The Utility of EEG Band Power Analysis in the Study of Infancy and Early Childhood

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Abstract

Research employing electroencephalographic (EEG) techniques with infants and young children has flourished in recent years due to increased interest in understanding the neural processes involved in early social and cognitive development. This review focuses on the functional characteristics of the alpha, theta, and gamma frequency bands in the developing EEG. Examples of how analyses of EEG band power have been applied to specific lines of developmental research are also discussed. These examples include recent work on the infant mu rhythm and action processing, frontal alpha asymmetry and approach-withdrawal tendencies, and EEG power measures in the study of early psychosocial adversity.

Within developmental science there remains great interest in integrating behavioral and neurophysiological measures in order to better explain developmental phenomena. This interest is being captured by the growing field of developmental cognitive neuroscience, a term which is used here in a broad sense to capture not only aspects of cognitive development but also social and emotional themes (Blakemore, Dahl, Frith, & Pine, 2011). In this respect there are a variety of methods available in the toolbox of the developmental cognitive neuroscientist. Our focus here is on the electroencephalogram (EEG) which has a rich history and (in our opinion) a bright future in terms of its continuing utility in the study of psychological development in infants and young children.

In the absence of being able to obtain functional neuroimaging data using other methods used to assess brain activity in adults (e.g., fMRI), measures derived from the EEG have continued to play an important role in the study of various domains of infant development (de Haan, 2007b). While developmental aspects of the EEG have been of interest to psychologists for decades, recent years have seen the emergence of new methods for assessing brain activity in infants. Two such methods are the magnetoencephalogram (MEG) and near-infrared spectroscopy (NIRS), both of which hold a good deal of promise for advancing our understanding of brain-behavior relations in early human development. Despite growing interest in such potentially very useful technologies, EEG remains very relevant due to a number of key strengths. First, EEG systems are relatively inexpensive and there is a good deal of choice in terms of application methods and options for hardware and software. Second, with the capacity to allow analyses on the millisecond timescale, the temporal precision of EEG methods is a clear strength. Third, EEG methods allow neurophysiological data to be collected in a relatively unconstrained laboratory environment. With appropriate strategies for data collection and analysis with infants and young children (see Hoehl & Wahl, in press), EEG data can be utilized from "real-time" laboratory tasks,

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with the potential to analyze electrophysiological data in relation to infants' ongoing behavior (Reynolds & Guy, in press).

Our particular emphasis in this article is on the analysis of EEG band power via the traditional approach of differentiating between functionally distinct bands such as theta, alpha, beta, and gamma. This approach involves the decomposition of the EEG signal into component frequency bands, each of which has different functional characteristics. In adults, typical frequency bands and their approximate spectral boundaries are delta (1–3 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (30–100 Hz). As we later note in some detail, the boundaries of corresponding bands appear to be lower in infants and children.

The decomposition of the overall power in the EEG signal into individual bands is commonly achieved through Fourier transforms and related methods for spectral analysis (see Dumermuth & Molinari, 1987). Prior to the advent of such computational methods in the 1970s, different EEG frequency components were identified using more qualitative methods. Indeed, early developmental work on the human EEG involved visual analysis of waveforms in order to identify dominant frequencies and to describe fluctuations in amplitude at these frequencies that could be induced by various kinds of sensory stimulation.

In terms of analysis approaches, one distinction that can be made in the developmental literature is between the quantification of band power over a period of tens of seconds or minutes (to index more tonic activity) or the quantification of phasic changes in band power over much shorter time intervals, on the order of hundreds of milliseconds or a few seconds. While much of the EEG research in social and cognitive development in infancy has employed the former approach, the latter paradigm is gaining traction in the developmental EEG literature. This approach often involves the use of event-related methods for assessing changes in band power that are time-locked to a particular event. This form of frequency analysis may also involve the computation of a continuous measure of band power or amplitude, with time-frequency plots being a related, useful tool for visualizing frequency-specific, event-related changes in EEG power. Note that such changes are not phase-locked to the event of interest and therefore require frequency analysis rather than the averaging process that characterizes the commonly used event-related potential (ERP) measures that are also derived from EEG responses to discrete events (for a review of ERP methods with infants see Hoehl & Wahl, in press). Short-term, frequency-specific changes in the EEG signal take the form of transient increases or decreases in band power relative to a baseline or other reference condition.

Infant EEG Bands

In this review we primarily consider the alpha, theta, and gamma frequency bands, since they have been the main bands of interest for developmental cognitive neuroscientists. In contrast, there is much less research in this area on delta or beta-range rhythms in infants and young children, and we will not discuss these bands further here.

In part because of their historical predominance in the study of infant EEG development, we begin with a general summary of work on alpha-range rhythms in infancy, followed by a consideration of developmental research on theta and gamma rhythms. We then move on to describe three specific examples of how EEG measures have informed the study of early social and cognitive development: 1) Central mu rhythms and action processing in infancy; 2) Frontal EEG alpha asymmetry and approach-withdrawal tendencies; 3) The use of EEG band power measures in the study of early psychosocial adversity.

Alpha-range Rhythms

Posterior alpha rhythms—Early studies of the development of the EEG signal noted a dominant occipital rhythm that emerged around 3 months of age with a peak frequency of 3–5 Hz which increased to 6–7 Hz by 12 months of age (for a review of ERP methods with infants see Lindsley, 1938, 1939; Smith, 1938a; Smith, 1938b, 1941). These authors labeled this rhythm "alpha" since its posterior dominance resembled the classical alpha rhythm in adults, which oscillates in the frequency range of 8–13 Hz and is strongest at occipital sites. Ever since Hans Berger's classic work in the early 1930s, it has been known that the classical posterior alpha rhythm in adults is sensitive to qualitative changes in visual input, being increased in amplitude when the eyes are closed and becoming reduced in amplitude when the eyes are opened.

Early work by Lindsley (1938) found the infant posterior rhythm to be reduced in amplitude by visual stimulation, suggesting a functional similarity to the adult alpha rhythm. More recent work has solidified this suggestion. In a detailed study of EEG development in 7- to 12-month-old infants, Stroganova, Orekhova, and Posikera (1999) recorded EEG under two conditions: Complete darkness and visual attention to an interesting stimulus (soap bubbles). Changes in power between these two conditions were then examined over a range of narrow frequency bins in order to specifically identify the infant alpha band at occipital sites. During darkness compared to visual attention, spectral amplitude in the 5.6–9.6 Hz range was maximal at occipital electrode sites and was significantly attenuated in amplitude during visual attention. Stroganova et al. (1999) suggested that the properties of this rhythmic activity at occipital sites are consistent with the reactivity and scalp distribution of the classical adult alpha rhythm. In this respect it is notable that mapping between infant and adult bands may be clearer for posterior alpha than for other alpha-range rhythms or for other frequency bands. Indeed, some infant EEG researchers (e.g., Bell & Wolfe, 2008) remain reticent to firmly apply adult labels to infant bands, preferring to refer to particular frequency ranges rather than labeling specific bands.

In terms of frequency changes, Stroganova et al. (1999) reported that the mean peak frequency of the occipital rhythm increased from 6.24 Hz in infants aged 7–9 months to 6.78 Hz in infants aged 10–12 months. A recent study of younger infants reported a modal peak frequency of 4 Hz for infants between one week and one month of age, with this frequency increasing to 5 Hz for 3-month-old infants (Diego, Jones, & Field, 2010). The results of Stroganova et al. (1999) and Diego et al. (2010) are broadly similar to those of much earlier studies (using visual analysis) which reported that the primary frequency of the posterior rhythm in infants increased from 3–5 Hz at 3 months of age to 6–7 Hz at 12 months of age (Smith, 1938b, 1941).

The reduction in amplitude or power of the posterior alpha rhythm with qualitative changes in visual stimulation can be thought of as activity-related desynchronization of oscillatory activity in the visual cortex. In this sense, high amplitude states of the alpha rhythm (i.e., synchronization) may represent an inactive or "idling" state of underlying cortical areas (Pfurtscheller, Stancak, & Neuper, 1996). Another possible mechanism for regional patterns of desynchronization and synchronization is that activation of one cortical area is accompanied by simultaneous inhibition of surrounding areas (Neuper & Pfurtscheller, 2001). Indeed, it has been suggested that synchronization in the adult alpha frequency range reflects active, top-down inhibition of task-irrelevant cortical areas (Klimesch, Doppelmayr, & Hanslmayr, 2006; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999). In infants, Orekhova, Stroganova, and Posikera (2001) extended this notion to the posterior alpha rhythm. EEG was collected from infants aged between 8 and 11 months during a peek-a-boo game. Infants who maintained anticipatory attention in the peek-a-boo game for longer periods showed greater synchronization of the alpha rhythm at parietal electrode sites

during the anticipatory phase compared to infants with shorter periods of anticipatory attention. This finding was interpreted as reflecting the suppression of information from the peripheral visual field and facilitating attention to the peek-a-boo game (Orekhova et al., 2001).

