ABSTRACT

Title of Thesis: AGE-RELATED DIFFERENCES IN KINEMATICS AND CEREBRAL CORTICAL PROCESSES DURING DISCRETE DRAWING MOVEMENTS IN CHILDREN AND ADULTS

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Research has shown developmental improvements in drawing movements during childhood. These changes may be related to protracted structural development and myelination of cortical brain structures underlying motor planning and control. However, no study to our knowledge has examined the relationship between cortical development and the emergence of accurate visuomotor behavior. This thesis characterized age-related differences in kinematics and cerebral cortical processes during the performance of discrete drawing movements in children, as compared to adults. Three groups were included in the study: young girls (6- to 7-year-olds), older girls (9- to 11-year-olds), and adult females (n=15, each). Participants performed 5cm center-out drawing movements with the dominant hand (right hand), while electroencephalography (EEG) was recorded. All participants exhibited similar task-related cortical communication (coherence) and activation (relative spectral power) in several frequency bands. Activation of motor neural resources (motor cortical potentials) in the midline pre-motor and motor regions was also similar across age groups. The similarity of the brain activation patterns for these measures may contribute to the comparable behavioral performance among all groups for root mean squared error (straightness) and movement length. However, other features of the young children’s brain activation patterns and motor control were different than the older children and/or adults. Specifically, the young children showed increased activation of frontal (executive process) areas, whereas the older children and adults exhibit increased relative activation in task-relevant sensorimotor areas (as measured by spectral power) in frequencies related to sensorimotor processes and attention. Similarly, increased coherence in the lower beta and gamma bands, indicative of local networking, was found in the adults between the frontal and central regions, and the frontal and parietal areas. Moreover, the adults show increased activation of the contralateral sensorimotor areas time-locked to the onset of movement, compared with the young children. The increased activation of the motor areas and visuomotor networks during movement planning may contribute to faster, smoother, and more consistent behavioral performance for the older children and adults, not evident in the young children.

AGE-RELATED DIFFERENCES IN KINEMATICS AND CEREBRAL CORTICAL PROCESSES DURING DISCRETE DRAWING MOVEMENTS IN CHILDREN AND ADULTS

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CHAPTER I

Overview

Adults are able to plan and control goal-directed movements, such as drawing and reaching, automatically and efficiently. In contrast, the behavioral performance of children on these types of tasks can be highly effortful and often results in less accurate performance for a particular goal. Many studies examining the development of drawing and reaching movements have found age-related improvements in motor performance. Authors have suggested that these changes may be related to protracted structural and myelination of brain structures underlying sensorimotor integration, motor planning and control. To bridge the relationship between cortical development and the emergence of accurate visuomotor drawing movements, the current study characterized age-related differences in kinematics and cerebral cortical processes, as measured by electroencephalography (EEG), during the performance of discrete drawing movements in children and adults.

Several studies have examined developmental trends in visuomotor behavior, that demonstrate improved accuracy, improved intralimb coordination patterns, and decreased variability with increasing age (Contreras-Vidal, 2006; Contreras-Vidal, Bo, Boudreau, & Clark, 2005; Konczak & Dichgans, 1997). These finding suggest that both the motor planning and control during the movement are refined with increased experience performing eye-hand coordinated tasks. In particular, age-related changes are thought to reflect the ability to utilize or integrate visual and proprioceptive inputs in the planning and online control of drawing movements during childhood (Contreras-Vidal et al., 2005; Hay, 1978; Hay, Bard, Ferrel, Olivier, & Fleury, 2005). For example, until the age of 5 or

6 years, children's movement performance is heavily reliant on vision, although these children do not appears to use of the visual feedback for online correction (Hay, 1978; Konczak et al., 1997; Konczak, Jansen-Osmann, & Kalveram, 2003). Despite significant improvements in kinematic accuracy during drawing movements through visually-guided feedback corrections, the arm movements of 7- and 8-year-olds still lack aspects of mature limb control. It has been suggested that these children lack the ability to efficiently utilize proprioceptive information (Hay et al., 2005). Redundancy between vision and proprioception allows optimized end effector localization during motor planning and more efficient error correction. The ability to efficiently utilize proprioception and importantly integrate it with visual information in the movement planning and control of limb trajectories is only fully reached in older children, over 9 years of age (Contreras-Vidal et al., 2005; Fayt, Schepens, & Minet, 1992; Ferrel, Bard, & Fleury, 2001; Ferrel-Chapus, Hay, Olivier, Bard, & Fleury, 2002). Moreover, the movement planning and control exhibited by older children often resembles the behavioral performance of adults.

The high temporal resolution of EEG allows delineation of the cortical activation patterns over the movement sequence from motor planning, movement initiation, and online control. Several electroencelphalography (EEG) techniques allow a characterization of the neurophysiological processes involved during goal-directed drawing movements that may be related to the changes associated with age-related structural development of the cerebral cortex. In particular, spectral analysis is useful to differentiate the frequency components of the brain waves to examine the age-related changes in power (or amplitude of the wave squared) during task performance. Previous studies investigated age-related changes in EEG spectral power at rest and have found that low-frequency components (theta and low alpha) decrease while high-frequency bands such as alpha and beta frequencies increase with increasing age (Clarke, 2001; Gasser, Jennen-Steinmetz, & Verleger, 1987; Gasser, Verleger, Bacher, & Sroka, 1988b). Gasser et al. (1988a; 1988b) found symmetrical patterns of the frequency distribution across the two hemispheres. However, these findings are not consistent with Clarke (2001), who reported differences in the developmental rates across the midline and two hemispheres. Specifically, beta power was found to increase in the midline sites at a faster rate than the lateral sites. Change in the frequency composition and regional activation may be attributed, in part, to physical growth during childhood and grey and white matter development in different cortical areas (Gasser et al., 1988b). Taken together, these studies provide a foundation for the age-related changes in spectral content in the EEG of children at rest. However, the changes in spectral power during any type of motor task performance have not been examined and it is unclear whether these documented age-related changes will be exhibited.

Although spectral power analyses provide information about the activity in different locations of the brain, it does not provide information about the functional coupling between areas of interest. Coherence analysis, on the other hand, quantifies the similarity of two signals (or electrode sites) in the time and frequency domains, indicative of the strength of their relationship. Previous developmental studies have found increased coherence at rest in frequency bands between 1.5 - 25Hz, with increasing age (Gasser, Jennen-Steinmetz, Sroka, Verleger, & Mocks, 1988a). It is unclear if lateralization of coherence is evident during childhood. Gasser et al. (1988b) reported that the intrahemispheric coherence estimates did not differ between the two hemispheres. However, Thatcher et al. (1987) found that long-range coherence between frontal and occipital regions increased only for the left hemisphere. Barry (2004), additionally found lateralized effects, in which the left hemisphere exhibited higher coherence than the right for several frequency bands. These finding suggest that the age-related increases in coherence, particularly for the long-range electrode distances, may be attributed to the development of long fibers and improved myelination during childhood particularly of the left hemisphere which is thought to be dominant in motor behavior.

One limitation to the previous developmental studies of coherence is that like those examining spectral content, they have primarily focused on resting conditions, and thus provided little information regarding active processing during the performance of motor tasks. However, several studies in adults have examined coherence during performance of coordinated visuomotor tasks. In a classic paper, Busk and Galbraith (1975) found that coherence increased when eye-hand coordination was necessary for task performance, as compared to eye-tracking and hand-tracking. The magnitude of this coherence depended on the functional properties of the visuo-motor system, such that highly connected areas such as the pre-striate to premotor areas and the premotor to primary motor areas demonstrated high levels of communication. Other studies have demonstrated increased inter-hemispheric coherence in the sensorimotor areas, even in children (Knyazeva et al., 1997). For example, Knyazeva et al., (Knyazeva et al., 1997) found that children exhibited lateralized intrahemispheric effects during right hand movements over the contralateral hemisphere. This would suggest that children show an increase in the lateralized functional connectivity between frontal, central, parietal and occipital regions related to right-hand motor behavior.

Event-related potentials (ERPs) provide a characterization of the time-locked response to a stimulus or behavioral event. ERPs reflect activity or processing from a population of neurons, and may be matched to the preparation and behavioral responses for a millisecond time-scale. Specifically, the Bereitschaftspotential (BP) or motor readiness potential, has previously been used to characterize the planning phase of self-initiated finger movements in children and adults prior to movement onset (Chiarenza, Villa, & Vasile, 1995; Jahanshahi & Hallett, 2003; Kristeva & Vladova, 1987). Adults exhibit increased negativity beginning 500ms to 1.5 seconds prior to movement onset and is maximal in electrodes placed above the supplementary motor area (SMA) (Deecke et al., 1984; Jahanshahi et al., 2003). A substantial increase in negativity is found between 500ms before the initiation of movement and movement onset, and is observed in the electrodes corresponding to SMA, premotor (PM) and primary motor area (M1). The waveform is symmetrical during the early portion and becomes increasingly more asymmetrical toward the peak amplitude which occurs around 50ms before movement onset (Jahanshahi et al., 2003). The asymmetry of the BP corresponds with larger values for the contralateral primary motor cortex (C3 > C4). This pattern reflects a left hemisphere dominance for motor processing (Deecke et al., 1984). Although BP is classically used to study finger movements, there is evidence that faster, more spontaneous and complex movements may be studied (Chiarenza, Papakostopoulos, Giordana, & Guareschi-Cazzullo, 1983; Deecke et al., 1984). The amplitude and latency of the BP is sensitive to increased movement complexity, coordination between various muscle groups and body segments, and inhibition of non-task associated behaviors (Chiarenza et al., 1995; Jahanshahi et al., 2003; Warren & Karrer, 1984).

The BP waveform is not consistently reported across developmental studies, particularly for young children, and may be characterized by either a negative to positive waveform evolution or the opposite with a high post-movement positive shift (Chisholm, Karrer, & Cone, 1984; Kristeva et al., 1987). The positive components preceding movement by about 200ms have been reported and may be indicative of inhibitory processes needed to increase the accuracy of the movement. On the other hand, post-movement positivity may indicate reception of feedback (Chisholm et al., 1984; Kristeva et al., 1987). Moreover, the youngest groups of children may exhibit a fronto-pareital response which may additionally reflect increased attention during task performance. The younger children exhibit much greater variability in their BP waveforms and in some reports do not show a modal peak BP, differing from the older children that exhibit modal BP profiles similar to adults.

Despite the variability of the waveforms for the young children, greater consistency is found in the waveforms of older children, similar to those exhibited by adults. These data support the ability of older children and adults to appropriately incorporate task relevant stimuli in motor plans. This ability may be in part be attributed to the maturation of the dorsolateral prefrontal cortex (DLPFC), which is thought to contribute to motor planning and development of the BP during self-paced movements (Jahanshahi, Dirnberger, Liasis, Towell, & Boyd, 2001; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000).

In the present study, these EEG techniques (relative spectral power, coherence, and event-related motor cortical potentials) were used to characterize the cerebral cortical patterns of activation in conjunction with the movement kinematics prior to and during the performance of discrete drawing movements in children and adults. It was hypothesized that the quality of the behavioral performance of the children and adults may be, in part, a product of the cerebral cortical processes and patterns of activation during motor planning and control. Thus, adult-like performance in the children may be related to the existence of adult-like brain patterns of activation, communication between brain areas of interest, and the neural facilitation of cortical motor resources related to goal-directed visuomotor behaviors. Conversely, a lack of similarity in these neural patterns may contribute to the behavioral differences between the children and adults.

In addition to this first introductory chapter (Chapter I), three additional chapters are included in this thesis. The second chapter contains a review of the relevant literature, including an examination visuomotor behavior (drawing) and the internal model framework, neurophysiology of visuomotor behaviors, and the electrophysiological techniques pertinent to this study. The third chapter is the complete manuscript that will be submitted separately for publication in a peer-reviewed journal and includes the methods, results, and discussion of the current study. The final chapter provides overall conclusions from this study and suggestions for future research.

CHAPTER II

Review of Literature

Overview

Previous research has provided a rich behavioral characterization of the development of arm movements in children. Similarly, on a neurophysiological level, electroencephalographic examinations in children have depicted the changes in cortical activation patterns, communication between functionally relevant cortical areas, and hemispheric lateralization. However, to date no study has concurrently examined age-related changes in brain dynamics and the movement kinematics related to drawing movements in children. This review is intended to provide a theoretical background and previous research investigating developmental changes in movement kinematics and brain dynamics, and provide justification for extending this line of research to include direct matching of motor planning and execution of the motor behavior with the cortical patterns of activations in childhood. The first portion of review will focus on the behavioral aspects from an internal model perspective of planning, execution, and control of reaching and pointing movements. The second portion of the review revisits the internal model perspective with respect to the development of key neurophysiological processes and structural development of cortical areas. The review will conclude with a discussion of the methods used in neurophysiological investigations to provide rationale for the use of these methods in the present investigation.

Visuomotor Behavior in Unimanual Drawing/Reaching Movements

Sensorimotor Transformations in Goal-Directed Movements: Internal Model (IM) Framework

The conceptual framework adopted for this study is the internal model approach to goal-directed reaching movements, detailed in Shadmehr and Wise (2005). This view of sensorimotor control holds that a sequence of computations is performed iteratively by the CNS to plan, execute and control the limb in space (see Figure 2.1). This framework conceptualizes how sensory information may be integrated during motor planning, and draws attention to the need for accurate and redundant sources of sensory information to optimize goal-directed limb movements.

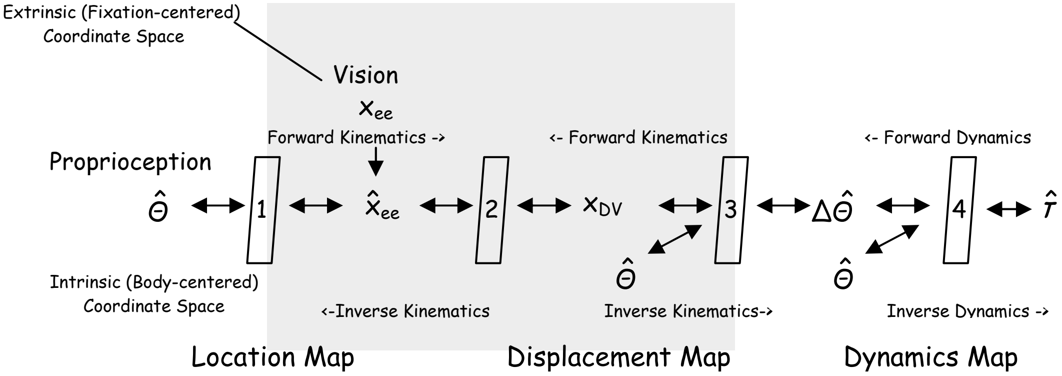


Figure 2.1 Sensorimotor transformations during visuomotor behaviors. The gray box depicts external (fixation-centered) coordinate space and all other portions are referenced to an intrinsic (body-centered) coordinate space. Based on figure 12.1 from Shadmehr & Wise, 2005.

Figure 2.1 depicts three components for motor planning and control hypothesized by the IM framework. The first component estimates the location of the limb effector and target (Location Map). The second component determines the approximate displacement between the limb and target (Displacement Map). The last component involves the determination of muscle forces needed to produce joint torques to move the limb to the (Dynamics Map). These events can be further decomposed into a series of sensorimotor transformations that allow integration between sensory modalities between internal (body-centered) and external (fixation-centered) coordinate frame of reference (depicted in the gray box in Figure 2.1). This sequence of events allows calibration between sensory afferents, increasing both the precision of the estimate of the end effector position in space and the accuracy in the motor commands to achieve the desired movement goals. The term internal model (IM) refers to the conceptualized stored neural representations of the relationship between a desired movement trajectory and the necessary motor commands to elicit the corresponding changes in joint torque - the output of the final sensorimotor transformation presented in Figure 2.1.

In order to fully understand this conceptual framework, the individual subcomponents must be examined. As mentioned, in order to generate the appropriate motor commands, the CNS must first locate the limb and target position in space. The first transformation (Figure 2.1, box 1) takes the proprioceptive estimate of the limb position and orientation of each joint from proximal to distal ($\hat{\theta}$), from an intrinsic or body-centered to extrinsic or fixation-centered coordinate space. Since it is held that vision provides extrinsic/fixation-centered information (x_{ee}), the transformation of proprioceptive afferents to this coordinate space facilitates integration between the two sensory modalities to provide an accurate estimate of the location of the limb effector ($\hat{x}_{ee}$) (Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003; Pouget, Ducom, Torri, & Bavelier, 2002). If additional sensory information, such as audition, is available, a similar transformation into a Cartesian coordinate system is also necessary. The next transformation (Figure 2.1, box 2) incorporates both the target and estimate of the limb location in external space to compute the displacement between the two (also referred to as the difference vector from the start position to the target). The magnitude and direction of the intended movement obtained in the displacement map, is transformed in the third step (Figure 2.1, box 3), to the corresponding joint configurations to achieve the goals of the movement (i.e., reach towards a spatial target). Thus, the transformation involves a mapping from the desired change in a fixation-centered, extrinsic coordinate frame to a joint-centered, intrinsic coordinate frame. The final step, the dynamics map, is the selection of the appropriate motor commands that will generate the muscle force needed to create joint configurations that will elicit movement from the start position to the desired position (Figure 2.1, box 4). After the initial motor command is generated, and movement has begun, feedback from both vision and proprioception supply information necessary for error-correction and subsequent update of motor commands, reinitiating the series of events.

The Development of an Internal Model

Exploring self-motion in the external environment throughout development provides the opportunity for calibration between internal (body-centered) and external (fixation-centered) coordinate systems. This calibration is a pre-requisite for developing an internal model of the relationship between the end effector and the external environment during limb movement. This process leads to increased precision in the motor plan at each of the aforementioned steps presented in Figure 2.1. In turn, increased precision of the motor outcome enhances the reliability in the sensory afferents for both motor planning and affecting motor execution (Contreras-Vidal et al., 2005; Metta, Sandini, & Konczak, 1999). Moreover, it is held that a primary function of the internal representation is to identify a discrepancy between the sensory afferents and the anticipated consequences of the motor commands (forward model), and drive the system to make online error corrections and adjust the system dynamics for future movements (Shadmehr & Wise, 2005). The latter outcome, referred to as state prediction, allows assessment of movement accuracy in spite of sensory feedback delays and noise in the system, both of which increase the uncertainty or variability in motor planning and control (Wolpert & Ghahramani, 2000).

Integration of Sensory Information to Reduce Uncertainty during Planning and Control

There are many sources of variability during visuomotor behaviors, including imprecise sensory information, noise or inherent variability in the central nervous system, and changing environmental and task constraints. These sources may contribute differentially during motor planning, execution, error-correction, and during the subsequent updating of future movement plans. However, errors that may accumulate during limb effector localization and during sensorimotor transformations, leading to poor motor planning, may also affect subsequent phases of motor control (Bays & Wolpert, 2007; Shadmehr et al., 2005). Moreover, task constraints may impinge on the availability of sensory information, forcing the individual to utilize other sources to augment sensory deficits. For example, limited lighting may force one to down-weight vision, resulting, in increased reliance on proprioception to provide a sense of initial position in space and guide the hand during the movement. Similarly, reweighting may reflect the salience of the sensory information. For example, in movements toward a visual target, visual information is weighted greater than proprioceptive information. However the opposite is the case when moving to proprioceptive targets. This allows the system to focus on relevant aspects of the task and privilege sources of information that may reduce errors and noise in the system. Taken together, differing weights are assigned to sensory modalities to increase the accuracy of movements during both motor planning and feedback dependent error correction, in order to optimize performance.

Furthermore, the system not only incorporates a flexible weighting strategy to account for the inherent variability of the sensorimotor system, but may also take into account previous experiences to inform the system of probable motor outcomes. By challenging the reliability of the sensory information, Kording and Wolpert (2004), found that the central nervous system also develops a probability distribution of prior knowledge. This information is incorporated with the estimated reliability of the sensory information to optimize performance and contribute to sensorimotor learning, using a Bayesian framework. As stated in Bays and Wolpert (2007), an improved state estimate [P(state|sensory input)] is the product of a probability of prior knowledge [P (state)] with the likelihood of a particular sensory outcome, given that predicted state [P(sensory input | state)], and normalized to the reliability of the sensory input [P(sensory input)].

$$\overbrace{P(\text{state}|\text{sensory input})}^{\text{Posterior}} = \frac{\overbrace{P(\text{sensory input}|\text{state})}^{\text{Likelihood}}\,\overbrace{P(\text{state})}^{\text{Prior}}}{P(\text{sensory input})}$$

The reweighing of sensory information would occur prior to this computation, and reflects the optimal combination that would produce the most reliable sensory estimate. Thus, the reliability of the state estimation during motor planning and the sensory predictions used in subsequent error correction may be finely tuned with experience.

Developmental Changes in the Role of Vision and Proprioception in Visuomotor Behavior

The reliability of the sensory afferents that inform the CNS of the environmental context is central for the development of an accurate internal model (Contreras-Vidal et al., 2005; Jeannerod, 1997). This is of particular importance in childhood, given the combination of motor inexperience and incomplete development of the neural system which result in movement errors during task performance. Thus, the refinement and utilization of visual and proprioceptive information is critical during the phases of motor planning, for error detection during movement production for online correction, and subsequent update of motor plans during future movements.

Several studies have examined developmental trends in visuomotor behavior that demonstrate improved accuracy, improved intralimb coordination patterns, and decreased variability with increasing age (Contreras-Vidal, 2006; Contreras-Vidal et al., 2005; Konczak et al., 1997). These finding suggest that both the motor planning and control during the movement are refined with increased experience performing eye-hand coordinated tasks. In order to assess these two components (planning and control) two phases of the movement kinematics are typically examined: a ballistic approach phase (evidence of the plan) and a decelerating terminal phase (evidence of control and online error correction). Konczak and Dichgans (1997) found that children 2- to 3-years-of-age are able to acquire targets during reaching movements with limited error correction, by virtue of learning the intralimb coordinative patterns. The authors reported that the development of stereotypic kinematic characteristics of reaching patterns, such as unimodal, bell-shaped velocity profiles and low end-point variability (aspects of motor planning) are established in toddlers. Although preplanned stereotyped movements may be sufficient for gross target acquisition, the movement precision and spatial characteristics are not refined. There is support that the ballistic pre-programming approach to goal-directed reaching continues to dominate behavior up to 5 and 6-years-of-age (Hay, 1978). As a result, similar performance is seen during movements in the presence or absence of vision for these children because they lack the ability to integrate feedback (both visual and proprioceptive) during motor execution (Bard, Hay, & Fleury, 1990). Although reliance on the initial motor plan alone is sufficient to attain targets, the inflexibility of this purely feed-forward motor strategy is clearly maladaptive under changing environmental contexts.

Significant features of adult-like limb control that allow adaptive motor execution are achieved in later stages of development. Control parameters such as endpoint precision and an optimized movement trajectory are not realized until feedback mechanisms are assimilated during the terminal phase of the movement (Hay, 1978; Hay et al., 2005; Jeannerod, 1997). Integration of visual feedback in the updating of relative target and hand locations produces longer deceleration during the terminal phase of the movement. Since this process needs to be calibrated, the optimization of these parameters are not completely realized and discontinuities may be evident in the kinematic (velocity) profile of 7- and 8-year-olds (Fayt et al., 1992; Hay, 1978). Once the children are able to gradually update and control limb trajectories based on visual errors, a decreased variability in movement amplitude, unimodal velocity profiles, and straight movement trajectories emerge.

These findings demonstrate the reliance on vision during the development of accurate online limb control particularly for the deceleration (terminal) phase of movement. Despite significant improvements in kinematic accuracy during reaching through the use of visual feedback, the arm movements of 7 and 8-year-olds still lack aspects of mature limb control. The reason for this is that these children do not appear able to use proprioceptive feedback to plan and control arm movements. Thus, it is in the absence of vision, when proprioceptive feedback is necessary to guide reaching, that this inability is made apparent. Favilla (2006) found that if visual feedback of the movement trajectory was removed, the younger children were able to make accurate, single, quick, uncorrected movements towards the visual targets. However, adult-like precision was reached for only the older, 8- to 9-year-old children. In a similar vein, a study by Redon, et al. (1994), found that 5-year-old children were able to detect the effect of a tendon vibration and correctly mirror the felt movement with the non-vibrated arm, they were not however, able to modulate the response. Older children, on the other hand, were able to modulate the response of the unaffected arm to reflect the perceived angular velocity induced by the tendon vibration. These results suggest that it is at a later stage of development when information provided by proprioception is comprehended and becomes efficiently employed to guide limbs and produce accurate movements.

The transition from visually-dominated feedback to increased incorporation of multisensory afferents is paramount for mature reaching to evolve. The continual integration of both visual and proprioceptive afferents in the control of limb trajectories has only been shown in older children, typically over 9 years of age (Ferrel et al., 2001; Ferrel-Chapus et al., 2002; Konczak et al., 2003). The accumulation of motor experience and the ability to integrate multiple sources of sensory in older children further develops the sensorimotor relationships that are necessary for motor planning and control.

Moreover, the sensorimotor mapping, or internal model, is adaptable such that the older children can learn how to accurately execute limb movements despite novel environmental contexts. For example, when presented with a distortion such as a visual feedback rotation or a dynamic perturbation (velocity dependent force fields), 8- year-old children are able to adapt the preexisting visuomotor mapping (or internal model) to accommodate environmental changes (Contreras-Vidal et al., 2005; Ferrel et al., 2001; Ferrel-Chapus et al., 2002). Thus, adaptation of the sensorimotor mapping requires a reweighting of visual and proprioceptive information to facilitating adaptive behavior.

To conclude, the quality of goal-directed reaching behaviors depends on appropriate motor planning through calibration and integration of sensory information. The estimation of the location of the limb effector in space (location map), the computation of the displacement between the start and target location (displacement map), and the estimation of the joint torques and muscle forces (dynamics map), are all contingent on the reliability of multiple sources of sensory information. The reliability of the state estimation during motor planning and the sensory predictions (forward model) used in subsequent error correction may be finely tuned with experience and with the development of refined sensory perception. The development of forward models or mechanisms that predict the sensory consequences of the motor commands allow the developing system to compensate for highly variable and noise-contaminated sensory estimation during motor planning and execution. Therefore, in order for children to elicit accurate and adaptive movements learning to efficiently utilize the sensory information during motor planning phase is critical.

Neurophysiology of Visuomotor Behavior

The planning, execution and control of limb effectors for reaching movements result from multifaceted interactions between many distinct neural structures (for a comprehensive review of both cortical, subcortical, and peripheral components see (Day & Brown, 2001; Jeannerod, 1997; Shadmehr et al., 2005). However, since the neuroimaging methods used in this investigation are limited to cortical structures, the focus of this review is to highlight associations and patterns of activations in cortical areas of interest. Thus, the only subcortical contribution to eye-hand coordination will be limited to the superior colliculus, as it is important during initial orienting behavior, and discussed with respect to its effect on cortical projections to the extrastriate areas.

The motor planning phase is initiated though the localization of target objects and of the limb effectors in extrinsic space. Although, various sensory inputs contribute to this localization, extra-retinal and retinal visual afferents dominate this phase (Batista, Buneo, Snyder, & Andersen, 1999). Excitation of the peripheral retina (extra-foveal area) initiate orientation behaviors that enable target fixation via the retinotectal pathway in the midbrain (Stein, 1998). The superior colliculus - the relay station for this pathway, receives inputs from the brainstem, basal ganglia, and multiple areas of the cortex, in addition to visual afferents. Cortical modulation of the superior colliculus allows low-level sensorimotor integration of these divergent sources and adaptive weighting of salient information (Jiang & Stein, 2003; Perrault, Jr., Vaughan, Stein, & Wallace, 2003; Salinas & Thier, 2000). Transformations between sensory mapping (primarily retinocentric) located on the superficial aspects of the superior colliculus and motor maps embedded within the deep aspects, allow coordination between eye and head movements (particularly saccadic movements) and reflexive projection (and/or withdrawal) of the limb toward the target (Prablanc, Pelisson, & Goodale, 1986; Stuphorn, Bauswein, & Hoffmann, 2000).

