Published in final edited form as:

Brain Cogn. 2010 July ; 73(2): 75–84. doi:10.1016/j.bandc.2010.03.001.

An extended motor network generates beta and gamma oscillatory perturbations during development

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Abstract

This study examines the time course and neural generators of oscillatory beta and gamma motor responses in typically-developing children. Participants completed a unilateral flexion-extension task using each index finger as whole-head magnetoencephalography (MEG) data were acquired. These MEG data were imaged in the frequency-domain using spatial filtering and the resulting event-related synchronizations and desynchronizations (ERS/ERD) were subjected to voxel-wise statistical analyses to illuminate time-frequency specific activation patterns. Consistent with adult data, these children exhibited a pre-movement ERD that was strongest over the contralateral postcentral gyrus, and a post-movement ERS response with the most prominent peak being in the contralateral precentral gyrus near premotor cortices. We also observed a high-frequency (~80 Hz) ERS response that coincided with movement onset and was centered on the contralateral precentral gyrus, slightly superior and posterior to the beta ERS. In addition to pre- and post-central gyri activations, these children exhibited beta and gamma activity in supplementary motor areas (SMA) before and during movement, and beta activation in cerebellar cortices before and after movement. We believe the gamma synchronization may be an excellent candidate signal of basic cortical motor control, as the spatiotemporal dynamics indicate the primary motor cortex generates this response (and not the beta oscillations) which is closely yoked to the initial muscle activation. Lastly, these data suggest several additional neural regions including the SMA and cerebellum are involved in basic movements during development.

Keywords

precentral; ERD; ERS; synchronization; cortex; MEG; cerebellum; magnetoencephalography; somatosensory; mu; child

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Introduction

Previous electrophysiological studies of motor function have characterized the oscillatory dynamics of neural responses culminating in the sensorimotor cortices. Such oscillatory behavior begins several hundred milliseconds preceding the movement onset and continues for several seconds after movement termination. These responses are commonly segregated into two quasi-distinct frequency bands, a lower frequency mu rhythm (8–16 Hz) and a higher frequency beta rhythm (15–30 Hz). The generous bandwidth partitioned for each rhythm reflects their underlying spectral nature and that the peak frequency of mu and beta responses typically differs between subjects. A large array of sensorimotor events have been shown to modulate these rhythms, including tactile stimulation (Neuper and Pfurtscheller, 2001; Cheyne et al., 2003; Muller et al., 2003; Gaetz and Cheyne, 2006; Houdayer et al., 2006), passive movements (Cassim et al. 2001), voluntary movements (Salmelin et al., 1995; Pfurtscheller et al., 1996; Cassim et al., 2001; Houdayer et al., 2006; Jurkiewicz et al., 2006; Parkes et al., 2006), imagined movements (Pfurtscheller and Neuper, 1997; Pfurtscheller et al., 2005; de Lange et al., 2008), and even observing another agent's movements (Hari et al., 1998; Koelewijn et al., 2008). Generally, such modulation entails a sharp decrease in power several hundred milliseconds (up to 1500 ms) preceding the movement onset that occurs in both beta and mu frequency bands. Once the movement is terminated, a sharp increase in power occurs for the beta band within the next 1–2 seconds, whereas power in the mu rhythm increases along a shallow slope lasting several seconds (Pfurtscheller and Lopes da Silva, 1999; Pineda, 2005). The pre-movement decrease in power is typically termed an event-related desynchronization or pre-movement ERD, and the post-movement increase is an event-related synchronization (ERS) or in this literature, the post-movement beta rebound (PMBR). These oscillatory changes are normally gauged relative to a baseline period that occurred 3–5 seconds from the most recent movement (i.e., before and after movement). For excellent reviews, see Hari and Salmelin (1997) or Pfurtscheller and Lopes da Silva (1999).