Central alpha rhythms—Early studies of EEG development documented a rhythm at central sites in infants that appeared to fall within the same frequency range as the occipital alpha rhythm. In his classic work, Smith (1939, 1941) reported the emergence of a 7 Hz oscillation at central recording sites around 4 months of age. The mean frequency of this rhythm increased to 8 Hz by 18 months of age. Smith labeled this rhythm "central alpha" and hypothesized that its development was linked to the loss of infant reflexes and the emergence of voluntary motor control. Hagne, Persson, Magnusson, and Petersen (1973) also observed a central rhythm in a cross-sectional study of EEG development during the first year of life. In this sample, a distinct central rhythm was not visible in power spectra from infants at 4 months of age, but could be observed by 6 months of age. Hagne et al. (1973) reported the peak frequency of the central rhythm increased from 6 Hz at 6 months to 7 Hz by 12 months of age. In line with the ideas of Smith (1941), these authors speculated that the development of the central rhythm was related to the development of motor abilities.

More recent work has confirmed the early reports of the development of a central rhythm. In a longitudinal study from infancy to early childhood, Marshall, Bar-Haim, and Fox (2002) observed a distinct rhythm over central sites at 10, 14, 24, and 51 months of age during periods of quiet attention to a visual stimulus. No similar peak was visible at 5 months. The rhythm had a peak frequency of 7–8 Hz at the infant assessments, increasing to 9 Hz in early childhood.

While early work established the presence of a prominent alpha-range central rhythm in the EEG of infants, more recent work has examined the functional correlates of this rhythm. In their study of 7- to 12-month-old infants, Stroganova et al. (1999) found that the central rhythm in infancy showed quite different functional reactivity compared with the posterior alpha rhythm. In contrast to the posterior rhythm, the central rhythm (which occurred in the range of 6.0–8.8 Hz) was synchronized during visual processing and was desynchronized during darkness. Based on this finding, Stroganova et al. (1999) speculated that the central rhythm in infancy was a developmental analog of the adult mu rhythm. In adults, the mu rhythm occurs in the same frequency range as the posterior alpha rhythm (8–13 Hz), but is considered a distinct alpha-range oscillation due to its different topographical and functional properties (Niedermeyer, 1997).

Early work on the adult mu rhythm by Gastaut, Dongier, and Courtois (1954) showed a desynchronization of the mu rhythm during overt movement, a finding that has been followed up by an array of more recent work (Pfurtscheller & Lopes da Silva, 1999). In addition, a number of other recent studies have found that the adult mu rhythm is also desynchronized during the observation of movement (Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, & McNair, 2004; Perry & Bentin, 2009; Pineda, Allison, & Vankov, 2000). Recent work with infants has suggested the central rhythm in the infant EEG shows a similar desynchronization during action production and action observation (Marshall, Young, & Meltzoff, 2011; Southgate, Johnson, Osborne, & Csibra, 2009). More details of this work will be discussed in the specific section on central mu rhythms and action processing later in this manuscript.

Theta Rhythms

In adults, theta (4–8 Hz) oscillations are often observed during the transition from wakefulness to sleep. In the awake EEG, an increase in theta-range power has been

associated with the processing of emotional information (Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2001; Sammler, Grigutsch, Fritz, & Koelsch, 2007) and during memory-related tasks (Gevins, Smith, McEvoy, & Yu, 1997; Kahana, Seelig, & Madsen, 2001; Khader, Jost, Ranganath, & Rosler, 2010; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010).

While there has been less attention devoted to theta rhythms than to alpha rhythms in early development, some studies have attempted to relate lower frequency EEG activity in the theta band to cognitive and emotional functioning in infancy. Such studies have linked infant theta activity with the expression of positive (Kugler & Laub, 1971; Maulsby, 1971) and negative (Futagi, Ishihara, Tsuda, Suzuki, & Goto, 1998; Hagne, 1972) emotions, feeding (Futagi et al., 1998; Lehtonen, Kononen, Purhonen, Partanen, & Saarikoski, 2002; Paul, Dittrichova, & Papousek, 1996), drowsiness (Futagi et al., 1998), and the modulation of attention (Orekhova, Stroganova, & Posikera, 1999). Within this work, the specific frequency range of a putative infant theta band has been inconsistent across studies, with the modal frequency range used being approximately 3–6 Hz.

Adult work reports differing scalp topographies of the theta response for different tasks, with these various patterns likely representing the contribution of different cortical networks (Kirk & Mackay, 2003). Similarly, the topographical distribution of infant theta appears to depend on the behavior under study. In a group of infants from 2 to 11 months of age, Futagi et al. (1998) found that theta activity was maximally synchronized over frontal regions during handling of toys, over posterior regions during feeding and crying, and over central and parietal regions during gazing. Another set of infant studies has linked frontal theta to the executive control of attention (Orekhova et al., 1999; Stroganova, Orekhova, & Posikera, 1998). These authors recorded EEG from infants aged between 7 and 11 months during a peek-a-boo game and during quiet visual attention (watching soap bubbles). Theta activity (which was assessed as power in the 3.6–4.8 Hz range) was significantly greater over frontal regions during the anticipatory period of the peek-a-boo game compared to periods of quiet attention (Orekhova et al., 1999). In general, greater increases in theta amplitude were observed among younger infants compared to older infants, although there were other, somewhat complex effects involving age. Specifically, the magnitude of theta synchronization was positively correlated with duration of visual attention in infants aged 7–8 months, but negatively correlated in infants aged 9–10 months. According to Orekhova et al. (1999), the task of maintaining attention may become easier with age and therefore the amount of frontal activation needed for the task decreases. This is consistent with the adult literature, in which greater frontal theta synchronization for more demanding tasks has been reported (for review see Inanaga, 1998).

Further links between frontal theta and executive control of attention were suggested in a study with 5-month-old infants (Bazhenova, Stroganova, Doussard-Roosevelt, Posikera, & Porges, 2007). Infants sat facing an adult experimenter who alternated between smiling and looking blankly at the infant. Power in the theta band increased at frontal sites when the adult's smiling face was replaced with the blank expression. Looking time analyses revealed that infants showed a significant increase in attention to the blank face compared to the smiling face. Based on this, Bazhenova et al. (2007) suggested that the increase in theta amplitude at frontal sites reflected activation of areas involved in executive control of attention, in this case related to infants' attempts to reengage with the experimenter.

Phasic increases in power in the putative infant theta band have been observed in infants as young as 18 to 26 weeks of age in response to feeding (Paul et al., 1996), with Lehtonen et al. (2002) reporting an age-related increase in this response from 3 to 6 months of age. A larger study of infants between 2 and 11 months of age also found a developmental increase

in the theta response to feeding (Futagi et al., 1998), although it is not clear from other studies whether there is a developmental increase in theta amplitude during other tasks or activities. In addition, unlike the infant alpha rhythm, there is very little extant information on changes in the frequency of the theta rhythm during infancy (Stroganova & Orekhova, 2007).

During childhood, the resting EEG of typically developing children displays a developmental decrease in the relative contribution of low-frequency rhythms (i.e., theta) and an increase in the salience of higher-frequency rhythms (i.e., alpha and beta) (Corbin & Bickford, 1955; Gibbs & Knott, 1949; John et al., 1980; Matousek & Petersen, 1973). In line with this pattern, theta-range power is particularly evident in EEG power spectra from infant samples, but is less salient for adults, with higher-frequency rhythms (particularly alpha and beta) being more prevalent (Miller, 2007). It has been suggested that the high levels of theta in the EEG of infants and young children reflect a brain state that is optimal for synaptic plasticity (Stroganova & Orekhova, 2007). This suggestion is partly based on a growing body of literature linking the adult theta rhythm to the formation of long-term memories (Khader et al., 2010; Klimesch, Doppelmayr, Russegger, & Pachinger, 1996). In line with this work, a recent theoretical proposal linked infant theta activity to visuomotor learning. Working on the assumption that theta activity occurs in a suitable range to promote Hebbian learning processes between different brain regions, Del Giudice, Manera, and Keysers (2009) proposed a role for theta-range brain oscillations in the development of a neural system for relating visual, sensory, and motor information about ongoing events and actions. Part of this proposal is based on observations that frontal theta increases in amplitude during infants' reaching and handling of objects (Futagi et al., 1998).

At this point it is worth noting that while the above line of theory suggests that phasic increases in theta may be related to adaptive processes of plasticity, an excess of tonic theta activity in the resting EEG of infants and children has been associated with learning and attentional disorders (Barry, Clarke, & Johnstone, 2003; Clarke, Barry, McCarthy, & Selikowitz, 2002; Snyder & Hall, 2006). High levels of theta have also been observed in children raised in aversive environments such as institutions (Marshall, Fox, & the BEIP Core Group, 2004). The interpretation of such findings is reviewed in more detail in a later section of this manuscript.

