Electrocortical Dynamics Reflect Age-Related Differences in Movement Kinematics among Children and Adults

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Previous neuroimaging and behavioral studies demonstrated structural and functional changes in the motor system across childhood. However, it is unclear what functionally relevant electrophysiological processes in the cerebrocortical regions underlying movement-related activity reflect age-related changes in neural development and control during multijoint, goal-directed movements. The current study characterized age-related differences in electrophysiological processes during the performance of discrete aiming movements in children and adults. Electroencephalography and movement kinematics were recorded from 3 groups of participants (n = 15 each): young children (mean 6.7 years), older children (mean 10.2 years), and adults (mean 22.1 years). Age-related differences were evident in the electroencephalographic (EEG) signals. First, young children exhibited less movement-related activity in task-relevant motor areas compared with adults (movement-related cortical potentials). Second, young children exhibited greater activation (less alpha power) of the frontal areas and less activation of the parietal areas as compared with the other groups. At the behavioral level, young children made slower and jerkier movements, with less consistent directional planning compared with older children and adults. Significant correlations were also found between EEG and movement kinematic measures. Taken together, the results of this study provide evidence that age-related differences in the quality of motor planning and performance are reflected in the differences in electrophysiological dynamics among children and adults.

Keywords: coherence, development, motor planning, movement-related cortical potentials, spectral analysis

Introduction

Planning and execution of goal-directed arm movements undergo continual refinement during childhood, as evidenced by age-related improvements in spatial and temporal accuracy (Bard et al. 1990; Yan et al. 2003), fine-tuning of intralimb coordination patterns (Thomas et al. 2000), and reduced variability (Contreras-Vidal et al. 2005; King et al. 2009). Improvements in motor behavior during this period of development parallel the protracted maturation of cerebrocortical brain regions and pathways critical for motor planning and control. Gogtay et al. (2004) reported that cortical gray matter maturation (gray matter refinement) is complete by around 5 or 6 years of age in regions mediating sensorimotor functions, such as the primary motor and sensory cortices. However, the maturation of cortical areas underlying motor coordination and higher-order multisensory integration, such as the prefrontal and parietal cortices, respectively, is not complete until later stages of childhood. Similarly, Paus et al. (1999) reported protracted development of the corticospinal and long-range cortical association tracts, which may facilitate the refinement in motor planning and behavioral performance with increasing age. However, the extent to which cortical development contributes to planning and control of movements in typically developing children remains unclear.

Very few studies have examined developmental changes in cerebrocortical processes during the performance of complex, goal-directed motor behavior. Previous studies predominantly investigated temporally sensitive electroencephalographic (EEG) correlates of motor preparation, such as movement-related cortical potentials (MRCPs) (Chiarenza et al. 1983; Warren and Karrer 1984b; Chiarenza et al. 1995) or contingent negative variation (CNV) (Bender et al. 2004; Bender et al. 2005) during simple button-press responses. Older children and adults exhibit these motor preparatory responses, which are characterized by large amplitude negative-going waveforms evident in the electrodes overlaying the supplementary motor area and contralateral primary motor cortex (Warren and Karrer 1984a; Chiarenza et al. 1995). In contrast to the adults and older children, the expected negative-going potentials are attenuated or absent in young children, indicating a lack of task-relevant cortical activation during movement preparation for simple movements. In addition to age-related modulation of the waveforms amplitudes, adults have shown that MRCPs are sensitive to increased movement complexity (Lang et al. 1983), visuomotor skill acquisition (Staines et al. 2002), as well as precision and movement selection (Shibasaki and Hallett 2006). However, developmental differences in these waveforms during movement preparation of multijoint and/or complex movements have yet to be examined.

Spectral analyses of EEG signals provide a complementary approach to examining developmental differences in EEG signals in the time domain (e.g., MRCPs). Specifically, differences in functional communication (coherence) among brain areas (Thatcher et al. 1986; Thatcher et al. 1987; Gasser et al. 1988a; Thatcher 1992; Barry et al. 2004) and oscillatory behavior (spectral power) of neuronal populations within a given region of interest (Gasser et al. 1988b; Clarke et al. 2001) have been investigated. These studies reported greater long-range functional communication within and across the brain hemispheres with increasing age during resting conditions (Thatcher et al. 1987; Gasser et al. 1988a; Thatcher 1992; Barry et al. 2004) and a shift in peak spectral power with age.
(Gasser et al. 1988b; Clarke et al. 2001). These studies provide a functional measure related to the structural developmental of cortical pathways and developmental changes in the activity of populations of cortical neurons at rest. However, no study to date has examined if these developmental differences may underlie age-related improvements in motor task performance.

