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EEG and ECG from 5 to 10 Months of Age: Developmental Changes in Baseline Activation and Cognitive Processing During a Working Memory Task

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Abstract

We recorded electroencephalogram (EEG) and electrocardiogram (ECG) from 20 infants monthly between 5 and 10 months of age during baseline and during performance on the looking A-not-B task of infant working memory. Analyses of baseline data showed age-related increases in EEG power (medial frontal, central, temporal, medial parietal, lateral parietal, occipital electrode sites) and coherence (frontal pole-medial frontal, medial frontal-lateral frontal, medial frontal-medial parietal, medial frontal-occipital electrode pairs), and decreases in heart rate (HR). Patterns of age-related change were similar for EEG power, EEG coherence, and HR. Analyses of task data relative to baseline revealed task-related increases in EEG power (all electrode sites), but no task-related changes in EEG coherence (medial frontal pairings) and HR. There was some evidence of localized task-related changes in EEG power by 10 months of age. These data highlight age-related changes in EEG and ECG, as well as the functional significance of these psychophysiological measures during baseline and during cognitive processing in the first year.

Keywords

infants; working memory; EEG power; EEG coherence; heart rate; A-not-B task

1. Introduction

Over the past 25 years, the use of psychophysiological measures in infancy research has become more prevalent. Our understanding of a variety of developmental constructs (e.g., attention, emotion regulation, temperament, memory) has been enhanced by the inclusion of both psychophysiological and behavioral measures (e.g., Bell and Fox, 1992; Doussard-Roosevelt et al., 2001; Fox and Davidson, 1987; Fox et al., 2001; Richards, 1989). The electrocardiogram (ECG) and the electroencephalogram (EEG) are two of the most preferred psychophysiological measures for use with awake, non-sedated infants because these measures are noninvasive and relatively resistant to motor artifacts (Casey and de Haan,

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2002; Reynolds and Richards, 2008). Although there is some literature about the developmental course of EEG and ECG during infancy, there is no study of both measures in the same participants across intensive month-to-month observations. As each of these measures demonstrates a great deal of change in baseline (i.e., a quiet attentive state; “resting” activation) recordings across the first year, information regarding the specific developmental patterns of EEG and ECG during baseline would inform the developmental psychophysiology literature. Furthermore, examination of the developmental patterns during specific psychological behavior (in this case, during an infant working memory task) would allow for examination of task-related changes in these psychophysiological measures.

In the present longitudinal study, EEG and ECG were recorded monthly from 5 to 10 months of age during a baseline condition and during performance of the looking version of the infant A-not-B task (Bell, 2001, 2002; Bell and Adams, 1999). The A-not-B task has been conceptualized as a measure of executive function during infancy, as it requires working memory and inhibitory control for successful task performance (Diamond et al., 1997). We analyzed age-related changes in baseline psychophysiology (EEG power, EEG coherence, and heart rate (HR)), as well as age-related changes in task psychophysiology, relative to baseline. In the following paragraphs, we first provide a brief overview of our infant working memory task. Next, we review the infant EEG and ECG on (a) baseline measures and (b) task-related measures during cognitive processing. Finally, we present research questions addressed by the current study.

1.1. Infant working memory task

In the classic version of the A-not-B working memory task, infants watch as a desirable object is hidden in one of two locations, there is a brief delay, and then infants lean and reach to one of the locations (e.g., Diamond, 1985). For the looking version of the task, infants respond by looking to one of the hiding locations rather than reaching (Bell and Adams, 1999; Pelphrey et al., 2004), thus allowing researchers to obtain relatively artifact-free EEG and ECG measures of cognitive processing (Bell, 2001, 2002; Bell, in press). Within-subjects comparisons of reaching and looking performance on the task have demonstrated equivalent task performance by 8 to 9 months of age (Bell and Adams, 1999; Cuevas and Bell, 2010; Pelphrey et al., 2004).

We are particularly interested in cognitive processing during the A-not-B working memory task because there is biobehavioral evidence that the dorsolateral prefrontal cortex is a major contributor to task performance (e.g., lesion studies with adult and infant nonhuman primates: Diamond, 1990; Diamond and Goldman-Rakic, 1989; near-infrared spectroscopy research with human infants: Baird et al., 2002). We tested infants between 5 and 10 months because this 6-month age range yields data during a period when there are dramatic shifts in A-not-B task performance (Cuevas and Bell, 2010; Diamond, 1985; Pelphrey et al., 2004) and frontal lobe maturation (Chugani, 1994; Huttenlocher, 1990). At 5 months, the youngest age that A-not-B data are available, the majority of infants make the A-not-B error after a brief delay (i.e., look to the incorrect (A) well; Cuevas and Bell, 2010). A-not-B task performance is normally distributed by 8 months of age (Bell & Adams, 1999), and by 10 months, most infants exhibit at least a basic level of proficiency on both looking and reaching versions of the task (Cuevas and Bell, 2010; Pelphrey et al., 2004). We asked whether the aforementioned age-related shifts in A-not-B task performance were associated with different patterns of task-related changes in psychophysiology.

In the following review, we are primarily interested in the development of working memory processing and corresponding changes in measures of continuous EEG and ECG. However, the limited psychophysiological research on the A-not-B task has only examined this question with 8-month-olds (Bell, 2001; Bell, in press). Attention and working memory may

both be essential for success on the A-not-B task (Bell & Adams, 1999). Thus, we also include developmental research on the psychophysiological correlates of attention tasks.