Gamma Rhythms

Studies of the gamma rhythm in infants and adults have mainly focused on the relation of higher frequency EEG oscillations to particular cognitive and perceptual processes. The gamma rhythm in adults (30–100 Hz) has been associated with the perceptual binding or the unification of various features of objects (Muller et al., 1996) - a phenomenon that was first described in animal work (Gray, Konig, Engel, & Singer, 1989). Subsequent studies of the adult gamma rhythm have solidified a link between gamma and object perception (Gruber & Muller, 2005; Gruber, Muller, & Keil, 2002) and also to attentional (Muller, Gruber, & Keil, 2000; Pantev et al., 1991; Tiitinen et al., 1993), and language-related (Pulvermuller et al., 1996) processes. Since many of the tasks used in this area involve active memory requirements, some researchers have also proposed that gamma activity reflects general processes related to retrieval (Engel, Fries, & Singer, 2001; Herrmann, Frund, & Lenz, 2010; Herrmann, Munk, & Engel, 2004). One of these proposals is the model of Herrmann et al. (2004) which states that gamma-band activity reflects the matching of sensory signals with memory contents. According to this hypothesis, familiar stimuli should evoke a greater gamma-band response compared to unfamiliar stimuli. This suggestion has been supported by studies in adults comparing gamma-band responses to words and pseudowords (Pulvermuller et al., 1996) as well as to upright faces versus inverted faces and abstract shapes (Keil, Muller, Ray, Gruber, & Elbert, 1999; Rodriguez et al., 1999).

In terms of infant work, it has been proposed that high-frequency oscillations (20–60 Hz) in the infant EEG map onto the adult gamma rhythm, with developmental changes in the gamma response relating to changes in infants' perceptual capacities. In an initial study of the infant gamma response, Csibra, Davis, Spratling, and Johnson (2000) showed 6- and 8-month-old infants static images of spatially separated elements arranged to form an illusory square (Kanizsa squares). Csibra et al. (2000) compared EEG responses to the presentation of the Kanizsa squares with responses to a control stimulus, which was composed of the same elements in a different (non-illusory) configuration. Based on a habituation study that found 7-month-old infants can reliably perceive such illusory objects, but younger infants cannot (Ghim, 1990), Csibra et al. (2000) predicted the presentation of the Kanizsa squares would evoke an increase in power for high-frequency (~40 Hz) oscillations in 8-month-olds, but not in 6-month-olds. These predictions were confirmed and were interpreted as reflecting an increased capacity for perceptual binding in the older age group.

In adults (Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998) and infants (Kaufman, Csibra, & Johnson, 2003, 2005), gamma oscillations have also been proposed as reflecting the active maintenance of objects in memory. In support of this, an increase in gamma activity was observed in the EEG of 6-month-old infants over the right temporal cortex during the occlusion of an object (Kaufman et al., 2003, 2005). Kaufman et al. (2003) included a condition in which the object was absent when the occluder was removed. For this condition, a second burst of gamma activity was observed over the right temporal cortex. The authors suggested that the initial increase in gamma reflected the maintenance of a representation of the occluded object, and that the second increase reflected infants' attempts to reconstruct the object from memory when it failed to reappear. A more recent study of 6-month-old infants also reported an increase in gamma during the occlusion of objects, with no increase being observed during the occlusion of faces (Southgate, Csibra, Kaufman, & Johnson, 2008). Southgate et al. (2008) also manipulated the objects and faces so that the objects and faces that were revealed after occlusion changed in terms of their surface features. The presentation of an old face following occlusion, but not a new face, was associated with a decrease in gamma activity. For the object condition, both old and new objects were associated with a decrease in gamma. According to Southgate et al. (2008), these results suggest that infants detected the change in the face, but did not detect the change in the object.

Also consistent with the properties of the adult gamma rhythm, the infant gamma rhythm is evoked more strongly for familiar stimuli compared to unfamiliar stimuli. Grossmann, Johnson, Farroni, and Csibra (2007) showed 4-month-old infants images of female faces with direct and averted eye gaze. The direct eye gaze evoked significantly greater gamma activity over the occipital and prefrontal regions compared to the averted gaze. According to Grossmann et al. (2007), this finding reflects the fact that infants are more familiar with a face with a direct gaze compared to a face with an averted gaze. More recent work has directly examined this idea that familiar stimuli elicit greater gamma activation compared to unfamiliar stimuli (Gliga, Volein, & Csibra, 2010). Infants were shown familiar objects that the infant recognized by name (e.g., duck, cup), familiar objects for which the infant did not know by name (e.g., clock, butterfly), and unfamiliar objects (e.g., sushi, harp). The items for each participant had been selected by the parent from a list to reflect their infant's familiarity with the objects and their verbal comprehension. Gliga et al. (2010) found that familiar objects with labels known to the infant evoked greater gamma activity over occipital scalp regions compared to familiar objects with no familiar label, as well as unfamiliar objects.

In addition to familiarity, gamma activity can be modulated by attention in both adults (Muller et al., 2000; Ray, Niebur, Hsiao, Sinai, & Crone, 2008; Tiitinen et al., 1993) and

infants (Reid, Csibra, Belsky, & Johnson, 2007). In adult subjects, gamma activity is greater when attention to the task is high (Muller et al., 2000; Ray et al., 2008; Tiitinen et al., 1993). Reid et al. (2007) extended this to infants by showing 8-month-old infants videos of complete and incomplete pouring actions. Bursts of gamma activity were observed over left frontal regions when the action abruptly ended. This increase in gamma activation was significantly greater than gamma activation during the corresponding point in the complete action condition. One explanation proposed by Reid et al. (2007) is that the greater gamma response to the incomplete condition reflected an increase in attention to the video stimuli, since the infants' expectations of seeing the completed action had not been met.

Specific Examples Relating EEG Rhythms to Early Social and Cognitive Development

After having reviewed historical and recent research on the functional properties of EEG bands in infancy, we now briefly summarize three specific lines of developmental research which have attempted to relate EEG band power to social and emotional functioning in infancy. These concern the study of central rhythms and infants' action processing, frontal alpha asymmetry and approach-withdrawal tendencies, and the effects of early psychosocial adversity on the developing EEG.

Central Mu Rhythms and Action Processing in Infancy

As noted earlier in this review, there is increasing interest in the alpha-range rhythm which is present at central sites in infants and which appears to bear a resemblance to the adult mu rhythm. It has been known since the 1950s that the rolandic mu rhythm in adults is desynchronized during overt movement (Gastaut et al., 1954), with more recent work showing how mu desynchronization varies prior to, during and following the execution of actions (e.g., Pfurtscheller, Neuper, & Krausz, 2000). In recent years, interest in the mu rhythm has been amplified by findings suggesting that this oscillation is not only desynchronized during action execution but responds in a similar (albeit more subtle) way during the observation of others' actions. Presaged by the observations of Gastaut and Bert (1954), a number of EEG studies with adults have reported mu rhythm suppression during both the observation and execution of actions (see Pineda, 2005).

These findings have generated interest in the mu rhythm from cognitive neuroscientists who study the neural systems involved in action perception and action understanding in adults (Hari, 2006). Given the relative ease of employing EEG methods with infants, and the apparent existence of a possible infant counterpart of the adult mu rhythm, developmental scientists have also become interested in the utility of mu for informing studies of early social cognitive development (Marshall & Meltzoff, 2011).

Although earlier work had suggested similarities between the infant central rhythm and the adult mu rhythm, the functional relationship between these rhythms – in terms of its reactivity to action execution and observation - was not investigated until quite recently. This recent work has examined the following premises: First, if it was similar to the adult rhythm, that the infant mu rhythm would be desynchronized during action execution and second, that the infant mu rhythm would also be reactive to action observation. In this respect there was some precedent in terms of developmental work. Lepage and Théoret (2006) found alpha-range desynchronization at central sites during action observation and execution in a group of older children with a mean age of 8 years.

In terms of infants, a small number of recent studies have addressed mu reactivity to action execution and action observation in the first two years of life. In a study of 9-month-old infants, Southgate et al. (2009) recorded EEG during an execution phase in which infants grasped small toys and during an observation phase in which infants observed an

experimenter reach for and grasp the toys. They reported a small but significant desynchronization in the alpha-range during both conditions, with their analyses being constrained to a cluster of electrodes straddling the central and parietal regions. In a second study of 9-month-olds, Southgate, Johnson, El Karoui and Csibra (2010) used a similar protocol to Southgate et al. (2009), but they manipulated whether or not the outcome of the observed action was likely to be goal-directed. In this fine-grained manipulation, infants saw a reaching hand disappearing behind an occluder, such that the outcome of the action was not seen. The hand was either in a grasping configuration or was upturned and flat, with desynchronization of the mu rhythm only being observed for conditions in which the grasping hand was seen. The results of this study were interpreted as showing mu desynchronization during action observation as being a predictive response related to the assumed outcome of the action. Although this interpretation fits with the theoretical framework of Csibra (2007), more research is needed to establish specifically whether the mu response relates to specific aspects of the observed action being "predicted", or whether the mu response reflects more general processes (see Marshall & Meltzoff, 2011).

Another outstanding question about the infant mu rhythm concerns the scalp distribution of alpha-range EEG desynchronization to action execution and observation. In a recent study, Marshall et al. (2011) examined this issue by recording EEG from 14-month-old infants during an imitative protocol involving the execution and observation of a button-press action. Compared to baseline epochs in which infants were shown abstract visual patterns, the mu band was significantly desynchronized during the execution and observation of the button press. As in studies of adults, the desynchronization of alpha-range power was specific to central sites during action execution (Muthukumaraswamy & Johnson, 2004) but was more widespread during action observation (Babiloni et al., 2002; Marshall, Bouquet, Shipley, & Young, 2009).