Changes in coherence and spectral power specific to motor planning and execution (task-related coherence [TRCoh] or task-related spectral power [TRPow], respectively) have been well characterized for adults (Rappelsberger et al. 1994; Gerloff et al. 1998; Manganotti et al. 1998). Increased TRCoh and decreased TRPow (with respect to resting/baseline conditions) in the alpha and beta bands is evident with increased movement complexity particularly among sensorimotor areas prior to the onset of movement (Rappelsberger et al. 1994; Gerloff et al. 1998; Manganotti et al. 1998; Neuper and Pfurtscheller 2001). Decreased TRPow or desynchronization is most prominent over the contralateral sensorimotor cortex and is thought to reflect movement preparation (Pfurtscheller 1989; Pfurtscheller and Andrew 1999; Pfurtscheller and Klimesch 1991; Neuper and Pfurtscheller 2001). Bender and colleagues have investigated alpha desynchronization in children (6- to 11-year-olds) and adolescents (12- to 18-year-olds) during the performance of a forewarned reaction time (CNV) task (Bender et al. 2004; Bender et al. 2005). Although less pronounced in young children, alpha desynchronization was evident and corresponded with the developmental changes observed in the time domain (i.e., age-related increases in CNV amplitude), indicating that the adolescents were engaged in task-specific movement preparatory processes in response to a warning stimulus. It is likely that self-initiated movements, in contrast to these externally cued movements, may elicit more pronounced desynchronization and may be more sensitive to age-related differences in movement preparation across childhood.

The current study examined age-related differences in cortical processes underlying the planning of goal-directed, multijoint aiming movements in children and adults. Time- and frequency-domain analyses were employed to characterize age-related differences in the EEG signals during motor planning and control. Specifically, MRCPs were analyzed to characterize the time-locked activation of cortical sensorimotor and motor planning regions. TRPow and TRCoh were used to examine differences in regional activity and functional coupling brain areas during motor planning, respectively. We hypothesized that developmental differences in motor performance would be related to greater neural facilitation of cortical motor resources, task-related activation, and efficient functional communication related to goal-directed visuomotor behaviors. Taken together, these results will provide insights into the potential functional relevance of electrocortical processes underlying the developmental differences in motor planning and control previously reported in school-age children.

Materials and Methods

Participants
Female participants were recruited for participation in the present study. Given that gender differences were not the focus of the current study, one gender was sought to preclude potential gender differences previously reported in EEG (Clarke et al. 2001; Barry et al. 2004). Two groups of female children ($n = 15$, each): 6- to 7-year-olds ($6.7 \pm 0.51$ years; mean age $\pm$ standard deviation [SD]) and 9- to 11-year-olds ($10.2 \pm 0.86$ years) were recruited from the area surrounding the university for participation in this study. An additional 5 children were recruited for the youngest age group but were unable to successfully complete the task and were not included in the analysis. A group of adult female undergraduate students ($n = 15$, 22.1 $\pm$ 2.0 years) was recruited as a "fully developed" control group. All participants were naive to the purpose of the experiment. The adult participants and the children's parents or legal guardians provided informed consent. 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 modest monetary compensation. Additionally, the children received a small age-appropriate prize for completing the experiment.

Inclusion Criteria
Study inclusion for the children participants was based on a neurological health screening completed by the parents of child participants prior to the testing session. Participants met the following inclusion criteria: uneventful prenatal, perinatal, and neonatal periods; no major head traumas or incidences of unconsciousness; no history of neuropsychological disorders (including depression and anxiety disorders); no learning disabilities (including attention-deficit hyperactivity disorder); no language impairments (including stuttering and language delays); no developmental physical or motor development delays (e.g., motor planning and execution deficits in memory or cognition); and no delays in the achievement of motor milestones (crawling, walking, writing). To ensure typical motor development, the children completed the Movement Assessment Battery for Children (Henderson and Sugden 1992). This standardized assessment evaluated the children's performance in the areas of manual dexterity, ball skills, and balance. All the children included in the study performed above the 30th percentile. The children's hand dominance was assessed by a 10-item laterality test (Fagard and Corroyer 2003). All children were right-hand dominant.

Adults completed the neurological health screening to ensure that they met the inclusion criteria and Edinburgh Handedness Inventory (Oldfield 1971) to ensure right-hand dominance. In addition, the adult participants were asked to abstain from caffeinated or alcoholic beverages and medication on the day of the testing session.

Experimental Apparatus and Procedures
The experimental procedures were consistent with a previous study in our laboratory (Contreras-Vidal and Kerick 2004). Figure 1 depicts the experimental setup. Participants sat comfortably at a table facing a computer monitor ($21^\circ$) positioned so that the center of the screen was at eye level. The participants used a chin rest to stabilize and maintain their head position. The height of the chair and chin rest were adjusted for each participant. Trunk displacement and rotation were minimized by back and chest support. Direct vision of the hand/arm was prevented via an occluding board upon which the computer screen was positioned; a digitizing tablet ($12^\circ \times 12^\circ$ WACOM Intuos) was placed underneath. A computerized pen was used to make line-drawing/aiming movements on the tablet in the horizontal plane with movement at the shoulder and elbow joints. The $x$ and $y$ coordinates of the pen on the digitizing tablet were sampled at 200 Hz using custom software written in OASIS (Kikosoft). OASIS generated event markers that were synchronized with the EEG data collection indicating the beginning of a trial, target appearance, movement onset, target acquisition, and the end of a trial. A laptop computer stored data for later processing and provided real-time visual feedback of pen movement on the computer screen.