1.2. Development of infant EEG and ECG

1.2.1. EEG frequency bands—Early longitudinal research from the 1930's through the 1970's was focused on describing infant EEG tracings and how the EEG changes with development (see Bell, 1998; Bell and Fox, 1994, for reviews). This early work demonstrated that infant EEG is at a much lower frequency than adult EEG, with rather dramatic changes in the dominant frequency from infancy through early childhood. More recently, researchers have focused on determining the predominant EEG frequencies at specific ages during infancy and early childhood (Bell and Fox, 1992; Marshall et al., 2002), as well as the functional significance of specific frequency bands (Bell, 2002; Lehtonen et al., 2002; Orekhova et al., 2006; Stroganova et al., 1999). The 6–9 Hz frequency band, labeled as infant “alpha” by Stroganova and Orekhova (2007), has emerged as a standard in infancy EEG research, and has been used to examine a variety of different constructs, much like the adult 8–13 Hz alpha band (e.g., visual attention, emotion expression and regulation, working memory and inhibitory control; Bell, 2001; Fox et al., 2001; Orekhova et al., 2001). An analysis of developmental changes in EEG measures in the 6–9 Hz frequency band is an essential reference for infancy EEG researchers who need to know how baseline measures of EEG power and EEG coherence potentially change across age.

1.2.2. EEG power—EEG measures have been used to examine brain development (i.e., scalp electrical activity related to cortical activity) in premature and full-term infants and children (e.g., Dreyfus-Brisac and Monod, 1975; Hudspeth and Pribram, 1992; Khazipov and Luhmann, 2006). Two commonly used EEG variables are power and coherence. EEG power reflects the excitability of groups of neurons and ontogenetic increases in power are considered to be indicative of brain development (Hudspeth and Pribram, 1992; see Bell, 1998, for review).

Baseline EEG recordings at 5 months and then again at 10 months of age show relative instability of 6–9 Hz power (Marshall et al., 2002), suggesting great developmental change across this time period. When and how does EEG power change between 5 and 10 months? Month-to-month longitudinal work using only six scalp electrodes demonstrated age-related increases in baseline 6–9 Hz power at medial frontal, medial parietal, and occipital electrode sites from 7 to 12 months (Bell and Fox, 1992, 1994). A case study of weekly baseline EEG recordings from 6 to 12 months of age across frontal and temporal electrodes showed similar increases in 6–9 Hz EEG power (Bell, 1998). These studies, in conjunction with the early infant EEG research that typically focused on a few posterior scalp locations (see Bell, 1998, for review), yield limited knowledge of developmental changes in EEG during the first year. Longitudinal studies with multiple data collection points during infancy are needed to inform age-related changes in power across the entire scalp.

Task-related changes in EEG power (in comparison to baseline) are hypothesized to represent “activation” of brain areas underlying specific scalp electrodes, and have been used as indicators of cognitive processing during attention and memory tasks with infants and adults (e.g., Bell, 2001, 2002; Orekhova et al., 2001; see Klimesch, 1999, for review). During infancy, task-related changes in continuous EEG have been found for both working memory and attention tasks. Eight- to 11-month-olds exhibit task-related changes in EEG amplitude during anticipatory attention (i.e., peek-a-boo): task-related increases at fronto-central (6.4–7.6 Hz) and lateral frontal (6.8–7.2 Hz) electrodes and task-related decreases at temporal (6.4–7.2 Hz) and occipital (6.8 Hz) electrodes (Orekhova et al., 2001). Likewise, 8-month-olds exhibit baseline to task increases in 6–9 Hz EEG power during the A-not-B

infant working memory task at all scalp locations (Bell, 2002; Bell and Wolfe, 2007). Infants exhibit substantial improvements in working memory between 5 and 10 months, and it is unknown whether younger or older infants would exhibit the same pattern of change in EEG power during working memory processing. EEG power, however, does not provide information about cortico-cortical connections.

1.2.3. EEG coherence—EEG coherence is the frequency-dependent squared cross-correlation between two scalp electrode sites (range: 0–1) and is a measure of axonal connectivity between two neuronal groups (Nunez, 1981; Thatcher et al., 1987). If the activity at two electrode sites is consistently in (or out) of phase then coherence values approach 1, and if there is no relation in phase (i.e., random changes in phase) then coherence values approach 0. Thatcher (1994) has proposed that resting coherence values reflect the number and strength of synaptic connections, which is also indicative of the level of connectivity between two scalp sites. Relatively higher levels of resting and task-related coherence reflect integration of function between two brain areas. Increases in resting coherence are particularly likely during infancy when there is widespread myelination of axons and synaptogenesis (Huttenlocher, 1990). Relatively lower levels of resting and task-related coherence reflect increased differentiation in function between two brain areas and may be related to increased speed and efficiency of information processing (Silberstein et al., 2004; Thatcher et al., 2005).

The initial developmental examination of baseline EEG coherence was completed by Thatcher et al. (1987) using a cross-sectional design. Age-related changes in coherence were characterized as being different for each set of electrode pairs between birth and 3 years; however, data from all infants less than 1 year were grouped together into a single category so that coherence development across the first year could not be examined. Bell and Fox (1994) used a longitudinal design, with monthly visits from 7 to 12 months, to examine the development of baseline EEG coherence during the first year. Medial frontal-medial parietal electrode pairs exhibited a U-shaped pattern in 6–9 Hz coherence as a function of age while medial frontal-occipital electrode pairs had stable coherence values across ages. A week-to-week case study (Schmauder and Bell, 1995), from 6 to 12 months of age, also found different developmental patterns of 6–9 Hz coherence as a function of electrode pairings. Age-related increases in coherence were found in both hemispheres for some electrode pairs (frontal pole-medial frontal), and only in the left hemisphere for others (medial frontal-temporal and medial frontal-lateral parietal). For some electrode pairs (medial frontal-lateral frontal), coherence was stable (29–38 weeks) and then exhibited a U-shaped pattern (39–43 weeks). A more encompassing study with multiple electrode pairs covering the entire scalp would provide valuable information regarding the early development of EEG coherence.