Other studies of the infant mu rhythm have examined its reactivity to action observation, but without an action execution condition. In one of the first studies on this topic, van Elk, van Schie, Hunnius, Vesper, and Bekkering (2008) recorded EEG from 14- to 16-month-old infants while they viewed videos of other infants crawling or walking. Based on studies with adults that have found greater mu desynchronization for the observation of well-practiced actions (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005), van Elk et al. (2008) predicted greater desynchronization for crawling than walking since infants of this age usually have more cumulative experience with crawling than with walking. The results supported this prediction, such that desynchronization in the infant alpha band was greater during the observation of crawling compared to walking, and the amount of desynchronization was correlated with the amount of infants' crawling experience (van Elk et al., 2008). This finding is consistent with behavioral evidence that first-hand experience with an action changes infants' subsequent perceptions of that action (Meltzoff & Brooks, 2008; Sommerville, Hildebrand, & Crane, 2008; Sommerville, Woodward, & Needham, 2005). However, findings from EEG studies investigating the influence of experience on the adult mu response have been inconsistent (Babiloni et al., 2010; Marshall et al., 2009; Quandt, Marshall, Bouquet, Young, & Shipley, 2011).

While the emerging work on the infant mu rhythm suggests intriguing possibilities for work in this area to expand our understanding of the neural processes involved in early action processing, there remain a number of issues that need to be clarified. Marshall and Meltzoff (2011) recently outlined a number of open questions related to the infant mu rhythm that need to be addressed in order for this nascent area of research to move forward. One such question concerns developmental changes in the mu rhythm response. Infant investigations of the mu rhythm (Marshall et al., 2011; Southgate et al., 2009) have reported much smaller reductions in mu power during action execution and action observation compared to that

reported for older children and adults (Lepage & Théoret, 2006; Muthukumaraswamy et al., 2004). However, methodological differences between existing developmental studies make these comparisons difficult, and more research is needed.

A second question about the infant mu rhythm relates to the nature of the purported overlap between EEG activity during action perception and action production. Marshall and Meltzoff (2011) note that finding broad similarities in EEG desynchronization during action execution and action observation does not mean that the same neural systems are active in both conditions. Technologies with finer spatial resolution which are also possible with infants (such as MEG) may help elucidate a more specific answer to this question, although firmly establishing the presence of an overlap in neural activation remains a significant issue.

Another ongoing question surrounding the mu rhythm response in both adults and infant research is characterizing what exactly mu rhythm desynchronization represents. Currently the most widely accepted view is that changes in mu amplitude reflect activation of the motor system (Pineda, 2005). However, as noted by Marshall and Meltzoff (2011), this view tends to underemphasize the fact that the mu rhythm appears to originate in primary somatosensory cortex (Hari & Salmelin, 1997). One intriguing possibility is that mu desynchronization during action observation relates to the somatosensory (e.g., proprioceptive or tactile) consequences of the observed action (Keysers, Kaas, & Gazzola, 2010), although this question remains to be specifically addressed.

As we note in the conclusion of this paper, bringing together brain and behavioral data is a complex endeavor, and we should ask critical questions about the relations between measures from very different domains of study. Going beyond the open questions on central rhythms in infancy, the hope is that EEG data would be able to enrich and inform theories of early social cognitive development, especially cognitive theories about imitation (Meltzoff & Moore, 1997). We note, however, that in many ways the cognitive theory presages the neuroscience data, which are meaningless in isolation. Future work in this area will hopefully result in a productive interface between neuroscience and developmental theory.

Frontal EEG Asymmetry and Approach-Withdrawal Tendencies

Taking more of an individual differences perspective, a body of work examining EEG correlates of social-emotional behavior in infancy and early childhood has concerned the relation of hemispheric asymmetries in EEG activity at frontal electrode sites and developing approach/withdrawal tendencies. Various research groups have been involved in this area of infant EEG research over the last three decades, and it remains an active area of inquiry. The focus in this area has been on hemispheric asymmetry in EEG power in the general range of around 3–12 Hz over the frontal region, with a particular emphasis on the 6–9 Hz band. It is notable that not all authors have been comfortable with labeling this latter band "alpha" (Smith & Bell, 2010), but much of the work in this area has proceeded under the premise that this band bears some functional resemblance to the alpha rhythms over other scalp regions. In this sense, activity in the 6–9 Hz band has typically been seen as being inversely related to cortical activity over a given scalp region.

A major impetus for the study of infant frontal EEG asymmetry came in the early 1980s from the work of Davidson and Fox, who stressed the primacy of approach and withdrawal tendencies in emotional development and who developed a model for examining the neural correlates of such tendencies (Fox & Davidson, 1984). Their model was based on a variety of work showing an association between asymmetries in the frontal cortical region and motivational responses to appetitive or aversive stimuli (Fox, 1991). In this perspective, the left frontal region promotes appetitive, approach-directed emotional responses, while the

right frontal region promotes withdrawal-directed responses to perceived aversive stimuli. Over the last three decades there has been steady interest in how individual differences in approach or withdrawal behaviors in infancy and early childhood relate to patterns of asymmetrical EEG activity over frontal electrode sites.

In the first of a series of early studies with 10-month-olds, Davidson and Fox (1982) showed that infants watching a video of an actress crying or smiling displayed differential EEG patterns to the two displays, with greater right frontal EEG activation during the crying segments (as evidenced by lower alpha power on the right side). Fox and Davidson (1987) went on to show that infants showed reductions in power of the right frontal region (taken as indicating greater right frontal "activation") during the approach of an unfamiliar adult, and that the relative level of asymmetry was concurrently related to the type of facial expression of emotion that the infant displayed.

Research in this area then went on to center on the construct of behavioral inhibition to the unfamiliar, which refers to the tendency of some toddlers and young children to be wary of unfamiliar people, objects, and contexts (Kagan, Reznick, Clarke, Snidman, & Garcia-Coll, 1984). In one longitudinal study, infants who were consistently behaviorally inhibited at multiple assessments up to 4 years of age exhibited stronger right frontal activation asymmetry at 9 and 14 months of age than infants who became less inhibited over time (Fox, Henderson, Rubin, Calkins, & Schmidt, 2001). Earlier work also showed that infants who displayed a stable pattern of greater right frontal activation during quiet visual attention across the first two years tended to be more behaviorally inhibited at both 14 and 24 months of age compared with infants who exhibited a pattern of stable greater left frontal activation (Fox, Calkins, & Bell, 1994). More recently, Smith and Bell (2010) reported that infants with stable right frontal asymmetry (at 10 and 24 months) were rated by their mothers as being higher in internalizing behaviors at 30 months of age. This latter study also suggested that infants who had stable left frontal asymmetry over the prior age points were rated as higher in externalizing behaviors. This finding reflects a growing interest in the association between left frontal asymmetry and approach-related emotions, including anger. This link was also a key part of a recent study by He et al. (2010), who found that that frontal EEG asymmetry at 9 months of age moderated the relation between the behavioral expression of anger at 4 months (elicited in response to arm restraint) and behavioral approach to an unpredictable toy at 9 months of age. Specifically, infant reactivity to arm restraint at 4 months predicted greater approach responses to an unpredictable toy at 9 months, but only among those infants who showed an overall left frontal EEG asymmetry at 9 months of age.

Much of the work described above has focused on individual differences in EEG asymmetry in relation to temperamental variations in approach and withdrawal behaviors in infancy and childhood. Work finding greater right frontal activation in infants of depressed mothers also suggests an important role for the influence of the social environment on EEG asymmetry (Dawson et al., 1999; Field, Fox, Pickens, & Nawrocki, 1995). Hane and Fox (2006) also emphasized the influence of caregiving styles on EEG asymmetries in infants. In an initial study, they examined frontal asymmetry in a sample of 9-month-olds who had been selected for high or low levels of temperamental reactivity at 4 months of age. While they did not report whether infants' 4-month-classifications were associated with later asymmetry patterns, they found that lower quality of maternal caregiving was concurrently associated with right frontal asymmetry at 9 months of age. Hane and colleagues then followed up this sample two years later, with quality of care at 9 months being associated with frontal alpha asymmetry at 3 years of age, with results going in a similar direction as in the previous study (Hane, Henderson, Reeb-Sutherland, & Fox, 2010).

In summary, investigating the correlates of frontal EEG asymmetry in infants remains an active area. In terms of future directions, there remain a number of questions about the nature of frontal EEG asymmetry. In particular, an overarching developmental model of EEG asymmetry has not been developed. Instead we are left with a mixture of findings which have not been fully integrated into a conceptual model which incorporates a detailed consideration of the possible neurophysiological origins of the observed asymmetries and their casual relation to affective processes (Miller, 2010).