Neuroscan Scan software (version 4.3; Hernndon) was used to collect and analyze continuous EEG from 11 surface tin electrodes housed within a stretchable lycra cap (Electro Cap International) consistent with the International 10/20 system. These sites included the following regions of interest: frontal (F3, Fz, F4), central (C3, Cz, C4), parietal (P3, Pz, P4), and occipital (O1, O2). Eye movement artifacts were monitored from electrodes placed superior and inferior to the left eye and on the orbital fossa of the left and right eyes. A common ground was used (FPz) and average mastoids served as the common reference. The impedances were maintained at or below 10 k$\Omega$ for all channels. However, acceptable impedances (below 10 k$\Omega$) for the occipital sites (O1 and O2) were difficult to obtain for some of the participants due to
interference caused by hair displacement. These sites were thus eliminated from the analysis. Continuous EEG signals were sampled at 512 Hz, amplified (×20 000) and digitally filtered (0.01 and 100 Hz) using Grass (12A5) Neurodata Acquisition Amplifiers (Grass Technology, Astro-Med, Inc.). Prior to the behavioral task, 2 min of eyes-open and eyes-closed resting EEG were recorded as baseline EEG measures.

The participants received an orientation to the behavioral task and 12 practice trials to become familiar with the digital pen, tablet, and computer display. Figure 2 depicts the behavioral task as presented on the computer monitor. For this “center-out” aiming task, the participants began a trial by moving the digital pen into the “home position” indicated by a circle (0.5 cm diameter) presented on the computer monitor corresponding to the center of the workspace. Upon entering the home position, 2 target circles (0.5 cm in diameter each) located at 135° and 315° were presented 5 cm from the home position. The participants were instructed to select one of the 2 targets. While holding the pen motionless in the home circle for at least 2 s, the participants were instructed to “plan or think how they will move quickly and accurately from the home position and stop in the target circle.” There was no external cue to move after the 2-s hold period; but, if the participants left the home position too soon (<2 s), the targets would disappear and the trial would restart. The purpose of this hold period was to provide the participants with sufficient time for target selection and movement planning and to allow ample time for electrophysiological data acquisition during this phase of the task. After the hold period, the participants made one swift aiming movement with the digitizing pen from the home position to the target. The pen trace was displayed on the computer screen in real time. Between trials, the experimenter periodically reminded the participants to move “as quickly and straight as possible” from the home position to the targets. Once the pen reached the target position, the targets and pen trace disappeared and the participant returned the pen to the home position to begin the next trial. Although the participants were free to choose the location of the target for each trial, they were instructed to move to each of the targets equally often during the 60 trials administered. The average number of movements per group to the target located at 135° (top) and 315° (bottom) were as follows: 48.8% and 51.2% for the young children ($\chi^2 = 0.04, P = 0.85$), 48.3% and 51.7% for the older children ($\chi^2 = 0.07, P = 0.80$), and 49.3% and 50.7% for the adults ($\chi^2 = 0.01, P = 0.96$).

**Data Analysis**

Behavioral data analyses were consistent with previously reported studies conducted in our laboratory (Contreras-Vidal and Kerick 2004; Kagerer et al. 2004; Contreras-Vidal et al. 2005; King et al. 2009). An 8-th-order dual-pass Butterworth filter (cutoff frequency: 10 Hz) was applied to the time series of $x$/$y$ pen positions for each trial. Automated algorithms were used to mark the time and $x$/$y$ position of the movement onset and offset; each trial was visually inspected and manually corrected if incorrect. The movement trajectory was computed as the time series of $x$/$y$ positions between the movement onset and offset. The following behavioral variables were computed from the movement trajectories: movement time (MT—s), movement length (ML—cm), root mean squared error (RMSE—cm), normalized jerk (NJ—unitless), and variable initial direction error (VIDE—degrees). MT was the total time obtained from the time series between movement onset and offset. ML was the total distance of the movement trajectory. RMSE was calculated as the average deviation between the ideal, straight-line trajectory between the start and target positions ($x_0$, $y_0$) and the actual movement trajectory ($x_i$, $y_i$):

$$\text{RMSE} = \sqrt{\frac{1}{N} \sum_{i=1}^{N} [(x_i - x_0)^2 + (y_i - y_0)^2]}$$

NJ was calculated as the rate of change of the acceleration ($j$) normalized by the MT and ML:

$$\text{NJ} = \frac{\text{MT}^T}{\text{ML}^2} \int \frac{j^2(t)}{\text{MT}^2} \, dt$$

Initial directional error (IDE) was calculated as the angular deviation between the ideal straight-line trajectory and the actual movement trajectory 80 ms after movement onset (initial movement direction prior to visual feedback correction). The VIDE was assessed as the variability (SD) of the IDE for each subject across all movements.

EEG recordings were processed off-line. All sites were referenced to average mastoids. These electrophysiological data were visually inspected for excessive movement and instrumental noise artifacts using Neuroscan. All the filters described were infinite impulse response filters with 24 dB/octave roll-off. Noise between 56 and 64 Hz frequencies were eliminated with a band-stop filter. For the spectral and coherence analyses, the following band-pass filters were used to separate the frequencies into the alpha (8–12 Hz) and beta (13–30 Hz) bands. These bands were selected for their relevance to motor tasks (Gerloff et al. 1998; Andres et al. 1999; Serrien and Brown 2003). For the MRCPs, data were low-pass filtered at 10 Hz. Continuous EEG data were epoched into 2000-ms windows beginning 1000 ms prior to and 1000 ms following movement onset. Each epoch was baseline corrected using a 100-ms pre-epoch interval. These epochs were again visually inspected prior to averaging in the frequency or time domains. Three separate signal-processing techniques were applied to the EEG data: 1) MRCPs, 2) TRPow, and 3) TRCoh.