Once the initial sensorimotor commands from the superior colliculus elicit orientation (head and eye movements) to the target, the target image is captured in foveal (central retina) vision. Retinal acquisition of the target and limb effector allows refinement of the locations map (Prablanc & Martin, 1992; Salinas et al., 2000). Visual information diverges into two corticocortical streams: the ventral and dorsal pathways (Goodale & Milner, 1992). The ventral pathway (occipitotemporal) travels from the striate cortex to prestriate areas, and moves bilaterally to the inferior temporal cortex by way of the corpus callosum. The ventral stream is associated static perceptual properties such as color, shape, orientation, and object recognition. Alternatively, the dorsal stream relays dynamic, movement-related visual information from the striate cortex to the posterior parietal cortex (Milner & Goodale, 1993). The retinal and extra-retinal afferents, along with subcortical and cortical contributions are combined to produce a single eye-centered representation of the target and the limb effectors (Shadmehr et al., 2005). Concurrently, limb effector location is computed from proprioceptive afferents in body-centered coordinates (Vindras, Desmurget, Prablanc, & Viviani, 1998). In the absence of vision, accurate proprioceptive localization is essential for the production of goal-directed reaching. However, the synthesis of both location maps (eye-centered and body-centered) through a coordinated network of neuronal populations in the premotor, and primary motor areas allows precise computation of a difference vector between the target and hand positions from in a common eye-centered reference frame (Battaglia-Mayer et al., 2003; Pouget et al., 2002).

In the context of the internal model framework, the computed movement amplitude and the direction (angle) are derived from the difference vector (displacement map). The difference vector is the computed the straight line trajectory between the start position and target position obtained from the combination of the visual and proprioceptive estimates of these positions. There is evidence of neuronal tuning in most of the cortical areas in the sensorimotor loop to these two parameters. In terms of the IM framework, the most influential forms of neuronal tuning are found in the premotor (dorsal premotor, PMd) and the parietal cortices, as they are related to changes in the gain fields (Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991; Crammond & Kalaska, 1996; DeSouza et al., 2000; Kettner, Schwartz, & Georgopoulos, 1988). The gain fields are multimodal representations that modulate the response amplitude of the receptive fields based on the gaze direction or position of the arm in a retinocentric coordinate frame. The gain fields appear the locus for computations between various sensory modalities during sensorimotor transformations across different reference frames (Salinas et al., 2000), particularly eye-centered and body-centered coordinates and motor commands (Buneo & Andersen, 2005; Pouget, Deneve, & Duhamel, 2002). With respect to reaching movements, sensorimotor transformations between reference frames allows translation of the difference vector (in extrinsic coordinate frames) into the intended configuration of joint angles or angular displacement (within an intrinsic coordinate frame) needed to move to the target. Moreover, feedback from these two sensory modalities allows precise updating of the displacement vector during the movement.

Modulation of neuronal activity is also present in neuronal populations of the primary motor cortex responsible for executing the motor plan with respect to kinematic and kinetic factors such as movement direction and amount of force needed to produce a given muscle torque (dynamic map), respectively (Burnod et al., 1992; Cisek, Crammond, & Kalaska, 2003; Georgopoulos, Ashe, Smyrnis, & Taira, 1992; Georgopoulos, Crutcher, & Schwartz, 1989). Studies involving force-field perturbations or movements with varying load forces depict large changes in neuronal population activity, over those observed under varying movement direction alone (Kalaska, Cohen, Hyde, & Prud'homme, 1989). Significant changes were also observed in comparisons between neuronal discharge related to proximal versus distal movements and contralateral versus ipsilateral arm movements. Ipsilateral activation of M1 in this context occurs to a small extent during limb transport and may reflect the role of the motor cortex in making compensatory adjustments to maintain stability and arm control (Kalaska et al., 1989; Verstynen, Diedrichsen, Albert, Aparicio, & Ivry, 2005). The ability of the primary motor areas to flexibly adapt to changes in movement parameters (position, direction, force production, additional muscle coordination) facilitates the kinematic and kinetic transformations for the dynamic map, and is requisite for the generation of motor commands and updates during online control.

In sum, the motor planning is the product of the activity of many neural substrates involved in the determination of the location, displacement, or dynamics maps discussed previously. The sequential nature of the interactions between brain areas allows modulation of sensory information, such as low-level sensory integration found in the superior colliculus, and adaptive weighting of sources of information, as in the changes in gain fields in the parietal and pre-motor areas. This pre-processing of sensory information, in turn, enables integration of salient sources of information during sensorimotor transformations. Thus, the motor commands sent for task execution will become more refined to the important task or environmental constraints, which will reduce the need for feedback based error corrections during task performance.

Cortical Lateralization

Investigations in both adult human and non-human primates provide evidence that unimanual hand skill is highly correlated to the size of the cortical representations in the contralateral somatosensory (Thoma, Yeo, Gangestad, Lewine, & Davis, 2002) and motor cortices (Kim et al., 1993; Volkmann, Schnitzler, Witte, & Freund, 1998). In these studies, comparisons between cerebral hemispheres in terms of structural and functional imaging techniques have demonstrated that increased lateralization is related to a greater difference in manual performance between dominant and non-dominant hands and with increased hand preference (selection of hand for a given task). In particular, there is asymmetrical activation in favor of the contralateral hemisphere related to visuomotor behavior and significant decreases in ipsilateral activation of the primary motor cortex (Dassonville, Zhu, Uurbil, Kim, & Ashe, 1997). Enlarged representational areas may foster greater cortical encoding of motor skills for the dominant hand within the motor cortex.

Additionally, intrahemispheric relations between specific areas are strengthened, facilitating efficient activation of finely-tuned regions within a ‘dominant hemisphere’ during motor tasks performed by both dominant and non-dominant hands (Serrien, Cassidy, & Brown, 2003). Although, right-handed subjects more consistently show this left-hemisphere bias, left- and mix-handed participants also exhibit similar asymmetric activation patterns in regions of the parietal cortex (inferior and superior parietal lobules, and intraparietal sulcus) and frontal, motor-related areas including the dorsal premotor and anterior cingulate areas (Astafiev et al., 2003; Thoenissen, Zilles, & Toni, 2002; Toni, Thoenissen, & Zilles, 2001). Similarities across modality (eye and hand movements), irrespective of the hand performing the movements, demonstrate that lateralized activation patterns are not solely due to mechanical factors but may reflect increased attention to task-relevant spatial information necessary for motor planning and movement execution during reaching. Further, Rushworth, Krams, and Passingham (2001) suggest that these effects are exclusively attributed to motor preparation of hand movements rather than to processes related to oculomotor orienting/attention or by verbal task preparation. The activation of recurrent left frontal-parietal networks may thus reflect processing of visuomotor transformations between extrinsic (retinal or fixation-centered) and internal (body-centered) reference frames during motor planning of limb movements. Importantly, these activation patterns are correlated with increased degree of handedness. Since hand preferences are strengthened over the course of childhood, it is reasonable to hypothesize that the activation patterns may also emerge between early and late childhood.

Developmental evidence indicates performance differences between dominant and non-dominant hands across childhood. Blank, Miller, and von Voß (2000) demonstrated that laterality of hand performance depends on factors including: the complexity of the task (combined or sequential movements), type of movement (wrist and elbow flexion/extension or finger circumduction) and joint topography (proximal versus distal). Additionally, these authors attribute these effects to the development of motor-neuronal populations of the primary motor cortex underlying movement generation discussed above (Blank, Miller, & von Voß, 2000). Developmental changes in these neuronal structures may relate to the functional changes evident in behavioral analyses of hand performance in children.

Structural Changes and Cortical Myelination

In comparison to the numerous imaging studies (EEG, fMRI, structural imaging) examining the development of hemispheric asymmetries related to language acquisition (see Toga & Thompson (2003) for a recent review), hemispheric asymmetries related to motor cortical areas are less often reported and appear inconsistent (Barry et al., 2004; Gasser et al., 1988a). However, several studies have shown structural changes in cerebral development throughout childhood and into adolescence that may contribute to behavioral changes in unimanual performance. For example, gray matter density increases through childhood until puberty due to increased dendritic arborization leading to an improvement in synaptic connections relaying sensory and motor information. Although the rate of change is attenuated after 7 years of age, the greatest volume is seen around 11 years in the frontal regions, and by 10 years in the parietal regions in girls (Gogtay et al., 2004). Giedd et al. (1999a) showed that gray matter decreases during puberty and through adolescence, indicative of maturational processes such as dendritic pruning, glial proliferation, and synaptic development, are earliest to emerge in the dorsal parietal regions closest to the sensorimotor areas spreading rostrally towards the primary motor regions and frontal areas. Correspondingly, the overall density of white matter tracts increases during this time and is essential for functional and efficient interactions between related brain areas (De Bellis et al., 2001; Giedd et al., 1999a; Giedd et al., 1999b; Paus et al., 1999). In particular, age-related changes in the internal capsule are attributed to increased axon diameter which in turn is related to increased myelination of the corticospinal tracts (Paus et al., 1999). On a functional level, the structural development of this fiber tract leads to improved conduction velocities into late childhood. Although peripheral conduction velocities reach adult levels by three years of age, these levels are usually not obtained much before the age of 10 for central conduction velocities (Muller, Ebner, & Homberg, 1994; Muller, Homberg, & Lenard, 1991). Thus, limitations on behavioral skill acquisition in motor behavior may be attributed to the protracted development of central rather than peripheral contributions.

Callosal Development

The corpus callosum is the major white matter bundle connecting homologous regions of the two cerebral hemispheres. The malformation or degeneration of the corpus callosum results in poor motor performance during unimanual and bimanual movements (Stancak, Cohen, Seidler, Duong, & Kim, 2003) and reduced interhemispheric transfer of sensory information (Chicoine, Proteau, & Lassonde, 2000; Sauerwein & Lassonde, 1994). Myelination of the posterior aspect of this major interhemispheric pathway during late childhood leads to transfer of task-relevant information particularly between association areas of the cortex (Chicoine et al., 2000; De Guise & Lassonde, 2001; Giedd et al., 1999b; Muller, Kass-Iliyya, & Reitz, 1997). Efficient integration of visual and somatosensory information across hemispheres is necessary for accurate motor planning and during error correction for visuomotor tasks in variable workspaces. Thus, the late development of the posterior callosal pathways, in particular, leads to behavioral differences in manual task performance between young and old children (Chicoine et al., 2000).

Typically the role of callosal pathways in motor planning and control is inferred through behavioral performance of crossed-uncrossed paradigms (Di Stefano & Salvadori, 1998; Fagard, Hardy-Leger, Kervella, & Marks, 2001; Hay & Velay, 2003; Konczak et al., 1997), or during unimanual transfer of learning tasks (Chicoine et al., 2000). Across these studies, the youngest children (6 to 7-year-olds) and patients with partial or complete callosal agenesis are consistently characterized similarly - longer transfer times during crossed conditions and poor transfer of practice between hands during unimanual performance. Rademaker (2004) examined motor performance and cross-sectional size of the corpus callosum in pre-term and typically-developing children. Strong correlations were found between increased callosal cross-sectional size and improved performance on the Movement Assessment Battery for Children (MABC) and the Developmental Test of Visual Motor Integration (VMI). Although, these results provide additional support for the role of these pathways in motor behaviors, the results must be interpreted cautiously as motor performance of the pre-term children may have been affected by additional deficits in cortical and subcortical motor areas that were not reported. Notwithstanding, it is clear that these pathways contribute to accurate motor performance and visuomotor integration.

Although the callosal tracts may serve to improve task-related information transfer across the hemispheres, there is an increased likelihood for homologous muscle activation of motor areas connected by transcallosal fibers. However, Lazarus (1987) found that the ability to inhibit non-task associated movements increases with increasing age. Thus, the effect of the development of the corpus callosum in enabling functional differentiation of the limb effectors during unimanual performance is two-fold: it facilitates transfer of task-related sensory information needed for motor planning and inhibits non-task related behaviors during motor execution.

There is good evidence that the prolonged development of specific neural structures may contribute to development of visuomotor skill acquisition across childhood. The evidence from neuroimaging and transcranial magnetic stimulation techniques complements the well documented behavioral characterization of visuomotor development. Moreover, it is possible to hypothesize that neural mechanisms either underlie or co-occur with the development of accurate and fast visuomotor abilities across childhood. However, the time course and extent to which these cortical areas play a role during the planning and control of accurate reaching in children in typically-developing children remains unclear.

Measurement of Neurophysiological Development Change

Several electroencephalography (EEG) techniques allow a comprehensive depiction of the neurophysiological processes involved during goal-directed reaching movements. In particular, spectral analysis allows an examination of age-related changes in the individual frequency contributions to a given brain wave signal across different brain regions. Coherence analysis quantifies the similarity of two signals (or electrode sites) in the time and frequency domains, indicative of the strength of their relationship and the underlying structural connections. Event-related potentials (ERPs) are also useful to examine the time-locked response to a stimulus or behavioral event. ERPs reflect activity or processing from a population of neurons, and may be matched to the preparation and behavioral responses from a millisecond time-scale. These methods have been validated for healthy infants and children, as well as pediatric patient populations, and prove useful in the study of cognitive, sensory, and motor functions (Taylor, 2002).

Power-Spectral Analysis

The power-spectrum of an EEG signal is obtained through fast Fourier transform (FFT). The magnitude of the amplitude and phase for each frequency component may be calculated from this method (Nunez, 1981). The following frequency bands contribute to the EEG signal: delta (<3Hz), theta (4-8Hz), low alpha (8-10Hz), upper alpha (11-13), low beta (14-20), upper beta (20-30), and gamma (30-70Hz). Relative power may be computed as the percentage contribution of these bands to the total EEG signal. By computing relative power, differences between individuals due to skull thickness and impedance may be attenuated. Moreover, this measure has been found to be sensitive to developmental changes (Gasser et al., 1988b). Although other more complex methods may be used to compute the changes in frequency bands and in the complexity of the EEG signal with age, the conventional FFT power estimates for each band are easily interpreted and better documented in the literature (Benninger, Matthis, & Scheffner, 1984). Overall, the value of power spectral analysis is that regional differences in activation and shifts in the frequency bands contributing to the overall brain signals may be determined.

Using traditional techniques, several developmental changes have been seen across frequency bands. One such change is a shift in the relative frequency contributions of these bands, in that alpha and beta contributions increase whereas those of the lower frequency bands decrease (Clarke, 2001; Gasser et al., 1988a; Gasser et al., 1988b). The topographical progression for these frequency shifts occur in different directions. For example, the lower frequencies (theta, low-alpha) develop first in the posterior regions and progressing forward, whereas the higher frequencies (high alpha and high beta) progress in the opposite direction (Benninger et al., 1984; Gasser et al., 1988b). These studies also reported symmetrical patterns of the frequency distribution across the two hemispheres across age, however, another study found developmental differences across the midline and two hemispheres (Clarke, 2001). In particular, beta power was found to increase in the midline sites at a faster rate than the lateral sites in children 8 to 12 years of age. These frequency shifts may be attributed to grey and white matter development and physical growth during childhood (Gasser et al., 1988a). Taken together, these studies provide a foundation for the age-related changes in spectral content in the EEG of children at rest. However, the changes in spectral power during motor task performance have not been examined to date. Since task-related cortical activity would exhibit different frequency, it is unclear as to degree of consistency with these documented age-related changes.

EEG Coherence

Although spectral power analyses provide information about the regional specificity and frequency composition of brain wave activity in different locations of the brain, they do not provide any information about the functional coupling between areas of interest. Coherence analysis, on the other hand, is useful to determine the strength of synaptic connections between spatially distant, but functionally related brain areas (Thatcher, 1992). This measure has been validated in children and used a measure of the development of cortical areas and functional communication between brain regions across age and gender (Barry et al., 2004; Thatcher, Walker, & Giudice, 1987).

Specifically, the calculation of coherence consistent with Halliday (1995) is given by the equation:

$$|R_{ab}(\lambda)|^2 = |f_{ab}(\lambda)|^2 \,/\, f_{aa}(\lambda)\, f_{bb}(\lambda)$$

where f represents the spectral estimate of two EEG signals a and b for a given frequency λ. The numerator is the cross-correlation for a and b (f_{ab}) and the denominator consists of the auto-correlation for a (f_{aa}) and for b (f_{bb}). The values range from 0 (no similarities between the two signals) and 1 (identical signals). Long-range and short range electrode pairs can be analyzed within a hemisphere (intrahemispheric coherence) or across the two hemispheres (interhemispheric coherence).

With increasing age, both measures increase, and are thought to reflect the cortical development (specifically, increased synaptic connections) underlying brain functions (Taylor, 2002). These developmental changes in coherence were found with increases in all frequency bands (1.5 - 25Hz) with increasing age (Gasser et al., 1988a). In addition, this study reported high interhemispheric frontal coherences, but very low coherence values across central electrodes. This study also reported high intrahemispheric coherence was found between frontal and central locations. The coherences values obtained from one hemisphere did not differ from those obtained from the other hemisphere. This was not the case in a study by Thatcher (1987), in which age-related increases in long-range coherence between frontal and occipital regions with increasing age for the left hemisphere were found. Barry (2004) additionally, found lateralized effects, in which left hemisphere exhibited higher coherence than the right for delta, theta, alpha, and beta frequency bands. These finding suggest that the age-related increases in coherence, particularly for the long-range electrode distances, may be attributed to the development of long fibers and improved myelination during childhood particularly of the left hemisphere.

One limitation to the developmental studies of coherence, like the spectral analyses discussed in the previous section, is that they have primarily focused on resting conditions, which provides little information regarding task-related communication specific to visuomotor behavior. However, several studies have examined coherence in adults while performing visuomotor tasks. In this context, alpha (8-12 Hz) and beta (13-30Hz) frequency bands are of interest during tasks requiring eye-hand coordination because they are associated with cognitive processes such as expectancy, attention, and behavioral preparation (alpha band), as well as the motor planning and execution during coordinated motor tasks (beta band) (Gerloff & Andres, 2002; Knyazeva et al., 1997; Serrien et al., 2003). In a classic paper, Busk and Galbraith (1975) found that coherence between 4 and 20Hz increased when eye-hand coordination was necessary for task performance, as compared to eye-tracking and hand-tracking. Moreover, the magnitude of the coherence depended on the functional properties of the visuomotor system, such that highly connected areas such as the pre-striate to premotor areas and the premotor to primary motor areas demonstrated high levels of communication. However, practice reduced the task complexity and correspondingly decreased the neural demand. The attenuation of coherence selectively affected the premotor to primary motor associations; however, since the visual-premotor connections are necessary for performance, coherence remained high between these areas.

Although interhemispheric coherence between the central electrodes (over the sensorimotor areas) was found to be the lowest among the other electrode pairings for this study, other studies have demonstrated increased inter-hemispheric coherence in these areas, even in children (Knyazeva et al., 1997; Mima, 2000). Both studies showed increases in the alpha and beta bands across hemisphere during motor tasks executed with the right hand. In addition to increased interhemispheric coherence between sensorimotor and parietal regions, Knyazeva et al. (1997) found that right-handed children also exhibited lateralized intrahemispheric effects during right hand movements over the contralateral hemisphere for the beta frequency band. Therefore, children show an increase in the lateralized functional connectivity between frontal, central, parietal and occipital regions related to right-hand motor behavior. These results are consistent with studies using various imaging techniques (EEG, fMRI and PET) confirming the necessary relationship between fronto-parietal and fronto-central regions during production of accurate visuomotor behavior, particularly during early learning (Koeneke, Lutz, Wustenberg, & Jancke, 2004; Krakauer et al., 2004; Staines, Padilla, & Knight, 2002).

Taken together, increased coherence across age suggests that there is continued neural development improving the strength and numbers of connecting fibers among different brain regions, throughout childhood. Results from both adults and child studies of arm and finger movements further support improved functional, task-related communication between areas subserving visuomotor behaviors. As children gain additional motor experience, as with practice, decreased coherence may reflect refinement of cortical processing and neural efficiency.

Event-Related Motor Cortical Potentials

The Bereitschaftspotential (BP) is an event-related motor readiness potential that has previously been used to characterize the planning phase of self-initiated finger movements in children and adults prior to movement onset (Chiarenza et al., 1995; Deecke et al., 1984; Jahanshahi et al., 2003; Kristeva et al., 1987). Figure 2.2 depicts the ideal BP waveform (typical of adults), which can be separated into a long lead (early BP) and a short lead (late and peak BP), based on the time-course evolution of the waveform and serial activation of cortical areas.

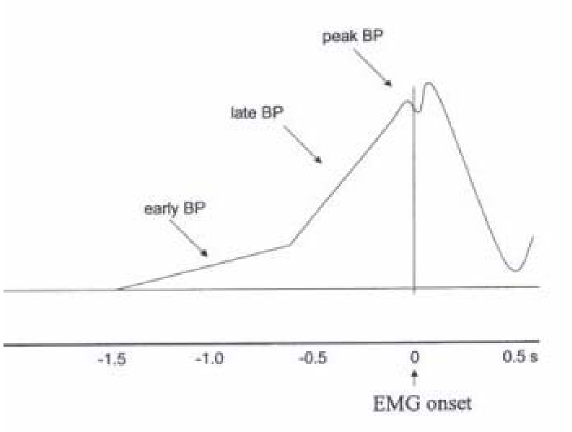


Figure 2.2. Depiction of the BP waveform time-locked to EMG onset. Positive vertical axis indicates a negative amplitude, in units of µV. Figure 1 from Jahanshahi and Hallett (2003).

The long lead activity is evident between 500ms to 1.5 seconds prior to movement onset and is maximal in electrodes placed above the SMA in adults (Deecke et al., 1984; Jahanshahi et al., 2003). The short lead activity is evident between 500ms before movement onset until the initiation of movement and is observed in the electrodes corresponding to SMA, PM and M1. The waveform is symmetrical during the long lead portion and becomes increasingly more asymmetrical toward the peak amplitude which occurs around 50ms before movement onset for Cz (Jahanshahi et al., 2003). Peak amplitudes differ across the electrode locations. The contralateral frontal maximum occurs approximately 500 ms before movement onset and but shifts to central sites approximately 100ms prior to onset. The asymmetry of the BP corresponds with larger values for the contralateral primary motor cortex (C3 > C4) and the ipsilateral visual association areas (P4>P3). This pattern reflects a left hemisphere dominance for motor processing and right parietal dominance in visuospatial processing (Deecke et al., 1984).

Although BP is classically used to study finger movements, there is evidence that faster, more spontaneous and complex movements may be studied (Chiarenza et al., 1983; Deecke et al., 1984). The amplitude and latency of the BP is sensitive to increased movement complexity, coordination between various muscle groups and body segments (Chiarenza et al., 1995; Jahanshahi et al., 2003; Warren et al., 1984). Specifically, during goal-directed hand movements, additional neural activation of the supplementary motor area (SMA), premotor (PM) areas, and primary motor (M1) areas may increase both the amplitude and latency of the BP.

The BP waveform is not consistently reported across developmental studies, particularly for young children, and may be characterized by either a negative to positive waveform evolution or the opposite with a high post-movement positive shift (Chisholm et al., 1984; Kristeva et al., 1987). The positive components preceding movement by about 200ms have been reported and may be indicative of inhibitory processes needed to increase the accuracy of the movement. On the other hand, post-movement positivity may indicate reception of feedback (Chisholm et al., 1984; Kristeva et al., 1987). Moreover, the youngest groups of children may exhibit a fronto-parietal response which may additionally reflect increased attention during task performance. The younger children exhibit much greater variability in their BP waveforms, and in some reports do not show a single peaked BP, differing from the older children that exhibit unimodal BP profiles similar to adults (Chiarenza et al., 1995; Chisholm et al., 1984; Kristeva et al., 1987).

Despite the variability of the waveforms for the young children, greater consistency is found in the waveforms of older children, similar to those exhibited by adults (depicted in Figure 2.2). These data support the ability of older children and adults to appropriately incorporate task relevant stimuli in motor plans. This ability may be, in part, attributed to the maturation of the dorsolateral prefrontal cortex (DLPFC), which is thought to contribute to motor planning and development of the BP during self-paced movements (Jahanshahi et al., 2001; Jenkins et al., 2000).

Summary

The development of adaptive motor planning and control is highly influenced by a multiplicity of factors, differentially contributing over the course of childhood. The changes in the behavioral performance of children during goal-directed reaching and drawing movements may not only reflect adjustments in response to physical and biomechanical constraints, but also may be indicative of tuning and reorganization of the central nervous system. By characterizing both the motor performance and the neurophysiology, it may be possible to gain a clearer understanding of the neurodevelopmental factors underlying changes in motor performance during reaching and drawing movements in children. The use of several types of the electrophysiological measures provides different windows to understanding age-related changes in neurophysiology. In particular, the development of task-related motor response preparation and communication between relevant brain areas, thought necessary to produce accurate motor planning and control, may be more clearly delineated.

CHAPTER III

Experiment 1: Age-related Difference in Kinematics and Cerebral Cortical Processes during Discrete Drawing Movements in Children and Adults

Introduction

Adults are able to plan and control goal-directed movements, such as drawing and reaching, automatically and efficiently. In contrast, the behavioral performance of children on these types of tasks can be highly effortful and often results in less accurate performance for a particular goal. Many studies examining the development of drawing and reaching movements have found age-related improvements in motor performance. Specifically, older children demonstrate improved accuracy, improved intralimb coordination patterns, and decreased variability, as compared with younger children (Contreras-Vidal et al., 2005; Hay, 1978; Hay et al., 2005). Age-related changes in motor behavior are thought to reflect the ability to utilize or integrate visual and proprioceptive inputs in the planning and online control of drawing movements during childhood. Redundancy between vision and proprioception allows optimized end effector localization during motor planning and allow more efficient error correction. Moreover, this information is necessary for the development of a forward model that predicts the motor output in response to a motor command and allows the CNS to better estimate the current and future state of the limb effector, despite delays in the sensory feedback loops (Contreras-Vidal, 2006; Desmurget & Grafton, 2000; Miall & Wolpert, 1996).

Authors have suggested that age-related changes in motor performance may be related to protracted structural development and myelination of brain structures underlying sensorimotor integration, motor planning and control. For example, age-related changes are evident in the cortical structures subserving integration and transfer between brain areas within and across the hemispheres (Barry et al., 2004; Paus et al., 1999; Rademaker, 2004; Thatcher et al., 1987). Myelination and white matter development of pathways between different functional brain areas during childhood leads to improved speed and fidelity of information transfer (Paus et al., 1999). Moreover, the development of the callosal tracts, the main white matter bundle connecting the homologous areas of the left and right cerebral cortical hemispheres, undergoes significant increases in size and the degree of myelination during childhood and adolescence (Giedd et al., 1999b) and may be related to task-related transfer of sensory information. Similar changes are also evident in the corticospinal and corticofugal tracts during this time (Paus et al., 1999). Importantly, the structural development of white matter tracts has widespread functional implications for improved sensory, motor, and cognitive functioning (Paus et al., 2001).

To bridge the relationship between cortical development and the emergence of accurate visuomotor drawing movements, the current study used kinematic analysis and electroencephalography (EEG) to delineate the cortical activation patterns during the movement sequence from motor planning, movement onset and online control. EEG relative spectral power, coherence, and event-related motor cortical potentials were used to map the brain activation patterns with goal-directed motor performance to better characterize the specific changes between young and older children, and adults during drawing movements. Relative spectral power has been used in previous developmental studies to examine age-related changes in the frequency contributions to the EEG signal during resting conditions (Benninger et al., 1984; Gasser et al., 1988a; Gasser et al., 1988b). Similarly, differences in coherence have also been found in school-aged children at rest (Barry et al., 2004; Gasser et al., 1988a; Thatcher, 1992; Thatcher et al., 1987) and during a tapping task (Knyazeva et al., 1997; Knyazeva, Kurganskaya, Kurgansky, Njiokiktjien, & Vildavsky, 1994). Several studies have investigated developmental changes in event-related motor cortical potentials related to motor planning during simple finger movements (button pressing, flexion/extension) (Chiarenza et al., 1995; Kristeva et al., 1987; Warren et al., 1984). However, only a few studies have examined complex goal-directed movements in terms of difference in the event-related motor readiness potentials (Grunewald-Zuberbier & Grunewald, 1978; Grunewald-Zuberbier, Grunewald, Homberg, & Schuhmacher, 1980) and error-related negativity (Contreras-Vidal & Kerick, 2004). However, to date no imaging study has examined the cerebral processes related to multi-joint, goal-directed visuomotor behaviors in children as compared to adults.