EEG Power Measures in the Study of Early Psychosocial Adversity

Our third example of the use of EEG power measures in the study of early social and emotional development concerns research on the effects of early psychosocial adversity. There is interest from a variety of perspectives on the effects of early adversity on different domains of children's functioning, including brain development. This interest is often framed from either of two perspectives; 1) the integrative perspective of developmental psychopathology, which encourages analyses of change across the behavioral, cognitive, and neurophysiological levels, and 2) the more deterministic perspective of biological psychiatry, which has tended to emphasize the long-lasting effects of early adversity through its effects on brain functioning (for discussion see Marshall & Kenney, 2009). From a developmental psychopathology viewpoint, there is also increasing interest in using EEG and related measures in research on psychosocial interventions for at-risk children (Bruce, McDermott, Fisher, & Fox, 2009). EEG is particularly suited to use in this kind of area given its portability, low cost and suitability for use with infants and young children.

One example of the use of EEG in research on early adversity comes from a recent intervention study of infants and children living in Bucharest, Romania. The Bucharest Early Intervention Project (BEIP; Zeanah et al., 2003) examined physical, social, cognitive, and biobehavioral characteristics of a group of children living in institutions in Bucharest, Romania. The study was aimed at gathering scientific data to inform policy concerning the care of abandoned children. This complex study implemented a design in which institutionalized children were randomly assigned to one of two conditions: 1) Foster care that was provided by the BEIP infrastructure; 2) care-as-usual in which placements followed the existing protocols of the state. A comparison group consisted of similar-aged children who lived with their families and who had never experienced institutionalization and who had been recruited from the local community. Because of a lack of foster care infrastructure in Romania at the onset of the study, a child-centered foster care system was developed for the study, with a team of Romanian social workers being trained to support foster parents with the challenges of caring for postinstitutionalized children (for further details on the intervention, see Smyke, Zeanah, Fox, & Nelson, 2009). For discussion of ethical issues and safeguards related to the BEIP see Millum and Emanuel (2007), Wassenaar (2006) and Zeanah et al. (2006).

As well as a variety of physical assessments, cognitive tests, social-emotional measures, and assessments of the caregiving environment, the BEIP also included electroencephalographic (EEG) measures in order to allow the investigation of the effects of the foster care intervention on aspects of brain development. This study presented an opportunity to examine questions concerning the effects of early experience on brain and behavioral development, as well as to investigate integrative relations between physiological and behavioral measures in the context of early intervention.

There are very few studies which have examined EEG measures in relation to early intervention in infancy or early childhood. In a randomized study carried out in Mauritius, Raine et al., (2001) observed a reduction in EEG theta power in a group of children who had received an enriched preschool intervention, compared with a group of children who

received typical care. This reduction in slow power in the intervention group was taken as an indicator of faster cortical maturation, since the amplitude of power in low frequency bands would be expected to decrease with age. Along these lines, it has been proposed that excessive theta activity in a child's EEG partly reflects a maturational lag in cortical development (Corning, Steffy, & Chaprin, 1982). These notions are based on a variety of findings that that the EEG of typically developing children shows a developmental increase in high-frequency rhythms (i.e., alpha and beta) and a decrease in low-frequency rhythms such as theta (Matousek & Petersen, 1973). Indeed, excessive levels of theta activity and concomitant reductions in higher-frequency activity have been associated with learning and attentional disorders, especially attention-deficit hyperactivity disorder (Barry et al., 2003). This EEG pattern in children has also been associated with high levels of psychosocial risk factors related to poverty (Harmony, Marosi, Diaz de Leon, Becker, & Fernandez, 1990).

In line with the above findings, in the initial EEG assessment of the children in the BEIP a profile of increased low-frequency power and reduced higher-frequency power in the EEG signal was characteristic of the institutionalized children in the study (Marshall et al., 2004). At the time of the initial baseline assessment, which occurred prior to randomization, children were aged between 5 and 31 months, although the EEG analyses only considered children older than 9 months. Compared with the comparison group of never-institutionalized community children, the children showed a higher proportion of theta power in the EEG, as well as lower levels of alpha and beta power. A recent analysis of the BEIP EEG data extended this finding by examining later behavioral assessments at 54 months of age in relation to the EEG profile at baseline. Consistent with the prior literature on slow EEG activity and attention problems, this analysis showed that levels of resting theta activity at the initial baseline assessment was a mediator of later attention deficit hyperactivity disorder (ADHD) symptoms among children who experienced institutionalization (McLaughlin et al., 2010).

In terms of the effect of the foster care intervention on children's EEG profiles, Marshall, Reeb, Fox, Nelson and Zeanah (2008) analyzed EEG power from follow-up assessments of the BEIP sample at 30 and 42 months of age. The aim of these analyses was to compare the EEG profiles of the two groups (foster care and care-as-usual) at these assessments in early childhood in order to assess the impact of the intervention. The primary hypothesis concerning EEG power was that the foster care intervention may remediate the high levels of slow (theta) power and the low levels of higher-frequency (alpha and beta) power in the EEG signal that were observed across the institutionalized children at the baseline assessment. However, effects of the intervention on the EEG were limited, with no difference in EEG theta or alpha power between the two groups of children at 30 or 42 months of age (Marshall et al., 2008), despite significant differences in cognitive status between the groups (Nelson et al., 2007).

Given the variability in children's ages at placement into the BEIP foster care intervention (6 to 31 months of age), Marshall et al. (2008) were also able to assess the effect of placement age on the EEG profile at a later age point (42 months). The age range at placement was a product of the spread of ages at the initial baseline assessment and although age at placement was not controlled in the study, it allowed analyses of the effects of age at placement and/or duration of time in foster care. It was expected that earlier placement into foster care would be associated with decreased theta power and increased alpha and beta power at 42 months. This suggestion was partially confirmed, with an inverse association between placement age and the proportion of alpha power in the EEG signal at 42 months of age, but no effects on theta power. This pattern of results as reported by Marshall et al. (2008) at 42 months of age was similar to that described in a more recent report in which the EEG profile of children in the BEIP was assessed at 8 years of age (Vanderwert, Marshall,

Nelson, Zeanah, & Fox, 2010). In that report, there were minimal differences between the original groups of children, but there was a continued negative relation between age at foster care placement and alpha power in the resting EEG.

In summary, although it was used as a fairly nonspecific measure derived from a resting baseline, the EEG data from the BEIP provided a window on the neurophysiological effects of early adversity. However, the relative lack of effects of the intervention on EEG power measures, despite distinct changes in various other domains, resists simple explanations. On the one hand, the results may reflect the lack of an active task during EEG collection and the relatively diffuse nature of the EEG measures that were collected. However, it also illustrates the complexity involved in integrating neurophysiological data into studies of early adversity. This complexity was emphasized by Marshall and Kenney (2009) who discussed various issues related to conceptualizing the role of neurobiological measures in the study of early experience. Among these issues are the difficulty of translating from comparative work to research with human populations, and the lack of knowledge about the neurobiological processes that may be associated with sensitive periods in human development. However, this remains an active area of research, and it is certainly possible that EEG measures will play a useful role in filling some of the gaps in our knowledge as work in this important area progresses.

Conclusions and Future Directions

As can be seen from the diversity of research briefly reviewed here, the study of EEG oscillations in infants and young children has spanned a variety of areas within the domains of early social, emotional, and cognitive development. It has also encompassed both the documentation of generalities in early human development as well as illuminating the study of developing individual differences. However, there certainly remain outstanding questions and controversies, such as the specific nature and function of different EEG frequency bands in infants and their relations to more established rhythms in adults. A wider background issue concerns the role of EEG and related measures in developmental theory, which in our opinion has been somewhat neglected. In some ways, this reflects a more general confusion about the way in which neurobiological measures should be considered in developmental science. It is often implicitly espoused that neuroscience represents another "level of analysis" of a given phenomenon, and that "multi-level" approaches are better than approaches which only assess one "level" (e.g., behavior). However, in our opinion, EEG measures are best placed within an integrative framework which recognizes the bidirectional interplay between brain and behavior (Marshall & Meltzoff, 2011; Miller 2010), although even this recognition in itself does not do full justice to the complexity of the brain-behavior-environment interface (Marshall, 2009). In this respect, one future area of promise concerns the development of nonlinear methods for EEG analysis, an approach which has seen recent success in the field of autism research (Bosl, Tierney, Tager-Flusberg, & Nelson, 2011).

Also helpful would be approaches in which EEG data are used to test theories at the psychological level which cannot be easily parsed by behavioral measures alone. This kind of "forward inference" (Henson, 2006), where neuroscience data are used to play off competing hypotheses, is a particularly compelling approach to the use of EEG data in developmental research, but one that remains underutilized. In older children and adults, functional neuroimaging data have been used to test and support theories of brain development in relation to the development of motor, perceptual and cognitive abilities (Johnson, Grossmann, & Cohen Kadosh, 2009), but related research with younger children and EEG has been lacking. In part, this may reflect our relatively limited state of knowledge concerning the functional correlates of EEG oscillations in early development (de Haan,

2007a). However, as more research focuses on this area, hopefully the coming years will see the emergence of a more fully-fledged developmental cognitive neuroscience of EEG oscillations in the early months and years of life.