Task-related changes in EEG coherence reflect functional connectivity between two electrode sites. During a demanding working memory task, adults exhibit task-related *increases* in long-distance and posterior short-distance coherence (theta band) and *decreases* in anterior short-distance coherence (upper alpha band) (Sauseng et al., 2005). Research with 8-month-olds has investigated task-related changes in frontal 6–9 Hz EEG coherence (i.e., medial frontal electrode pairings) during working memory processing. Infants exhibited task-related decreases in coherence for each electrode pair (i.e., a whole head effect; Bell and Wolfe, 2007). As with EEG power, it is unknown whether this pattern of task-related change in EEG coherence during working memory processing is limited to 8 months of age. The maturation of the frontal lobe and improvements in working memory performance between 5 and 10 months of age might be associated with different patterns of functional connectivity during working memory processing.

1.2.4. Heart rate—The brain evokes changes in HR via activation of the parasympathetic and sympathetic nervous systems. According to the “intake-rejection” hypothesis (Lacey and Lacey, 1958), increased HR is associated with inhibition of cortical activity as a result of increased sensory thresholds while decreased HR is associated with decreased sensory thresholds (Lacey et al., 1962). HR and its inverse measure of heart period are frequently used in infancy research (see Reynolds and Richards, 2008, for review). The developmental progression of HR is well-established: HR decreases during the first year (e.g., Bar-Haim et al., 2000; Izard et al., 1991; Richards, 1989).

Cardiac measures have long been used to operationally define different phases of infant attention (see Richards, 2004, for review). Sustained attention is associated with infant-controlled cognitive processing and is characterized by a prolonged decrease in HR from baseline and increased distraction latencies. Using a cross-sectional sample, Courage et al. (2006) found that for a variety of different visual stimuli, older infants (39- and 52-week-olds) exhibited more HR deceleration than younger infants (14-, 20-, and 26-week-olds).

Sustained attention and working memory may be similar during infancy because both require information to be in “active” state (Diamond et al., 1997). Executive attention, which includes effortful attentional processes mediated by frontal neural circuits (Posner and Rothbart, 2000), is a component of Engle’s model of working memory (Kane and Engle, 2002) and exhibits initial development at 10 months (Posner and Rothbart, 2000). With research linking HR and attentional processes, it is plausible that HR might also provide information about infant working memory processing.

Only one study has examined HR during a working memory task. At 8 months of age, task-related changes in HR differed as a function of task performance: High performers exhibited task-related increases while low performers exhibited task-related decreases (Bell, in press). It is unknown whether older or younger infants would exhibit similar patterns of task-related changes in HR or whether the direction of task-related changes in HR shifts during development. The present study allows for the analysis of possible age-related changes in cardiac reactivity during working memory processing.

1.3. Research questions and hypotheses

Are there changes in psychophysiological measures during rest (baseline) from 5 to 10 months of age?—Based on previous psychophysiological research, we hypothesize that EEG power (6–9 Hz) will increase in all electrode sites as a function of age, while HR will decrease as a function of age. Age-related changes in EEG coherence (6–9 Hz) will be dependent on the particular electrode pairing with some pairs exhibiting increases (frontal pole-medial frontal) or decreases (medial frontal-medial parietal) in coherence and others exhibiting stable (medial frontal-lateral frontal, medial frontal-occipital) coherence values.

Which psychophysiological measures differentiate between baseline and working memory processing from 5 to 10 months of age?—Based on previous psychophysiological research, we hypothesize that baseline to task increases in 6–9 Hz EEG power will be exhibited at most, if not all, electrode sites. We also predict baseline to task decreases in 6–9 Hz EEG coherence in all electrode pairs. Our EEG predictions are based on non-longitudinal data, however. It may be that with longitudinal data, there will be initial evidence of localized, as compared to widespread, task-related changes in EEG power and coherence (Bell and Wolfe, 2007). Different patterns of HR change have been found at 8 months of age based on task performance (Bell, in press). We have no a priori hypotheses about the direction of task-related changes in HR.

2. Materials and methods

2.1. Participants

Twenty healthy full-term infants (6 girls, 14 boys; 17 Caucasian, 2 African American, 1 Hispanic) were participants in this longitudinal study. Infants were born to middle- and upper-middle-class parents. All parents had at least a high school diploma (5% technical degree; 67.5% bachelor's degree, 17.5% graduate degree). Mothers were approximately 30 years old (range 22–40) and fathers were approximately 31 years old (range 22–45). Infants were recruited via birth announcements placed in local newspapers. All infants were born within 15 days of their calculated due dates and were healthy at the time of testing. Infants were seen in the laboratory monthly from 5 until 10 months of age, for a total of six sessions. Infants were seen within 15 days of their month “birthday.” The mean delay between monthly visits was 29.59 days ($SD = 4.38$). One infant began the study when he was 6 months. Parents were paid \$20 for each monthly visit to the research lab.

2.2. Procedure

2.2.1. EEG recordings—EEG was recorded during baseline and during the looking working memory task. Recordings were made from 16 left and right scalp sites: frontal pole (Fp1, Fp2), medial frontal (F3, F4), lateral frontal (F7, F8), central (C3, C4), temporal (T7, T8), medial parietal (P3, P4), lateral parietal (P7, P8), and occipital (O1, O2). All electrode sites were referenced to Cz during recording. EEG was recorded using a stretch cap (Electro-Cap, Inc.; Eaton, OH) with electrodes in the 10/20 system pattern (Jasper, 1958; Pizzagalli, 2007). After the cap was placed on the infant's head, recommended procedures regarding EEG data collection with infants were followed (Pivik et al., 1993). Specifically, a small amount of abrasive was placed into each recording site and the scalp gently rubbed. Following this, conductive gel was placed in each site. Electrode impedances were measured and accepted if they were below 5K ohms.