In the present study, it was hypothesized that the quality of the behavioral performance of the children and adults may be, in part, a product of the cerebral cortical processes and patterns of activation during motor planning and control. Thus, adult-like performance in the children may be related to the existence of adult-like brain patterns of activation, communication between brain areas of interest, and the neural facilitation of cortical motor resources related to goal-directed visuomotor behaviors. Conversely, a lack of similarity in these neural patterns may contribute to the behavioral differences between the children and adults.

Method

Participants

In order to reduce group heterogeneity only female participants were included in the present study. Two groups of girls (n = 15, each): 6- to 7- year olds (6.7 ± 0.51 years; mean age ± SD) and 9- to 11-year-old (10.2 ± 0.86 years) were recruited from the surrounding areas, local camps, and from campus flyers for participation in this study. Five additional children were recruited for the young group, but were unable to successfully complete the task and were not included in the final analysis. One group of adult female undergraduate students (n= 15, 22.1 ± 2.0 years) was also recruited from summer courses as a "fully-developed" control group and used for comparison with the children. All participants were naïve to the purpose of the experiment. The adult participants and the children's parents or legal guardians signed informed consent forms (Appendix A and Appendix B). The children signed assent forms, similar to the informed consent, but written in age-appropriate language (Appendix C). All procedures were approved by the Institutional Review Board at the University of Maryland – College Park. For their participation in the study, the adults and children received a small monetary compensation. Additionally, the children also received a small toy prize for completing the experiment.

Inclusion Criteria

The adult participants or the parents of the child participants completed the neurological health screening either via phone interview or paperwork completed prior to the testing session (Appendix D and Appendix E). Inclusion was based on the following criteria: uneventful prenatal, perinatal, and neonatal periods, no major head traumas or incidences of unconsciousness, no history of convulsive disorders, no history of neuropsychological disorders (including depression and anxiety disorders), no diagnosis for learning disabilities (including ADHD), no language impairment (including stuttering and language delays), no deviation from physical or mental development (including no impairments in memory or cognition), no delays in the achievement of motor milestones (crawling, walking, writing). The adult participants were asked to abstain from caffeinated or alcoholic beverages and medication on the day of the testing session. The children also completed the Movement Assessment Battery for Children (Henderson & Sugden, 1992) during the testing session to evaluate their performance in the areas of manual dexterity, ball skills, and balance (Appendix F- manual dexterity tasks). All of the children included in the study performed above the 20th percentile (61% ± 21.8%; mean percentile ± SD) which is the cut-off for motor skill deficits as assessed with the MABC.

Only right-handed participants were included in the study. The adult participants were assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) and the children completed a 10-item test (Fagard & Corroyer, 2003) to determine the extent of the participant's handedness and laterality (Appendix G and Appendix H, respectively). The items on the child assessment included: throwing a ball, raising one hand, using an eraser, combing hair, brushing teeth, using a hammer, cutting with scissors, retrieving marbles from a cup, unscrewing a lid and rewinding a tape. These items were chosen for their familiarity to young children and the reliability compared to other measures of handedness. The children and the adults demonstrated a strong preference for their right hands with at most one item that was classified as mixed-handed.

Apparatus and Procedures

Figure 3.1 depicts the experimental set up. Participants sat comfortably at a table facing a 15”computer monitor positioned so that the center of the screen was kept at the child’s eye level. The participants used a chin rest to stabilize and maintain the head position. The height of the chair was also adjusted so that the child’s hand could move freely on the digitizing tablet. The child’s back was firmly supported, and his/her sternum was in contact with the tabletop. This had the effect of minimizing rotation of the torso, thereby reducing trunk movement and constraining the drawing movements to the arm at the shoulder and elbow joints. Direct vision of the hand/arm was prevented via an occluding board located between the computer screen and the digitizing tablet. A computerized pen was used to make line-drawing movements upon a digitizing tablet (12”×12” WACOM In-Tuos, Vancouver, Canada) in the horizontal plane. The digitizing tablet recorded the X-Y coordinates of the pen position at a sampling rate of 200 Hz using custom software written in OASIS (Kikosoft, Nijmegen). A laptop computer stored the data for later processing and provided real-time visual feedback of pen movement on the computer screen.

Figure 3.1 The experimental set-up

The participants began a trial presented on the computer monitor by moving the digital pen into a red circle (0.5cm diameter) in the center of the workspace (home position). Figure 3.2 depicts the behavioral task as presented on the computer monitor. Upon entering this home position, two blue targets circles (each 0.5cm in diameter) located at 135 and 315 degrees, were presented 5cm from the home position. The participant was instructed to self-select one target among the two. They had to remain motionless in the home circle for at least two second, and were told to "use this time to plan how to move as quickly and accurately as possible and stop in the target circle". There was no external cue to move after the 2 second hold period, but if the participant left the home position too soon, the targets would disappear and the trial would restart. The purpose of this wait period was to not only provide the participants with sufficient time for target selection and movement planning, but also to allow ample time for electrophysiological data acquisition during this phase of the movement. After the hold period, the participants drew a line between the home position and the target. Several times during the session the requirements to move to the target as "quickly and straight as possible" from the home position were reiterated. The targets and movement trajectory disappeared once the participant reached the target position, and subsequently, the participant would return to the home position to begin the next trial.

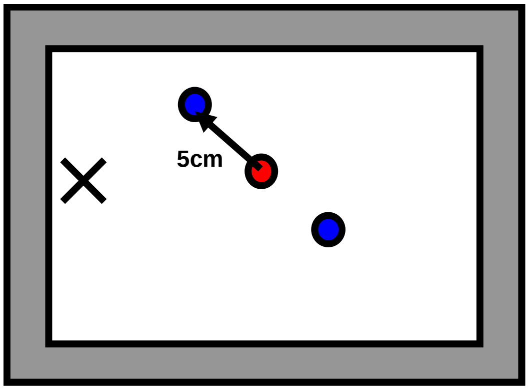


Figure 3.2 Task presentation on the computer monitor. The participant placed the left hand on the “x” during the task performance of the right hand. The red circle indicates the home position with the two target locations (blue) at 135° and 315°.

Prior to test performance, the subjects received a general orientation to the behavioral set up. The participants were instructed to move across all areas of the workspace to become familiar with the digital pen, tablet, and computer display. A formal set of practice trials consisted of 12 trials, 6 trials to each target. Testing constituted total of 60 trials. Although the subjects were free to choose the location of the target for each trial, they were instructed to move to each of the targets equally (average 30 trials to each target).

Behavioral dependent variables.

Post-acquisition data analysis with visual inspection of the pen trajectory data for each trial using Matlab 7.0 (The Mathworks Inc.™). Movement onset was defined as time when the pen left the circular home position. Movement offset was defined as the first sample when the pen entered the target circle and remained still for 250ms. Automatic routines were used to select the time and position of the movement onset and offset, and each trial was visually inspected and these positions were manually re-selected if incorrect, to ensure accurate marking of these events. The movement trajectory characterized the entire pen trace between the movement onset and offsets. The behavioral variables included in the statistical analysis to assess limb control during the task included: movement time, movement length, root mean squared error, normalized jerk, and initial direction error (IDE). In addition, prior to the statistical analysis, the trials exceeding 2.5 standard deviations from the mean for each of the behavioral variables (see below) were considered statistical outliers and were eliminated. Less than 5% of trials were eliminated prior to statistical analysis.

Movement length (total distance, mm) was computed from the pen trajectory between the home and the target. The straightness of the movements was measured by calculating the root mean square error (RMSE, in mm) for each trial. RMSE scores were calculated to assess the average deviation of the movement trajectory from the "ideal" straight line connecting the start and target position (the temporal structure of the ideal trajectory was therefore characterized by a uniform velocity profile), as follows:

$$RMSE(\text{inmm}) = \sqrt{\sum_{i=1}^{N} \left[(x_a - x_i)^2 + (y_a - y_i)^2 \right] \frac{1}{N}} \qquad (1)$$

where (x_a, y_a) and (x_i, y_i) are corresponding points of the re-sampled trajectory and the ideal trajectory, respectively, and N is the number of points in the path. The smoothness of the movement was measured by calculating the normalized jerk (NJ, unit free) of the temporally sampled pen trajectory. NJ scores were calculated as follows:

$$NJ = \sqrt{\frac{MT^5}{TD^2} \int j^2(t)\,\mathrm{d}t} \qquad (2)$$

where $j^2(t)$ is the rate of change of acceleration (i.e. jerk), MT is the total time from the movement onset to offset, and TD is the distance covered during the movement. The initial directional error (IDE, in degrees) was measured as the angular difference between a vector linking the home and target and a vector from the home to the pen position computed at 80 ms after movement onset (e.g., the initial direction of pen movement). Assessment of the IDE score at 80ms allows for the calculation of directional error before visual feedback is available for online corrections, and is thought to represent a measure of movement direction planning. In addition, IDE absolute and variable error were also computed to determine directional bias and consistency of the motor planning.

All behavioral dependent variables were subjected to separate one-way analysis of variance (ANOVA) with age group (young children, older children, adults) as the independent factor, using the mixed procedure in SAS® 9.1 software (SAS Institute Inc.). Tukey's post hoc multiple comparisons tests were used to follow-up significant effects.

Electrophysiological Data Acquisition

During the task, the participant's head was stabilized using an adjustable chin rest to reduce the amount of movement artifact present during the electroencephalographic data collection. Prior to behavioral task performance, two minutes of EEG were collected during both baseline conditions: resting eyes-open and eyes-closed. Neuroscan Scan acquisition software (version 4.1) was used to collect EEG from twelve unipolar surface electrodes sites using tin electrodes housed within a stretchable lycra cap (Electro Cap International) consistent with the international 10/20 montage (Benninger et al., 1984). As depicted in Figure 3.3, these sites included frontal left (F3), frontal midline (Fz), frontal right (F4), central left (C3), central midline (Cz), central right (C4), parietal left (P3), parietal midline (Pz), parietal right (P4), occipital left (O1) and occipital right (O2). Eye movements were monitored from tin electrodes placed superior (VEOU) and inferior (VEOL) to the left eye and on the orbital fossi of the left (HEOL) and right eyes (HEOR). A common ground was used and linked mastoids (M1 and M2) served as the reference signals). The impedances were maintained below 10kΩ using a Grass electronic impedance meter (model EXM 5D). Grass model (12A5) amplifiers were used to amplify the signals by 50,000 times for the scalp and mastoid electrodes and 20,000 for the eye electrodes. The a high-pass filter of 0.01Hz and a low-pass filters set at 100Hz

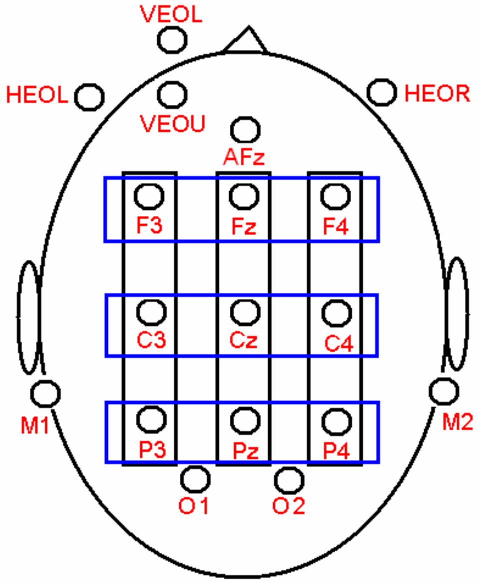


Figure 3.3 The electrode montage. Each of the areas (frontal, central and parietal, occipital) were divided into left, central, and right positions. Additionally, right and left occipital areas, and the anterior frontal midline (ground) were recorded. The black boxes indicate the electrode groups for the intra-hemispheric coherence analysis assessed within the left (F3, C3, P3) and right (F4, C4, P4) hemispheres and the midline (Fz, Cz, Pz). The blue boxes indicate the electrode groups used for the inter-hemispheric across the frontal (F3, Fz, F4), central (C3, Cz, C4), and parietal (P3, Pz, P4) areas.

Electrode recordings were processed off-line. All sites were algebraically referenced to the linked mastoid sites. Acceptable impedances (below 10kΩ) were difficult to obtain for the occipital sites (O1 and O2), due to interference caused by hair displacement. These sites were eliminated from the analysis for this reason. Continuous EEG data were epoched into 2,000ms sections beginning 1000ms prior to and 1000ms following movement onset. These electrophysiological data were visually inspected off-line for excessive movement and instrumental noise artifacts using Neuroscan Scan (version 4.3) software. All of the filters described were infinite impulse response (IIR) filters with 24dB/octave roll-off. Noise between 56Hz and 64Hz frequencies were eliminated with a band-stop filter. A 70-Hz low-pass filter was also applied to all data. For the spectral and coherence analyses, the following band-pass filters were used to separate the frequencies of interest: broad band (1-50Hz), theta (4-8Hz), lower alpha (8-10Hz), upper alpha (11-13Hz), lower beta (13-20Hz), upper beta (20-30Hz), and gamma (36-44Hz). For the BP analysis these data were low-pass filtered at 10Hz. Finally, epochs were baseline corrected and again visually inspected, prior to averaging.

Power-spectral analysis.

The power-spectrum of an EEG signal is obtained through fast Fourier transform (FFT). Power spectral analysis was performed on one-second epoched data from the baseline (eyes-open) condition, and from the one second before movement onset during the behavioral performance. Nine electrodes of interest (Fz, F3, F4, Cz, C3, C4, Pz P3, P4) for each of six narrow frequency bands (theta, lower alpha, upper alpha, lower beta, upper beta, and gamma) were analyzed. Structural differences (increased head size, increased skull thickness, greater changes of synaptic arborization) across age may change the total power contribution of the absolute spectral frequencies of interest (John et al., 1980). Relative spectral power is suggested to have better rest-retest reliability (Clarke, 2001; Gasser et al., 1988b) and to be more sensitive than absolute spectral power to age-related changes in the frequency composition (Gasser et al., 1988b). Thus, the relative spectral power was calculated as the summation of the absolute spectral power in a particular frequency band was normalized to the summation of the absolute spectral power from 1 to 50Hz (broad band spectral power).

In order to meet the requirement of normality for parametric statistics, the relative power for each electrode was then log transformed defined by Gasser (1988b) and expressed as the equation: $Y = \log(Z / 1 - Z)$, where Z is relative power. The log-transformed relative spectral power for each of the frequency bands was subjected to a 3 x 3 x 3 repeated-measures analysis of covariance (ANCOVA), with group (young children, older children, adults) as the between subjects factor, anterior-posterior location (frontal, central, parietal) and mediolateral location (midline, left, right) as repeated-measures within subjects factors, and the log-transformed relative spectral power at baseline as the covariate. Tukey's post hoc multiple comparisons tests were used for the significant main effects. Post hoc contrasts for significant interactions were written in SAS to analyze the interactions to test age-related difference effects of the other independent variables (Levin & Marascuilo, 1972).

Coherence analysis.

The calculation of coherence was consistent with Halliday et al., (Contreras-Vidal, 2006; Contreras-Vidal et al., 2005) and defined by the equation:

$$|R_{ab}(\lambda)|^2 = |f_{ab}(\lambda)|^2 / f_{aa}(\lambda) f_{bb}(\lambda)$$

where f represented the spectral estimate of two EEG signals a and b for a given frequency λ. The numerator was the cross-spectrum for a and b (f_{ab}) and the denominator consists of the autospectra for a (f_{aa}) and for b (f_{bb}). The coherence between Fz (coherence reference) and each of eight electrodes (F3, F4, Cz, C3, C4, Pz P3, P4) were calculated. Since the electrodes are all paired with Fz, these data were treated as an incomplete factorial (without a midline electrode in the frontal location). Again, the coherence for each of the frequency bands were subjected to a 3 x 3 x 3 repeated-measures analysis of covariance (ANCOVA), with group (young children, older children, adults) as the between subjects factor, anterior-posterior location (frontal, central, parietal) and mediolateral location (midline, left, right) as repeated-measures within subjects factors, and the coherence obtained at the baseline as the covariate. Tukey's post hoc multiple comparisons tests were used for the significant main effects. Post hoc contrasts for significant interactions were written in SAS to analyze the interactions to test age-related difference effects of the other independent variables (Levin et al., 1972).

Event-related potentials (ERP).

The ERP waveforms were obtained for each subject as the time-locked, averaged epochs from all trials. Three 250ms time windows before movement onset (-750 to -500ms, -500ms to -250ms, -250ms to movement onset) and one time window following movement onset (movement onset to 250ms) were included in the 3 (age group) x 4 (time) repeated-measures analysis of variance (ANOVA). Again, Tukey's post hoc multiple comparisons tests were used for the significant main effects and the interactions tested age-related difference effects of the other independent variables.

Results

EEG Spectral Content

Relative spectral power: power decreased across age groups with differences in regional activation in young children compared with older children and adults

Table 1 (Appendix I) reports the significant results for the relative spectral power from the ANCOVA for each frequency band of interest (theta, lower alpha, lower beta, upper beta, and gamma) including the *F* values, degrees of freedom, *p* values (indicated by asterisks), and post hoc comparisons. Upper alpha is absent from this table since no significant results were found for this frequency band. Significant group main effects were found for the mean log-transformed relative theta ($F_{(2,\ 39)} = 12.06$ $p < 0.01$) and lower alpha spectral power ($F_{(2,\ 39)} = 12.75$, $p < 0.0001$). Figure 4.1 shows the group main effect for mean log relative theta spectral power (Appendix I, Figure 4.1.1 for the analogous graph presented as a proportion).

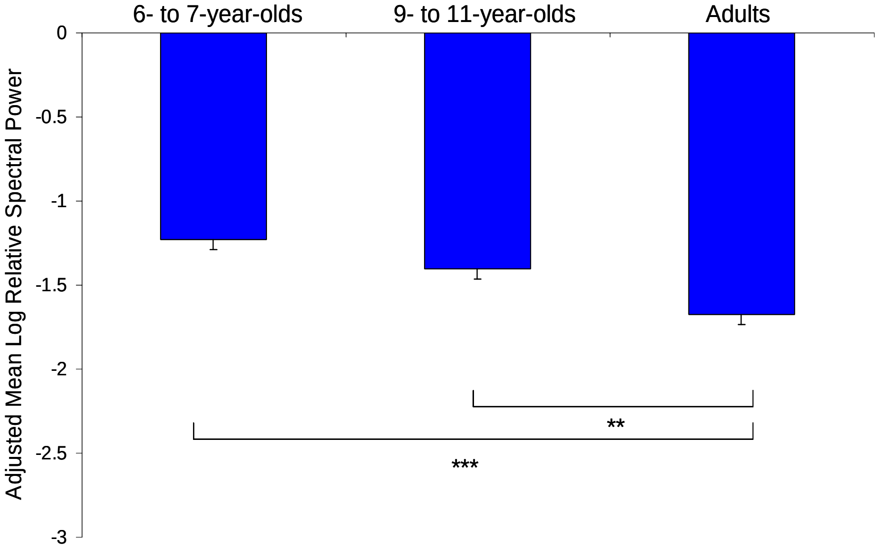


Figure 4.1. Adjusted mean log relative theta spectral power for each group. The error bars indicate one standard error for each group mean. ***Significance level of $p < 0.0001$; **Significance level of $p < 0.01$.

Tukey's post hoc analyses for theta revealed that the young children and older children exhibit significantly greater (less negative log relative) spectral power than the adults ($p < 0.001$ and $p < 0.01$, respectively). However, there was no significant difference between the young and old children for these measures ($p > 0.05$).

A significant group x anterior-posterior location x mediolateral location interaction was found for the lower alpha band ($F_{(8,\ 155)} = 2.35$, $p < 0.05$). Figure 4.2 shows the anterior-posterior location x mediolateral location for each of the three age groups (Appendix I, Figure 4.2.1 for the analogous graph presented as a proportion).

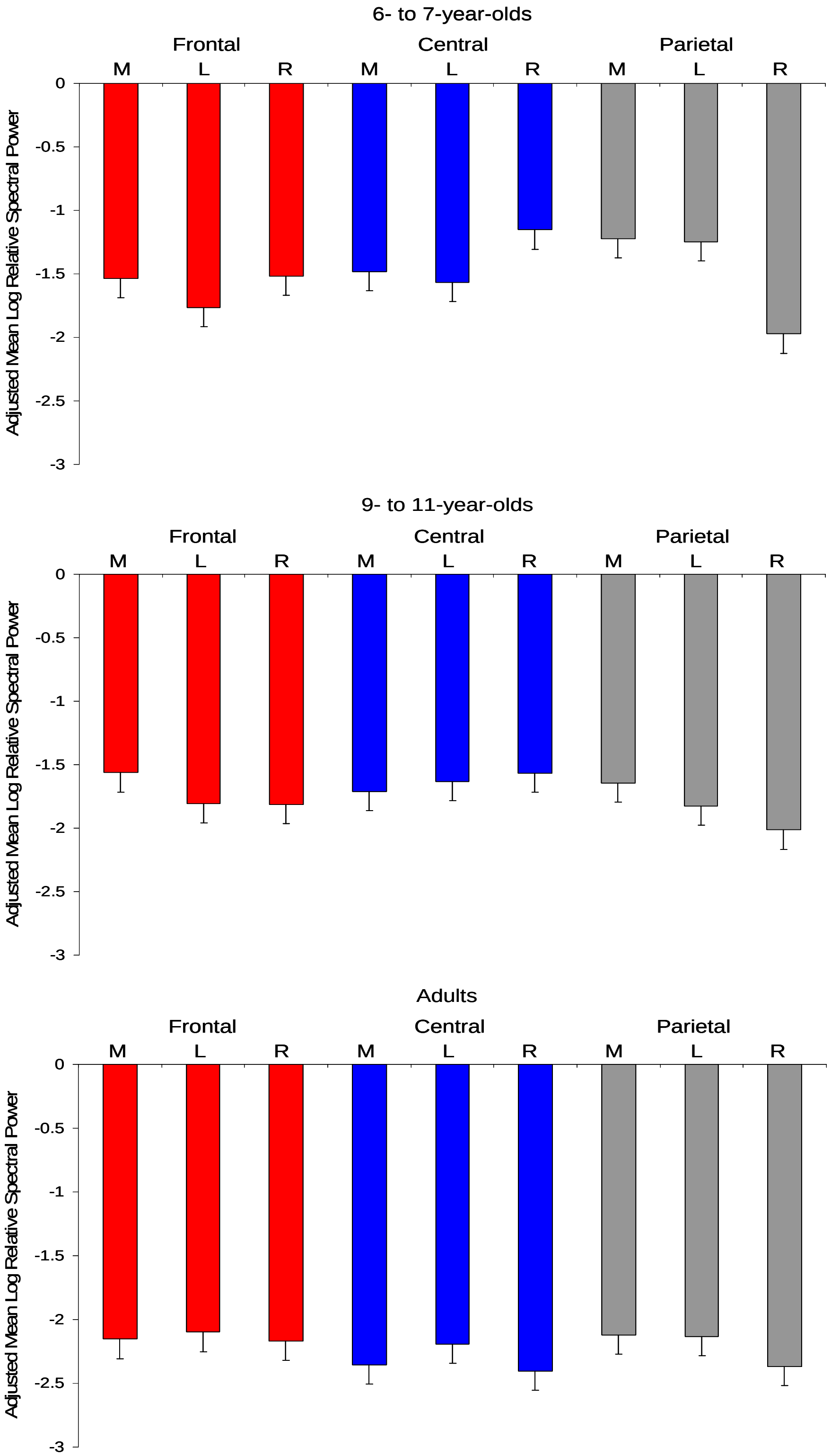


Figure 4.2. Adjusted mean log relative lower alpha spectral power three-way interaction. Age group: 6- to 7-year olds (top), 9- to 11-year-olds (middle), and adults (bottom). Anterior-posterior locations: frontal (red), central (blue), and parietal (gray). Mediolateral locations: M (midline); L (left), and R (right). The error bars indicate one standard error for each group mean**.**

Post hoc analysis of the interactions revealed that the young children were significantly different from the older children and the adults ($p < 0.05$) between the right and left electrodes in the central and parietal regions. The young children were also significantly different from the adults between the midline and right electrodes in the parietal region. These significant differences are driven by the high spectral power (less negative log relative spectral power) in the central and parietal locations exhibited by the young children. No significant differences between age groups were found for the midline and left electrodes for any of the anterior-posterior locations ($p > 0.05$). Moreover, no significant differences were found between the older children and the adults ($p > 0.05$).

Relative spectral power: increased log relative spectral power for the midline and left hemisphere for frontal and parietal locations, but decreased power in central locations for all groups.

Significant anterior-posterior x mediolateral location interactions were found for theta, upper beta, and gamma (Appendix I, Table 1 for the exact F and p values). Figure 4.3 shows the mean log relative spectral power for theta (Appendix I, Figure 4.3.1 for the analogous graph presented as a proportion); mean log relative spectral power for upper beta and gamma is similar (Appendix I, Figure 4.3.2 and Figure 4.3.3 for the graphs upper beta; Figure 4.3.4 and 4.3.5 for gamma). Post hoc analysis of the interactions revealed that the difference between the frontal and parietal or the central and parietal regions across the midline and right electrodes were significantly different ($p < 0.01$). Differences between the frontal and parietal or the central and parietal regions between the left and right electrodes were also significantly different ($p < 0.01$). Overall, there was greater log relative spectral power (indicated as a less negative value) at the midline and left for the frontal and parietal locations, compared to the right electrodes. The opposite was true for the central electrodes, in which less log relative spectral power was evident in the midline and left, compared to the right electrodes. In addition, post hoc analysis of the interactions for the mean log relative spectral power in the upper beta and gamma bands revealed that for comparisons between the frontal and central the differences between the midline and right were also significant ($p < 0.05$). This was largely due to the significant decrease in the log relative spectral power in these bands for the frontal right electrode.

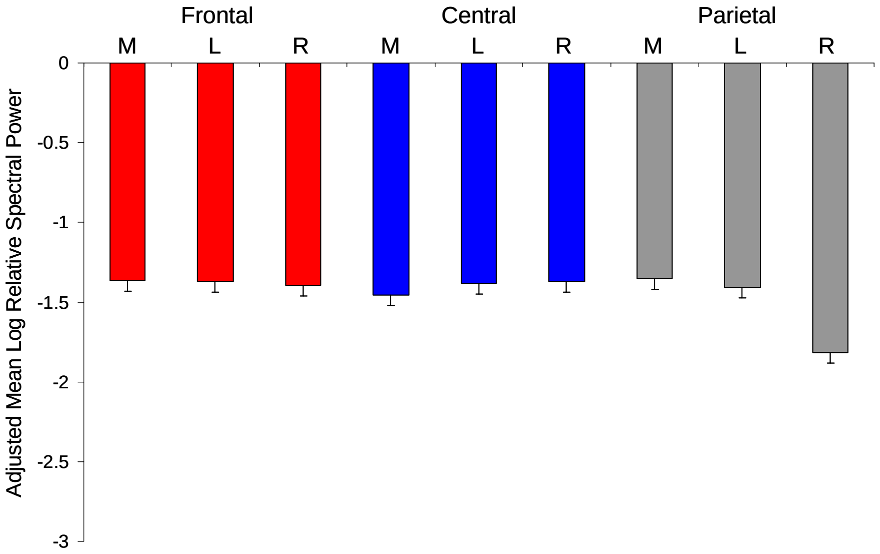


Figure 4.3. Adjusted mean log relative theta spectral power for the anterior-posterior x mediolateral interaction. Anterio-posterior locations: frontal, central, and parietal. Mediolateral locations: M (midline), L (left), and R (right). The error bars indicate one standard error for each group mean.