Acknowledgments

References

Aftanas L, Varlamov A, Pavlov S, Makhnev V, Reva N. Event-related synchronization and desynchronization during affective processing: emergence of valence-related time-dependent hemispheric asymmetries in theta and upper alpha band. International Journal of Neuroscience. 2001; 110:197–219. [PubMed: 11912870]

Babiloni C, Babiloni F, Carducci F, Cincotti F, Cocozza G, Del Percio C, et al. Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: a high-resolution EEG study. Neuroimage. 2002; 17:559–572. [PubMed: 12377134]

Babiloni C, Marzano N, Infarinato F, Iacoboni M, Rizza G, Aschieri P, et al. "Neural efficiency" of experts' brain during judgment of actions: a high-resolution EEG study in elite and amateur karate athletes. Behavioural Brain Research. 2010; 207:466–475. [PubMed: 19891991]

Barry RJ, Clarke AR, Johnstone SJ. A review of electrophysiology in attention-deficit/hyperactivity disorder: I. Qualitative and quantitative electroencephalography. Clinical Neurophysiology. 2003; 114:171–183. [PubMed: 12559224]

Bazhenova OV, Stroganova TA, Doussard-Roosevelt JA, Posikera IA, Porges SW. Physiological responses of 5-month-old infants to smiling and blank faces. International Journal of Psychophysiology. 2007; 63:64–76. [PubMed: 17056142]

Bell, MA.; Wolfe, CD. The use of the electroencephalogram in research on cognitive development. In: Schmidt, LA.; Segalowitz, SJ., editors. Developmental psychophysiology: Theory, systems, and methods. New York: Cambridge University Press; 2008. p. 150-170.

Blakemore SJ, Dahl RE, Frith U, Pine DS. Developmental cognitive neuroscience. Developmental Cognitive Neuroscience. 2011; 1:3–6. [PubMed: 22436415]

Bosl W, Tierney A, Tager-Flusberg H, Nelson C. EEG complexity as a biomarker for autism spectrum disorder risk. BMC Medicine. 2011; 9:18. [PubMed: 21342500]

Bruce J, McDermott JM, Fisher PA, Fox NA. Using behavioral and electrophysiological measures to assess the effects of a preventive intervention: A preliminary study with preschool-aged foster children. Prevention Science. 2009; 10:129–140. [PubMed: 19030992]

Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P. Action observation and acquired motor skills: An fMRI study with expert dancers. Cerebral Cortex. 2005; 15:1243–1249. [PubMed: 15616133]

Clarke AR, Barry RJ, McCarthy R, Selikowitz M. EEG analysis of children with attention-deficit/hyperactivity disorder and comorbid reading disabilities. Journal of Learning Disabilities. 2002; 35:276–285. [PubMed: 15493324]

Corbin HP, Bickford RG. Studies of the electroencephalogram of normal children: comparison of viscal and automatic frequency analyses. Electroencephalography and Clinical Neurophysiology. 1955; 7:15–28. [PubMed: 14353017]

Corning WC, Steffy RA, Chaprin IC. EEG slow frequency and WISC-R correlates. Journal of Abnormal Child Psychology. 1982; 10:511–530. [PubMed: 7161442]

Csibra, G. Action mirroring and action understanding: an alternative account. In: Haggard, P.; Rosetti, Y.; Kawato, M., editors. Sensorimotor Foundations of Higher Cognition: Attention and Performance. Vol. XXII. Oxford: Oxford University Press; 2007. p. 435-459.

Csibra G, Davis G, Spratling MW, Johnson MH. Gamma oscillations and object processing in the infant brain. Science. 2000; 290:1582–1585. [PubMed: 11090357]

Davidson RJ, Fox NA. Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. Science. 1982; 218:1235–1237. [PubMed: 7146906]

Dawson G, Frey K, Self J, Panagiotides H, Hessl D, Yamada E, et al. Frontal brain electrical activity in infants of depressed and nondepressed mothers: relation to variations in infant behavior. Developmental Psychopathology. 1999; 11:589–605.

de Haan, M. Current and future directions in infant electrophysiology. In: de Haan, M., editor. Infant EEG and Event-Related Potentials. New York: Psychology Press; 2007a. p. 305-314.

de Haan, M., editor. Infant EEG and event-related potentials. New York: Psychology Press; 2007b.

Del Giudice M, Manera V, Keysers C. Programmed to learn? The ontogeny of mirror neurons. Developmental Science. 2009; 12:350–363. [PubMed: 19143807]

Diego MA, Jones NA, Field T. EEG in 1-week, 1-month and 3-month-old infants of depressed and non-depressed mothers. Biological Psychology. 2010; 83:7–14. [PubMed: 19782119]

Dumermuth G, Molinari L. Spectral analysis of the EEG. Some fundamentals revisited and some open problems. Neuropsychobiology. 1987; 17:85–99. [PubMed: 3306442]

Engel AK, Fries P, Singer W. Dynamic predictions: oscillations and synchrony in top-down processing. Nature Reviews Neuroscience. 2001; 2:704–716.

Field T, Fox NA, Pickens J, Nawrocki T. Relative right frontal EEG activation in 3- to 6-month-old infants of "depressed" mothers. Developmental Psychology. 1995; 31:358–363.

Fox NA. If it's not left, it's right: Electroencephalograph asymmetry and the development of emotion. American Psychologist. 1991; 46:863–872. [PubMed: 1928939]

Fox NA, Calkins SD, Bell MA. Neural plasticity and development in the first two years of life: Evidence from cognitive and socioemotional domains of research. Development & Psychopathology. 1994; 6:677–696.

Fox, NA.; Davidson, RJ. Hemispheric substates of affect: A developmental approach. In: Fox, NA.; Davidson, RJ., editors. The Psychobiology of Affective Development. Hillsdale, N.J: Erlbaum; 1984. p. 353-381.

Fox NA, Davidson RJ. Electroencephalogram asymmetry in response to the approach of a stranger and maternal separation in 10-month-old infants. Developmental Psychology. 1987; 23:233–240.

Fox NA, Henderson HA, Rubin KH, Calkins SD, Schmidt LA. Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. Child Development. 2001; 72:1–21. [PubMed: 11280472]

Futagi Y, Ishihara T, Tsuda K, Suzuki Y, Goto M. Theta rhythms associated with sucking, crying, gazing and handling in infants. Electroencephalography and Clinical Neurophysiology. 1998; 106:392–399. [PubMed: 9680150]

Gastaut H, Dongier M, Courtois G. On the significance of "wicket rhythms" in psychosomatic medicine. Electroencephalography and Clinical Neurophysiology. 1954; 6:687.

Gastaut HJ, Bert J. EEG changes during cinematographic presentation; moving picture activation of the EEG. Electroencephalography and Clinical Neurophysiology. 1954; 6:433–444. [PubMed: 13200415]

Gevins A, Smith ME, McEvoy L, Yu D. High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. Cerebral Cortex. 1997; 7:374–385. [PubMed: 9177767]

Ghim H. Evidence for perceptual organization in infants: Perception of subjective contours by young infants. Infant Behavior and Development. 1990; 13:221–248.

Gibbs FA, Knott JR. Growth of the electrical activity of the cortex. Electroencephalography and Clinical Neurophysiology. 1949; 1:223–229. [PubMed: 18149593]

Gliga T, Volein A, Csibra G. Verbal labels modulate perceptual object processing in 1-year-old children. Journal of Cognitive Neuroscience. 2010; 22:2781–2789. [PubMed: 20044900]

Gray CM, Konig P, Engel AK, Singer W. Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. Nature. 1989; 338:334–337. [PubMed: 2922061]

Grossmann T, Johnson MH, Farroni T, Csibra G. Social perception in the infant brain: gamma oscillatory activity in response to eye gaze. Social Cognitive Affective Neuroscience. 2007; 2:284–291.

Gruber T, Muller MM. Oscillatory brain activity dissociates between associative stimulus content in a repetition priming task in the human EEG. Cerebral Cortex. 2005; 15:109–116. [PubMed: 15238442]

Gruber T, Muller MM, Keil A. Modulation of induced gamma band responses in a perceptual learning task in the human EEG. Journal of Cognitive Neuroscience. 2002; 14:732–744. [PubMed: 12167258]

Hagne I. Development of the EEG in normal infants during the first year of life. A longitudinal study. Acta Paediatrica Scandinavica. Supplement. 1972; 232:1–53.

Hagne, I.; Persson, J.; Magnusson, R.; Petersen, I. Spectral analysis via fast fourier transform of waking EEG in normal infants. In: Kellaway, P.; Petersen, I., editors. Automation of clinical EEG. New York: Raven; 1973. p. 3-48.