For the MRCP analysis, the focus of the present study is the late negative slope of the readiness and motor potentials that may be captured in the period 250 ms prior to and following movement onset (Gerloff et al. 1998; Staines et al. 2002; Bahbholi et al. 1999; Shibasaki...
and Hallett 2006). Given that previous developmental studies did not observe a single-peak waveform in young children (Warren and Karrer 1984a; Chiarenza et al. 1995), the average amplitude was computed before and after movement onset (∼250 to 250 ms) for all trials to determine whether the children exhibited the expected negativity even when they did not exhibit a single peak.

For the TRPow and TRCoh analyses, the power spectrum was obtained using fast Fourier transform (FFT) from 1-s epoched data from the baseline (eyes open) condition and from the 1-s before movement onset during the behavioral task. For the TRPow analysis, consistent with Gerloff et al. (1998) and Andres et al. (1999), the average spectral power during the baseline (eyes open) condition and during the task performance were log-transformed to meet the normality and homogeneity of variance assumptions for the statistical analyses. TRPow was computed by subtracting the log-transformed spectral power during baseline from the log-transformed spectral power during the task. For the TRCoh analysis, following the FFT computation, coherence was calculated consistent with Halliday et al. (1995) as:

\[
\text{Coh}_{ab}(f) = \left[ \frac{\text{f}(f) \cdot \text{f}(b)}{\text{f}(f) \cdot \text{f}(b)} \right]^{1/2}
\]

where \(f\) represents the spectral estimate of 2 EEG signals \(a\) and \(b\) for a given frequency \(f\). The numerator is the cross-spectrum for \(a\) and \(b\) (\(f_{ab}\)), and the denominator is the auto-spectra for \(a\) (\(f_a\)) and for \(b\) (\(f_b\)). Coherence was calculated for the following regional connections: left hemisphere to the mesial frontocentral region (F3-Fz, C3-Fz, P3-Cz, C3-Cz, and P3-Cz) and right hemisphere to the mesial frontocentral region (F4-Fz, C4-Fz, P4-Fz, F4-Cz, C4-Cz, and P4-Cz). In order to meet the assumption for homogeneity of variance and normality for the statistical analysis, an inverse hyperbolic tangent transformation was applied to all coherence data. Consistent with Gerloff et al. (1998) and Andres et al. (1999), TRCoh was calculated by subtracting the transformed coherence during baseline (eyes open) from the transformed values obtained during the task for each electrode pair.

**Statistical Analysis**

All dependent behavioral 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.). Scheffé’s post hoc multiple comparisons were used to decompose significant main effects. Mixed-model ANOVAs were used for the MRCPs, TRPow, and TRCoh analyses. Traditional repeated-measures ANOVAs assume a spherical (or compound symmetric) variance-covariance structure. Given that the electrode locations are fixed and nested, the sphericity assumption is violated; thus, it would be inappropriate to assume a compound symmetric variance-covariance structure. Accordingly, the mixed procedure in SAS permits the variance-covariance structure to be estimated based on the actual data rather than assuming compound symmetry. Moreover, the mixed-model ANOVA prevents a loss of degrees of freedom that result from corrections such as Greenhouse-Geisser or Huynh-Feldt corrections whenphericity is violated. Thus, the models employed in the current study have greater sensitivity than traditional repeated-measures ANOVAs and have been previously reported for EEG and movement kinematics in adults (Kerrick et al. 2004).

For the MRCPs, the analysis was restricted to Fz, Cz, C3, and C4; these electrodes were selected for their relevance to motor planning and control as previous studies have reported MRCPs at these locations (Warren and Karrer 1984a). For each of the 4 electrode sites, a group (3) x time (2) mixed-model ANOVA was employed. The time variable consisted of the two premovement periods (∼250 ms to movement onset) and immediate postmovement period (movement onset to 250 ms). This time range was selected based on the adult literature to capture the sharp negative slope of the MRCP (Gerloff et al. 1998, Staines et al. 2002, Babiloni et al. 1999, Contereras-Vidal and Kerick 2004). For the TRPow analyses, each frequency band was analyzed using 2 mixed-model ANOVAs—one for the electrodes overlying the 2 hemispheres (lateral electrodes) and the other for the midline data. For the first analysis, a group (3) x hemisphere (2) x region (3; frontal, central, parietal) design was implemented. For the midline data, a group (3) x region (3; frontal, central, parietal) design was implemented. For TRCoh, a group (3) x regional connection (2; left hemisphere to the mesial frontocentral region and right hemisphere to the mesial frontocentral region) mixed-model ANOVA was used for each frequency band. For each of the EEG-dependent measures, significant main effects were decomposed using Scheffé’s post hoc multiple comparisons. Significant interactions were decomposed with respect to differential effects (difference of difference comparisons) (Levin and Marascoiu 1972).

In order to assess the relationship between the EEG and behavioral variables, Pearson’s correlations were examined with respect to the following variables: the mean amplitude of the MRCPs before and after movement for Fz and C3, the mean alpha TRPow for the frontal and central regions, the mean alpha and beta TRCoh between Fz-C3 and Cz-C3 and all 5 behavioral measures. These EEG measures were selected for their relevance to motor planning and control. For all statistical analyses, the level of significance was set to \(P < 0.05\).