These oscillatory perturbations are thought to reflect large scale changes in the synchronicity of sensorimotor networks. Essentially, somatosensory and primary motor networks are thought to synchronize at mu and beta frequencies, respectively, in the absence of internal and/or external sensorimotor inputs. In the case of volitional movements, the pre-movement ERD indicates a large-scale desynchronization due to input disturbing the resting or idling frequency of sensorimotor cortices. Although the ERD reflects a decrease in power, the underlying mechanism is believed to be activation of a small patch(s) of cortex which serves the tactile perception and/or motor output (Pfurtscheller and Lopes da Silva, 1999; Pineda, 2005). Thus, pre-movement ERDs are large-scale decreases in power that are putatively accompanied by a small-scale activation near the centroid or peak of the frequency-specific ERD. In contrast, the PMBR may indicate the return of sensorimotor cortices to their highly synchronous resting state following completion of the sensory or motor task (i.e., the idling hypothesis; Pfurtscheller, 1992; Pfurtscheller et al., 1996, 1999); albeit, other models suggest the PMBR results from active inhibition (Salmelin et al. 1995; Pfurtscheller and Neuper, 1997; Cassim et al., 2001) and/or somatosensory reafferent input to the motor cortex (Cassim et al., 2001; Houdayer et al., 2006). Likewise, the post-movement mu rebound may reflect an analogous phenomena for this lower frequency band, but unlike the PMBR response, mu rebound is slower, less intense, and does not exceed the degree of baseline power in this brain area (i.e., before the pre-movement ERD; Salmelin and Hari, 1994; Salmelin et al., 1995). Studies of volitional movement in adults have shown mu and beta responses localize to somatotopic areas of the postcentral and precentral gyrus, respectively (Pfurtscheller et al., 1994; Salmelin et al., 1994; Salmelin et al., 1995; Pfurtscheller and Lopes da Silva, 1999). These studies did not note spatial differences between pre- and post-movement responses in either frequency band. However, beta band responses more closely followed somatotopic organization and showed more laterality than mu activity, being stronger in the cortices contralateral to the movement.

More recent studies, especially those using magnetoencephalography (MEG), have refined understanding of the pre- versus post-movement responses in these bands. These studies have shown both pre- and post-event (ERD and ERS) rhythmic mu activity localizes to the post-central gyrus, shows moderate contralateral dominance, and roughly follows the somatotopic organization of these cortices (motor: Jurkiewicz et al., 2006; tactile stimulation: Cheyne et al., 2003; Gaetz and Cheyne, 2006). In regards to the oscillatory beta activity, these studies found pre-event beta ERD to be generated in the postcentral gyrus and that the neural correlates of the post-event beta ERS are slightly anterior in the precentral motor cortex (Jurkiewicz et al., 2006; Cheyne et al., 2003; Gaetz and Cheyne, 2006). Contralateral dominance and somato- or motorotopic mapping was stronger for beta versus mu responses, especially for the PMBR. However, a combined electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) study recently reported a postcentral gyrus focus for the PMBR motor response, thus indicating that the source of this beta rebound remains somewhat uncertain (Parkes et al., 2006).

Although the regions generating PMBR activity remain an area of contention, another facet of oscillatory motor behavior has only recently seen widespread interest and thus, is far less characterized. Essentially, using invasive methods, a number of studies in epilepsy patients have described high-frequency gamma responses in the 65–100 Hz range during sustained muscle contractions, continuous movements, and a few other motor tasks (Pfurtscheller et al., 2003; Szurhaj et al., 2006; Brovelli et al., 2005; Miller et al., 2007). The brain areas generating this activity are near precentral gyrus and other motor areas, but their precise location has been limited to the region where the grid or subdural electrode was placed during surgery. Likewise, the motor tasks used in these studies have limited extraction of time course information. However, a few recent MEG studies have described similar gamma activity in sensors near motor cortex (Schoffelen et al., 2005; Waldert et al., 2008), or precisely in the hand region of primary motor cortex (Cheyne et al., 2008; Tecchio et al., 2008). Cheyne and colleagues (2008) demonstrated that high-frequency gamma responses coincided with the movement onset, were strongly lateralized to the contralateral hemisphere, and largely followed the somatotopic organization of the primary motor cortex with respect to the foot, bicep and index finger. These findings have not yet been replicated, but their spatiotemporal dynamics are intriguing as the response could reflect the initial activation of primary motor neurons serving movement, or a form of feedback allowing advanced control of discrete movements (see Cheyne et al., 2008). As noted above, a previous study by this same group found PMBR activity also localized to the contralateral primary motor area. Indeed, for the same right index finger movement, the PMBR activation peak in the earlier study (Jurkiewicz et al., 2006) was within 1mm on x- and y-axes and only 5mm superior (z-axis) to the peak for high-gamma activity (Cheyne et al., 2008). This could indicate a common population of neurons generates the two responses at different stages of movement execution, with the time course and spectral content simply reflecting the diverse functions necessary for these distinct phases of movement. Although it is worth noting that the spatial similarity between PMBR and high-frequency gamma could be artificial, as to date the two responses have not been characterized in the same group of participants. Thus, even in healthy adults, the precise neural generators of gamma- and beta-frequency oscillatory motor responses, their spatiotemporal relationships, and their neurobehavioral functions remain a work in progress. In regards to parcellating function within the motor system, a substantial body of fMRI data is now available although it is difficult to directly link with neural oscillatory activity. The primary motor cortices appear to be the most basic element and are involved in the initiation of movement amongst many other functions (Passingham et al., 1997; Ween, 2008). Several studies have shown the supplementary motor cortex is intricately involved in coordinating bimanual movements (Swinnen 2002; Koeke et al., 2004) and unimanual movements that involve sequencing or maintaining an internal pace (Passingham, 1989; Jenkins et al. 2000). There is also strong evidence that multiple regions of the premotor cortex and the cerebellum are involved in bimanual tasks, and that these regions