The electrical activity from each lead was amplified using separate SA Instrumentation Bioamps (San Diego, CA) and bandpassed from .1 to 100 Hz. Activity for each lead was displayed on the monitor of an acquisition computer. The EEG signal was digitized on-line at 512 samples per second for each channel so that the data were not affected by aliasing. The acquisition software was Snapshot-Snapstream (HEM Data Corp.; Southfield, MI) and the raw data were stored for later analyses. Prior to the recording of each subject a 10 Hz, 50 uV peak-to-peak sine wave was input through each amplifier. This calibration signal was digitized for 30 s and stored for subsequent analysis.

2.2.2. EEG analysis—Spectral analysis of the calibration signal and computation of power at the 10 Hz frequency band was accomplished. The power figures were used to calibrate the power derived from the subsequent spectral analysis of the EEG. EEG data were examined and analyzed using EEG Analysis System software developed by James Long Company (Caroga Lake, NY). First, the data were re-referenced via software to an average reference configuration (Lehmann, 1987). Average referencing, in effect, weighted all the electrode sites equally and eliminated the need for a noncephalic reference. Active (F3, F4, etc.) to reference (Cz) electrode distances vary across the scalp. Without the re-referencing, power values at each active site may reflect interelectrode distance as much as they reflect electrical potential. For example, using an infant EEG sample that was recalculated with three different reference montages, Stroganova and Orekhova (2007) showed that average reference and linked ears montages exhibit similar EEG rhythms at the same scalp locations, whereas the Cz reference montage yields a pattern of amplitude changes at very different scalp sites, especially for the electrode sites furthest away from Cz. The average reference configuration requires that a sufficient number of electrodes be

sampled and that these electrodes be evenly distributed across the scalp. Luck (2005) has demonstrated with event-related potential recordings that voltage can be affected by average reference montage when only mid-line electrodes, as opposed to an entire scalp of electrodes, are used. Currently, there is no agreement concerning the appropriate number of electrodes (Davidson et al., 2000; Hagemann et al., 2001; Luck, 2005), although the 10/20 configuration that we used does satisfy the requirement of even scalp distribution.

The re-referenced EEG data were artifact scored for eye blinks using Fp1 and Fp2 (Myslobodsky et al., 1989) and for gross motor movements and these artifact-scored epochs were eliminated from all subsequent analyses. The data then were analyzed with a discrete Fourier transform (DFT) using a Hanning window of 1-s width and 50% overlap. Across the 20 infants, the mean number of artifact-free DFT windows during baseline and task, respectively, was 72 ($SD = 21$) and 73 ($SD = 40$) at 5 months, 66 ($SD = 20$) and 78 ($SD = 41$) at 6 months, 61 ($SD = 20$) and 102 ($SD = 62$) at 7 months, 56 ($SD = 18$) and 91 ($SD = 41$) at 8 months, 58 ($SD = 17$) and 76 ($SD = 41$) at 9 months, 62 ($SD = 17$) and 92 ($SD = 51$) at 10 months. Power was computed for the 6–9 Hz frequency band. The power was expressed as mean square microvolts and the data were transformed using the natural log ($\ln$) to normalize the distribution. Coherence between medial frontal and all other electrode sites within each hemisphere was computed for the 6–9 Hz band using an algorithm by Saltzberg et al. (1986).

2.2.3. ECG recordings—ECG also was measured during baseline and task from two neonatal disposable electrodes using modified lead II (right collarbone and lower left rib; Stern et al., 2001), grounded at the scalp near electrode site Fz. The cardiac electrical activity was amplified using a SA Instrumentation Bioamp and the QRS complex was displayed on the acquisition computer monitor along with the EEG data. The cardiac signal was digitized at 512 samples per second. The acquisition software was Snapshot-Snapstream and the raw data were stored for later analyses.

2.2.4. ECG analysis—Heart data were examined and analyzed using IBI Analysis System software developed by James Long Company. First, R waves were detected and movement artifact, designated by the absence of at least 3 consecutive R waves, was scored. These artifact-scored epochs were eliminated from all cardiac calculations. Across the 20 infants, the mean duration (in s) of artifact-free data during baseline and task, respectively, was 50 ($SD = 16$) and 80 ($SD = 38$) at 5 months, 56 ($SD = 17$) and 87 ($SD = 48$) at 6 months, 52 ($SD = 13$) and 115 ($SD = 48$) at 7 months, 55 ($SD = 16$) and 112 ($SD = 37$) at 8 months, 60 ($SD = 10$) and 95 ($SD = 49$) at 9 months, 51 ($SD = 16$) and 106 ($SD = 53$) at 10 months. HR was calculated as beats per minute (bpm).

2.2.5. Baseline—Baseline EEG and ECG were recorded for 1 min ($M = 64.2$ s, $SD = 6.7$) while the infant sat on the mother's lap. It is a common practice for infant EEG researchers to obtain approximately 1 min of baseline recording (e.g., Bell, 2001, 2002; Marshall et al., 2002; Orekhova et al., 1999, 2001; Stroganova et al., 1998; Thatcher et al., 1987). During the baseline recording, a research assistant manipulated a toy containing brightly colored balls on top of the testing table, 1.1 m in front of the infant. This procedure quieted the infant and yielded minimal eye movements and gross motor movements. Mothers were instructed not to talk to infants during the EEG recording. Immediately after baseline, the recording of EEG and ECG continued as the looking task was administered.

2.2.6. A-not-B working memory task—Much like the reaching version of the infant A-not-B working memory task (Diamond 1985, 1990; Diamond et al., 1997), the looking version requires the infant to constantly update memory of where the toy was hidden through a series of displacements and to inhibit looking back toward a previously rewarded

hiding place (Bell and Adams, 1999). Thus, the infant “searched” for a hidden toy by making an eye movement to one of two possible hiding locations (e.g., Bell and Adams, 1999; Pelphrey et al., 2004). Our comparison of looking and reaching working memory task performance from 5 to 10 months of age in these same infants is published elsewhere (Cuevas and Bell, 2010).