**Results**

**MRCP: Age-Related Differences in Negativity over the Premotor/Supplementary Motor Areas and Contralateral Motor Areas between Children and Adults**

To assess the functionally relevant and temporally sensitive patterns of cortical activity during motor planning and motor control, the MRCP waveforms were analyzed. Figure 3 depicts the group-ensemble time-averaged waveforms for the 4 electrodes of interest (Fz, Cz, C3, and C4). A significant group by time interaction was found for Fz (F2,42 = 3.25, \(P < 0.05\)). Differential contrasts (Levin and Marascoiu 1972) revealed that the 6- to 7-year-olds exhibited similar negativity prior to and following movement onset, whereas the adults exhibited an increase in negativity across the 2 time windows (\(T_{1,42} = 6.48, P < 0.05\)). Significant group and time main effects were found for C3 (\(F_{2,42} = 6.91, P < 0.01\) and \(F_{1,42} = 6.46, P < 0.05\), respectively). Scheffé’s post hoc analysis revealed the adults exhibited greater negativity than the 6- to 7- and the 9- to 11-year-olds (\(T_{1,42} = 3.57, P < 0.01\), and \(T_{1,42} = 2.67, P < 0.05\), respectively). In addition, there was significantly greater negativity in the contralateral motor area (C3) during the time window immediately following movement onset (\(T_{1,42} = 2.54, P < 0.05\)). The group by time interaction was not significant for C3. No significant main effects or interactions were found for Cz and C4, indicating that all groups showed a similar magnitude of negativity for both time windows. Overall, age-related differences in the temporal aspects of the EEG were found between the 2 groups of children and adults in brain areas relevant to motor planning and control.

**TRPow: Regional Differences in TRPow between 6- to 7-Year-Olds and the Other 2 Groups**

TRPow was analyzed to assess age-related differences in regional and hemispheric activation. Table 1 reports the results for the TRPow analysis. Figure 4 depicts the TRPow for the lateral electrodes for the alpha band by region and hemisphere. A significant region by hemisphere interaction was found (Fig. 4; \(P < 0.01\)). Post hoc contrasts revealed that the difference in alpha TRPow between the 2 hemispheres in the central region was significantly different than the difference in TRPow between the 2 hemispheres in the frontal region. Consistent with previous research (Gerloff et al. 1998; Manganotti et al. 2002, Babiloni et al. 1999, Contereras-Vidal and Kerick 2004).
1998), this result is driven by the magnitude of activation (negative TRPow) in the contralateral sensorimotor region during motor planning.

Figure 5 shows the TRPow by group and region for the lateral electrodes for the alpha band (A), midline electrode for the alpha band (B), and midline electrodes for the beta band (C). No hemisphere main effects were found. Group by region interactions were found for the lateral electrodes in the alpha band ($P < 0.01$), midline electrodes in the beta band ($P < 0.01$), and were marginally significant for the midline electrodes in the alpha band ($P = 0.058$).

Post hoc difference contrasts decomposing the significant group by region interaction for lateral electrodes in the alpha band revealed that the difference between the frontal and parietal regions for the 6- to 7-year-olds was significantly different than the frontal-parietal differences in both the 9- to 11-year-olds and the adults (Fig. 5A and Table 1). Moreover, for both the 6- to 7-year-olds and the adults, the values for the frontal and parietal regions were significantly different than 0 ($P < 0.05$), indicating that the alpha TRPow during completion of the task was significantly different from baseline (eyes open). The difference in alpha TRPow between the frontal and central regions for the 6- to 7-year-olds was significantly different than the frontal-central difference for the adults. The activation patterns of the 9- to 11-year-olds appeared to be in a transition period in that their values for

| Table 1 |
|---|---|---|---|
| **Alpha results by frequency band** |   | $F$ or $T$ | $P$ |
| Lateral | Group | $F_{2,39} = 0.91$ | 0.413 |
| Region | $F_{2,39} = 3.24$ | 0.045* |
| Group × region | $F_{4,78} = 4.64$ | 0.002** |
| Hemisphere | $F_{1,39} = 0.03$ | 0.870 |
| Midline | Group | $F_{2,39} = 0.49$ | 0.615 |
| Region | $F_{2,39} = 5.01$ | 0.009** |
| Group × region × hemisphere | $F_{4,78} = 0.51$ | 0.726 |
| Contrast | 6- to 7-year olds and adults (frontal-central) | $T_{1,78} = 6.40$ | 0.013* |
| 6- to 7-year-olds and 9- to 11-year-olds (frontal-parietal) | $T_{1,78} = 7.73$ | 0.007** |
| 6- to 7-year-olds and adults (frontal-parietal) | $T_{1,78} = 17.48$ | <0.001*** |
| Left hemisphere and right hemisphere (frontal-central) | $T_{1,78} = 10.02$ | 0.002** |
| Beta | Lateral | All nonsignificant |
| Midline | | |
| Group | $F_{2,39} = 3.30$ | 0.053 |
| Region | $F_{2,39} = 2.38$ | 0.056 |
| Group × region | $F_{4,78} = 0.15$ | 0.895 |
| Contrast: | 6- to 7-year-olds and adults (frontal-parietal) | $T_{1,78} = 9.04$ | 0.004** |
| $*$ $P < 0.05$; $**P < 0.01$; $***P < 0.001$. |
all regions were in between the values for the 6- to 7-year-olds and adults.