A significant main effect for mediolateral location was also found for lower beta ($F_{(2, 78)} = 64.35$, $p < 0.05$). Figure 4.4 shows the significant mediolateral location main effect was found for lower beta (Appendix I, Figure 4.4.1 for the analogous graph presented as a proportion).

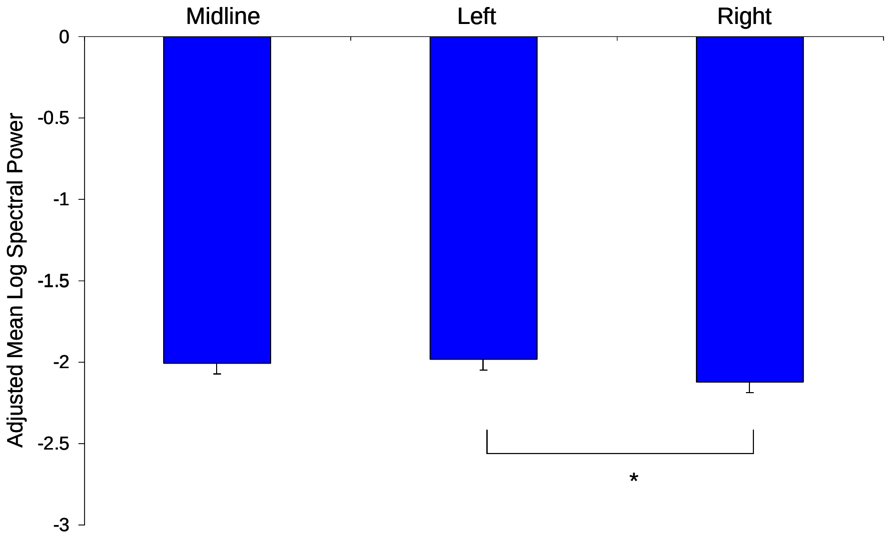


Figure 4.4. Adjusted mean log relative lower beta spectral power main effect for mediolateral locations. M = Midline, L = Left hemisphere, R= Right hemisphere. The error bars indicate one standard deviation above the mean for each group. *Significance level of $p < 0.05$.

The mean log relative spectral power is significantly less (larger negative log relative spectral values) for the electrodes on the right hemisphere versus the left hemisphere ($p < 0.05$).

EEG Coherence

The results from the mean spectral analysis indicate some developmental differences in the frequency contributions that may be regionally specific. However, spectral analysis does not provide any evidence for functional communication among these areas that may lead to improved performance during the drawing task. Therefore, coherence analyses were performed to gain insights on developmental changes in regional specialization and functional connectivity.

Coherence: adults demonstrate greater coherence between the frontal midline and central electrode.

Table 2 (Appendix I) reports the significant results from the coherence ANCOVA for each frequency band of interest (theta, lower alpha, upper alpha, lower beta, upper beta, and gamma) including the *F* values, degrees of freedom, *p* values (indicated by asterisks), and post hoc comparisons. A significant group x anterior-posterior interactions were found for lower beta and gamma ($F_{(4, 78)} = 6.07$, $p < 0.01$ and $F_{(4, 78)} = 4.43$, $p < 0.01$, respectively). Figure 4.5 depicts the interaction for the lower beta frequency band; the graph for the gamma frequency band is similar (Appendix I, Figure 4.5.1). Significant differences were found between the older children and the adults between the frontal and central electrodes and between the central and parietal electrodes ($p < 0.01$ and $p < 0.05$, respectively). The differences between the young children and adults between the frontal and central electrodes were marginally significant ($p = 0.0589$). For the gamma band, both the young children significantly differed from the adults in comparisons between frontal and central, and frontal and parietal electrodes ($p < 0.05$). Overall, for both frequencies the adults showed increased coherence between Fz and central electrode pairs, similar in magnitude to the coherence between Fz and the frontal lateral sites (F3 and F4). For the gamma band, coherence increases between Fz and parietal sites were also found for the adults, as compared to the two groups of children.

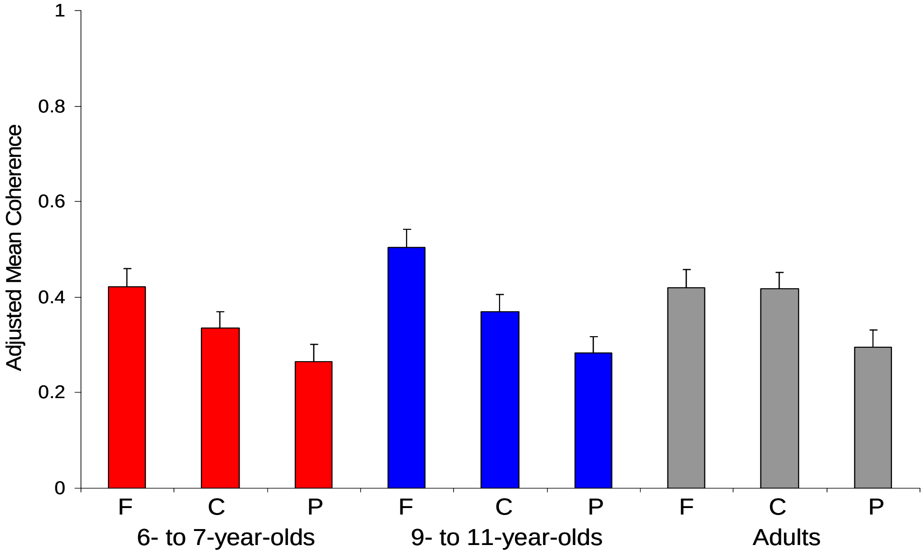


Figure 4.5. Adjusted mean coherence for the lower beta frequency for each group x anterior-posterior interaction. 6- to 7-year olds (left - red), 9- to 11-year-olds (middle – blue), and adults (right – gray). The anterior-posterior locations: F (Frontal), C (Central), and P (Parietal). The error bars indicate one standard error for each group mean.

No additional significant age group effects were found for any of the mean coherence values, for any of the frequency bands ($p > 0.05$).

Coherence: coherence decreased in long-range electrode pairs and increased in the midline and left hemisphere pairs similarly for all groups.

Significant main effects for anterior-posterior location ($p < 0.001$) were found for all frequency bands. Figure 4.6 depicts the mean coherence for the theta band; the graphs for lower alpha and upper beta are nearly identical (see Appendix I, Figure 4.6.1 and 4.6.2). The main effects for upper alpha will be discussed with regards to the anterior-posterior x mediolateral interaction, below. Tukey's post hoc analyses revealed significant differences between all combination of electrode locations for the mean coherence for theta, lower alpha, and upper beta frequency bands (see Table 2 for *p* values for the post hoc tests). Specifically, the coherence between Fz (frontal midline) and F3 (frontal left) and F4 (frontal right) electrodes are larger than the coherence between Fz and the other electrodes in the central and parietal regions ($p < 0.01$).

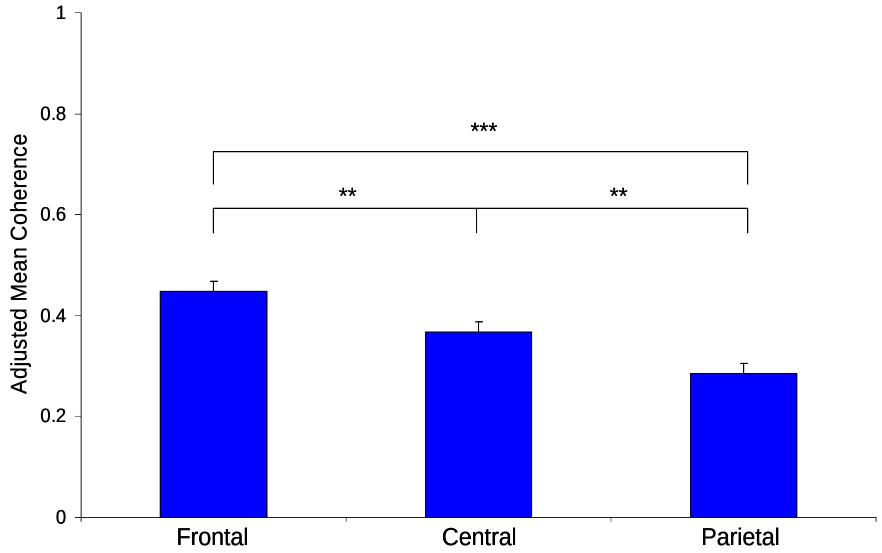


Figure 4.6. Adjusted mean coherence for the three anterior-posterior electrode distances in the theta frequency band. F= Fz to Frontal, C = Fz to Central, P = Fz to Parietal electrodes. Error bars indicate one standard error for the mean of each group. ***Significance level of $p < 0.0001$; **Significance level of $p < 0.01$.

Significant main effects for the mediolateral locations were found for lower alpha, upper alpha bands, lower beta, and upper beta. Figure 4.7 depicts the lower alpha mean coherence for the mediolateral direction; the graph for upper beta is nearly identical (Appendix I, Figure 4.7.1). Again, the main effects for upper alpha will be discussed with regards to the anterior-posterior x mediolateral interaction, below. The mean coherence between Fz and the left hemisphere electrodes demonstrated the higher values than the mean coherence for Fz to the right hemisphere electrodes. On the other hand, the upper alpha frequency band showed the largest mean coherence values in the right hemisphere, followed by the left and midline.

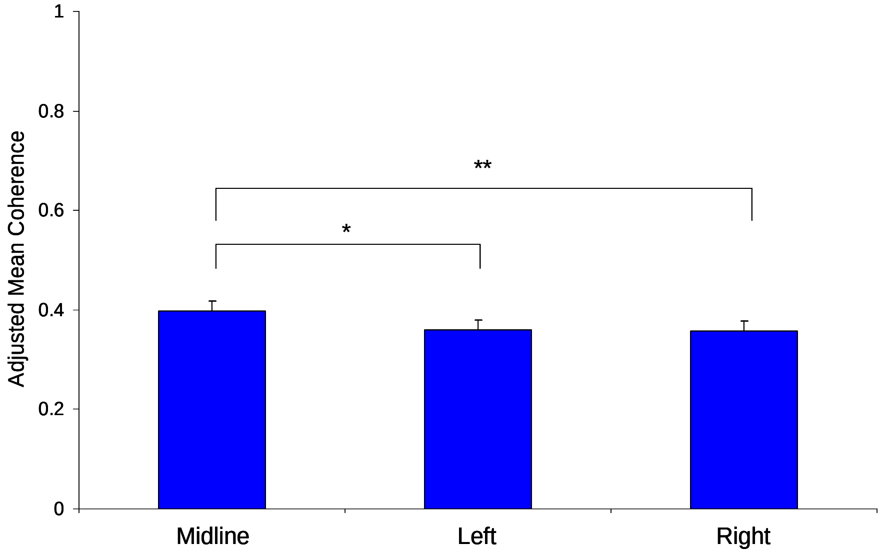


Figure 4.7. Adjusted mean coherence for the three mediolateral electrode locations in the lower alpha frequency band. Midline= Fz to Midline electrodes; Left = Fz to Left hemisphere electrodes; Right = Fz to Right hemisphere electrodes. Error bars indicate one standard error for the mean of each group. **Significance level of $p < 0.01$; *Significance level of $p < 0.05$.

As mentioned, significant interactions between the anterior-posterior location and the mediolateral locations were found for the upper alpha frequency band. Figure 4.8 depicts the interaction for upper alpha.

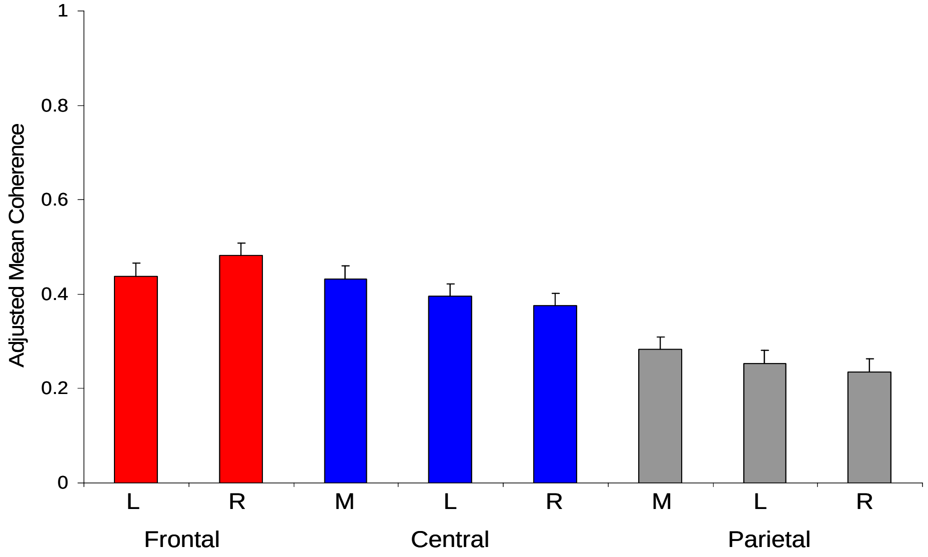


Figure 4.8. Adjusted mean coherence for the anterior-posterior x mediolateral location interaction for the upper alpha frequency band. Error bars indicate one standard deviation above the mean for each group.

Post hoc contrasts for the interaction excluded combinations involving the frontal midline and other electrodes, since the frontal midline was used as the reference electrode for all coherences derivations. These contrasts revealed that the differences in coherence between the frontal and central electrodes were significantly different for the midline to left and midline to right electrode pairs ($p < 0.01$). Significant differences were also found for the frontal and parietal electrodes between the midline and left and between the midline and right electrode pairs ($p < 0.05$). The increased coherence between Fz (frontal midline) and F4 (frontal right) was greater than between Fz and F3 (frontal left). The opposite was the case for both the central and parietal locations, in which Fz to left hemisphere electrodes (C3 and P3) were significantly greater than for right hemisphere electrodes (C4 and P4).

Event-Related Potentials (ERP)

Coherence analysis demonstrated increased functional communication between the frontal and central electrodes during the motor planning phase. To further assess the functionally relevant patterns of cortical activity during motor planning and motor control, the ERP waveforms were analyzed.

Midline ERP/ERN: facilitation of motor cortical resources and response monitoring in all groups.

Figure 4.9 depicts these time-domain, event-related cortical potentials for the midline electrodes (frontal (Fz), central (Cz), and parietal (Pz)). No significant group main effects were found for any of these electrodes; however, there was a significant time main effect ($F_{(3, 117)} = 2.82$, $p < 0.05$). Tukey's post hoc analysis revealed that there was significantly higher negativity ($p < 0.05$) during the last time window (movement onset to 250ms after) than the first one (750ms before the movement). These results indicate that all groups exhibited event-related negativity prior to and during the initial component of the movement, this is particularly clear with the steep negative ramping in the last two time windows. The group by time interaction almost reached significance ($F_{(6, 116)} = 2.12$, $p = 0.06$), with the adults showing a slightly higher amplitude than the children during the last time window.

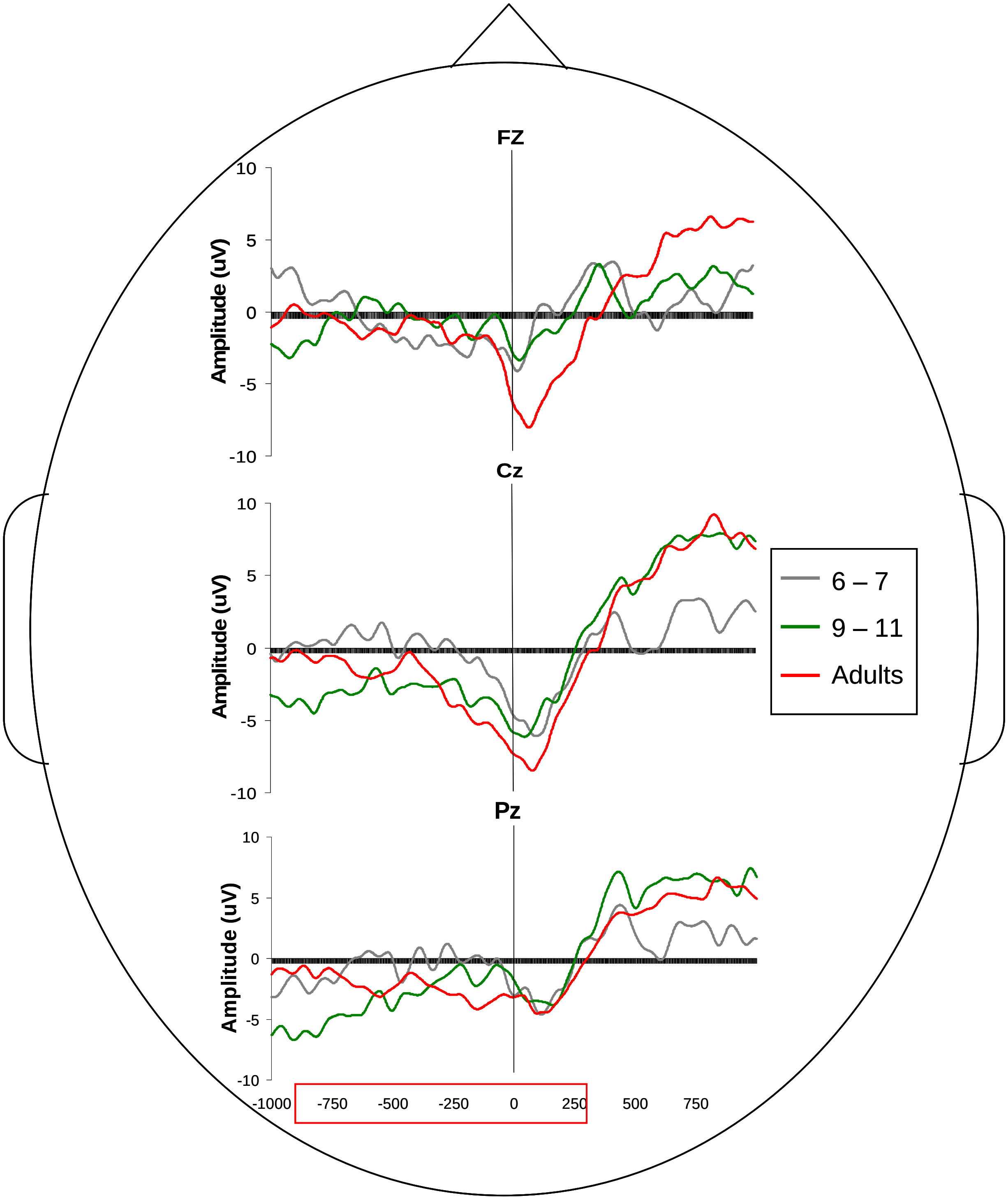


Figure 4.9. Mean midline ERP values by group. Frontal (Fz - top), Central (Cz - middle), and Parietal (Pz - bottom). Group means are presented for each location: 6- to 7-year-olds (young children) in gray, 9- to 11-year-olds (older children) in green, and adults in red. Movement onset is indicated as the vertical line through time = 0. The time values boxed in red (-750ms to -500, -500 to -250, -250 to movement onset, and movement onset - 250ms) are the 4 time windows in the ANOVA.

The central midline site, as expected, demonstrated the greatest negativity prior to and during the initial portion of movement. All groups demonstrated a unimodal waveform (negativity increasing to a single peak), with maximal negativity around movement onset immediately followed by a drastic positive shift. A significant time main effect was found for the central midline site ($F_{(3,\ 124)} = 5.71$, $p < 0.05$, see Appendix I, Figure 4.9.1). Tukey's post hoc analysis revealed that the last two time window (-250ms to movement onset and movement onset to 250ms) were significantly different from the first and second time windows. These results confirm that for all groups the negativity increases within a short period of time, over the course of the last two time windows, as seen in the Cz graphs. Again, there were no significant differences between groups between the children and the adults for Cz. These results indicate that all children recruited neural motor resources, signified by increased negative amplitudes similarly to the adults.

Since the parietal sites are not normally associated with motor-related cortical potentials, the parietal midline site was analyzed to ensure consistency between these results and previous literature. The negativity prior to movement for this site did not clearly lead towards a single peak for any of the groups. As expected, there was no main effect of time and no group main effect.

Lateral ERPs: increased contralateral activation during motor planning in adults only.

It is often the case that the left and possibly the right central sites also exhibit increased negativity and a unimodal ERP, which may indicate facilitation or priming of the primary motor areas. Figure 4.10 shows the waveform for the electrode overlying the sensorimotor cortex (C3 - central left and C4 - central right).

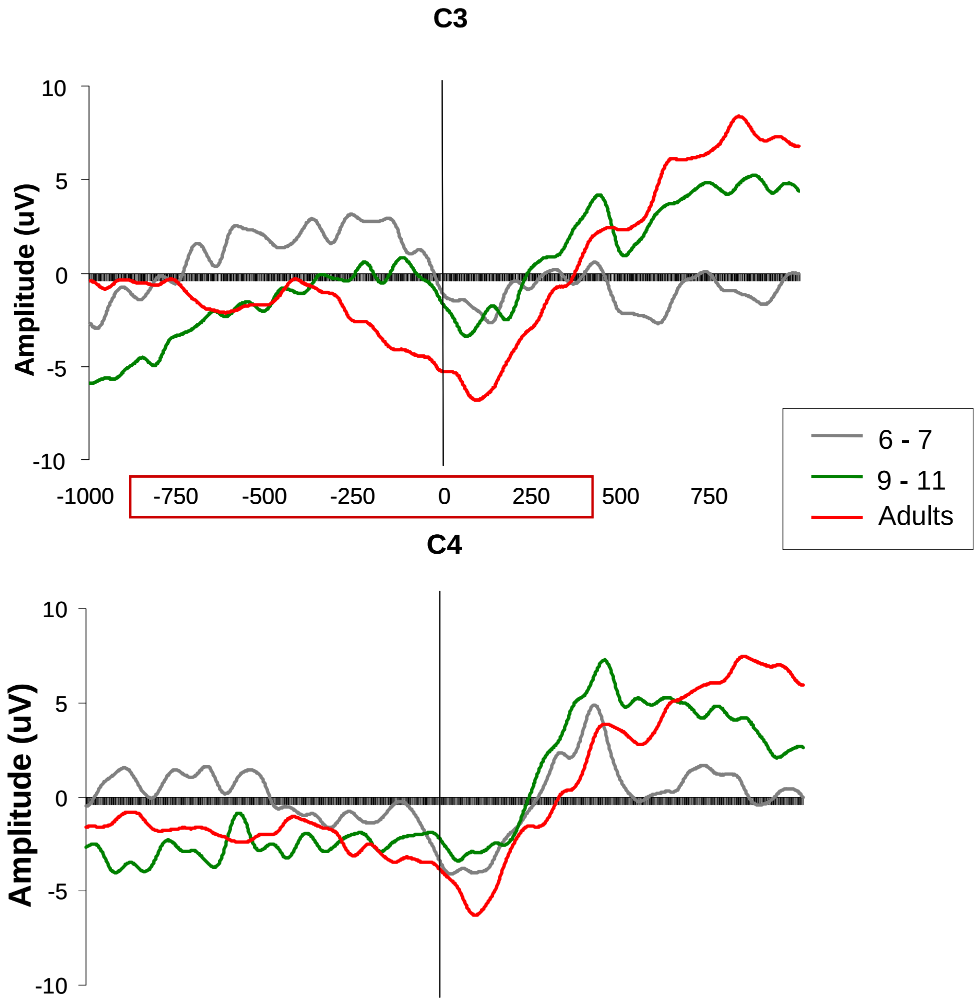


Figure 4.10 Mean lateral central ERP values by group. Central left (C3 - top) and central right (C4 - bottom). Group means are presented for each location: 6- to 7-year-olds (young children) in gray, 9- to 11-year-olds (older children) in green, and adults in red. Movement onset is indicated as the vertical line through time = 0. The time values boxed in red (-750ms to -500, -500 to -250, -250 to movement onset, and movement onset - 250ms) are the 4 time windows in the ANOVA.

A group main effect was found for C3 (left central site) ($p < 0.003$), but not for the right central electrode (C4). Tukey's post hoc analysis of the C3 results revealed that the adults differed from the young children significantly ($p < 0.002$). No significant differences were found between the two groups of children or between the older children and the adults ($p > 0.05$). These results indicate that neural facilitation, especially for the area over the contralateral motor cortex (C3) as measured by the BP, although similar in appearance to the adults, is not yet at the same level for the young children over the contralateral sensorimotor area.

Behavioral Results

It is expected that the task-related activation, increased regional specificity in intrahemispheric coherence, and neural facilitation of motor elements are expected to contribute to improved accuracy and efficiency of the motor performance. Kinematic analysis was used to gauge movement quality and performance consistency. The following variables were analyzed using a one-way ANOVA with group (3) as the between subjects factor: movement length, root mean squared error (RMSE), movement time, normalized jerk, and initial directional error (signed IDE, absolute IDE and IDE variable error).

Motor performance variables: continued improvements in the quality of movement performance across age.

Figure 4.11 depicts the mean movement trajectories for each of three groups: 6- to 7-year-olds (young children), 9- to 11-year-olds (older children), and adults.

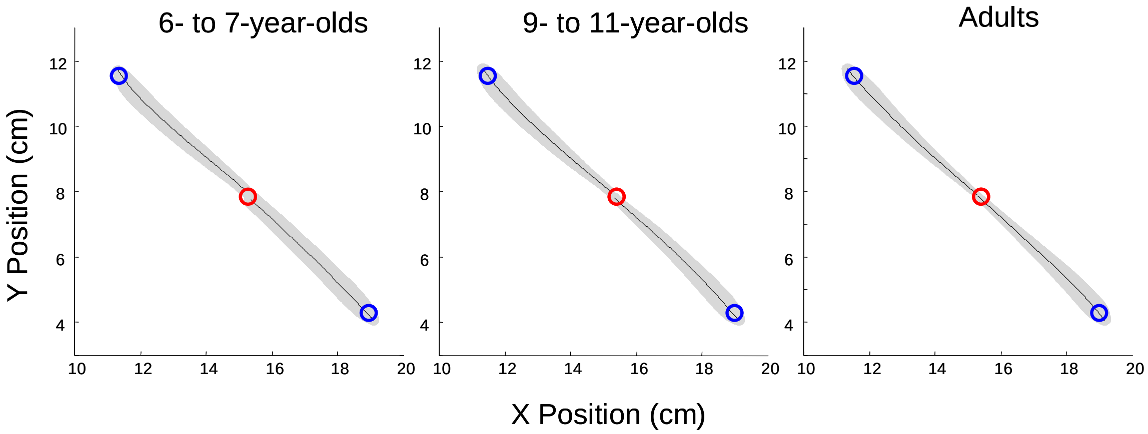


Figure 4.11. Mean movement trajectories by group. 6- to 7-year-olds (left), 9- to 11-year-olds (middle), and adults (right). Horizontal and vertical axes are in units of cm. The black line indicates the mean trajectory from the home position is located in the middle at point (14.5, 8) to the targets are located in the 135 and -45 degree directions, 5cm away from the home position. The gray shading represents one standard deviation from the group mean**.**

These movement trajectories for all groups were straight and accurate, as measured by RMSE and movement length, respectively. There were no significant differences between groups for movement length and RMSE (Appendix I, Table 3), measures of accuracy and straightness ($p > 0.05$, both). Therefore, all groups were equally able to perform the task with respect to accuracy for these measures.