become more strongly recruited as the task complexity increases (Debaere et al., 2004). Several excellent reviews of different components of the motor system are available (Passingham et al., 1997; Geyer et al., 2000; Rizzolatti and Luppino, 2001; Nachev et al., 2008).

In this study, we examine the oscillatory dynamics of basic motor circuitry by recording high-density MEG data during unilateral flexion-extension movements of each index finger in a group of typically-developing children and adolescents. Previous MEG and EEG investigations of oscillatory motor activity have focused exclusively on adults and have not studied the full gamut of responses. Thus, the aims of the current study were to derive the spatial and temporal relationship of the full range of oscillatory responses in a single group of participants, and to assess the effect of maturation on oscillatory motor activity. Our primary hypothesis was that children and adolescents would show greater involvement of neural regions outside the pre- and postcentral gyri than that observed in comparable adult studies of oscillatory motor responses. To this end, we subjected whole-head MEG data to a frequency-domain spatial filtering technique to image oscillatory neural responses that were roughly time-locked, but not necessarily phase-locked, to the onset of finger movements. We observed pre-movement beta ERD and post-movement beta ERS responses that resembled adult findings in rolandic regions, but with additional areas of activation in cerebellar cortices and the supplementary motor area (SMA). Likewise, we detected a high-frequency oscillatory component that coincided with the movement onset in the contralateral precentral gyrus, although again these children showed additional nodes in cerebellum and SMA where gamma synchrony increased in temporal unison. Such beta- and gamma-frequency activations outside rolandic regions may indicate additional nodes are involved in each phase of basic movement performance in the developing motor system.

Methods and Materials

Subject Selection

We studied 10 typically-developing children and adolescents (4 male), all of whom were recruited from the local community. The mean age of participants at time of scan was 11.3 years-old (range: 8–15 years), all were strongly right handed (Annett, 1985), and of average intelligence (mean full-scale IQ: 110). Exclusionary criteria included any medical illness affecting CNS function, psychiatric or neurological disorder, history of head trauma, and current substance abuse. Informed consent was obtained in accord with guidelines of the Colorado Multiple Institutional Review Board.

Experimental Paradigm

Participants were seated within the magnetically-shielded room (MSR) in a custom-made child booster-seat below a PVC stand designed specifically for this task. The stand consisted of two plastic rods attached at 90 degrees to plastic arm braces that allowed elbow to hand to be fully extended. The arm braces were attached to two plastic pipes, near the elbow, which connected to the MEG chair providing stability to the overall contraption. Participants rested both arms on the stands and wrapped their hands around the two rods. Accelerometer chips were attached to each index fingertip, using Delrin rings, to precisely quantify each movement onset. Participants were instructed to fixate on a cross hair presented centrally and to perform a single knuckle flexion-extension of an index finger each time a dot reached the 12 o'clock position. This dot completed one full revolution, around a clock-like circle without numbers or tick marks, every 6 s (see Figure 1 for an illustration). Each participant performed approximately 105 trials per finger, with the order of finger moved randomized across participants, making the overall recording time 21 minutes.