Post hoc difference contrasts decomposing the significant group × region interaction for midline electrodes in the alpha band revealed that the difference between the frontal and parietal regions for the 6- to 7-year-olds was significantly different than the frontal–parietal differences in both the 9- to 11-year-olds and the adults (Fig. 5B and Table 1). Again, the values for the frontal and parietal regions were significantly different than 0 for the 6- to 7-year-olds and the adults (P < 0.05). Moreover, these results mirror that of the lateral electrodes in the alpha band (Fig. 5A). The difference in alpha TRPow between the central and parietal regions for the 6- to 7-year-olds was significantly different than the central–parietal difference for the adults.

Consistent with the lateral and midline electrodes in the alpha band, the difference in beta TRPow between the frontal and parietal regions for the 6- to 7-year-olds was different than that of the adults (Fig. 5C and Table 1). Given that negative TRPow in the alpha and beta frequency bands reflect regional cortical activation of the somatosensory and motor systems, respectively (Gerloff et al. 1998; Manganotti et al. 1998), these results collectively indicate that the 6- to 7-year-olds exhibit the greatest activation of the frontal regions, whereas adults and the older children show less reliance on the frontal areas for motor planning.

**TRCoh: Selective Increases in Task-Related Alpha Coherence by Region for the Left Hemisphere**

TRCoh analyses were performed to assess developmental differences in functional connectivity during motor planning. Table 2 reports the results for the TRCoh analysis. No significant main effects or interactions were found for the beta frequency band. No significant group main effects were found for the alpha frequency (P > 0.05). Figure 6 depicts a significant region by hemisphere interaction for alpha TRCoh. Post hoc contrasts indicated that the difference between the 2 hemispheres in the central region was significantly different than the difference between the 2 hemispheres in both the frontal and parietal regions. These data indicate that the 3 regions in the right hemisphere and the central region in the left hemisphere exhibit selective and significant positive TRCoh (significantly different than 0, P < 0.05, Figure 6). In particular, as expected, the greatest TRCoh is found the mesial frontal central regions and the contralateral sensorimotor region in comparison to the other regions.

**Behavioral Results: Age-Related Difference in the Quality of Movement Performance**

Figure 7 depicts the mean movement trajectories for the 3 age groups. Although the 6- to 7-year-olds appear, on average, to make straight and accurate movements to the targets, these children are much more variable across the entire movement trajectory (wider SD) compared with the other 2 groups. To quantify age-related differences in the movement kinematics, movement control was assessed with the following variables: ML, MT, RMSE, and NJ. In order to determine the consistency of the directional planning, VIDE was analyzed.

There were no significant differences between groups for ML and RMSE (P > 0.05, both). Therefore, all groups achieved a similar degree of straightness and accuracy. Figure 8 depicts the significant age main effects for MT, NJ, and VIDE. Significant group differences were found for the mean MT and mean NJ (F_{1,42} = 5.49 and 8.03, respectively, P < 0.001 for both). Scheffé’s post hoc analysis demonstrated that the 6- to 7-year-olds exhibited significantly longer MTs compared with the 9- to 11-year-olds and adults (F_{1,42} = 5.49 and 8.03, respectively, P < 0.001 for both). Similar significant differences were found...
between the 6- to 7-year-olds and the other 2 groups for NJ ($F_{1,42} = 5.01$ and $6.24$, respectively, $P < 0.001$ for both). No significant differences ($P > 0.05$) were found between the 9- to 11-year-olds and adults for these measures.

A significant group effect was found for VIDE ($F_{2,42} = 14.77$, $P < 0.001$). Scheffe’s post hoc analysis revealed that 6- to 7-year-old children exhibited significantly more variable directional planning than the 9- to 11-year-olds and adults ($F_{1,42} = 3.00$ and $5.43$, $P < 0.01$ and $P < 0.001$, respectively). Taken together, these results suggest that important aspects of adult-like performance have not yet developed in the 6- to 7-year-old children. Although this group exhibited similar spatial accuracy (ML and RMSE) as the other groups, they were slower, jerkier, and were highly variable in their directional planning.

### Relationships between the Brain Function and Behavior

Figure 9 depicts the scatter plots for the significant Pearson’s correlations between the EEG and behavioral variables. Each individual is depicted with respect to their age group to highlight the contribution of each group to the overall correlations. MT, VIDE, and NJ were positively correlated with the mean MRCP amplitude from Fz following movement onset ($r = 0.409$, $0.382$, and $0.338$, respectively; $P < 0.01$ for all) and the mean MRCP amplitude from C3 before movement onset ($r = 0.388$, $0.373$, and $0.433$, respectively; $P < 0.01$ for all). No significant correlation was found for ML or RMSE with the MRCPs. This suggests that greater movement-related negativity in the supplementary motor (Fz) and contralateral motor cortex (C3) was related to faster, more consistent directional planning, and smooth movements.

MT and NJ were inversely related to the alpha TRPow in the frontal region ($r = -0.281$ and $-0.325$, respectively; $P < 0.05$ for both). In other words, less task-related frontal activation (positive alpha TRPow) was related to faster and smoother movement performance, whereas greater frontal activation (negative alpha TRPow) is related to poorer movement performance. Taken together, these results provide evidence that age-related improvements in movement kinematics are related to age-related differences in the underlying brain activation patterns.