Significant group differences were found for the mean movement time and mean normalized jerk ($F_{(2, 42)} = 28.81$, $p < 0.0001$ and $F_{(2, 42)} = 21.84$, $p < 0.0001$, respectively). Tukey's post hoc test demonstrated that the young children exhibited significantly longer movement times and were significantly jerkier ($p < 0.0001$). No significant differences ($p > 0.05$) were found between the older children and adults for these measures. Figure 4.12 and 4.13 show the differences between the age groups for these measures. Therefore, the young children moved slowly in order to produce accurate movements. On the other hand, the older children and adults were able to produce both accurate and smooth movements, while moving very quickly. Thus, these important aspects of adult-like performance have not yet developed in the young children.

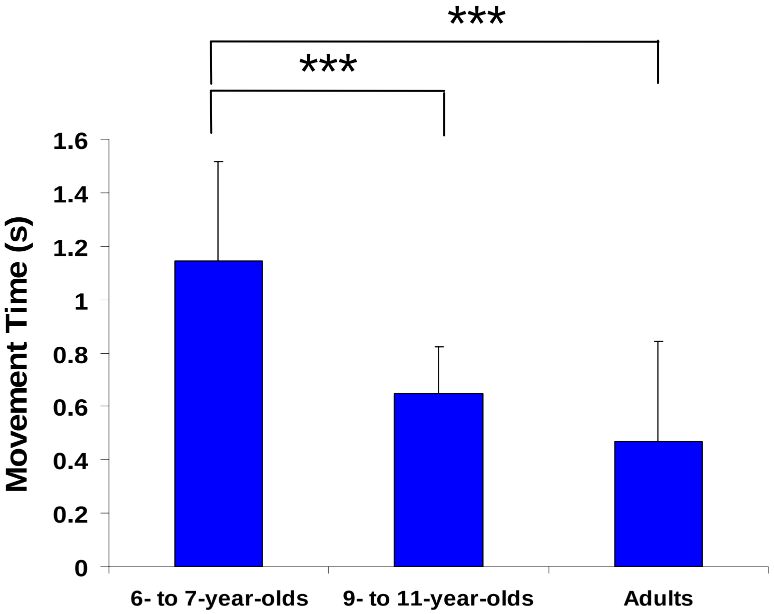


Figure 4.12. Mean movement time (in seconds) by group. *** Significance level of $p < 0.001$. Error bars represent one standard deviation above the mean for each group.

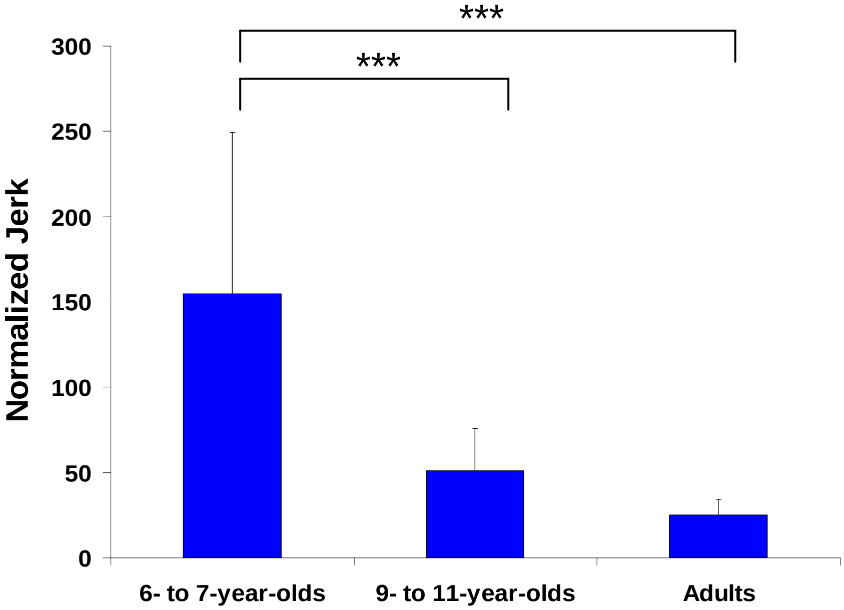


Figure 4.13. Mean normalized jerk by group. *** Significance level of $p < 0.001$. Error bars represent one standard deviation above the mean for each group.

Motor planning variables: improved consistency in motor planning across age.

Figure 4.14 depicts the mean signed IDE values for the three age groups. On average, all groups performed with 3.5 degrees or less deviation in the initial movement direction. However, there was a significant group main effect ($F_{(2, 42)} = 3.39$, $p < 0.05$) for this variable. Tukey's post hoc analysis revealed significantly higher IDE values for the adult group compared to the youngest children (but not the older children), with $p = 0.04$. These results would indicate that the youngest children were able to produce at movement initiation the movement trajectory that deviated least from the ideal of the three age groups. However, IDE is calculated with signed (+/-) errors. To further explore this result for IDE, two additional analyses were conducted.

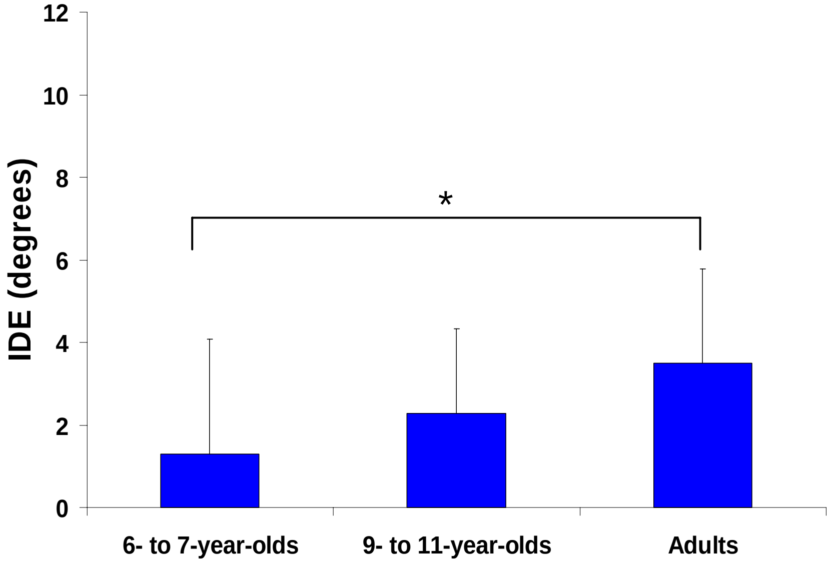


Figure 4.14 Mean signed initial directional error (IDE) values (in degrees) by group. * Significant level of $p < 0.05$. Error bars indicate one standard deviation above the mean for each group.

The first supplementary analysis used unsigned error. Mean absolute IDE values were calculated for each group (Figure 4.15). This analysis revealed no significant group differences. The mean absolute IDE values for the young children increases to a greater degree than the other groups, and that the mean signed IDE values presented in Figure 4.16 may have been artificially attenuated by negative IDE values in the signed calculation of IDE. These results suggest that this group does not show a directional bias in their initial movement trajectory towards the targets. The older children and the adults on the other hand, demonstrate more consistent performance, although the deviation remains slightly greater than that of the young children.

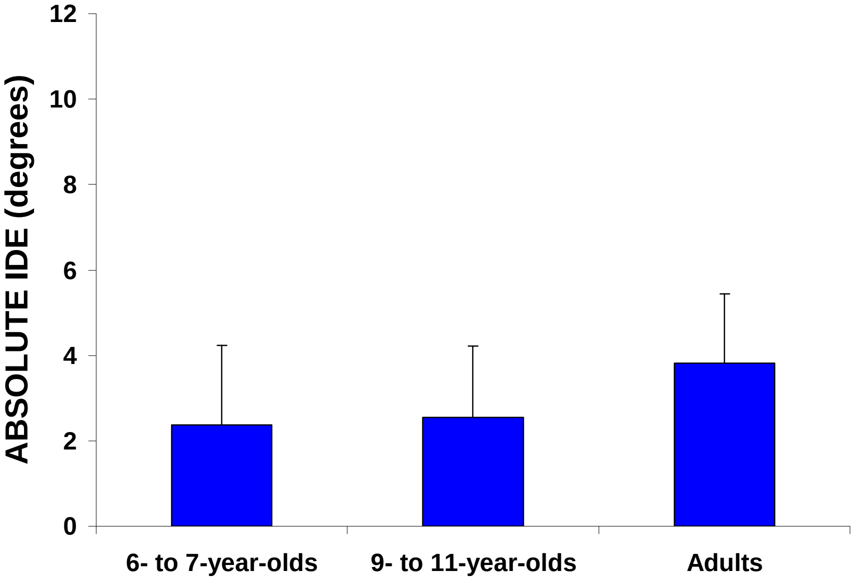


Figure 4.15 Mean absolute IDE values (in degrees) by group. Error bars indicate one standard deviation above the mean for each group.

In order to determine the consistency of the initial movement direction for each of these groups IDE variable error was also analyzed. For this measure, the means for each group were calculated from the standard deviations of the IDE values for each subject (Figure 4.16). A significant group main effect was found ($F_{(2, 42)} = 14.77$, $p < 0.0001$) The youngest group of children were significantly more variable than the older children and adults ($p< 0.014$ and $p< 0.001$, respectively), indicating a less consistent performance in movement trajectories over the first 80 ms.

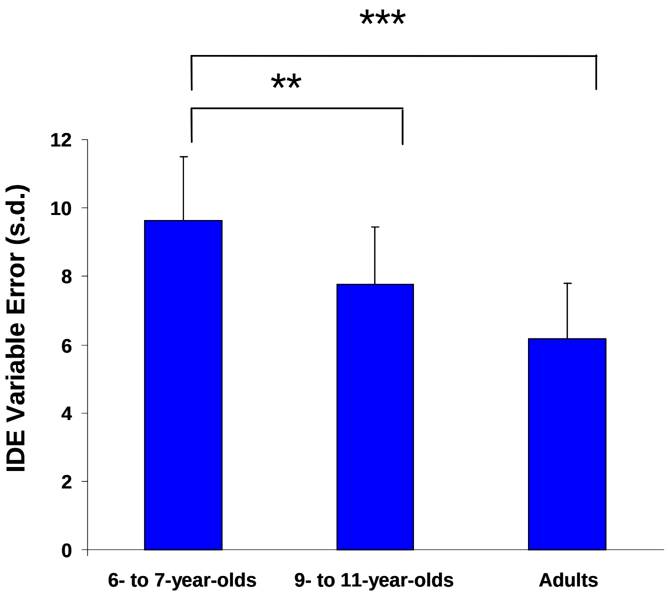


Figure 4.16. Mean IDE variable error by group. Means depicted were calculated from the standard deviation of the IDE values. Error bars indicate one standard deviation above the mean for each group.

These results suggest that although the young children are able to plan the trajectory of their movements and produce low directional error on average, their trial-by-trial planning is highly variable. These behavioral results are consistent with the results from the lateral BP indicating that motor planning for the young children has not developed to adult levels.

Discussion

This study is the first to characterize children's electro-cortical brain activation patterns during behavioral performance of a drawing task compared to adults. The use of multiple analysis techniques (spectral, coherence, and event-related motor cortical potentials) provides increased sensitivity to age-related differences between the groups of children and adults during motor tasks. Some similarities were found for the EEG measures in a few of the frequency bands across groups. For example, no age-related difference were found for the either beta bands and the gamma band for the spectral analysis. Theta, both alpha frequencies, and upper beta coherences were also similar across groups. The midline motor potentials, discussed in details below, were also similar between the groups. The similarities among groups for these measures may be attributed to basic processes that are necessary for motor task performance, such as attention processes, sensorimotor activities, and rudimentary motor planning. Consistent with these similarities in cortical processes, in terms of the kinematic performance, no group differences were found for the movement length and RMSE. These results may be due in part to the fact that the young children moved more slowly, which may have allowed them to move straight to the target with little over- or under-shoot. These results may also have resulted from the fact that the movements were much smaller than the movements in previous studies (Contreras-Vidal, 2006; Contreras-Vidal et al., 2005; Kagerer, Bo, Contreras-Vidal, & Clark, 2004) and that veridical visual feedback was provided during the entire session. In larger movements, or those without visual feedback, the movement preparation and online control would be much more demanding and behavioral deficits may be more apparent.

However, age-related differences were found in the movement kinematics that may be related to the quality of the cerebral cortical processes during motor planning and control. Consistent with previous behavioral studies from this lab for a similar task (Contreras-Vidal, 2006), significant aspects of the motor performance were not evident in the behavioral performance of the younger children. This group was on average slower, less smooth, and exhibited less finely-tuned initial movement directions, as compared to the older children and adults. These results provided evidence of 'less tuned' planning and feed-forward control mechanisms, compromising the accuracy of the young children's motor plans and efficiency during the online error correction for visuomotor behaviors(Contreras-Vidal et al., 2004). Similar to previous studies (Luu & Tucker, 2001; Luu, Tucker, & Makeig, 2004), bias in the movement direction was evident for the older children and adults, which may have elicited online error compensation to improve the overall motor performance. Notwithstanding, overall improvements in the movement kinematics were found as a function of age, and the older children and adults exhibited improved accuracy and consistency.

There is evidence that increased theta power particularly in the midline frontal regions is related to evaluation of an action plan and exhibited before and after a motor response (Gerloff et al., 1998). All groups demonstrated increased frontal theta power. However, the overall magnitude of the theta power was significantly less for the children compared to the adults. Moreover, differences in lower alpha spectral power were found across the three age groups in terms of regional specialization that may be related to motor task planning. Decreased spectral power for the lower alpha band have been found during internally paced movement compared to those externally cued, and reflect activation of the premotor and contralateral sensorimotor cortices (Gerloff et al., 1998) Compared to the young children, older children and adults exhibited increased activation of the frontal and central left hemisphere sites, over the premotor and sensorimotor cortices in the lower alpha band. These finding are appropriate given that all of the subjects performed the task with their right hands, thus eliciting activation of the premotor and contralateral primary motor areas which are lateralized towards the left of the midline. On the other hand, the younger children exhibited decreased activation in the areas directly overlaying the sensorimotor cortex, as compared to older children and adults. Moreover, the younger children show a relative increase in frontal engagement, meaning that executive areas may have needed to contribute to the motor planning for the task performance, whereas older children and adults rely more on the sensorimotor (central) areas during task performance.

The present study is consistent with previous coherence analysis during visuomotor behaviors. Specifically, Busk & Galbraith (1998) and Gerloff et al. (1975) both reported a high coherence between the frontal and central sites. The high coherence between the frontal and central midline in particular, may be due to increased communication between these sites or may be caused by another area affecting the frontal and central electrode similarly. Likely candidates are the anterior cingulated area or the supplementary motor areas which are situated between Fz and Cz at the vertex, and may be involved in motor planning and action monitoring. The increased coherence between all central electrodes with Fz, in the adults is clearly different for the two groups of children, for both the lower beta and gamma frequency bands. Increased coherence between the frontal midline (cingulate, supplementary motor, and premotor areas) with the sensorimotor areas for the adults suggest increased task-related networking between these regions. This interpretation is consistent with the results from the ERP analysis, discussed in more detail in the following section.

Decreased coherence was evident for mid- and long-range coherence for both groups of children (frontal-central and frontal-parietal associations) in both the lower beta and gamma frequency bands. This is reasonable given that coherence will decrease with increased distance between electrodes and was also similar to the results in Busk and Galbraith (2003). It is possible that rather, a common area such as the central midline may serve as an intermediary during information transfer for the children. Moreover, these results suggest that the frontal areas may not be directly involved in the functional communication between the lateral central regions and the parietal areas. However, increased long-range coherence between the frontal and parietal regions was evident in the adults for the gamma frequency band.

These regionally specific differences in functional communication across age groups could be related to the structural growth enabling better communication between functional areas within and between the hemispheres. The present study examined the communication between premotor areas in the frontal midline, considered motor planning regions, with all other electrodes. Lateralization effects in the upper alpha band were observed for both the central and parietal locations, in which Fz to left hemisphere electrodes (C3 and P3) are significantly greater than for right hemisphere electrodes (C4 and P4). These results are consistent with Serrien (1990) suggesting a dominant role of the left hemisphere during motor task performance.

Interhemispheric coherence (between sites across the left and right hemispheres) was not gauged between homologous areas, such as between the left and right electrodes directly, but rather inferred from interactions between the frontal midline and the lateral electrodes. For the lower alpha, lower beta, and upper beta bands the coherence between the frontal midline and the other midline electrodes were greater than the coherence with the left and right hemisphere electrodes. This is consistent with Colebatch (Deecke et al., 1984; Grunewald-Zuberbier et al., 1978; Grunewald-Zuberbier et al., 1980), since the movements performed in the present study were small, but required muscle activation of proximal (shoulder and elbow) as opposed to distal (wrist and fingers), both contralateral and ipsilateral motor areas contributed to the movement planning and execution. However, it is possible that the similarity between the coherence values of the left and right hemisphere electrodes may be due in part to the direct interhemispheric tracts connect homologous brain areas.

Overall, the regional specialization in coherence between the children and adults suggest different patterns of networking between brain areas that appear to be primarily related to motor planning and involve pre-motor and sensorimotor areas. The results from ERP analysis are consistent with the spectral and coherence results, supporting increased activity in the frontal midline and central midline during motor planning. For goal-directed movements, event-related negativity related to visuomotor behavior continues until the completion of the movement (Contreras-Vidal et al., 2004). This negativity may be associated with the facilitation of motor resources as well as action-monitoring and has been exhibited by adults performing a similar task (Grunewald-Zuberbier et al., 1980). Although, several studies examining short ballistic movements have reported an absence of negative motor cortical potentials for young children, the younger children in the current study exhibited adult-like waveforms along the frontal and central midline sites. These results suggest that the young children do exhibit activation patterns indicating a facilitation of motor planning resources and the presence of action monitoring.

However, the adults exhibited increased negative magnitude for the contralateral ERP waveforms over the sensorimotor cortex, compared to both groups of children, although to a lesser extent in the older children. These findings are consistent with previous reports, in which goal-directed movement potential are large over the contralateral sensorimotor area (2000). The lack of contralateral activation, may suggest deficient motor planning of areas directly related to the task performance and online error-correction. Blank suggests that development changes in the recruitment of motor-neuronal populations in the primary motor cortex underlying movement generation discussed above may relate to the functional changes evident in behavioral analyses of hand performance in children. Therefore, the increased negativity, or activation of contralateral motor areas in the adults may positively contribute to the quality of the movement performance.

Conclusion

This study was the first to provide evidence that age-related differences in movement kinematics may be related to disparate patterns of cerebral cortical processes underlying motor planning and control between children and adults. In particular, given several age-related differences in the brain activation patterns related to motor planning and action monitoring, it was expected that the kinematic performance of the young children would be poorer than the other two groups. These results indicate that although children exhibit some similarities in the cortical dynamics (spectral power and coherence in several bands, and midline motor cortical potentials) and behavioral performance (movement length and RMSE), many aspects of young children's brain patterns (relative spectral power, coherence between frontal midline and central electrodes and lateral BP) and motor performance (movement time, normalized jerk, and variable IDE), differ from the older children and adults.

Future investigations may include more complex and coordinated movements (i.e. bimanual movements), which may more dramatically draw out the cortical laterality and performance differences between the groups. Alternatively, examinations of purely feed-forward movements with little online feedback may be able to heighten the need for motor planning and increase the recruitment of neural resources needed for accurate motor performance.

CHAPTER IV

Summary and Future Directions

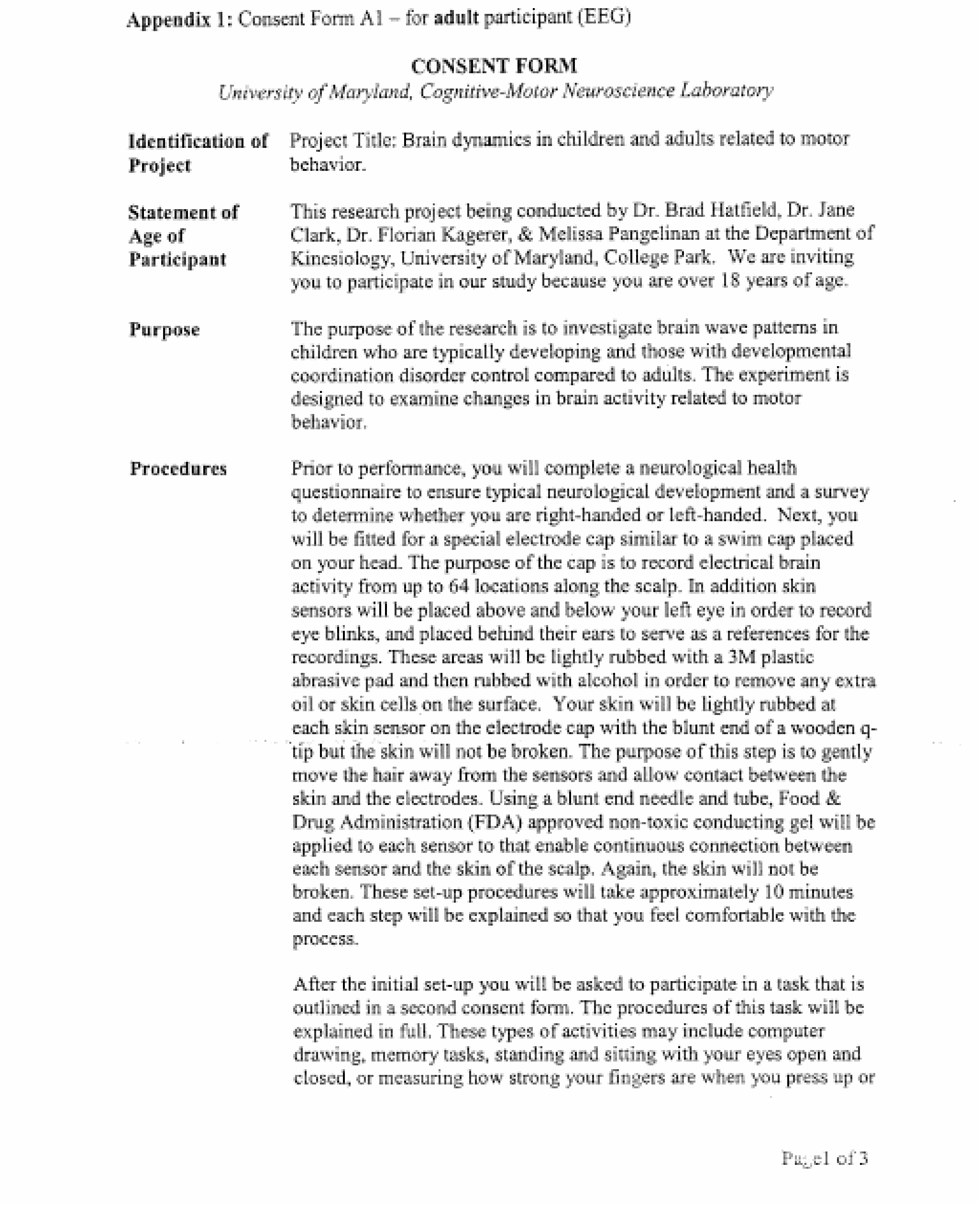
This study was the first to provide evidence that age-related differences in movement kinematics may be related to disparate patterns of cerebral cortical processes underlying motor planning and control between children and adults. In particular, given several age-related differences in the brain activation patterns found before movement onset and during the movement, it was expected that the kinematic performance of the young children would be poorer than the other two groups. These results indicate that although children exhibit some similarities in the cortical dynamics (coherence in several bands, midline BP) and behavioral performance (movement length and RMSE), many aspects of young children's brain patterns (relative spectral power, coherence between frontal midline and central electrodes and lateral BP) and motor performance (movement time, normalized jerk, and variable IDE), differ from the older children and adults. Taken as a whole, this study demonstrated that EEG spectral power, coherence, and event-related potentials are sensitive measures of the electro-cortical processes related to multi-joint, goal-directed visuomotor behavior in children and adults.

However, it is of note to mention that because the study required the children to remain silent, attentive, and patient, several young children were unable to complete the task and their data were not included in the final analysis. Therefore, children much younger or those children with impulsivity, inattention, or difficulty remaining still, will find this task extremely challenging. The older children and adults had no difficulties with the testing and probably could complete many more trials using a similar task. Also, although measures were taken to reduce displacement of the electrodes due to long hair in the girls and young women, acceptable impedances were difficult to obtain for the occipital sites. As a result, those data obtained from the occipital sites were excluded from the analysis, and no conclusions could be made regarding the role of the occipital region during visuomotor processing. If these sites are to be included in future studies, children with short hair would be preferable to reduce impedance difficulties.

Future investigations may include more complex and coordinated movements (i.e. bimanual movements), which may more dramatically draw out the cortical laterality and performance differences between the groups. Alternatively, examinations of purely feed-forward movements with little online feedback may be able to heighten the need for motor planning and increase the recruitment of neural resources needed for accurate motor performance.

APPENDICES

Appendix A. Consent Form for Adult Participation



Appendix 1: Consent Form A1 – for **adult** participant (EEG)

CONSENT FORM

University of Maryland, Cognitive-Motor Neuroscience Laboratory

Identification of Project	Project Title: Brain dynamics in children and adults related to motor behavior.
Statement of Age of Participant	This research project being conducted by Dr. Brad Hatfield, Dr. Jane Clark, Dr. Florian Kagerer, & Melissa Pangelinan at the Department of Kinesiology, University of Maryland, College Park. We are inviting you to participate in our study because you are over 18 years of age.
Purpose	The purpose of the research is to investigate brain wave patterns in children who are typically developing and those with developmental coordination disorder control compared to adults. The experiment is designed to examine changes in brain activity related to motor behavior.
Procedures	Prior to performance, you will complete a neurological health questionnaire to ensure typical neurological development and a survey to determine whether you are right-handed or left-handed. Next, you will be fitted for a special electrode cap similar to a swim cap placed on your head. The purpose of the cap is to record electrical brain activity from up to 64 locations along the scalp. In addition skin sensors will be placed above and below your left eye in order to record eye blinks, and placed behind their ears to serve as a references for the recordings. These areas will be lightly rubbed with a 3M plastic abrasive pad and then rubbed with alcohol in order to remove any extra oil or skin cells on the surface. Your skin will be lightly rubbed at each skin sensor on the electrode cap with the blunt end of a wooden q-tip but the skin will not be broken. The purpose of this step is to gently move the hair away from the sensors and allow contact between the skin and the electrodes. Using a blunt end needle and tube, Food & Drug Administration (FDA) approved non-toxic conducting gel will be applied to each sensor to that enable continuous connection between each sensor and the skin of the scalp. Again, the skin will not be broken. These set-up procedures will take approximately 10 minutes and each step will be explained so that you feel comfortable with the process. After the initial set-up you will be asked to participate in a task that is outlined in a second consent form. The procedures of this task will be explained in full. These types of activities may include computer drawing, memory tasks, standing and sitting with your eyes open and closed, or measuring how strong your fingers are when you press up or

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down. These tasks are completed during this one visit and range in time from 30-minutes to 1.5-hours.

Confidentiality

All information collected in the study is strictly confidential except as you specify on the signed permission form for video and image illustrations, and your name will not be identified at any time. The data you provide will be grouped with data others provide for reporting and presentation. Data will be stored in a locked file cabinet in the Cognitive-Motor Neuroscience Laboratory. Only the investigators and their collaborators will have access to this locked file. All those with access to the data are NIH certified in the procedures for protecting participants in scientific experiments. Your information may be shared with representatives of the University of Maryland, College Park and government authorities if we are required to do so by law.

Risk

As result of your participation in this study, and specifically wearing the electrode cap to measure brain activity, you may experience some slight sensation and irritation of the skin as the scalp is lightly rubbed at the electrode sites. Additionally, you may experience a modest degree of fatigue from the concentration required during the performance of the test but there are no other known risks and no long-term effects associated with participation in this study.