Data Acquisition

With an acquisition bandwidth of 0.1–200 Hz, neuromagnetic responses were sampled continuously at 508 Hz using a Magnes 3600 WH equipped with 248 first-order axial-gradiometers (4-D Neuroimaging, San Diego, CA, USA). MEG data were subjected to a global noise filter subtracting the external, non-biological noise obtained through the MEG reference channels. Following MEG data acquisition, T1-weighted coronal images were acquired on a GE 3.0T MR scanner using a 3-dimensional IR-SPGR sequence with the following parameters: TE = 1.9, TR = 9 ms, TI = 500 ms, Flip angle = 10°, FOV = 240×240 mm, matrix = 256×256, slice thickness/gap = 1.7/0 mm. The imaged volume contained the scalp surface through the cerebellum, including the external auditory meati bilaterally, with a voxel resolution of 0.94 × 1.7 × 0.94 mm.

Prior to MEG measurement, five coils were attached to the subject's head and the locations of these coils, together with the three fiducial points and scalp surface, were determined with a 3-D digitizer (Fastrak 3SF0002, Polhemus Navigator Sciences, Colchester, VT, USA). Once the subject was positioned inside the MSR, an electric current was fed to the coils. This induced a measurable magnetic field and allowed the coils to be localized in reference to the sensors. Since coil locations were also known in head coordinates, all MEG measurements could be transformed into a common coordinate system. With this coordinate system (including the scalp surface points) we coregistered each participant's MEG data with structural T1-weighted MRI data using the BrainVoyager QX 1.7 software (Brain Innovations, The Netherlands).

MEG Pre-Processing

Artifact rejection was based on a fixed threshold method (MEG level exceeding ± 1.2 pT), supplemented with visual inspection. Epochs were of 6 s duration (−3s to 3s), with 0 ms defined as the movement onset and the baseline being the −3000 to −2200 ms window. Artifact-free epochs from each condition were transformed into the time-frequency domain using complex demodulation (Paap and Ktonas, 1977; Hoechstetter et al., 2004), and the resulting spectral density power estimations per sensor were averaged over trials to generate time-frequency displays of complex spectral density. These data were normalized by dividing the power value of each post-stimulus time-frequency bin by the respective frequency's baseline power, calculated as the mean power during the period preceding stimulus onset. This normalization procedure allowed task-related power fluctuations to be readily visualized in sensor space, and once identified the neural regions generating these event-related synchronizations (ERS; power increases) or desynchronizations (ERD; power decreases) could be scrutinized by examining these time-frequency windows with a beamformer.

For beta ERS/ERD, we imaged the 16–28Hz band separately using −300ms to 400ms time window (pre-movement ERD) and a 1700 to 2400 time window (post-movement ERS). The gamma ERS responses were imaged using the 74–86Hz passband and the −50 to 200ms time window. All passbands and time bins were chosen to focus on maximum responses (i.e., MEG signal) across the sample, thus sacrificing some precision on the single-subject level to achieve a consistent analytical approach across participants.

MEG Source Imaging

Cortical networks were imaged through an extension of the linearly constrained minimum variance vector beamformer (Gross et al., 2001), which employs spatial filters in the frequency domain to calculate source power for the entire brain volume. The single images are derived from the cross spectral densities of all combinations of MEG sensors averaged over the time-frequency range of interest, and the solution of the forward problem for each location on a grid specified by input voxel space. The voxelized source space for each subject was determined from a piecewise Talairach transform for each subject's co-registered MRI into a standard

anatomical space using BrainVoyager (Talairach and Tournoux, 1988). Following convention, the source power in these images was normalized per condition and subject using a separately averaged pre-stimulus noise period of equal duration and bandwidth (van Veen et al., 1997). In principle, the beamformer operator generates a spatial filter for each grid point, which passes signals without attenuation from the given neural region while minimizing interference from activity in all other brain areas. The properties of these filters are entirely determined from the MEG covariance matrix and the forward solution for each grid point in the image space, which are used to allocate sensitivity weights to each sensor in the array for each voxel in the brain (for a review, see Hillebrand et al., 2005). Normalized source power was computed for the selected frequency bands over the entire brain volume per condition.