### Discussion

This study is the first to provide evidence regarding the potential functional relevance of children’s EEG activation patterns in both the frequency- and the time domains with respect to planning multijoint goal-directed movements. The EEG signal analyses revealed several significant age-related differences. First, 6- to 7-year-old children exhibited less facilitation or priming of the premotor/supplementary motor areas compared with adults, as indicated by a relatively reduced amplitude of the MRCPs. In addition, both groups of children exhibited less priming of the contralateral primary motor cortex compared with adults.

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**Table 2**

<table>
<thead>
<tr>
<th>Effects</th>
<th>$F$ or $T$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alpha</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group</td>
<td>$F_{2,38}$ = 0.85</td>
<td>0.435</td>
</tr>
<tr>
<td>Region</td>
<td>$F_{2,38}$ = 3.36</td>
<td>0.0401</td>
</tr>
<tr>
<td>Group × region</td>
<td>$F_{2,38}$ = 1.51</td>
<td>0.208</td>
</tr>
<tr>
<td>Hemisphere</td>
<td>$F_{2,38}$ = 1.62</td>
<td>0.211</td>
</tr>
<tr>
<td>Region × hemisphere</td>
<td>$F_{2,38}$ = 3.14</td>
<td>0.027**</td>
</tr>
<tr>
<td>Group × region × hemisphere</td>
<td>$F_{2,38}$ = 0.77</td>
<td>0.544</td>
</tr>
<tr>
<td>Contrast:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left hemisphere and right</td>
<td>$T_{1,38}$ = 12.45</td>
<td>&lt;0.001***</td>
</tr>
<tr>
<td>hemisphere (frontal-central)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left hemisphere and right</td>
<td>$T_{1,38}$ = 4.35</td>
<td>0.038**</td>
</tr>
<tr>
<td>hemisphere (frontal-parietal)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Beta</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All nonsignificant</td>
<td></td>
<td></td>
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</tbody>
</table>

*P < 0.05; **P < 0.01; ***P < 0.001.
Second, 6- to 7-year-olds exhibited greater task-related activation (desynchronization) of the frontal areas and less task-related activation (synchronization) of the parietal areas than the adults. The 9- to 11-year-old children exhibited activation patterns that appear to be in a transition between the patterns exhibited by younger children and adults. Third, although age-related differences were not found for the TRCoherence measures, all groups exhibit greater networking between the left (contralateral) motor areas with the mesial frontocentral areas. With respect to the movement kinematics, age-related differences were found across the 3 groups and were consistent with previous behavioral studies (Contreras-Vidal et al. 2005; King et al. 2009). The 6- to 7-year-olds children’s movements were slower, jerkier, and exhibited less consistent directional planning, compared with 9- to 11-year-olds children and adults. Moreover, these behavioral variables were found to be significantly related to the underlying brain activation patterns, namely MRCPs and TRPower. Collectively, these results provide evidence that the electrocortical dynamics reflect age-related differences in movement kinematics among young children, older children, and adults. Specifically, the poor quality of movement planning and control in young children is related to less task-relevant activation of relevant sensorimotor planning regions compared with older children and adults.
Less Priming of Contralateral Sensorimotor Areas in Young Children

The results from the analysis of MRCPs and the correlation analysis suggest that greater priming of areas relevant to motor planning may, in part, contribute to developmental improvements in task performance during multijoint, goal-directed movements. For example, the 6- to 7-year-old children exhibited adult-like waveforms overlaying the midline and right sensorimotor areas (Cz and C4). However, the amplitude of the movement-related waveforms over the midline frontal (Fz) and contralateral sensorimotor area (C3) was attenuated in the 6- to 7-year-olds compared with adults. In addition, differences in the magnitude of the MRCPs overlying the contralateral sensorimotor area (C3) between the 9- to 11-year-olds and adults suggest that this group of children does not utilize relevant sensorimotor regions to the same extent as adults.

Previous developmental studies using simple, ballistic finger movements did not find negative-going waveforms for any scalp locations for young children (Warren and Karrer 1984a; Kristeva and Vladova 1987). In contrast to these previous studies, this study found negative-going waveforms exhibited by all groups, which likely resulted from the self-initiated, self-selected, and precise nature of these movements. Notwithstanding, it is clear that both groups of children do not exhibit priming of sensorimotor resources to the same extent as the adults. Thus, given that MRCPs reflect the facilitation or priming of sensorimotor resources (Grunewald-Zuberbier et al. 1980; Dececke et al. 1984), a lack of adult-like MRCP waveforms may directly impact the quality of motor performance in the 2 groups of children. Furthermore, Blank et al. (2000) suggested that developmental changes in the recruitment of motor-neuronal populations in the primary motor cortex underlying movement generation is related to the functional changes evident in behavioral analyses of hand performance in children.