The testing apparatus was a table measuring 90 cm (L) × 60 cm (W) × 75 cm (H) and the hiding sites were bright orange and blue plastic tubs that measured 17 cm in diameter and 11 cm deep. The infant sat on the parent’s lap 1.1 m from the edge of the testing table as the experimenter manipulated a toy and hid it under one of the two (17.5 cm on either side of midline) plastic tubs. After the toy was hidden, the infant’s gaze to the hiding site was broken and brought to the experimenter’s face at midline by the experimenter calling the infant’s name and asking, “Where’s the toy?”. The direction of the infant’s first eye movement after being brought to midline was scored as either correct or incorrect. A video camera was placed behind and above the experimenter’s head and focused so as to maintain a close-up view of the infant’s face.

Initial side of hiding was counterbalanced among infants and the pattern of toy placement was determined by the infant’s performance. Two consecutive successful eye movements toward the same side (for example, toward the infant’s right) resulted in the toy then being hidden under the tub on the opposite side (toward the infant’s left; i.e., Right-Right-Left). Regardless of whether or not the infant was successful on the “reversal” trial, new “same-side” trials commenced at the reversal site and continued until two consecutive successful eye movements were executed, initiating another reversal (i.e., L-L-R). Thus, flawless performance by an infant would result in this pattern of trials: R-R-L-L-R-etc. In reality, most infants were not flawless in performance and some needed multiple same-side trials in order to achieve two consecutive successful eye movements prior to reversal trials. Infants who made an eye movement toward the correct tub on reversal trials in two out of three attempts were then tested with a delay. The delay was initiated during the time the infant’s gaze to the hiding site was broken and brought to the experimenter’s face at midline. In the delay condition, the experimenter called the infant’s name, counted out the delay period, and then asked, “Where’s the toy?”. Subsequent delays were initiated until the infant looked at the incorrect tub in two out of three reversal trials at any given delay. Delay was incremented in 2-s intervals throughout the longitudinal study. In reality, even during the “no delay” trials at the beginning of the assessment the infants experienced a brief delay as their gaze to the tub was broken and brought to midline. This brief delay was unavoidable because of the necessity of breaking the infant’s gaze so that the direction of their first eye movement could be determined. Assessment terminated when the infant made an eye movement toward the incorrect tub in two out of three reversal trials at either no delay or a timed delay.

An event marker was used in conjunction with the EEG and ECG recordings so that it was possible to mark which portions of the electrophysiological record were associated with the most cognitively demanding sections of the looking task. The task-related EEG and ECG used in data analyses was that associated with the simultaneous use of the cognitive skills of working memory and inhibition (Bell, 2001, 2002). The task-related EEG and ECG started with the covering of the hiding site(s) with the tubs, continued through the distraction and delay periods, and stopped when the experimenter lifted a tub prior to giving the infant appropriate verbal feedback. Thus, electrophysiological data *not* included in the analyses were those recorded when the experimenter was manipulating the toy prior to hiding it and those recorded when the experimenter was giving appropriate feedback to the infant after the infant’s eye movement to one of the hiding sites. The artifact-free EEG and ECG data from all trials, correct and incorrect, were used in the analyses. The average number of trials

(combining same-side and reversal trials) from which electrophysiological data were collected was 8.45 ($SD = 3.93$), 10.75 ($SD = 3.81$), 14.35 ($SD = 4.45$), 17.45 ($SD = 6.46$), 15.05 ($SD = 5.09$), and 20.00 ($SD = 5.21$) per infants at 5, 6, 7, 8, 9, and 10 months of age, respectively. Because task administration was based on infant performance, there were more trials as infants became older and were more proficient at the task.

2.2.7. Statistical analysis—To examine each of the research questions, the analyses consisted of repeated-measures multivariate analysis of variance (MANOVA) with region, hemisphere, and age (i.e., development), as well as condition (i.e., cognitive processing) as within-subjects factors. Main effects and interactions with a p value of $\leq .10$ are noted in the tables for information purposes; however, only p values of $\leq .05$ are highlighted in the results section. Of major interest for the specific analyses associated with each question were the main effects and the interactions involving age (development) and condition (cognitive processing) factors. Region was of interest for all EEG power and coherence analyses as our EEG hypotheses examined age-related changes in the localization of working memory processing.

3. Results

Data were missing for one infant at 5 months who did not enter the study until 6 months of age. To avoid having this participant dropped from all of the multivariate analyses because of missing data, values of the missed session were interpolated from the data collected at the session adjacent to the missed session (i.e., 6 month visit). The interpolation procedure was chosen, as opposed to substituting the mean value of all subjects at the first visit, because the interpolation procedure yielded a substituted value that more closely resembles the individual infant's initial performance level. An additional infant had no useable ECG data at 8 months of age. Values for the missed session were interpolated from the data at the two sessions adjacent to the missed session (i.e., 7 and 9 month visits).

3.1. EEG power

Separate repeated-measures MANOVAs were performed on the ln EEG power values for each region (i.e., frontal pole, medial frontal, lateral frontal, central, temporal, medial parietal, lateral parietal, occipital) to assess power differences as a function of development and working memory processing. The within-subjects factors were age (i.e., 5, 6, 7, 8, 9, or 10 months), condition (i.e., baseline or task), and hemisphere (i.e., left or right). These analyses tested our hypotheses that (a) a main effect for age would occur at each electrode site, (b) baseline to task increases in power would occur at most, if not all, electrode sites, and (c) infants might exhibit initial evidence of localized activation between 5 and 10 months of age.