In order to use a standardized atlas of anatomical labels for the ROI analyses (see below), a 6-parameter affine transformation was applied between each subject's Talairach-scaled MRI images and the T1-template in SPM2 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, London, UK). The resulting MNI transformation was then applied to the beamformer output images so that results could be reported using MNI coordinates (Montreal Neurological Institute, Montreal, Canada). The MNI-space beamformer volumes were resampled during the application of the affine transformation to $4.5 \times 4.5 \times 4.5$ mm resolution prior to computing statistics.

We probed activation patterns for the three time-frequency components (TFC) of interest using a random effects analysis for each TFC per condition. To reduce the risk of false positive results while increasing sensitivity, a masking procedure was used to circumvent statistical problems posed by whole-brain analyses (i.e., multiple comparisons). This mask included only cortical regions directly involved in motor behavior or programming, plus cerebellar areas, with the primary goal of ensuring statistical tests were performed only on neural areas of a priori interest. This mask included bilateral cerebellar regions, pre- and post-central gyri, and supplementary motor areas (SMA; see Figure 2) as defined with the automated anatomical labeling template (AAL; Tzourio-Mazoyer et al., 2002) implemented in the WFU Pickatlas (Maldjian et al., 2003, 2004).

Results

Sensor Space Analyses

In agreement with previous studies, finger movements generated robust beta rhythm ERDs several hundred milliseconds preceding movement onset, which also extended into the movement period (Pfurtscheller and Lopes da Silva, 1999; Jurkiewicz et al., 2006). Likewise, after the movement terminated, a beta frequency ERS was observed and this response had a variable duration from subject-to-subject, but was typically 500–900ms. Unlike beta, mu rhythms were not significantly reactive to impending movements and did not show any rebound effect after movement termination, instead transforming into low amplitude ERD that was often only slightly distinguishable from mu power during the baseline period. Relative to the strong beta ERD and ERS oscillatory components, the lack of post-movement mu reactivity is consistent with other studies (e.g., Jurkiewicz et al., 2006). Given the lack of rhythmic power, mu frequency responses were not subjected to the beamformer analyses (see below). Lastly, we observed a high frequency gamma ERS component coinciding with the movement onset, and this response dissipated substantially before movement termination (see Figure 3). We focused on beta ERS and ERD responses and the gamma ERS in this study to decipher how the high-frequency response is linked with the other well-described oscillatory motor responses.

Source Space Analyses

All resulting statistical parametric maps were thresholded at a false discovery rate (FDR) of $p < 0.01$ and inspected for regions of significant ERS or ERD. Table 1 shows the brain regions and coordinates for the cluster maxima for each of the TFCs per condition. We observed considerable similarity in the activation maxima contralateral to movement across the two conditions, along with more ipsilateral activity for movements of the non-dominant index finger. We describe results for the pre-movement ERD, the high-frequency movement ERS, and the post-movement ERS for each index finger in turn.

Right Finger Movements—The FDR-corrected pre-movement ERD maps indicated flexion-extension of the right index finger strongly activated bilateral SMA, left postcentral gyrus (see Figure 4A), right cerebellum crus II (Figure 5). Smaller and weaker clusters of ERD activity were also found in anterior and inferior portions of the left and right precentral gyri (i.e., premotor areas) and the right postcentral gyrus. High-frequency ERS activity coinciding with movement onset was found centered near the hand “knob” region (Yousry et al., 1997) of the left precentral gyrus, and extended into the left postcentral gyrus and bilateral SMA (see Figure 4B). The post-movement beta rebound (PMBR) response was strongest in the left precentral gyrus (anterior and lateral to the high-frequency ERS), within the premotor cortices (see Figure 4C). This activation stretched superior toward the hand area of primary motor cortices and posterior into the adjacent somatosensory cortex. Finally, smaller and spatially separate PMBR clusters were found in superior areas of bilateral cerebellum, including lobules IV, V, and VI and right cerebellum crus I. Peak activity for each TFC component is shown in Figure 6A–B.