Greater Task-Related Activation of the Frontal Regions in Young Children

The 6- to 7-year-olds exhibited a relative engagement of frontal cortical areas (negative task-related power) in comparison to the other cortical regions of interest and in comparison to the other 2 age groups. Negative TRPow, or desynchronization, is generally thought to indicate attention and movement preparation (Neuper and Pfurtscheller 2001; Gómez et al. 2006), sensorimotor processing (Manganotti et al. 1998), and/or reflect gating of information between thalamocortical neural substrates related to motor planning of limb movements (Neuper and Pfurtscheller 2001). Bender et al. (2005) found that alpha desynchronization in 6- to 11-year-old children emerged over the contralateral sensorimotor area during simple reaction time tasks. In contrast, the current study suggests that more complex motor tasks may require greater attention and frontally mediated motor planning in 6- to 7-year olds. However, the adults, and to some degree the older children as well, exhibit much less engagement of the frontal regions. Moreover, these results are consistent with the MRCP analysis in that the pattern of regionally specific activation exhibited by the 9- to 11-year-olds appears to be in a transition between the patterns exhibited by young children and adults. Taken together, these data suggest that efficient activation of task-relevant sensorimotor areas and reduced reliance on frontal regions of the brain during motor planning are relevant to age-related improvements in movement kinematics.

Hemispheric and Regionally Specific Differences in Task-Related Activation and Functional Communication

Although age-related differences in regional and hemispheric specialization were expected, interestingly, all groups exhibited similar and corresponding interactions between region and hemisphere for TRPow and TRCoh in the alpha band. All groups exhibited TRPow decreases for the left (contralateral) central area and an increase in TRCoh between that area and the frontocentral mesial region. In addition, the right frontal region exhibited a similar trend. These results are consistent with results from Manganotti et al. (1998) for sequential finger movements in adults. These results are also consistent with previous studies examining developmental trends in coherence at rest, in which changes in coherence appear to be found only for long-range coherence pairs or short-range coherence pairs within the frontal regions (Thatcher et al. 1987; Barry et al. 2004). Taken together, these results suggest that the short-range functional communication and differential hemispheric activation during motor planning are established by 6 years of age. However, despite these similar patterns of hemispheric activation and functional communication across these age groups, the 6- to 7-year-olds, and to some extent the 9- to 11-year-olds, lack the efficient activation of task-related resources that may underlie age-related differences in movement kinematics.

Continued Improvements in Movement Kinematics across Age

Given the age-related differences in the brain activation patterns during motor planning, it was expected that the quality of the movement performance of the 6- to 7-year-olds would be inferior compared with the other 2 groups. Consistent with previous behavioral studies from this laboratory for a similar task (Contreras-Vidal et al. 2005; Contreras-Vidal 2006), the 6- to 7-year-old children were slower, jerkier, and exhibited less consistent movement planning, as compared with the 9- to 11-year-olds and adults. These results provide support for “less-tuned” feed forward control mechanisms, compromising the accuracy of the young children’s motor plans and efficiency during the performance of visuomotor behaviors (Contreras-Vidal 2006). Notwithstanding, the quality of the movement kinematics was found to increase as a function of age, and the 9- to 11-year-olds and adults exhibited greater speed, smoothness, and consistency. Collectively, these results provide a brain-behavior explanation for the observed age-related differences in the quality of movement performance in the current study and behavioral results reported in the extant developmental literature.

Motor Planning and Performance Measures Are Related to the Patterns of Activation in Relevant Sensorimotor Regions

This study provides evidence that efficient activation of task-relevant sensorimotor areas and reduced reliance on frontal regions of the brain during motor planning are related to better quality of movement performance. Since age-related
differences were found for these EEG measures and for the movement kinematic variables, it appears that these electrophysiological processes are functionally relevant to the age-related improvements in movement kinematics found in the current study and those previously reported (Bard et al. 1990; Thomas et al. 2000; Contreras-Vidal et al. 2005; King et al. 2009).

**Potential Mechanisms for Age-Related Changes in Brain Dynamics and Movement Kinematics**

Although this study is an important first step to understanding the brain–behavior relationships with respect to goal-directed motor planning in school-aged children and adults, the mechanisms that may underlie these developmental differences are not clear. Many researchers have suggested that differences in brain function evident across childhood are attributed to maturation of the underlying brain structures (Thatcher et al. 1986; Paus et al. 1999; Barry et al. 2004; Gogtay et al. 2004). However, in addition to maturational changes of underlying brain structures, motor experience also appears to be critical for functional plasticity and eliciting improvements in behavioral performance. Many studies have found that motor skill training results in cortical and subcortical neuronal plasticity even on a short-time scale in adults (Karni et al. 1998; Sanes 2003; Doyon and Benali 2005). More recently, similar effects have been found for pediatric populations. For example, extensive piano practice has been found to induce plastic changes in the brain that extend beyond the primary sensorimotor areas in children (Schlaug et al. 2005; Hyde et al. 2009). Future longitudinal studies are necessary to disambiguate maturational and experiential effects on motor planning and control in children.

**Conclusion**

The functional brain measures employed in the present study were found to be sensitive electrocortical markers of age-related differences in movement planning and control in children and adults. By mapping the electrocortical dynamics with movement kinematics, we provide a neurobiological foundation for future studies investigating the development of complex movements including those requiring coordination between limb effectors (e.g., bimanual coordination) or adaptive planning (e.g., target switching or visuomotor adaptation). Importantly, by characterizing typically developing children, this study also provides a basis for comparison with children exhibiting motor coordination impairments such as developmental coordination disorder and attention-deficit hyperactivity disorder. Using similar methods for investigating brain–behavior relationships in populations with atypical development, we may determine if the behavioral deficits in motor planning and control observed in these children are reflected in different or delayed electrophysiological processes.

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**References**