The results of the MANOVAs are displayed in Table 1. Only main effects and interactions involving age and condition are highlighted. There were main effects for age using baseline and task data at medial frontal ($\eta_p^2 = .72$), central ($\eta_p^2 = .71$), temporal ($\eta_p^2 = .72$), medial parietal ($\eta_p^2 = .71$), lateral parietal ($\eta_p^2 = .60$), and occipital ($\eta_p^2 = .57$) electrode sites. Visual inspection of Figure 1 reveals that baseline and task power values increased as a function of age.

To provide a detailed analysis of monthly age-related changes in baseline power, pairwise comparisons were conducted for regions that exhibited significant main effects for age (see Table 2). As can be seen, all regions exhibited similar patterns of age-related changes in baseline EEG power. EEG from adjacent months did not exhibit increases in baseline power values, with the exception of 7 to 8 months. There were significant increases in baseline

power values for most regions when intervals longer than 1 month were compared. However, after 8 months, there were few age-related changes in baseline EEG power.

In addition to the main effects for age noted in the preceding paragraphs and specific to our examination of cognitive processing, the separate regional analyses also showed that there was a main effect of condition for all electrode sites ($\eta_p^2 = .40 - .70$). Power values were higher during the task than during baseline (see Table 1 and Figure 1). Likewise, there was a Condition $\times$ Age interaction for the medial parietal, $\eta_p^2 = .55$, and lateral parietal, $\eta_p^2 = .65$, electrode sites. For lateral parietal electrode sites, post-hoc analyses confirmed that there was a main effect of condition at each age, all p s $\leq .051$, with EEG power values higher at task than during baseline. Visual inspection of Figure 1 suggests that the magnitude of task-related changes in power was greater for younger infants than older infants. For medial parietal electrodes, post-hoc analyses revealed that the main effect of condition was only present from 5 to 7 months of age, when task EEG power values were higher than at baseline (Figure 1).

3.1.2. EEG coherence—Separate repeated-measures MANOVAs were performed on the EEG coherence values for each regional electrode pair (i.e., frontal pole-medial frontal, medial frontal-lateral frontal, medial frontal-central, medial frontal-temporal, medial frontal-medial parietal, medial frontal-lateral parietal, medial frontal-occipital) to assess coherence differences as a function of development and working memory processing. The within-subjects factors were age, condition, and hemisphere. These analyses tested our hypotheses that (a) some electrode pairs would exhibit a main effect for age and other electrode pairs would not, (b) baseline to task decreases in coherence would occur in all electrode pairs, and (c) infants might exhibit initial evidence of localized activation between 5 and 10 months.

The results of the MANOVAs are displayed in Table 3. Only main effects and interactions involving age are highlighted. A main effect of age was found in four electrode pairs using baseline and task data: frontal pole-medial frontal ($\eta_p^2 = .74$), medial frontal-lateral frontal ($\eta_p^2 = .53$), medial frontal-medial parietal ($\eta_p^2 = .61$), medial frontal-occipital ($\eta_p^2 = .74$). Visual inspection of Figure 2 reveals that baseline and task coherence values increased for those electrode pairs as a function of age.

Pairwise comparisons of monthly baseline coherence values were conducted for electrode pairs that exhibited significant main effects for age (see Table 2). As can be seen, most electrode pairs exhibited similar patterns of age-related changes in monthly baseline EEG coherence values. Baseline coherence values obtained at 5 months were relatively stable until 8 months of age when infants exhibited significantly higher coherence values. Between 6 and 8 months, infants exhibited increases in baseline coherence after intervals of 1 month or longer. Just as with baseline EEG power, after 8 months of age, there were few monthly changes in baseline EEG coherence values.

In addition to the main effects for age noted in the preceding paragraphs and specific to our examination of cognitive processing, the separate regional analyses revealed no main effects of condition in any of the electrode pairs (see Table 3), in contrast to the main effects of condition seen in the EEG power data.

3.1.3. ECG—To assess HR differences as a function of development and working memory processing, a repeated-measures MANOVA was completed using age and condition as within-subjects factors. There was a main effect for age, $F(5, 15) = 7.35$, $p = .001$, $\eta_p^2 = .71$. As can be seen in Figure 3, HR decreased as a function of age across baseline and task data. Pairwise comparisons of month-to-month changes of HR are reported in Table 2. Baseline HR values at 5 months remained relatively stable until 8 months of age when infants

exhibited significantly lower HR. At 6, 7, and 9 months of age, infants exhibited decreases in baseline HR after intervals of 1 month or longer. There was no main effect or interaction involving condition.

4. Discussion

We used a longitudinal design to investigate age-related changes in EEG power, EEG coherence, and HR during baseline and as a function of cognitive processing during the infant working memory task. These data provide a unique contribution to the literature by assessing the same psychophysiological measures monthly between 5 and 10 months of age. Furthermore, these data yield valuable information regarding the particular psychophysiological correlates of working memory processing as a function of age.

4.1. Development of EEG and ECG: 5 to 10 months

Baseline levels of EEG power increased as a function of age for all electrode sites except frontal pole and lateral frontal. Infant EEG researchers have considered increasing EEG power values as a function of age to be indicative of brain maturation and our findings confirm previous evidence of age-related increases in power (Marshall et al., 2002; see Bell, 1998; Bell and Fox, 1994, for reviews). In follow-up analyses, the increases in baseline EEG power were not evident in 1-month intervals, except between 7 and 8 months of age, but the increases were evident in 2-month or more intervals, except at 8 to 10 months of age. We have previously focused our research efforts on 8-month-old infants (Bell, 2001, 2002; Bell, in press) because that age group offers the greatest variability of performance on the A-not-B task (Bell & Adams, 1999). It may be that the changes in EEG power around 8 months are associated with the wide range in task performance at that same age. Unfortunately, these data cannot reveal whether the changes in EEG power are driving the variability in task performance or vice versa.