Hane AA, Fox NA. Ordinary variations in maternal caregiving influence human infants' stress reactivity. Psychological Science. 2006; 17:550–556. [PubMed: 16771807]

Hane AA, Henderson HA, Reeb-Sutherland BC, Fox NA. Ordinary variations in human maternal caregiving in infancy and biobehavioral development in early childhood: A follow-up study. Developmental Psychobiology. 2010; 52:558–567. [PubMed: 20806328]

Hari R. Action-perception connection and the cortical mu rhythm. Progress in Brain Research. 2006; 159:253–260. [PubMed: 17071236]

Hari R, Salmelin R. Human cortical oscillations: a neuromagnetic view through the skull. Trends in Neurosciences. 1997; 20:44–49. [PubMed: 9004419]

Harmony T, Marosi E, Diaz de Leon AE, Becker J, Fernandez T. Effect of sex, psychosocial disadvantages and biological risk factors on EEG maturation. Electroencephalography and Clinical Neurophysiology. 1990; 75:482–491. [PubMed: 1693893]

He J, Degnan KA, McDermott JM, Henderson HA, Hane AA, Xu Q, et al. Anger and approach motivation in infancy: Relations to early childhood inhibitory control and behavior problems. Infancy. 2010; 15:246–269.

Henson R. Forward inference using functional neuroimaging: dissociations versus associations. Trends in Cognitive Sciences. 2006; 10:64–69. [PubMed: 16406759]

Herrmann CS, Frund I, Lenz D. Human gamma-band activity: a review on cognitive and behavioral correlates and network models. Neuroscience & Biobehavioral Reviews. 2010; 34:981–992. [PubMed: 19744515]

Herrmann CS, Munk MH, Engel AK. Cognitive functions of gamma-band activity: memory match and utilization. Trends in Cognitive Sciences. 2004; 8:347–355. [PubMed: 15335461]

Hoehl S, Wahl S. Recording Infant ERP Data for Cognitive Research. Developmental Neuropsychology. (in press).

Inanaga K. Frontal midline theta rhythm and mental activity. Psychiatry and Clinical Neurosciences. 1998; 52:555–566. [PubMed: 9895201]

John ER, Ahn H, Prichep L, Trepetin M, Brown D, Kaye H. Developmental equations for the electroencephalogram. Science. 1980; 210:1255–1258. [PubMed: 7434026]

Johnson MH, Grossmann T, Cohen Kadosh K. Mapping functional brain development: Building a social brain through interactive specialization. Developmental Psychology. 2009; 45:151–159. [PubMed: 19209998]

Kagan J, Reznick JS, Clarke C, Snidman N, Garcia-Coll C. Behavioral inhibition to the unfamiliar. Child Development. 1984; 55:2212–2225.

Kahana MJ, Seelig D, Madsen JR. Theta returns. Current Opinion in Neurobiology. 2001; 11:739–744. [PubMed: 11741027]

Kaufman J, Csibra G, Johnson MH. Representing occluded objects in the human infant brain. Proceedings of the Royal Society of London B: Biological Sciences. 2003; 270(Suppl 2):S140–143.

Kaufman J, Csibra G, Johnson MH. Oscillatory activity in the infant brain reflects object maintenance. Proceedings of the National Academy of Sciences. 2005; 102:15271–15274.

Keil A, Muller MM, Ray WJ, Gruber T, Elbert T. Human gamma band activity and perception of a gestalt. Journal of Neuroscience. 1999; 19:7152–7161. [PubMed: 10436068]

Keysers C, Kaas JH, Gazzola V. Somatosensation in social perception. Nature Reviews Neuroscience. 2010; 11:417–428.

Khader PH, Jost K, Ranganath C, Rosler F. Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. Neuroscience Letters. 2010; 468:339–343. [PubMed: 19922772]

Kirk IJ, Mackay JC. The role of theta-range oscillations in synchronising and integrating activity in distributed mnemonic networks. Cortex. 2003; 39:993–1008. [PubMed: 14584563]

Klimesch W, Doppelmayr M, Hanslmayr S. Upper alpha ERD and absolute power: their meaning for memory performance. Progress in Brain Research. 2006; 159:151–165. [PubMed: 17071229]

Klimesch W, Doppelmayr M, Russegger H, Pachinger T. Theta band power in the human scalp EEG and the encoding of new information. Neuroreport. 1996; 7:1235–1240. [PubMed: 8817539]

Klimesch W, Doppelmayr M, Schwaiger J, Auinger P, Winkler T. 'Paradoxical' alpha synchronization in a memory task. Brain Research Cognitive Brain Research. 1999; 7:493–501. [PubMed: 10076094]

Kugler J, Laub M. "Puppet show" theta rhythm. Electroencephalography and Clinical Neurophysiology. 1971; 31:532–533.

Lehtonen J, Kononen M, Purhonen M, Partanen J, Saarikoski S. The effects of feeding on the electroencephalogram in 3- and 6-month-old infants. Psychophysiology. 2002; 39:73–79. [PubMed: 12206297]

Lepage JF, Théoret H. EEG evidence for the presence of an action observation-execution matching system in children. European Journal of Neuroscience. 2006; 23:2505–2510. [PubMed: 16706857]

Lindsley DB. Electrical potentials of the brain in children and adults. Journal of Genetic Psychology. 1938; 19:285–306.

Lindsley DB. A longitudinal study of the occipital alpha rhythm in normal children: frequency and amplitude standards. Journal of Genetic Psychology. 1939; 55:197–213.

Marshall PJ. Relating psychology and neuroscience: Taking up the challenges. Perspectives on Psychological Science. 2009; 4:113–125.

Marshall PJ, Bar-Haim Y, Fox NA. Development of the EEG from 5 months to 4 years of age. Clinical Neurophysiology. 2002; 113:1199–1208. [PubMed: 12139998]

Marshall PJ, Bouquet CA, Shipley TF, Young T. Effects of brief imitative experience on EEG desynchronization during action observation. Neuropsychologia. 2009; 47:2100–2106. [PubMed: 19467360]

Marshall PJ, Fox NA. the BEIP Core Group. A comparison of the electroencephalogram between institutionalized and community children in Romania. Journal of Cognitive Neuroscience. 2004; 16:1327–1338. [PubMed: 15532128]

Marshall PJ, Kenney JW. Biological perspectives on the effects of early psychosocial experience. Developmental Review. 2009; 29:96–119.

Marshall PJ, Meltzoff AN. Neural mirroring systems: Exploring the EEG mu rhythm in infancy. Developmental Cognitive Neuroscience. 2011; 1:110–123. [PubMed: 21528008]

Marshall PJ, Reeb BC, Fox NA, Nelson CA, Zeanah CH. Effects of early intervention on EEG power and coherence in previously institutionalized children in Romania. Development and Psychopathology. 2008; 20:861–880. [PubMed: 18606035]

Marshall PJ, Young T, Meltzoff AN. Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. Developmental Science. 2011; 14:474–480. [PubMed: 21477187]

Matousek M, Petersen I. Automatic evaluation of EEG background activity by means of age-dependent EEG quotients. Electroencephalography and Clinical Neurophysiology. 1973; 35:603–612. [PubMed: 4128155]

Maulsby RL. An illustration of emotionally evoked theta rhythm in infancy: hedonic hypersynchrony. Electroencephalography and Clinical Neurophysiology. 1971; 31:157–165. [PubMed: 4104705]

McLaughlin KA, Fox NA, Zeanah CH, Sheridan MA, Marshall P, Nelson CA. Delayed maturation in brain electrical activity partially explains the association between early environmental deprivation and symptoms of attention-deficit/hyperactivity disorder. Biological Psychiatry. 2010; 68:329–336. [PubMed: 20497899]

Meltzoff AN, Brooks R. Self-experience as a mechanism for learning about others: A training study in social cognition. Developmental Psychology. 2008; 44:1257–1265. [PubMed: 18793060]

Meltzoff AN, Moore MK. Explaining facial imitation: a theoretical model. Early Development and Parenting. 1997; 6:179–192.

Miller GA. Mistreating psychology in the decades of the brain. Perspectives on Psychological Science. 2010; 5:716–743. [PubMed: 21949539]

Miller R. Theory of the normal waking EEG: from single neurones to waveforms in the alpha, beta and gamma frequency ranges. International Journal of Psychophysiology. 2007; 64:18–23. [PubMed: 16997407]

Millum J, Emanuel EJ. The ethics of international research with abandoned children. Science. 2007; 318:1874–1875. [PubMed: 18096792]

Muller MM, Bosch J, Elbert T, Kreiter A, Sosa MV, Sosa PV, et al. Visually induced gamma-band responses in human electroencephalographic activity--a link to animal studies. Experimental Brain Research. 1996; 112:96–102.