Benefits, Freedom to Withdraw and to ask questions

Your participation is completely voluntary. The experiment is not designed to help you specifically, but it may have substantial impact on understanding how the brain controls movement. You are free to ask questions or to withdraw from participation at any time without penalty. A signed copy of this consent form will be given to you and that the investigators will provide you with the results of this study.

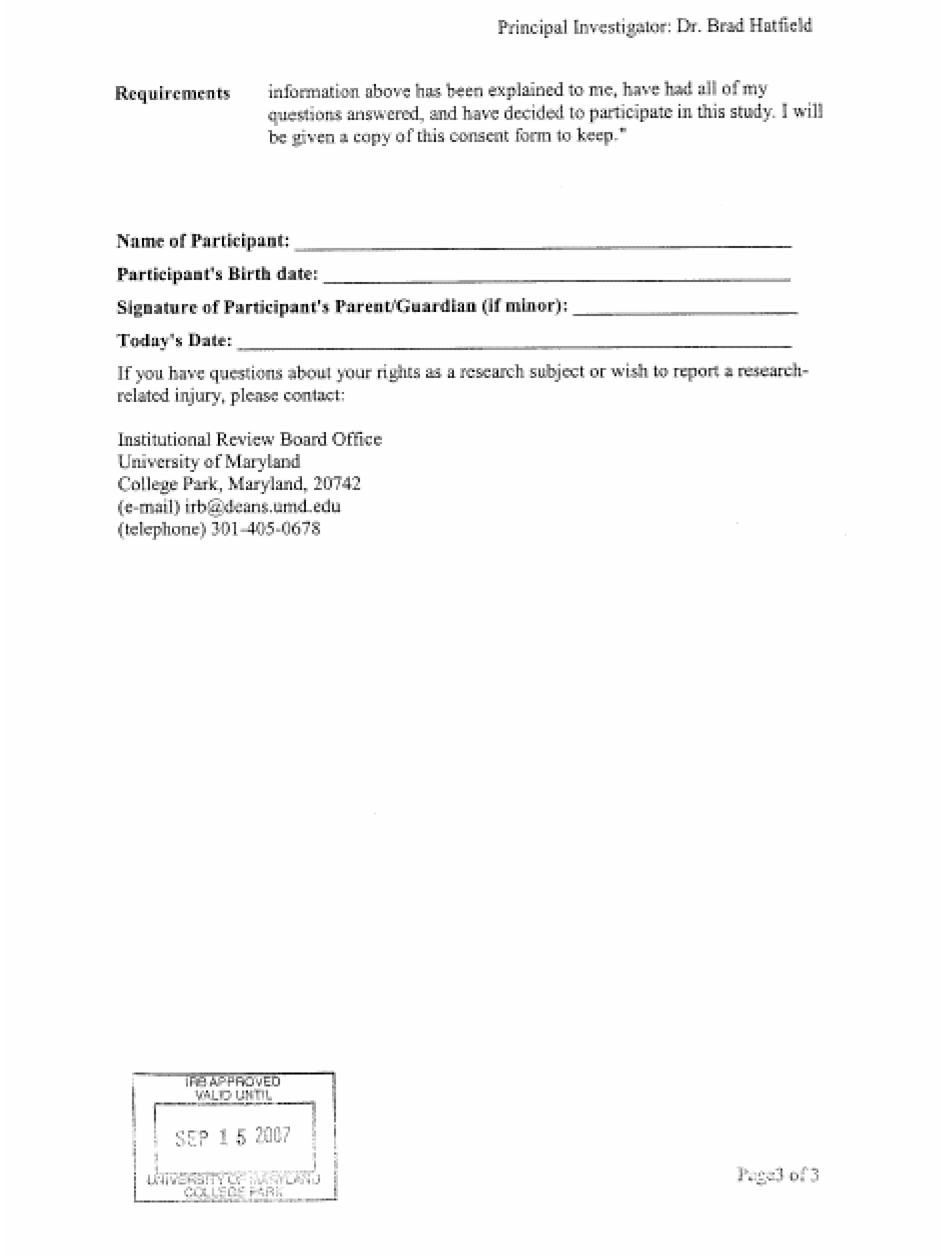
The University of Maryland does not provide any medical or hospitalization insurance coverage for participants in the research study nor will the University of Maryland provide any compensation for any injury sustained as a result of participation in this study except as required by law.

Investigators

Dr. Brad Hatfield (PI),
Dr. Jane Clark (Co-PI),
Dr. Florian Kagerer (Collaborator),
Melissa Pangelinan (graduate student)
Department of Kinesiology, 2303 HHP Bldg
University of Maryland, College Park, MD 20742
(301)-405-2495

Informed Consent

"I am voluntarily making a decision whether or not participate in the research study described above. My signature indicates that the



Principal Investigator: Dr. Brad Hatfield

Requirements information above has been explained to me, have had all of my questions answered, and have decided to participate in this study. I will be given a copy of this consent form to keep."

Name of Participant: ______________________________

Participant's Birth date: ______________________________

Signature of Participant's Parent/Guardian (if minor): ______________

Today's Date: ______________________________

If you have questions about your rights as a research subject or wish to report a research-related injury, please contact:

Institutional Review Board Office
University of Maryland
College Park, Maryland, 20742
(e-mail) irb@deans.umd.edu
(telephone) 301-405-0678

IRB APPROVED
VALID UNTIL
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UNIVERSITY OF MARYLAND
COLLEGE PARK

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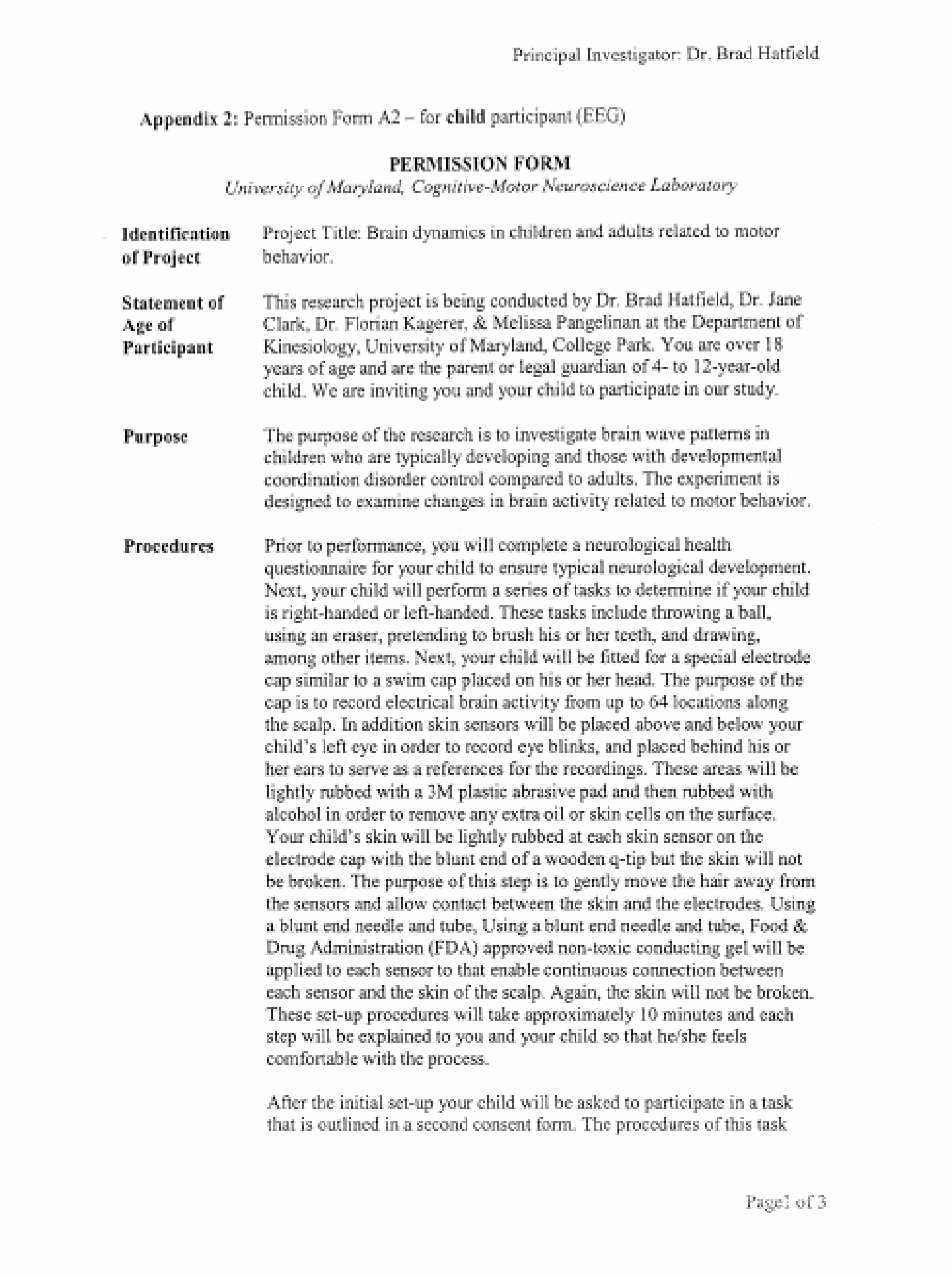
Appendix B. Parental Consent (Permission Form) for Child Participation



Principal Investigator: Dr. Brad Hatfield

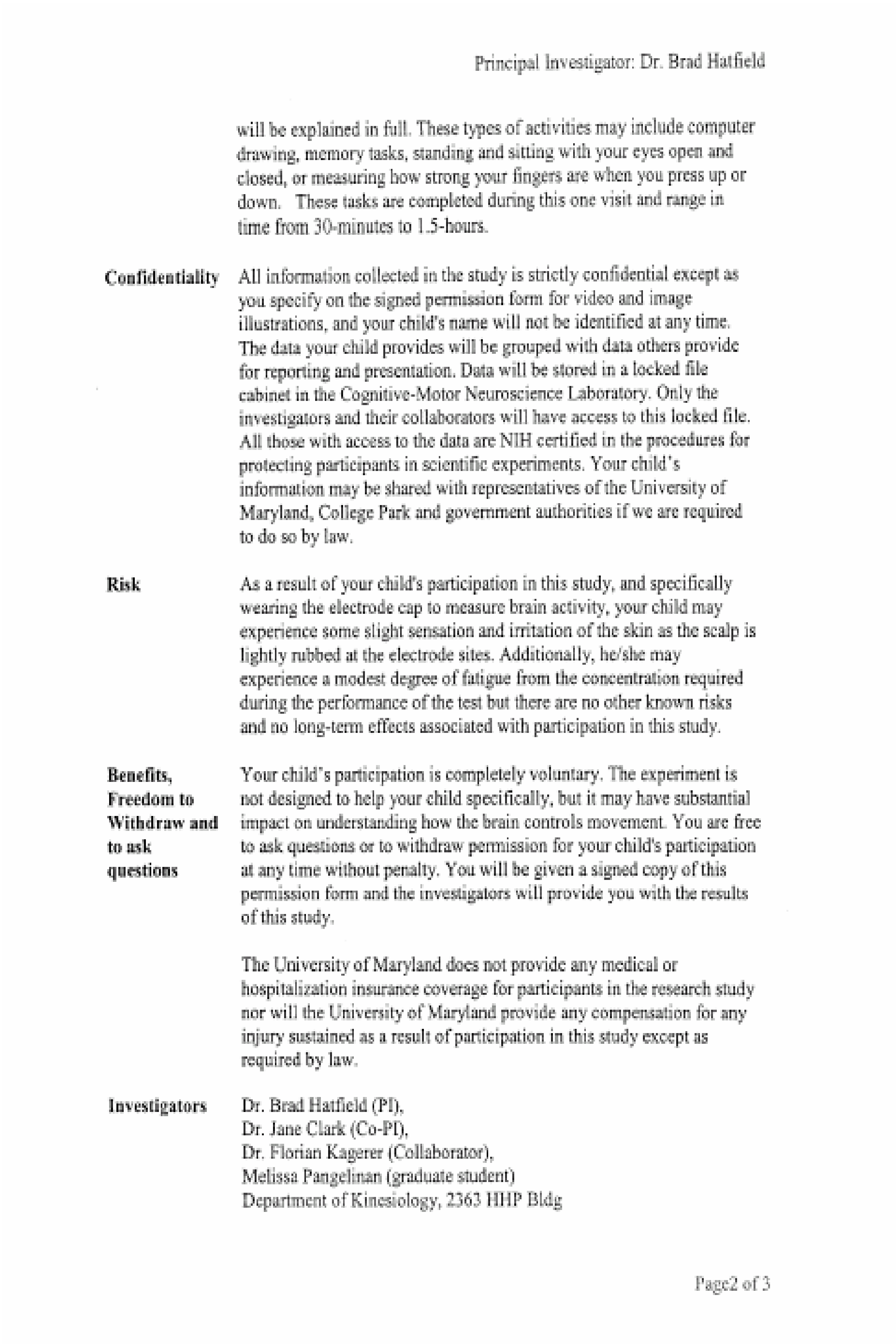
Appendix 2: Permission Form A2 – for **child** participant (EEG)

PERMISSION FORM

University of Maryland, Cognitive-Motor Neuroscience Laboratory

Identification of Project	Project Title: Brain dynamics in children and adults related to motor behavior.
Statement of Age of Participant	This research project is being conducted by Dr. Brad Hatfield, Dr. Jane Clark, Dr. Florian Kagerer, & Melissa Pangelinan at the Department of Kinesiology, University of Maryland, College Park. You are over 18 years of age and are the parent or legal guardian of 4- to 12-year-old child. We are inviting you and your child to participate in our study.
Purpose	The purpose of the research is to investigate brain wave patterns in children who are typically developing and those with developmental coordination disorder control compared to adults. The experiment is designed to examine changes in brain activity related to motor behavior.
Procedures	Prior to performance, you will complete a neurological health questionnaire for your child to ensure typical neurological development. Next, your child will perform a series of tasks to determine if your child is right-handed or left-handed. These tasks include throwing a ball, using an eraser, pretending to brush his or her teeth, and drawing, among other items. Next, your child will be fitted for a special electrode cap similar to a swim cap placed on his or her head. The purpose of the cap is to record electrical brain activity from up to 64 locations along the scalp. In addition skin sensors will be placed above and below your child's left eye in order to record eye blinks, and placed behind his or her ears to serve as a references for the recordings. These areas will be lightly rubbed with a 3M plastic abrasive pad and then rubbed with alcohol in order to remove any extra oil or skin cells on the surface. Your child's skin will be lightly rubbed at each skin sensor on the electrode cap with the blunt end of a wooden q-tip but the skin will not be broken. The purpose of this step is to gently move the hair away from the sensors and allow contact between the skin and the electrodes. Using a blunt end needle and tube, Using a blunt end needle and tube, Food & Drug Administration (FDA) approved non-toxic conducting gel will be applied to each sensor to that enable continuous connection between each sensor and the skin of the scalp. Again, the skin will not be broken. These set-up procedures will take approximately 10 minutes and each step will be explained to you and your child so that he/she feels comfortable with the process. After the initial set-up your child will be asked to participate in a task that is outlined in a second consent form. The procedures of this task

Page1 of 3



will be explained in full. These types of activities may include computer drawing, memory tasks, standing and sitting with your eyes open and closed, or measuring how strong your fingers are when you press up or down. These tasks are completed during this one visit and range in time from 30-minutes to 1.5-hours.

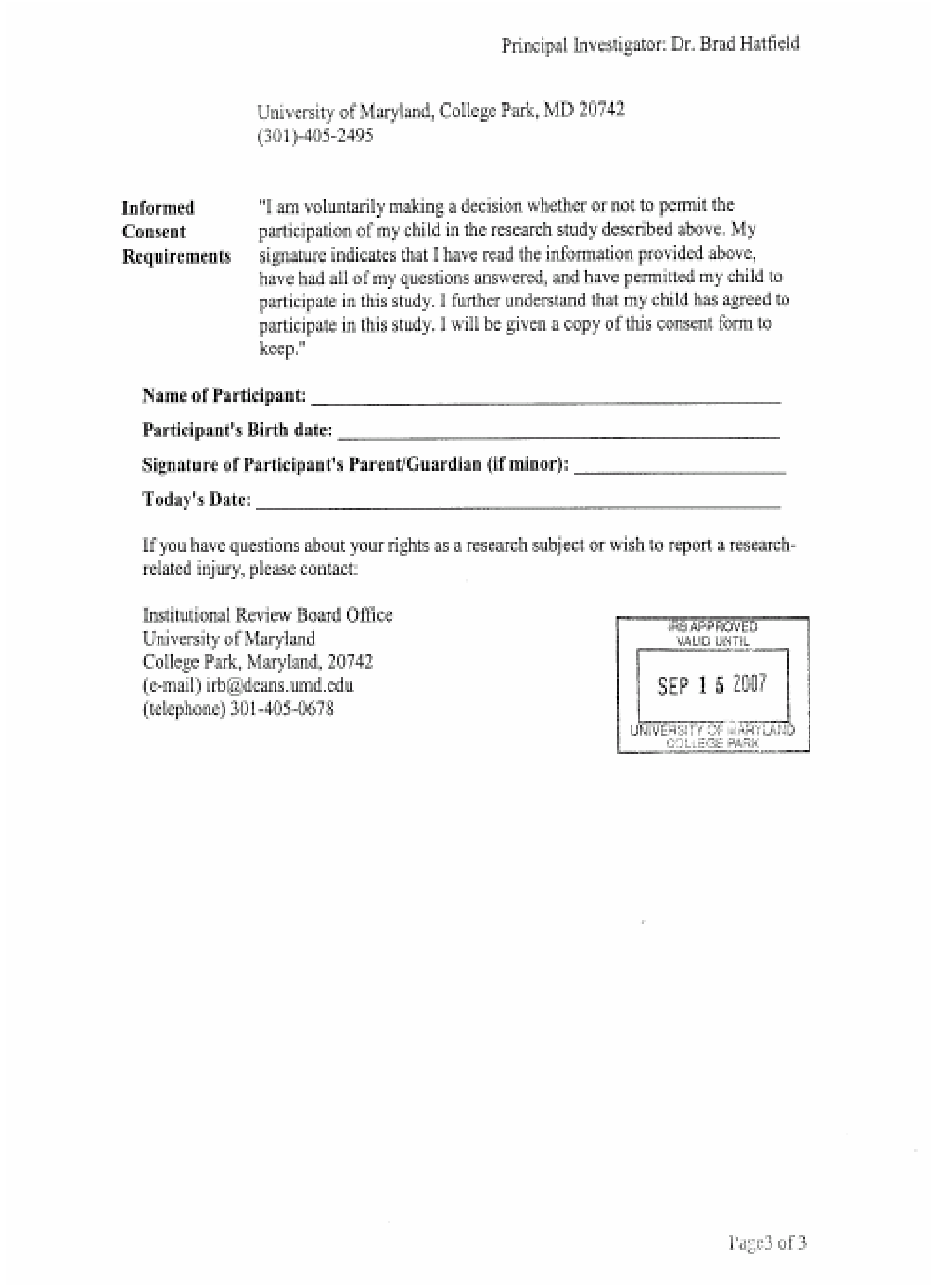
Confidentiality All information collected in the study is strictly confidential except as you specify on the signed permission form for video and image illustrations, and your child's name will not be identified at any time. The data your child provides will be grouped with data others provide for reporting and presentation. Data will be stored in a locked file cabinet in the Cognitive-Motor Neuroscience Laboratory. Only the investigators and their collaborators will have access to this locked file. All those with access to the data are NIH certified in the procedures for protecting participants in scientific experiments. Your child's information may be shared with representatives of the University of Maryland, College Park and government authorities if we are required to do so by law.

Risk As a result of your child's participation in this study, and specifically wearing the electrode cap to measure brain activity, your child may experience some slight sensation and irritation of the skin as the scalp is lightly rubbed at the electrode sites. Additionally, he/she may experience a modest degree of fatigue from the concentration required during the performance of the test but there are no other known risks and no long-term effects associated with participation in this study.

Benefits, Freedom to Withdraw and to ask questions Your child's participation is completely voluntary. The experiment is not designed to help your child specifically, but it may have substantial impact on understanding how the brain controls movement. You are free to ask questions or to withdraw permission for your child's participation at any time without penalty. You will be given a signed copy of this permission form and the investigators will provide you with the results of this study.

The University of Maryland does not provide any medical or hospitalization insurance coverage for participants in the research study nor will the University of Maryland provide any compensation for any injury sustained as a result of participation in this study except as required by law.

Investigators Dr. Brad Hatfield (PI),
Dr. Jane Clark (Co-PI),
Dr. Florian Kagerer (Collaborator),
Melissa Pangelinan (graduate student)
Department of Kinesiology, 2363 HHP Bldg



Principal Investigator: Dr. Brad Hatfield

University of Maryland, College Park, MD 20742
(301)-405-2495

Informed Consent Requirements

"I am voluntarily making a decision whether or not to permit the participation of my child in the research study described above. My signature indicates that I have read the information provided above, have had all of my questions answered, and have permitted my child to participate in this study. I further understand that my child has agreed to participate in this study. I will be given a copy of this consent form to keep."

Name of Participant: ______________________________

Participant's Birth date: ______________________________

Signature of Participant's Parent/Guardian (if minor): ______________

Today's Date: ______________________________

If you have questions about your rights as a research subject or wish to report a research-related injury, please contact:

Institutional Review Board Office
University of Maryland
College Park, Maryland, 20742
(e-mail) irb@deans.umd.edu
(telephone) 301-405-0678

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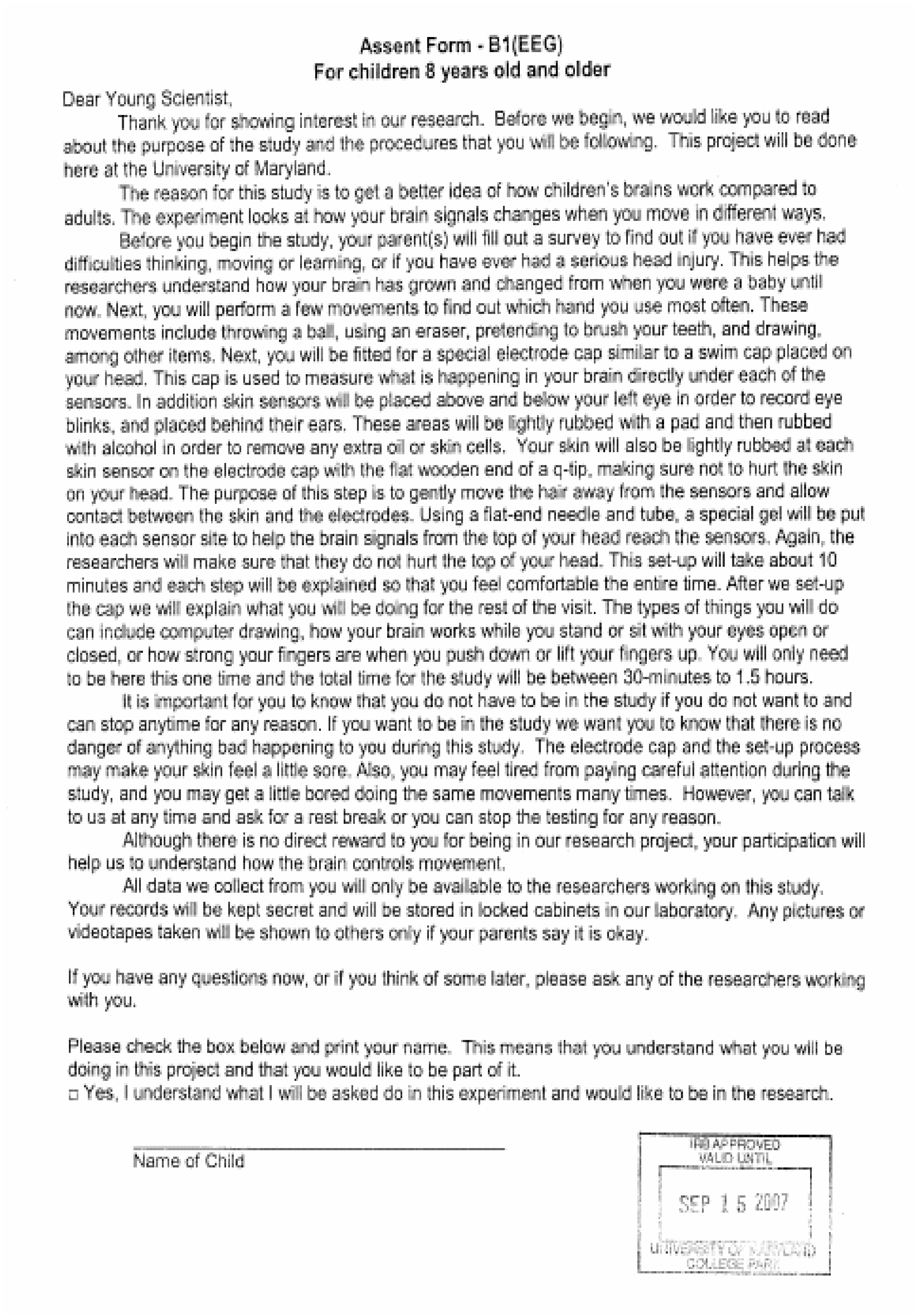
Appendix C. Minor Ascent Form for Child Participation



Assent Form - B1(EEG)
For children 8 years old and older

Dear Young Scientist,

Thank you for showing interest in our research. Before we begin, we would like you to read about the purpose of the study and the procedures that you will be following. This project will be done here at the University of Maryland.

The reason for this study is to get a better idea of how children's brains work compared to adults. The experiment looks at how your brain signals changes when you move in different ways.

Before you begin the study, your parent(s) will fill out a survey to find out if you have ever had difficulties thinking, moving or learning, or if you have ever had a serious head injury. This helps the researchers understand how your brain has grown and changed from when you were a baby until now. Next, you will perform a few movements to find out which hand you use most often. These movements include throwing a ball, using an eraser, pretending to brush your teeth, and drawing, among other items. Next, you will be fitted for a special electrode cap similar to a swim cap placed on your head. This cap is used to measure what is happening in your brain directly under each of the sensors. In addition skin sensors will be placed above and below your left eye in order to record eye blinks, and placed behind their ears. These areas will be lightly rubbed with a pad and then rubbed with alcohol in order to remove any extra oil or skin cells. Your skin will also be lightly rubbed at each skin sensor on the electrode cap with the flat wooden end of a q-tip, making sure not to hurt the skin on your head. The purpose of this step is to gently move the hair away from the sensors and allow contact between the skin and the electrodes. Using a flat-end needle and tube, a special gel will be put into each sensor site to help the brain signals from the top of your head reach the sensors. Again, the researchers will make sure that they do not hurt the top of your head. This set-up will take about 10 minutes and each step will be explained so that you feel comfortable the entire time. After we set-up the cap we will explain what you will be doing for the rest of the visit. The types of things you will do can include computer drawing, how your brain works while you stand or sit with your eyes open or closed, or how strong your fingers are when you push down or lift your fingers up. You will only need to be here this one time and the total time for the study will be between 30-minutes to 1.5 hours.

It is important for you to know that you do not have to be in the study if you do not want to and can stop anytime for any reason. If you want to be in the study we want you to know that there is no danger of anything bad happening to you during this study. The electrode cap and the set-up process may make your skin feel a little sore. Also, you may feel tired from paying careful attention during the study, and you may get a little bored doing the same movements many times. However, you can talk to us at any time and ask for a rest break or you can stop the testing for any reason.

Although there is no direct reward to you for being in our research project, your participation will help us to understand how the brain controls movement.

All data we collect from you will only be available to the researchers working on this study. Your records will be kept secret and will be stored in locked cabinets in our laboratory. Any pictures or videotapes taken will be shown to others only if your parents say it is okay.

If you have any questions now, or if you think of some later, please ask any of the researchers working with you.

Please check the box below and print your name. This means that you understand what you will be doing in this project and that you would like to be part of it.