Frontal pole and lateral frontal scalp locations were the only areas that failed to exhibit age-related increases in EEG power between 5 and 10 months, even though medial frontal electrode sites did show age-related changes. The frontal lobe exhibits protracted development (e.g., Chugani, 1994; Huttenlocher, 1990; Richards, 2010), and it is likely that developmental changes in EEG power at frontal pole and lateral frontal electrode sites would have been exhibited if infants were tested at slightly older ages.

EEG coherence values also increased as a function of age for frontal pole-medial frontal, medial frontal-lateral frontal, medial frontal-medial parietal, and medial frontal-occipital electrode pairs. Previous longitudinal research between 7 and 12 months had found U-shaped (medial frontal-medial parietal) and stable (medial frontal-occipital) patterns of coherence development (Bell and Fox, 1994). It is plausible that this discrepancy is related to slightly different beginning and end age points of data collection. Our data support case study findings of age-related increases in frontal pole-medial frontal coherence between 6 and 12 months (Bell, 1998; Schmauder and Bell, 1995). The pattern of age-related change in EEG coherence parallels the pattern in EEG power.

According to Thatcher (1994; Thatcher et al., 1987), resting EEG coherence values reflect the number and strength of synaptic connections, thus indicating the level of connectivity between two scalp electrode sites (and, possibly two cortical areas). Coherence values have been hypothesized to be indicative brain organization because, unlike EEG power, they are not affected by arousal, opening or closing of the eyes, or changes in state (Thatcher, 1994). Recent cross-sectional research has found age-related increases in coherence values (13–25 Hz frequency band) for both short and long interelectrode distances from approximately 5 months to 4 years (Thatcher et al., 2008). Thus, there is initial evidence that increases in

coherence during the first few years may be related to brain organization. The pattern of changes in coherence in the present study is intriguing. Despite the absence of age-related changes in EEG power at frontal pole and lateral frontal electrodes, the same frontal electrodes exhibited increases in EEG coherence. Age-related increases in EEG coherence were also found between frontal and posterior electrodes. These increases in coherence among frontal electrodes and between frontal and posterior electrodes could potentially be setting the neurological foundations for early working memory development. Infants typically show a great deal of variability in A-not-B working memory performance around 8 months, the same time there is beginning to be noticeable growth in dendritic branches in the prefrontal cortex (Diamond, 2002). Frontal-parietal interactions are essential to spatial working memory (Nelson et al., 2000; Ungerleider et al., 1998), and age-related increases in medial frontal-parietal coherence might reflect increasing connectivity between these regions. These findings might also be interpreted as the result of increased myelination of long-distance axons between frontal and posterior sections and short-distance axons within the frontal cortex (e.g., Almli et al., 2007; Richards, 2010).

Finally, consistent with previous research (e.g., Bar-Haim et al., 2000), we found that HR decreased as a function of age between 5 and 10 months. A comparison of baseline EEG and HR measures revealed a similar pattern of relative stability from 5 to 7 months of age. We did not anticipate this finding. There are reports of correlations between EEG and HR changes in preterm infants (e.g., Pfurtscheller et al., 2008), but these reports are specific recordings at one point in time, not month-to-month associations between the two measures. More work is needed to determine if there is coupling between EEG and ECG measures in early development.

4.2. EEG and ECG during working memory processing: 5 to 10 months

Differences in brain electrical activation between baseline and task has been used an indicator of cognitive processing in both infants and adults (e.g., Bell, 2001, 2002; see Klimesch, 1999, for review). In the present study, infants exhibited task-related increases in EEG power values for all electrode sites. This finding confirms previous evidence of task-related changes in EEG power during working memory and anticipatory attention tasks (Bell, 2001, 2002; Orekhova et al., 2001). However, working memory-related changes in EEG power were previously only examined at 8 months of age (Bell, 2001, 2002). Our findings provide initial evidence that infants, as young as 5 months, exhibit changes in brain electrical activation as a function of working memory processing.

The localization of cognitive processing is an intriguing aspect of development. By 4.5 years, children exhibit localized (medial frontal electrode sites) task-related changes in EEG power during a working memory task (Bell and Wolfe, 2007). In the current study, for most scalp locations, infants between 5 and 10 months of age exhibited the same pattern of task-related changes in EEG power. However, there was initial evidence of localized, as compared to widespread, changes in EEG power; for medial parietal scalp locations, only younger infants (5–7 months) exhibited task-related changes in EEG power, and for lateral parietal scalp locations, the magnitude of task-related changes in EEG power appeared greater for younger infants than older infants (see Figure 1). We hypothesize that infants older than 10 months would not exhibit task-related changes in EEG power at lateral parietal scalp locations.

Our longitudinal data failed to show task-related changes in medial frontal EEG coherence for any electrode pair. Previous studies that have found task-related changes in medial frontal EEG coherence at 8 months of age had larger sample sizes (Bell, 2001; Bell, in press; Bell and Wolfe, 2007). It is plausible that the present study did not have sufficient statistical power to reveal a main effect of condition for medial frontal EEG coherence measures.

According to Thatcher (1994), EEG resting coherence reflects the strength and number of synaptic connections between two cortical areas. Between 3 and 9 months of age, there are extensive increases in frontal white matter (i.e., myelinated axons) (Almli et al., 2007; Richards, 2010). Thus, prior to substantial myelination of frontal axons, medial frontal EEG coherence may not be as robust of a measure of cognitive processing as EEG power. Future research with larger sample sizes will provide additional information about the development of task-related changes in medial frontal EEG coherence between 5 and 10 months of age.