Muller MM, Gruber T, Keil A. Modulation of induced gamma band activity in the human EEG by attention and visual information processing. International Journal of Psychophysiology. 2000; 38:283–299. [PubMed: 11102668]

Muthukumaraswamy SD, Johnson BW. Changes in rolandic mu rhythm during observation of a precision grip. Psychophysiology. 2004; 41:152–156. [PubMed: 14693010]

Muthukumaraswamy SD, Johnson BW, McNair NA. Mu rhythm modulation during observation of an object-directed grasp. Brain Research Cognitive Brain Research. 2004; 19:195–201. [PubMed: 15019715]

Nelson CA, Zeanah CH, Fox NA, Marshall PJ, Smyke AT, Guthrie D. Cognitive recovery in socially deprived young children: The Bucharest Early Intervention Project. Science. 2007; 318:1937–1940. [PubMed: 18096809]

Neuper C, Pfurtscheller G. Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. International Journal of Psychophysiology. 2001; 43:41–58. [PubMed: 11742684]

Niedermeyer E. Alpha rhythms as physiological and abnormal phenomena. International Journal of Psychophysiology. 1997; 26:31–49. [PubMed: 9202993]

Orekhova EV, Stroganova TA, Posikera IN. Theta synchronization during sustained anticipatory attention in infants over the second half of the first year of life. International Journal of Psychophysiology. 1999; 32:151–172. [PubMed: 10380948]

Orekhova EV, Stroganova TA, Posikera IN. Alpha activity as an index of cortical inhibition during sustained internally controlled attention in infants. Clinical Neurophysiology. 2001; 112:740–749. [PubMed: 11336888]

Pantev C, Makeig S, Hoke M, Galambos R, Hampson S, Gallen C. Human auditory evoked gamma-band magnetic fields. Proceedings of the National Academy of Sciences. 1991; 88:8996–9000.

Paul K, Dittrichova J, Papousek H. Infant feeding behavior: development in patterns and motivation. Developmental Psychobiology. 1996; 29:563–576. [PubMed: 8911772]

Perry A, Bentin S. Mirror activity in the human brain while observing hand movements: a comparison between EEG desynchronization in the mu-range and previous fMRI results. Brain Research. 2009; 1282:126–132. [PubMed: 19500557]

Pfurtscheller G, Lopes da Silva FH. Event-related EEG/MEG synchronization and desynchronization: Basic principles. Clinical Neurophysiology. 1999; 110:1842–1857. [PubMed: 10576479]

Pfurtscheller G, Neuper C, Krausz G. Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement. Clinical Neurophysiology. 2000; 111:1873–1879. [PubMed: 11018505]

Pfurtscheller G, Stancak A Jr, Neuper C. Event-related synchronization (ERS) in the alpha band--an electrophysiological correlate of cortical idling: a review. International Journal of Psychophysiology. 1996; 24:39–46. [PubMed: 8978434]

Pineda JA. The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing". Brain Research Reviews. 2005; 50:57–68. [PubMed: 15925412]

Pineda JA, Allison BZ, Vankov A. The effects of self-movement, observation, and imagination on mu rhythms and readiness potentials (RP's): toward a brain-computer interface (BCI). IEEE Transactions on Rehabilitation Engineering. 2000; 8:219–222. [PubMed: 10896193]

Pulvermuller F, Eulitz C, Pantev C, Mohr B, Feige B, Lutzenberger W, et al. High-frequency cortical responses reflect lexical processing: an MEG study. Electroencephalography and Clinical Neurophysiology. 1996; 98:76–85. [PubMed: 8689998]

Quandt LC, Marshall PJ, Bouquet CA, Young T, Shipley TF. Experience with novel actions modulates frontal alpha EEG desynchronization. Neuroscience Letters. 2011; 499:37–41. [PubMed: 21624433]

Raine A, Venables PH, Dalais C, Mellingen K, Reynolds C, Mednick SA. Early educational and health enrichment at age 3–5 years is associated with increased autonomic and central nervous system arousal and orienting at age 11 years: evidence from the Mauritius Child Health Project. Psychophysiology. 2001; 38:254–266. [PubMed: 11347871]

Ray S, Niebur E, Hsiao SS, Sinai A, Crone NE. High-frequency gamma activity (80–150Hz) is increased in human cortex during selective attention. Clinical Neurophysiology. 2008; 119:116–133. [PubMed: 18037343]

Reid VM, Csibra G, Belsky J, Johnson MH. Neural correlates of the perception of goal-directed action in infants. Acta Psychologica. 2007; 124:129–138. [PubMed: 17074296]

Reynolds GD, Guy MW. Brain-behavior relations in infancy: Intergrative approaches to examining infant looking behavior and event-related potentials. Developmental Neuropsychology. (in press).

Rodriguez E, George N, Lachaux JP, Martinerie J, Renault B, Varela FJ. Perception's shadow: long-distance synchronization of human brain activity. Nature. 1999; 397:430–433. [PubMed: 9989408]

Sammler D, Grigutsch M, Fritz T, Koelsch S. Music and emotion:electrophysiological correlates of the processing of pleasant and unpleasant music. Psychophysiology. 2007; 44:293–304. [PubMed: 17343712]

Sauseng P, Griesmayr B, Freunberger R, Klimesch W. Control mechanisms in working memory: a possible function of EEG theta oscillations. Neuroscience and Biobehavioral Reviews. 2010; 34:1015–1022. [PubMed: 20006645]

Smith CL, Bell MA. Infant frontal asymmetry as a predictor of toddlerhood internalizing and externalizing behaviors. Developmental Psychobiology. 2010; 52:158–167. [PubMed: 20175143]

Smith JR. The electroencephalogram during normal infancy and childhood: I. Rhythmic activities present in the neonate and their subsequent development. The Journal of Genetic Psychology. 1938a; 53:431–453.

Smith JR. The electroencephalogram during normal infancy and childhood: The nature and growth of the alpha waves. Electroencephalography and Clinical Neurophysiology. 1938b; 53:455–469.

Smith JR. The occipital and precentral alpha rhythms during the first two years. Journal of Psychology. 1939; 7:223–226.

Smith JR. The frequency growth of the human alpha rhythms during normal infancy and childhood. The Journal of Psychology. 1941; 11:177–198.

Smyke AT, Zeanah CH Jr, Fox NA, Nelson CA 3rd. A new model of foster care for young children: the Bucharest early intervention project. Child and Adolescent Psychiatric Clinics of North America. 2009; 18:721–734. [PubMed: 19486847]

Snyder SM, Hall JR. A meta-analysis of quantitative EEG power associated with attention-deficit hyperactivity disorder. Journal of Clinical Neurophysiology. 2006; 23:440–455. [PubMed: 17016156]

Sommerville JA, Hildebrand EA, Crane CC. Experience matters: the impact of doing versus watching on infants' subsequent perception of tool-use events. Developmental Psychology. 2008; 44:1249–1256. [PubMed: 18793059]

Sommerville JA, Woodward AL, Needham A. Action experience alters 3-month-old infants' perception of others' actions. Cognition. 2005; 96:B1–11. [PubMed: 15833301]

Southgate V, Csibra G, Kaufman J, Johnson MH. Distinct processing of objects and faces in the infant brain. Journal of Cognitive Neuroscience. 2008; 20:741–749. [PubMed: 18052786]

Southgate V, Johnson MH, El Karoui I, Csibra G. Motor system activation reveals infants' on-line prediction of others' goals. Psychological Science. 2010; 21:355–359. [PubMed: 20424068]

Southgate V, Johnson MH, Osborne T, Csibra G. Predictive motor activation during action observation in human infants. Biology Letters. 2009; 5:769–772. [PubMed: 19675001]

Stroganova, TA.; Orekhova, EV. EEG and infant states. In: de Hann, M., editor. Infant EEG and event-related potentials. New York: Psychology Press; 2007. p. 251-287.

Stroganova TA, Orekhova EV, Posikera IN. Externally and internally controlled attention in infants: an EEG study. International Journal of Psychophysiology. 1998; 30:339–351. [PubMed: 9834890]

Stroganova TA, Orekhova EV, Posikera IN. EEG alpha rhythm in infants. Clinical Neurophysiology. 1999; 110:997–1012. [PubMed: 10402087]

Tallon-Baudry C, Bertrand O, Peronnet F, Pernier J. Induced gamma-band activity during the delay of a visual short-term memory task in humans. Journal of Neuroscience. 1998; 18:4244–4254. [PubMed: 9592102]

Tiitinen H, Sinkkonen J, Reinikainen K, Alho K, Lavikainen J, Naatanen R. Selective attention enhances the auditory 40-Hz transient response in humans. Nature. 1993; 364:59–60. [PubMed: 8316297]

van Elk M, van Schie HT, Hunnius S, Vesper C, Bekkering H. You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. Neuroimage. 2008; 43:808–814. [PubMed: 18760368]

Vanderwert RE, Marshall PJ, Nelson CA, Zeanah CH, Fox NA. Timing of intervention affects brain electrical activity in children exposed to severe psychosocial neglect. PLoS One. 2010; 5:e11415. [PubMed: 20617175]

Wassenaar DR. Commentary: Ethical considerations in international research collaborations: The Bucharest Early Intervention Project. Infant Mental Health Journal. 2006; 27:577–580.

Zeanah CH, Koga SF, Simion B, Stanescu A, Tabacaru C, Fox NA, et al. Ethical considerations in international research collaboration: The Bucharest Early Intervention Project. Infant Mental Health Journal. 2006; 27:559–576.

Zeanah CH, Nelson CA, Fox NA, Smyke AT, Marshall P, Parker SW, et al. Designing research to study the effects of institutionalization on brain and behavioral development: The Bucharest Early Intervention Project. Development and Psychopathology. 2003; 15:885–907. [PubMed: 14984131]