☐ Yes, I understand what I will be asked do in this experiment and would like to be in the research.

____
Name of Child

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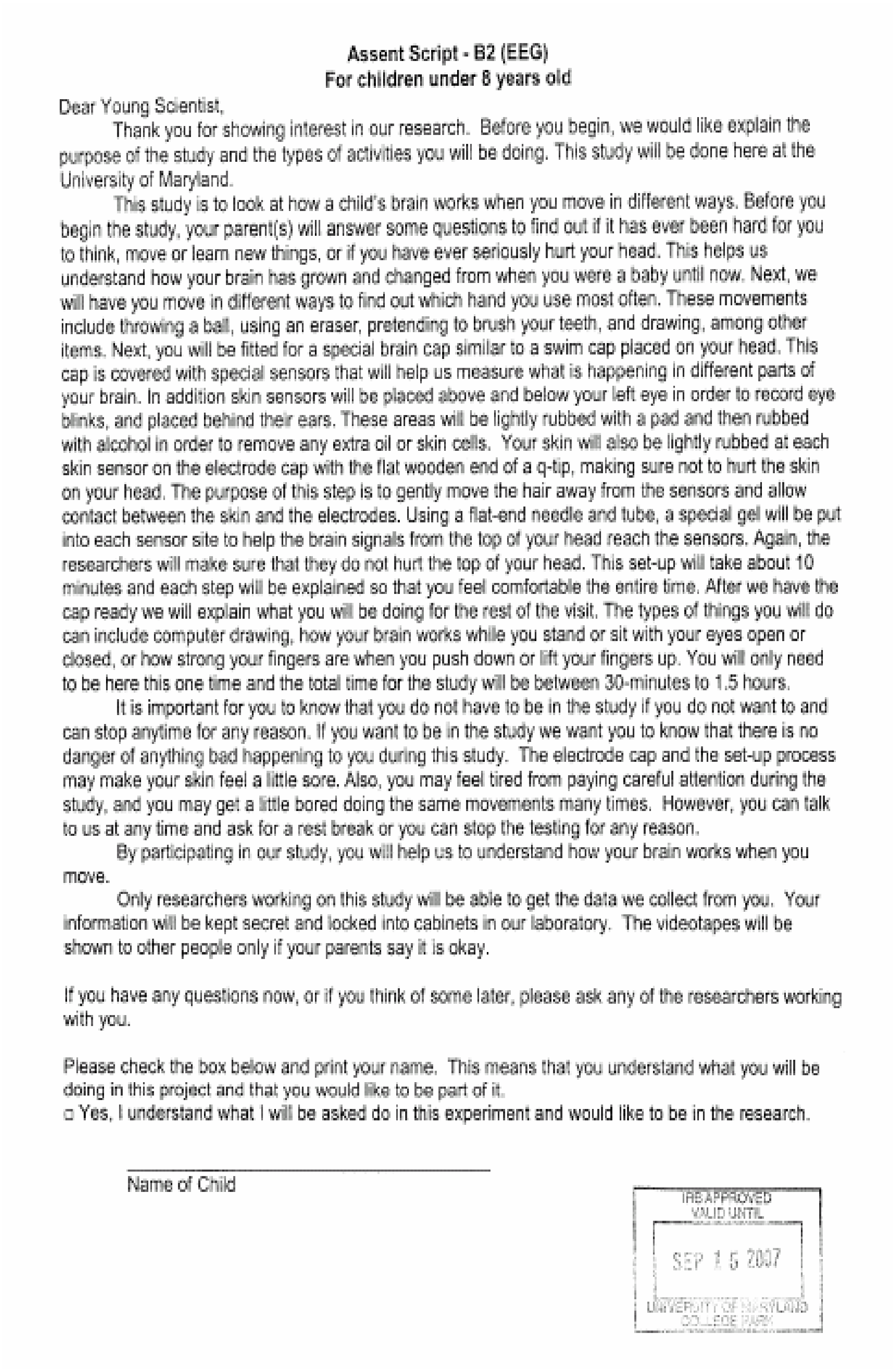

Assent Script - B2 (EEG)
For children under 8 years old

Dear Young Scientist,

Thank you for showing interest in our research. Before you begin, we would like explain the purpose of the study and the types of activities you will be doing. This study will be done here at the University of Maryland.

This study is to look at how a child's brain works when you move in different ways. Before you begin the study, your parent(s) will answer some questions to find out if it has ever been hard for you to think, move or learn new things, or if you have ever seriously hurt your head. This helps us understand how your brain has grown and changed from when you were a baby until now. Next, we will have you move in different ways to find out which hand you use most often. These movements include throwing a ball, using an eraser, pretending to brush your teeth, and drawing, among other items. Next, you will be fitted for a special brain cap similar to a swim cap placed on your head. This cap is covered with special sensors that will help us measure what is happening in different parts of your brain. In addition skin sensors will be placed above and below your left eye in order to record eye blinks, and placed behind their ears. These areas will be lightly rubbed with a pad and then rubbed with alcohol in order to remove any extra oil or skin cells. Your skin will also be lightly rubbed at each skin sensor on the electrode cap with the flat wooden end of a q-tip, making sure not to hurt the skin on your head. The purpose of this step is to gently move the hair away from the sensors and allow contact between the skin and the electrodes. Using a flat-end needle and tube, a special gel will be put into each sensor site to help the brain signals from the top of your head reach the sensors. Again, the researchers will make sure that they do not hurt the top of your head. This set-up will take about 10 minutes and each step will be explained so that you feel comfortable the entire time. After we have the cap ready we will explain what you will be doing for the rest of the visit. The types of things you will do can include computer drawing, how your brain works while you stand or sit with your eyes open or closed, or how strong your fingers are when you push down or lift your fingers up. You will only need to be here this one time and the total time for the study will be between 30-minutes to 1.5 hours.

It is important for you to know that you do not have to be in the study if you do not want to and can stop anytime for any reason. If you want to be in the study we want you to know that there is no danger of anything bad happening to you during this study. The electrode cap and the set-up process may make your skin feel a little sore. Also, you may feel tired from paying careful attention during the study, and you may get a little bored doing the same movements many times. However, you can talk to us at any time and ask for a rest break or you can stop the testing for any reason.

By participating in our study, you will help us to understand how your brain works when you move.

Only researchers working on this study will be able to get the data we collect from you. Your information will be kept secret and locked into cabinets in our laboratory. The videotapes will be shown to other people only if your parents say it is okay.

If you have any questions now, or if you think of some later, please ask any of the researchers working with you.

Please check the box below and print your name. This means that you understand what you will be doing in this project and that you would like to be part of it.

☐ Yes, I understand what I will be asked do in this experiment and would like to be in the research.

____
Name of Child

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Appendix D. Adult Neurological Health Questionnaire

Have you ever…(Please circle yes or no)
1) been seen by a neurologist or neurosurgeon? Yes No
    if yes, please explain____________________________________
2) had a head injury involving unconsciousness? Yes No
    if yes, how long?_______________________________________
3) required overnight hospitalization for a head injury? Yes No
    if yes, please explain?_______________________________________
4) had any illness that caused a permanent decrease in memory or cognition? Yes No
    if yes, please explain____________________________________
5) had a seizure? Yes No
    if yes, please explain____________________________________
6) had any illness that caused a permanent decrease in motor ability (including speech)? Yes No
    if yes, please explain____________________________________
7) had difficulty using your hands? Yes No
    if yes, please explain____________________________________

Appendix E. Pediatric Neurological Health Questionnaire

Child's Name____
Sex___________ Age___________ Date of Birth___________

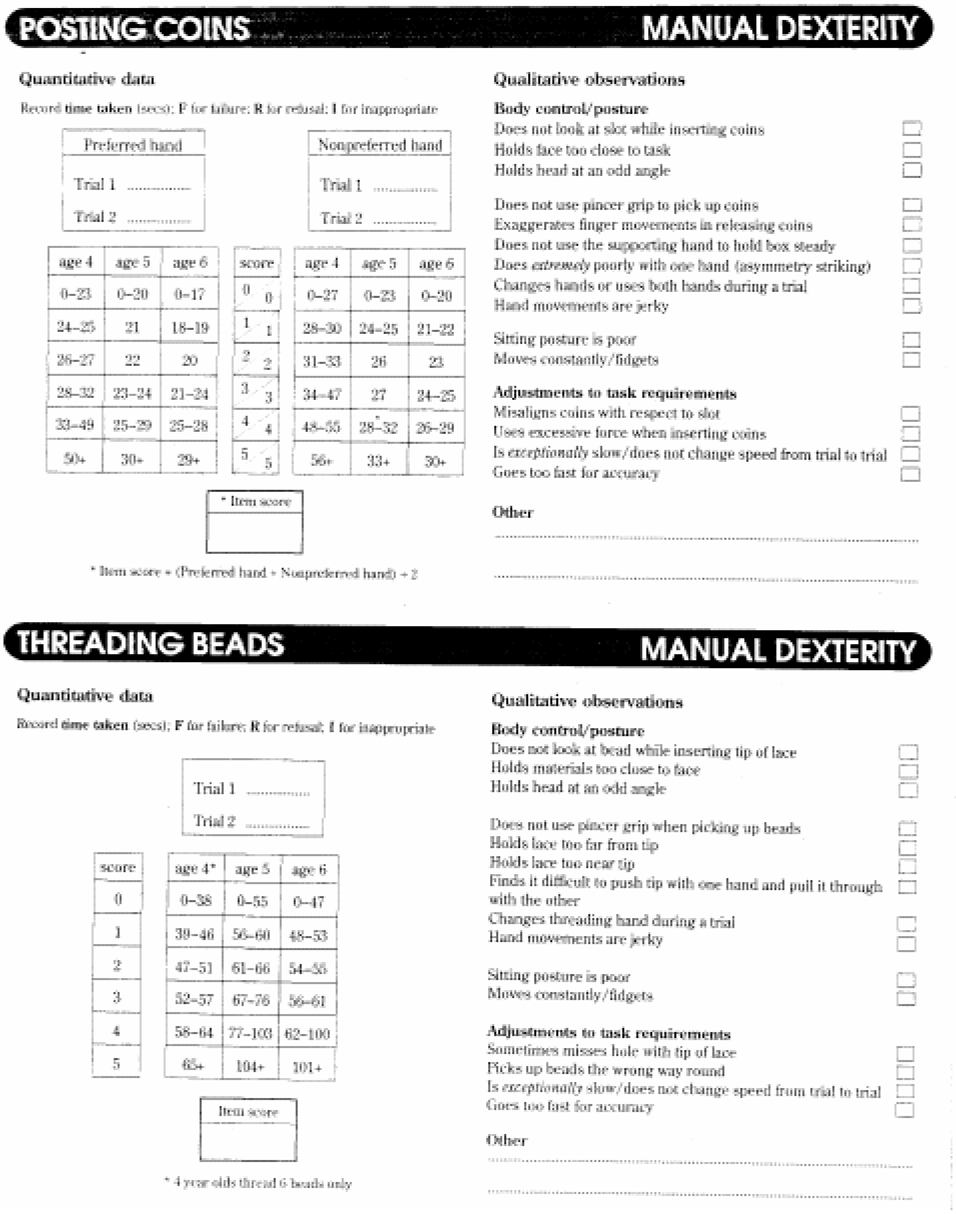
Past Medical History
Please list any prior major illnesses and/or injuries:

Birth History:
1) Any problems with the pregnancy? Yes No
if yes, what?____
2) Was your child born full term? Yes No
if no, how early?______________
3) Medical problems at birth? Yes No
if yes, what?____
Hospitalization/Surgery/Injury:
4) Except at birth, has your child been hospitalized? Yes No
if yes, list age(s) and reason________________________________
5) Has your child ever had surgery? Yes No
if yes, list age(s), and reason_______________________________
6) Has your child ever had a head injury involving unconsciousness? Yes No
if yes, how long?_______________________________________
7) Has your child had any illness that caused a permanent decrease in memory or cognition? Yes No
if yes, please explain_____________________________________
8) had any illness that caused a permanent decrease in motor ability (including speech)?
if yes, please explain_____________________________________

Review of Neurological Systems
Please circle yes or no to the following. Does your child have or has your child ever had… (if yes, please explain):
9) Seizure disorder? Yes No
____
10) Developmental delay? Yes No
____
11) Speech Delay? Yes No
____
12) Learning disabilities? Yes No
____

The above information is accurate to the best of my knowledge.
Signature of Parent or Guardian_____________________________
Printed Name of Parent or Guardian__________________________
Date_______________

Appendix F. Sample Manual Dexterity Items for Age Band 1 (4-6 years) from the Movement Assessment Battery for Children (Henderson & Sugden, 1992)



POSTING COINS **MANUAL DEXTERITY**

Quantitative data

Record **time taken** (secs); **F** for failure; **R** for refusal; **I** for inappropriate

Preferred hand
Trial 1 ....
Trial 2 ....

Nonpreferred hand
Trial 1 ....
Trial 2 ....

age 4	age 5	age 6	score		age 4	age 5	age 6
0–23	0–20	0–17	0	0	0–27	0–23	0–20
24–25	21	18–19	1	1	28–30	24–25	21–22
26–27	22	20	2	2	31–33	26	23
28–32	23–24	21–24	3	3	34–47	27	24–25
33–49	25–29	25–28	4	4	48–55	28–32	26–29
50+	30+	29+	5	5	56+	33+	30+

* Item score

* Item score = (Preferred hand + Nonpreferred hand) ÷ 2

Qualitative observations

Body control/posture

- Does not look at slot while inserting coins ☐
- Holds face too close to task ☐
- Holds head at an odd angle ☐

- Does not use pincer grip to pick up coins ☐
- Exaggerates finger movements in releasing coins ☐
- Does not use the supporting hand to hold box steady ☐
- Does *extremely* poorly with one hand (asymmetry striking) ☐
- Changes hands or uses both hands during a trial ☐
- Hand movements are jerky ☐

- Sitting posture is poor ☐
- Moves constantly/fidgets ☐

Adjustments to task requirements

- Misaligns coins with respect to slot ☐
- Uses excessive force when inserting coins ☐
- Is *exceptionally* slow/does not change speed from trial to trial ☐
- Goes too fast for accuracy ☐

Other

....

....

THREADING BEADS **MANUAL DEXTERITY**

Quantitative data

Record **time taken** (secs); **F** for failure; **R** for refusal; **I** for inappropriate

Trial 1 ....

Trial 2 ....

score	age 4*	age 5	age 6
0	0–38	0–55	0–47
1	39–46	56–60	48–53
2	47–51	61–66	54–55
3	52–57	67–76	56–61
4	58–64	77–103	62–100
5	65+	104+	101+

Item score

* 4 year olds thread 6 beads only

Qualitative observations

Body control/posture

- Does not look at bead while inserting tip of lace ☐
- Holds materials too close to face ☐
- Holds head at an odd angle ☐

- Does not use pincer grip when picking up beads ☐
- Holds lace too far from tip ☐
- Holds lace too near tip ☐
- Finds it difficult to push tip with one hand and pull it through with the other ☐
- Changes threading hand during a trial ☐
- Hand movements are jerky ☐

- Sitting posture is poor ☐
- Moves constantly/fidgets ☐

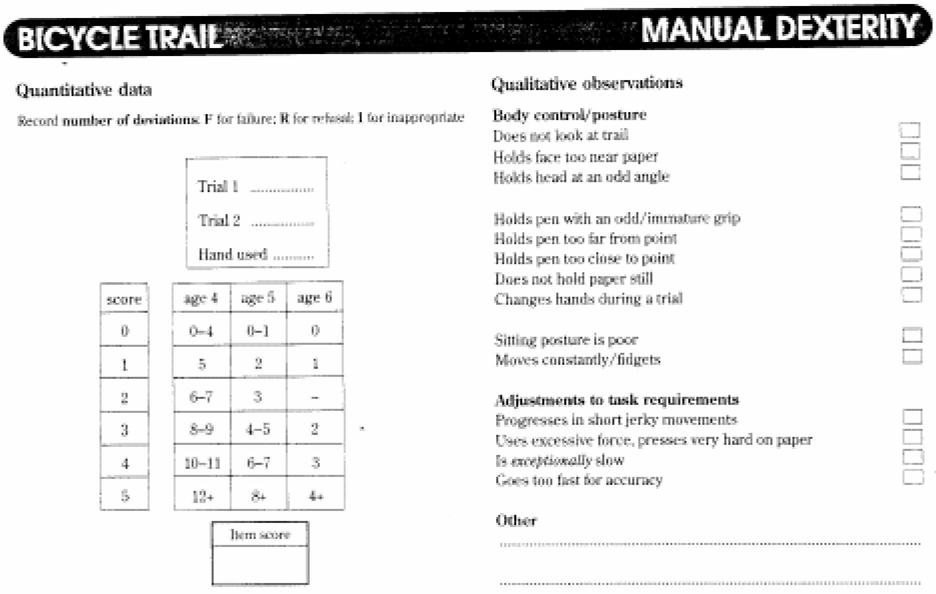
Adjustments to task requirements

- Sometimes misses hole with tip of lace ☐
- Picks up beads the wrong way round ☐
- Is *exceptionally* slow/does not change speed from trial to trial ☐
- Goes too fast for accuracy ☐

Other

....

....



BICYCLE TRAIL — MANUAL DEXTERITY

Quantitative data

Record **number of deviations**: F for failure: R for refusal: I for inappropriate

Trial 1 ....
Trial 2 ....
Hand used ....

score	age 4	age 5	age 6
0	0–4	0–1	0
1	5	2	1
2	6–7	3	–
3	8–9	4–5	2
4	10–11	6–7	3
5	12+	8+	4+

Item score

Qualitative observations

Body control/posture

Does not look at trail ☐
Holds face too near paper ☐
Holds head at an odd angle ☐

Holds pen with an odd/immature grip ☐
Holds pen too far from point ☐
Holds pen too close to point ☐
Does not hold paper still ☐
Changes hands during a trial ☐

Sitting posture is poor ☐
Moves constantly/fidgets ☐

Adjustments to task requirements

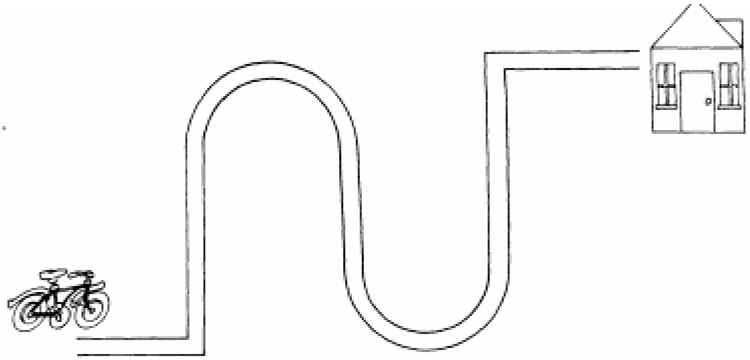
Progresses in short jerky movements ☐
Uses excessive force, presses very hard on paper ☐
Is *exceptionally* slow ☐
Goes too fast for accuracy ☐

Other

....

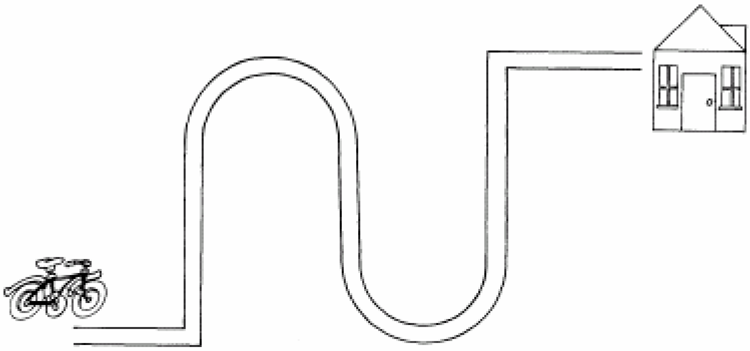
....

BICYCLE TRAIL



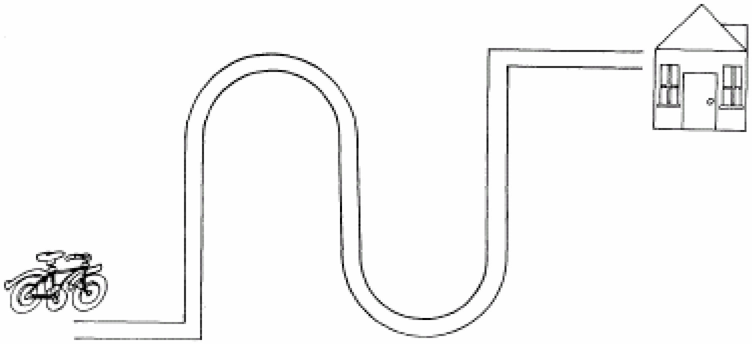
Name ....

BICYCLE TRAIL



Name ....

BICYCLE TRAIL



Name ....

Appendix G. Edinburgh Handedness Inventory

Please indicate your preferences in the use of hands in the following activities by putting + in the appropriate column.

Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, put ++. If in any case you are really indifferent put + in both columns.

Some of the activities require both hands. In these cases the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all of the questions, and only leave a blank if you have no experience at all of the object or task.

		Left	Right
1	Writing		
2	Drawing		
3	Throwing		
4	Scissors		
5	Toothbrush		
6	Knife (without fork)		
7	Spoon		
8	Broom (upper hand)		
9	Striking match (match)		
10	Opening box (lid)		
i.	Which foot do you prefer to kick with?		
ii.	Which eye do you use when using only one?		

Appendix H. Child Handedness Assessment

Item	Left	Right	Comments
throwing a ball			
raising one hand			
using an eraser			
combing hair			
brushing teeth			
using a toy hammer			
cutting with scissors			
retrieving marbles from a cup			
unscrewing a lid			
rewinding a tape or turning the hour hand on a play clock			

Appendix I. Additional Tables and Figures

Frequency Band	Factor	*F*	Post Hoc (Tukey's for Main Effects or Contrasts for Interactions)
Theta (4-7 Hz)	Group (2, 39)	12.06**	Young Children vs. Adults*** Older Children vs. Adults**
	Anterior-Posterior (2, 78)	5.73**	(see simple effects from interaction below)
	Medio-Lateral (2, 78)	5.13**	(see simple effects from interaction below)
	Anterior-Posterior*Medio-Lateral (4, 154)	6.98***	Frontal vs. Parietal Midline – Right** Central vs. Parietal Midline – Right*** Frontal vs. Parietal Left – Right** Central vs. Parietal Left – Right**
Lower Alpha (8-10 Hz)	Group (2, 39)	12.75***	(see simple effects from interaction below)
	Group * Anterior-Posterior * Medio-Lateral (8, 155)	2.35*	Young Children vs. Older Children: Frontal vs. Central Midline – Right* Young Children vs. Older Children: Frontal vs. Parietal Midline – Right** Young Children vs. Adults: Frontal vs. Parietal Midline – Right** Young Children vs. Older Children: Central vs. Parietal Midline – Right*** Young Children vs. Adults: Central vs. Parietal Midline – Right*** Young Children vs. Older Children: Frontal vs. Parietal Left – Right** Young Children vs. Adults: Frontal vs. Parietal Left – Right** Young Children vs. Older Children: Central vs. Parietal Left – Right*** Young Children vs. Adults: Central vs. Parietal Left – Right***
Lower Beta (13-20 Hz)	Medio-Lateral (2, 78)	64.35*	Left vs. Right*
Upper Beta (21-30 Hz)	Anterior-Posterior (2, 78)	24.25***	(see simple effects from interaction below)
	Medio-Lateral (2, 78)	23.23***	(see simple effects from interaction below)
	Anterior-Posterior*Medio-Lateral (4, 154)	7.67***	Frontal vs. Central Midline – Right* Frontal vs. Parietal Midline – Right** Central vs. Parietal Midline – Right*** Frontal vs. Parietal Left – Right** Central vs. Parietal Left – Right***
Gamma (36-44 Hz)	Anterior-Posterior (2, 78)	221.41***	(see simple effects from interaction below)
	Medio-Lateral (2, 78)	175.45***	(see simple effects from interaction below)
	Anterior-Posterior*Medio-Lateral (4, 154)	389.80***	Frontal vs. Central Midline – Right* Frontal vs. Parietal Midline – Right** Central vs. Parietal Midline – Right*** Frontal vs. Parietal Left – Right** Central vs. Parietal Left – Right***

Table 1. Log-transformed relative spectral power results for all frequency bands. *F* values, *p* values (indicated by asterisks), and Tukey's post hoc (main effects) or Contrasts (interactions) results. Degrees of freedom for numerator and denominator indicated in parentheses for each factor. For the post hoc analysis *** indicates $p < 0.0001$, ** indicates $p < 0.01$, * indicates $p < 0.05$.

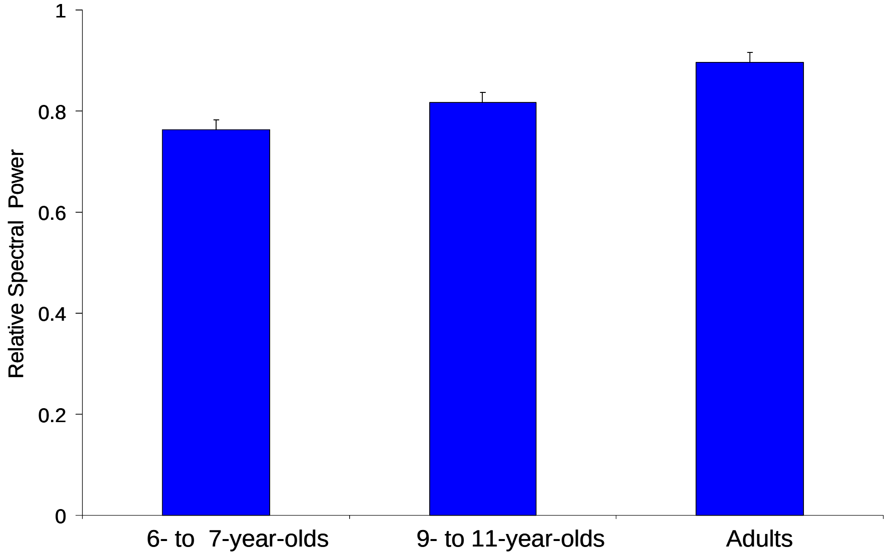


Figure 4.0. Adjusted mean relative delta spectral power (proportion) for each group. The error bars indicate the standard error above the mean for each group. *The delta frequency band was not subjected to statistical analysis for this study. However, this band appeared to comprise greater than 75% of the total spectral power for all electrodes. Therefore, all other frequencies contributed to less than 25% of the total broad-band power.