Finally, there were no task-related changes in HR between 5 and 10 months of age. This finding was unexpected: Working memory research with 8-month-olds has found that the direction of task-related changes in HR varied as a function of task performance (Bell, in press). Perhaps we failed to find task-related changes in HR because we did not analyze these findings in relation to individual differences in task performance. On the other hand, decreases in HR have been reported in studies of infant attention which typically obtain a prestimulus baseline prior to each look trial (Courage et al., 2006; see Richards, 2004, for review). Although a continuously updated baseline is not compatible with the design of the A-not-B task, it likely provides a more sensitive measure of HR changes during cognitive processing than a baseline measure taken prior to the experimental manipulation. Clearly, additional research is necessary to determine whether our null findings were related to variability in task performance or the sensitivity of our HR measure.

In sum, our data showed age-related baseline increases in EEG power (all electrode sites except frontal pole and lateral frontal), increases in EEG coherence (medial frontal paired with frontal pole, lateral frontal, medial parietal, or occipital), and decreases in HR. The age-related patterns were similar for EEG power, coherence, and HR. Likewise, across age, there were task-related increases in EEG power (all electrode sites except medial parietal). There were no task-related changes in medial frontal EEG coherence or HR. These data provide developmental researchers with a longitudinal reference of age- and working memory-related changes in psychophysiological measures from 5 to 10 months. Only one task of infant working memory was used in the present study, and future research with other infant working memory tasks is needed to assess the generalizability of these findings.

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Figure 1.

EEG power values (ln 6–9 Hz) during baseline (filled symbols) and task (open symbols) for infants between 5 and 10 months age.

Figure 2. EEG coherence values (6–9 Hz) during baseline (filled symbols) and task (open symbols) for infants between 5 and 10 months.

Figure 3. Heart rate during baseline (filled symbols) and task (open symbols) for infants between 5 and 10 months age.

Developmental and Cognitive Processing Analyses of EEG Power: Summary of Multivariate Analyses F Values for Baseline and Task Activation Comparisons

Table 1

	df	Fp1/Fp2	F3/F4	F7/F8	C3/C4	T7/T8	P3/P4	P7/P8	O1/O2
Age	5,15	2.29 ⁺	7.63***		7.25***	7.74***	7.51***	4.50**	4.02*
Hemi	1,19				3.98 ⁺	4.43*			
Condition	1,19	27.80***	12.57**	34.16***	12.70**	29.36***	14.62***	44.01***	25.85***
Age × Hemi	5,15			2.70 ⁺					
Age × Cond	5,15						3.68*	4.12*	
Hemi × Cond	1,19								4.15 ⁺
A × H × C	5,15								

Note. Fp1/Fp2 = frontal pole; F3/F4 = medial frontal; F7/F8 = lateral frontal; C3/C4 = lateral central; T7/T8 = temporal; P3/P4 = medial parietal; P7/P8 = lateral parietal; O1/O2 = occipital.

p ≤ .001;

**
p ≤ .01;

*
p ≤ .05;

+
p ≤ .10.

Table 2

Month-to-Month Pairwise Comparisons of EEG Power, EEG Coherence, and Heart Rate

F3/F4	C3/C4	T7/T8	P3/P4	P7/P8	O1/O2	Fp1-F3 Fp2-F4	F3-F7 F4-F8	F3-P3 F4-P4	F3-O1 F4-O2	HR
5-6				+	**					
5-7	*	+		+	*	+				
5-8	*	*	*	**	**	*	**	*	*	**
5-9	***	***	***	***	***	***	**	*	**	**
5-10	**	**	**	**	***	***	*	*	***	***
6-7						*		+		
6-8	**	***	**	**	+	*	+	**	*	**
6-9	***	***	***	***	***	***	+	***	***	*
6-10	***	***	**	**	**	***		**	***	***
7-8	**	+	**	*	*		*	*		+
7-9	***	**	***	***	*	***	*	*	***	
7-10	***	***	***	**	*	*	+		***	*
8-9	+					*			*	
8-10		*				+			*	
9-10										*

Note. F3/F4 = medial frontal; C3/C4 = central; T7/T8 = temporal; P3/P4 = medial parietal; P7/P8 = lateral parietal; O1/O2 = occipital; Fp1-F3/Fp2-F4 = frontal pole-medial frontal; F3-F7/F4-F8 = medial frontal-lateral frontal; F3-P3/F4-P4 = medial frontal-medial parietal; F3-O1/F4-O2 = medial frontal-occipital; HR = heart rate.

p ≤ .001;

**
p ≤ .01;

*
p ≤ .05;

+
p ≤ .10.

Developmental and Cognitive Processing Analyses of EEG Coherence: Summary of Multivariate Analyses F Values for Baseline and Task Activation Comparisons

Table 3

	<i>df</i>	Fp1-F3	F3-F7	F3-C3	F3-T7	F3-P3	F3-P7	F3-O1
		Fp2-F4	F4-F8	F4-C4	F4-T8	F4-P4	F4-P8	F4-O2
Age	5,15	8.69***	3.40*			4.61**	2.46 ⁺	8.65***
Hemi	1,19	12.62**			12.79**			
Condition	1,19		3.13 ⁺					
Age × Hemi	5,15							
Age × Cond	5,15							
Hemi × Cond	1,19							
A × H × C	5,15					2.85 ⁺		

Note. Fp1-F3/Fp2-F4 = frontal pole-medial frontal; F3-F7/F4-F8 = medial frontal-lateral frontal; F3-C3/F4-C4 = medial frontal-central; F3-T7/F4-T8 = medial frontal-temporal; F3-P3/F4-P4 = medial frontal-medial parietal; F3-P7/F4-P8 = medial frontal-lateral parietal; F3-O1/F4-O2 = medial frontal-occipital.

 $p \leq .001$;

**
 $p \leq .01$;

*
 $p \leq .05$;

+
 $p \leq .10$.