte & Angevine, 1995, pp. 134-137).

Figure 3. Average heart rate change as a function of stimulus following stimulus onset for the heart rate defined attention phases for infants from 3 to 6 months of age. From Richards & Casey, 1991.

Figure 4. 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 saccadic eye movements ("Reflexive Saccades"), voluntary saccadic eye movements ("Targeted Saccades"), and smooth pursuit eye movements ("Smooth Pursuit"). From Richards & Hunter, 1998.

Figure 5. The smooth pursuit EOG gain and saccade frequency (saccades per sec) as a function of stimulus tracking speed and testing age (8 and 14 weeks combined, 20 and 26 weeks combined). The top two plots were taken from the period when sustained heart rate deceleration was occurring, and the bottom two plots were taken from the period after heart rate had returned to its prestimulus level. Adapted from Richards & Holley, 1999, Figure 4, and Richards & Hunter, 1998, Figure 4.7.

Figure 6. 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 Richards & Hunter, 2002).

Figure 7. The duration of familiar exposure occurring during heart rate deceleration (sustained attention) and the percent fixation on the novel stimulus in the recognition memory test phase. The “No-Exposure Control” time (40%) should be considered the baseline percent fixation with no exposure to the familiar stimulus. Adapted from Richards, 1997, Figure 3.

Figure 8. The Nc component during attention and inattention. The ERP recording from 100 ms prior to stimulus onset through 1 s following stimulus is shown for the F_Z and C_Z electrodes for attentive (top figures) and inattentive (bottom figures) periods, combined over the three testing ages. The topographical scalp potential maps show the distribution of this component for the three memory stimulus types in attention and inattention. The topographical maps represent an 80 ms average of the ERP for the Nc component at the maximum point of the ERP response. The data is plotted with a cubic spline interpolation algorithm and represents absolute amplitude of the ERP. (Figure 2 from Richards, 2003).

Figure 9. The ICA component cluster for the prefrontal component. The topographical map of the average ICA loadings are similar to the topographical map of the grand average ERP of the Nc component. The ECD locations are displayed on several MRI slices, and each location represents an ICA from one individual. (Figure 4 in Reynolds & Richards, 2005).

Figure 10. The ICA activations for the frontal clusters for 1 s following stimulus onset. The left panel displays combined responses to frequent familiar and infrequent familiar stimulus presentations for separately for periods of attention and inattention. The right panel displays

responses to infrequent novel stimulus presentations separately for periods of attention and inattention. (Figure 6 in Reynolds & Richards, 2005).