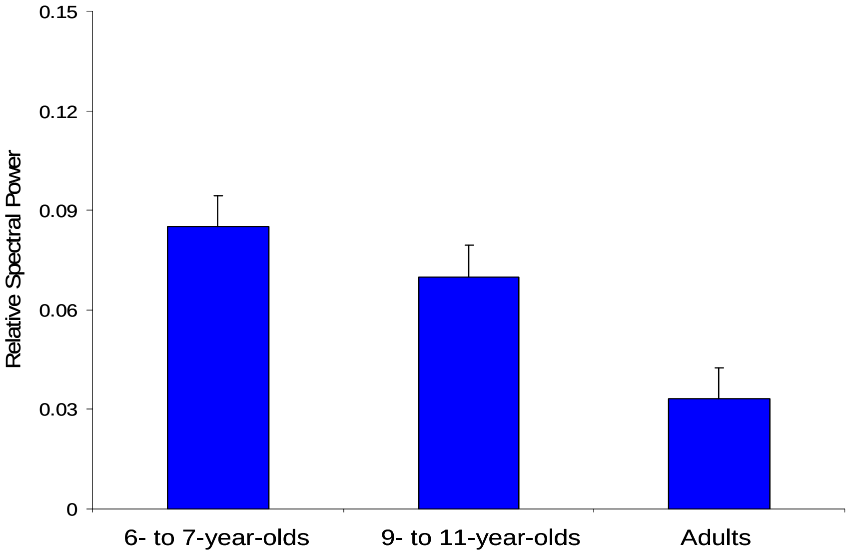
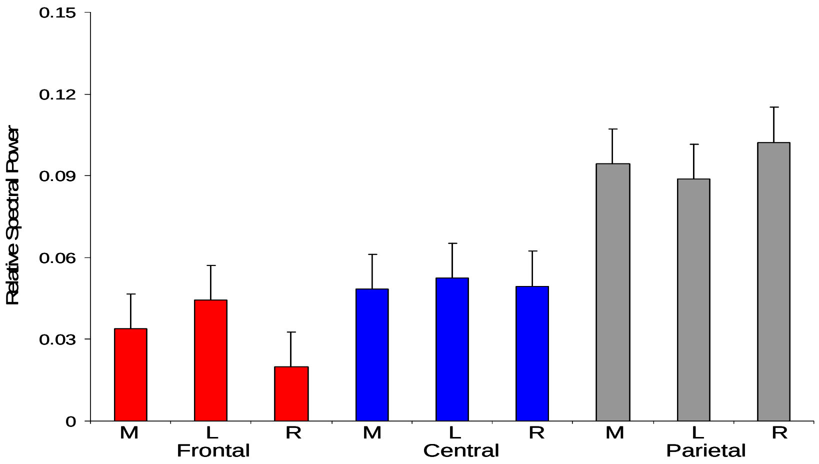
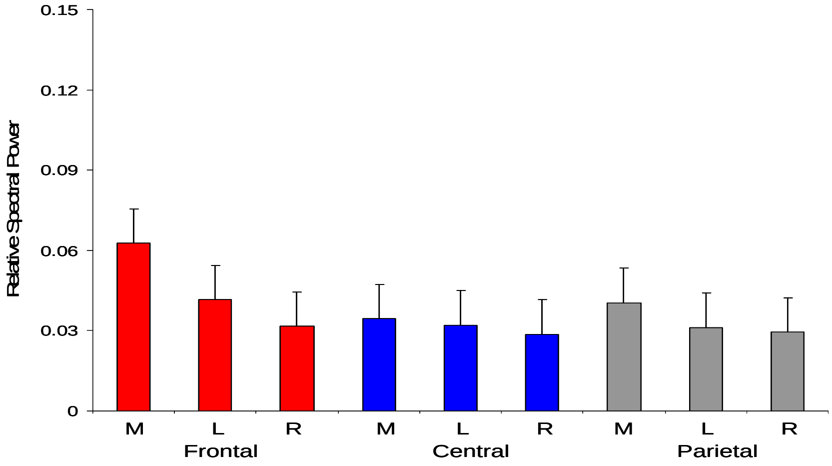


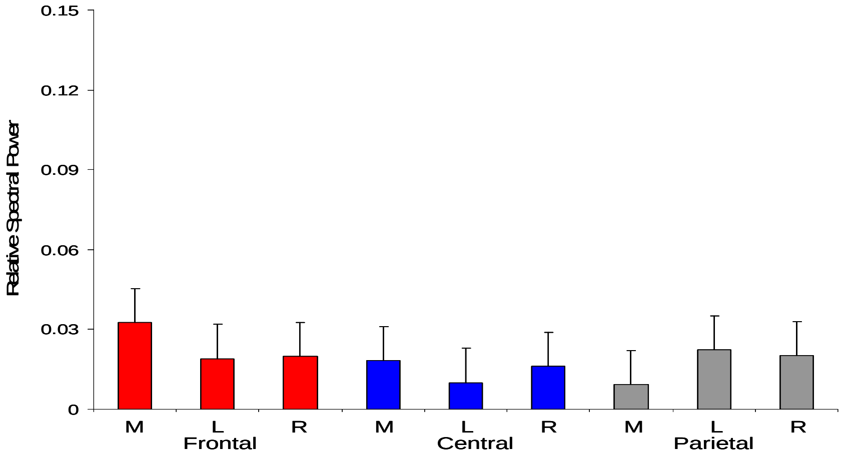
Figure 4.1.1 Adjusted mean relative theta spectral power (proportion) for each group. The error bars indicate the standard error above the mean for each group



6- to 7-year-olds



9- to 11-year-olds



Adults

Figure 4.2.1. Adjusted mean relative lower alpha spectral power (proportion) three-way interaction. Age group: 6- to 7-year olds (top), 9- to 11-year-olds (middle), and adults (bottom). Anterior-posterior locations: frontal (red), central (blue), and parietal (gray). Mediolateral locations: M (midline); L (left), and R (right). The error bars indicate one standard error for each group mean.

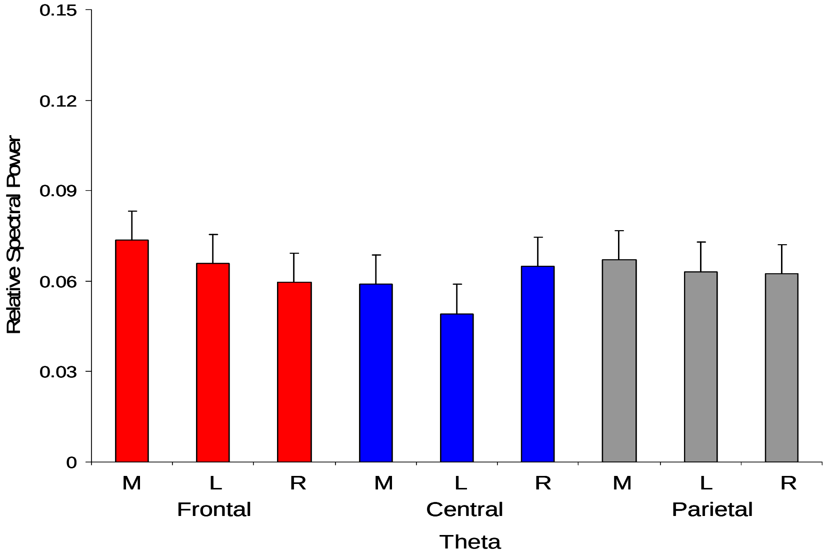


Figure 4.3.1 Adjusted mean relative theta spectral power (proportion) for anterior-posterior x mediolateral interaction. Anterio-posterior locations: frontal, central, parietal. Mediolateral locations: M (midline), L (left), and R (right). The error bars indicate one standard error for each group mean.

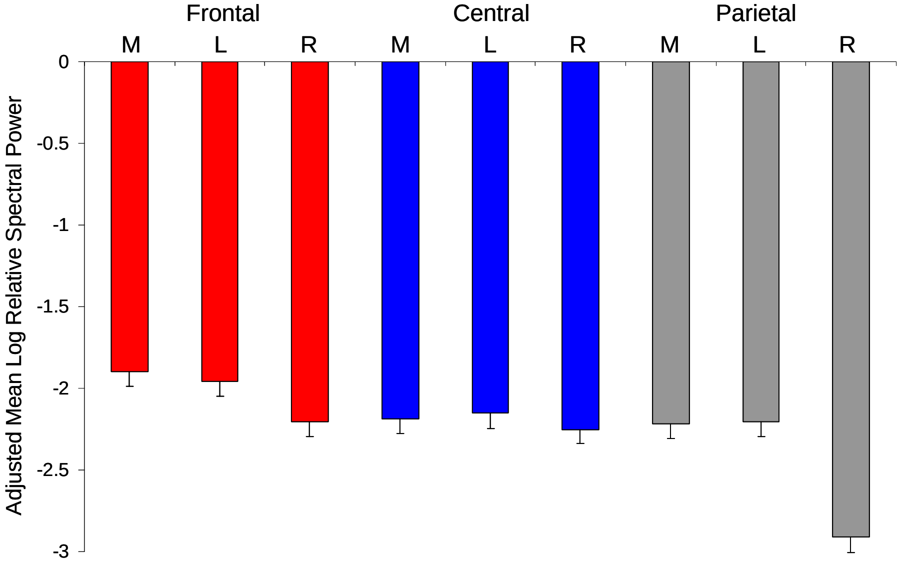


Figure 4.3.2. Adjusted mean log relative upper beta spectral power for the anterior-anterior-posterior x mediolateral interaction. Anterio-posterior locations: frontal, central, parietal. Mediolateral locations: M (midline), L (left), and R (right). The error bars indicate one standard error for each group mean.

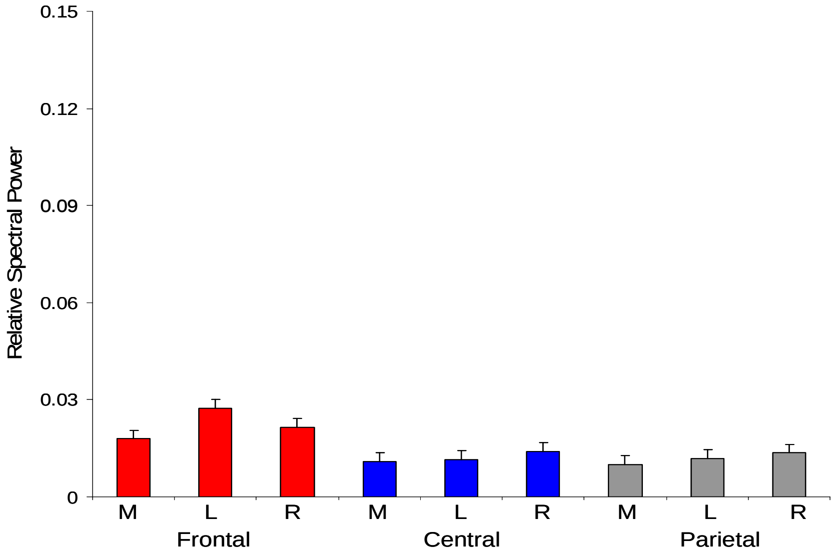


Figure 4.3.3. Adjusted mean relative upper beta spectral power (proportion) for the anterior-posterior x mediolateral interaction. Anterio-posterior locations: frontal, central, parietal. Mediolateral locations: M (midline), L (left), and R (right). The error bars indicate one standard error for each group mean.

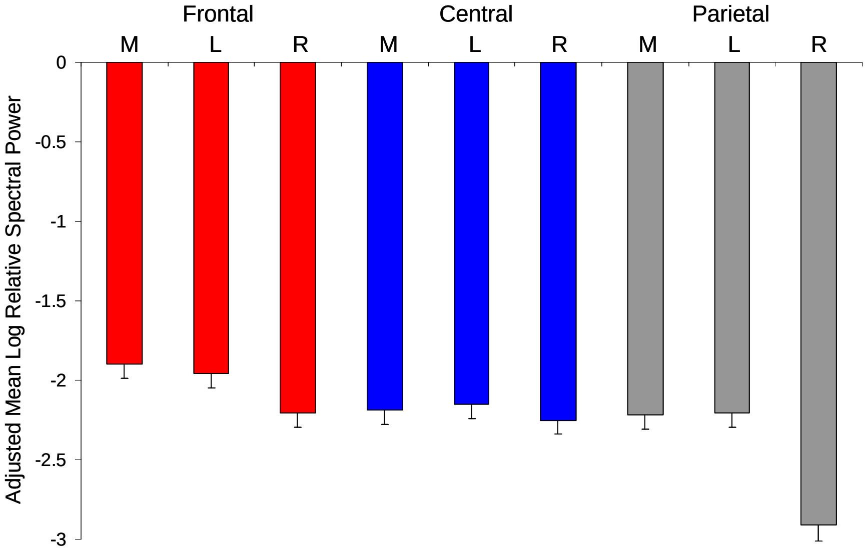


Figure 4.3.4. Adjusted mean log relative gamma spectral power for the anterior-posterior x mediolateral interaction. Anterio-posterior locations: frontal, central, parietal. Mediolateral locations: M (midline), L (left), and R (right). The error bars indicate one standard error for each group mean.

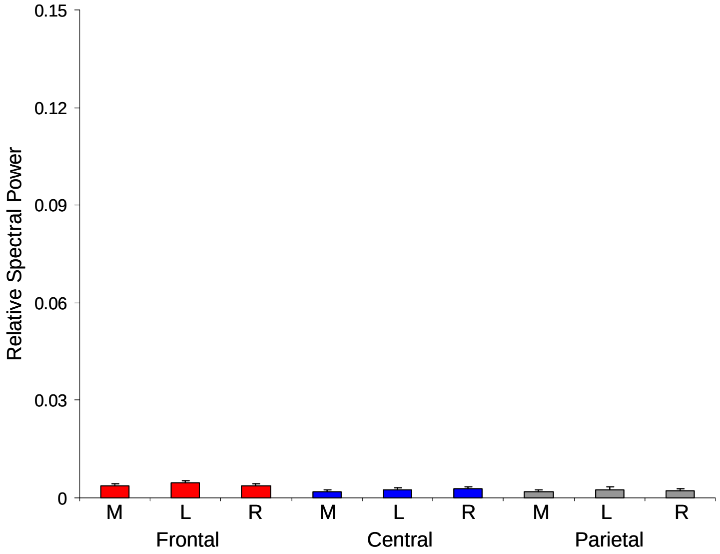


Figure 4.3.5. Adjusted mean relative gamma spectral power (proportion) for anterior-posterior x mediolateral interaction. Anterio-posterior locations: frontal, central, parietal. Mediolateral locations: M (midline), L (left), and R (right). The error bars indicate one standard error for each group mean.

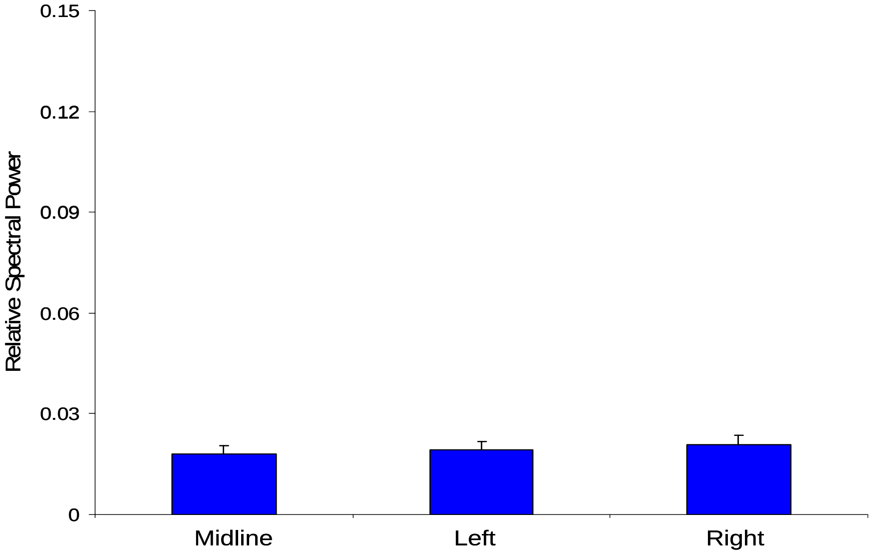


Figure 4.4.1. Adjusted mean relative lower beta spectral power (proportion) for the mediolateral locations (midline, left, and right). The error bars indicate one standard error for each group mean.

Frequency Band	Factor	*F*	Post Hoc (Tukey's for Main Effects or Contrasts for Interactions)
Theta (4-7 Hz)	Anterior-Posterior (2, 78)	23.54***	Frontal vs. Central** Frontal vs. Parietal *** Central vs. Parietal**
Lower Alpha (8-10 Hz)	Anterior-Posterior (2, 78)	29.56***	Frontal vs. Central** Frontal vs. Parietal *** Central vs. Parietal***
	Medio-Lateral (2, 78)	6.21**	Midline vs. Left *; Midline vs. Right**
Upper Alpha (11-13 Hz)	Anterior-Posterior (2, 78)	12.78***	(see simple effects from interaction below)
	Medio-Lateral (2, 78)	4.57*	(see simple effects from interaction below)
	Anterior-Posterior * Medio-Lateral (3, 116)	3.10*	Frontal vs. Central Left-Right ** Frontal vs. Parietal Left-Right*
Lower Beta (14-20 Hz)	Anterior-Posterior (2, 78)	30.51***	(see simple effects from interaction below)
	Medio-Lateral	9.07***	Midline vs. Left**; Midline vs. Right**
	Group*Anterior-Posterior (4, 78)	6.07**	Older Children vs. Adults Frontal – Central ** Older Children vs. Adults Central – Parietal*
Upper Beta (21-30 Hz)	Anterior-Posterior (2, 78)	21.69***	Frontal vs. Central ** Frontal vs. Parietal *** Central vs. Parietal**
	Medio-Lateral (2, 78)	6.14**	Midline vs. Left * Midline vs. Right**
Gamma (36-44 Hz)	Anterior-Posterior (2, 78)	17.02***	(see simple effects from interaction below)
	Group * Anterior-Posterior (4, 78)	4.43**	Young Children vs. Adults Frontal – Central** Older Children vs. Adults Frontal – Central* Young Children vs. Adults Frontal – Parietal* Older Children vs. Adults Frontal – Parietal*

Table 2. Coherence results for all frequency bands. *F* values, p values (indicated by asterisks), and Tukey's post hoc (main effects) or Contrasts (interactions) results. Degrees of freedom for numerator and denominator indicated in parentheses for each factor. For the post hoc analysis *** indicates $p < 0.0001$, ** indicates $p < 0.01$, * indicates $p < 0.05$.

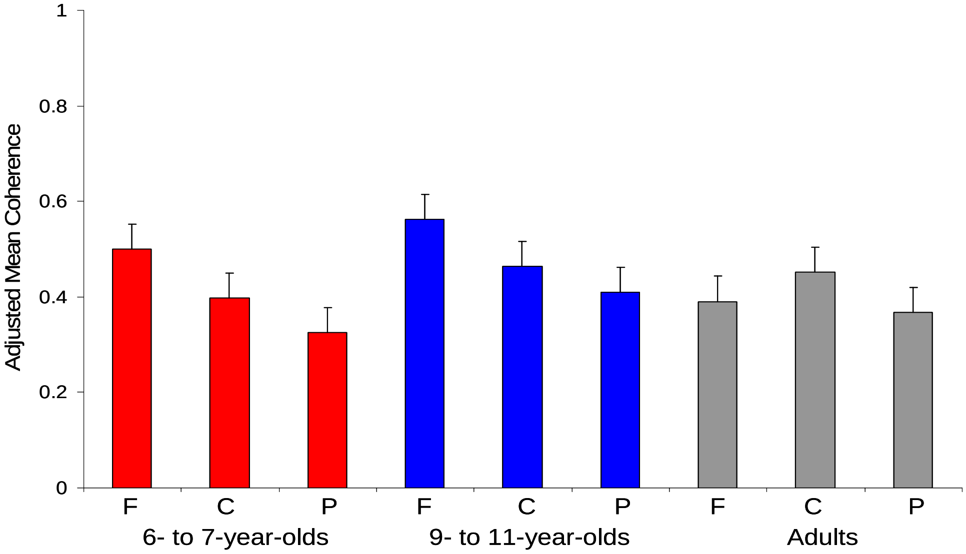


Figure 4.5.1 Adjusted mean coherence for the gamma frequency for the group x anterior posterior interaction. 6- to 7-year olds (left - red), 9- to 11-year-olds (middle – blue), and adults (right – gray). Anterior-posterior locations: F (Frontal), C (Central), and P (Parietal). The error bars indicate one standard error for each group mean.

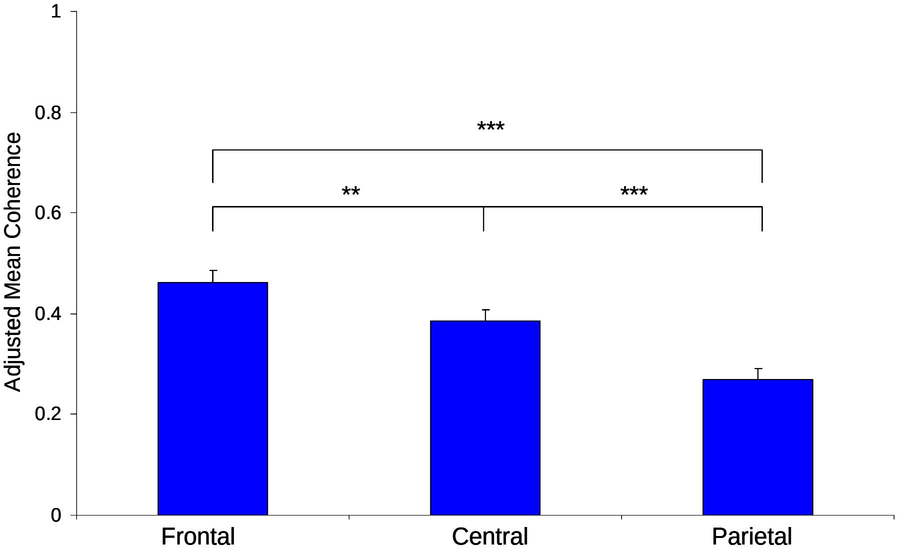


Figure 4.6.1 Adjusted mean coherence for the three electrode distances in the lower alpha frequency band. F= Fz to Frontal, C = Fz to Central, P = Fz to Parietal electrodes. Error bars indicate one standard error for the mean of each group. ***Significance level of $p < 0.0001$; **Significance level of $p < 0.01$.

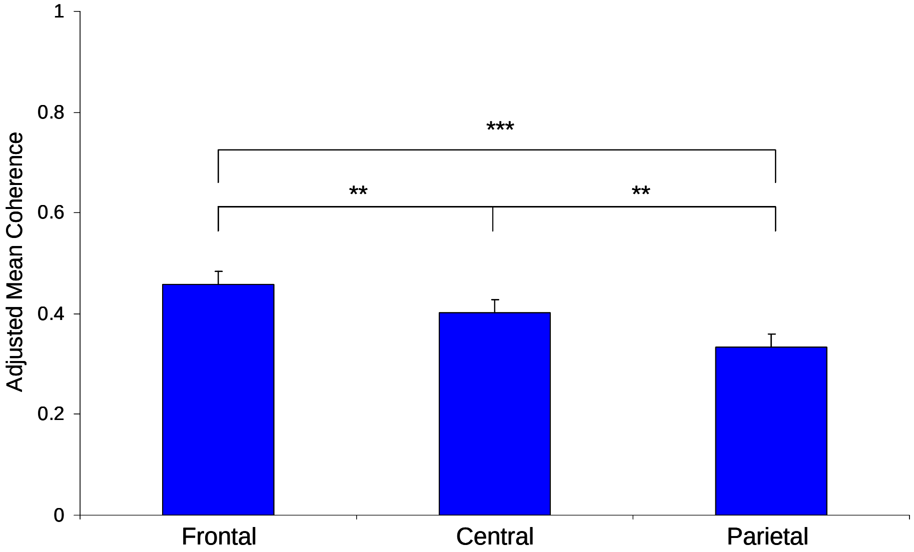


Figure 4.6.2 Adjusted mean coherence for the three electrode distances in the upper beta frequency band. F= Fz to Frontal, C = Fz to Central, P = Fz to Parietal electrodes. Error bars indicate one standard error for the mean of each group. ***Significance level of $p < 0.0001$; **Significance level of $p < 0.01$.

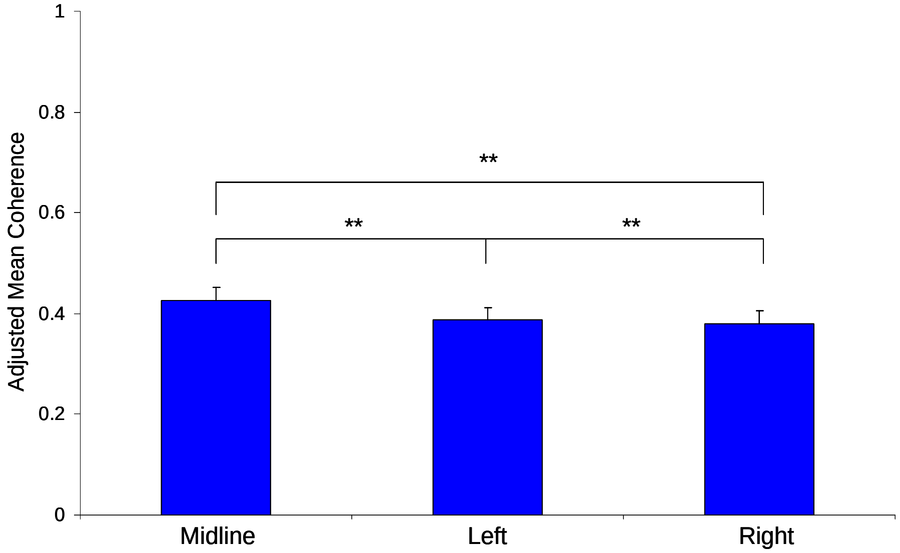


Figure 4.7.1 Adjusted mean coherence for the three mediolateral electrode locations in the upper beta frequency band. Midline= Fz to Midline electrodes; Left = Fz to Left hemisphere electrodes; Right = Fz to Right hemisphere electrodes. Error bars indicate one standard error for the mean of each group. **Significance level of $p < 0.01$.

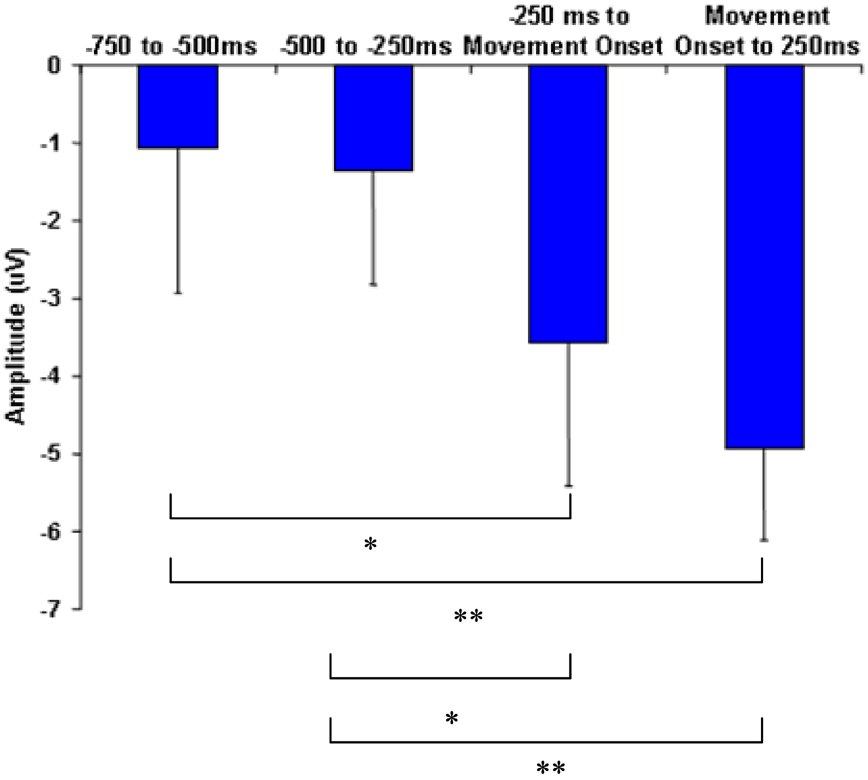


Figure 4.9.1. Central midline (Cz) main effect of time. ** Significance level of $p < 0.01$, * $p < 0.05$. Error bars indicate one standard deviation below the mean for each group.

	Movement Length (cm)	**RMSE (cm^2)**	**Movement Time (s)**	**Normalized Jerk**
6- to 7-year olds	5.654 (0.094)	0.210 (0.555)	1.143 (0.363)	154.660 (94.667)
9- to 11-year-olds	5.579 (0.088)	0.186 (0.050)	0.647 (0.211)	50.896 (24.924)
Adults	5.658 (0.124)	0.166 (0.058)	0.469 (0.117)	25.210 (9.195)

Table 3. Behavioral performance measures for all groups. Means are presented with standard deviations for each group indicated in parentheses.

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