Left Finger Movements—The pre-movement ERD associated with left index finger movement was strongest in bilateral SMA and the right postcentral gyrus/central sulcus (see Figure 6B). Weaker ERD activity was found in the left postcentral gyrus, small areas in each cerebellar hemisphere (right cerebellum crus I and II; left cerebellum lobules IV, V, and VI), and the right precentral gyrus. Analogous to that of the right, the high-frequency ERS response associated with left finger movement was centered on the hand “knob” region of the right primary motor cortex (Yousry et al., 1997; see Figures 6B and 7). High frequency activity in bilateral SMA (mostly right) and small separate areas of left inferior parietal cortex and the left precentral gyrus were also observed. The PMBR for left finger movements involved the right precentral gyrus (near the high-frequency ERS maxima; see Figure 6B) and a separate inferior cluster that included right premotor cortex. In addition, weaker but still significant activation was observed in the left postcentral gyrus extending to left inferior parietal cortices.

Correlation Analyses

To evaluate whether the participant’s age at the time of scan was related to the amplitude of oscillatory responses, we computed Pearson-correlation coefficients using peak values for each significant cluster of activation (See Table 1). These analyses indicated that age at scan was, overall, more strongly related to activation associated with movement of the non-dominant (left) hand and that these patterns were most clear for activation in the non-primary motor cortices (i.e., SMA and cerebellar regions). Specifically, age at scan was significantly correlated with left finger pre-movement ERD activation in the right SMA, $r(10) = 0.58$ ($p < 0.05$), and left cerebellum lobules IV–V, $r(10) = 0.57$ ($p < 0.05$). The high-frequency gamma ERS during left finger movements was also related to age in the right SMA, $r(10) = -0.68$ ($p = 0.01$), as was the PMBR response in the right precentral gyrus, $r(10) = 0.53$ ($p < 0.05$). In regards to right finger movements, the pre-movement ERD response was significantly correlated with age in the right cerebellum crus II, $r(10) = 0.63$ ($p < 0.05$), and trended that way in the ipsilateral postcentral gyrus, $r(10) = 0.48$ ($p = 0.08$). The gamma ERS response in the left SMA also trended in the predicted direction, $r(10) = -0.52$ ($p = 0.06$). Lastly, a weaker

developmental trend was found for right finger PMBR responses in the right cerebellum, $r(10) = -0.46$ ($p = 0.09$).

Discussion

We examined the oscillatory dynamics associated with knuckle flexion-extension movements of each index finger in a group of typically-developing adolescents. Consistent with adult findings, we observed a beta-frequency ERD response that predominated up to a second before and several hundred milliseconds after movement onset, as well as a beta ERS response (i.e., PMBR) that typically began 1.5 second after movement onset and continued for at least 700 milliseconds. The neural correlates of these ERD and ERS responses in rolandic areas, contralateral postcentral and precentral gyri, respectively were largely similar to those reported by other investigators. The main exceptions being the weaker lateralization of ERD and beta ERS activation observed in rolandic regions, robust ERD and ERS beta responses originating in SMA and cerebellar cortices, and the relatively anterior and inferior precentral gyrus peak for the beta ERS activation. We also observed high-frequency gamma bursts in these participants that coincided with the movement onset and included a network of cortical *motor* regions. High-frequency ERS occurring in unison with the movement onset has been reported using a similar task in adults, although such gamma activity was strongly restricted to the contralateral precentral gyrus (Cheyne et al., 2008). Thus, the additional activity we found in bilateral SMA and parietal cortices may reflect neural dynamics unique to maturing motor systems, as the correlation coefficients suggest, or simply slight analytical differences between the current study and those before. Below, we discuss the results of the current pediatric study, relate these data to previous work that used adult groups, and forward a hypothesis regarding the behavioral correlate of the high-frequency activity, which we believe may be the oscillatory signature of macroscopic activity (i.e., population responses) in columns of primary motor neurons.

As noted above, the beta ERD and ERS rolandic responses in these children were spatially and temporally analogous to those previously reported in adults (Salmelin et al., 1995; Pfurtscheller et al., 1996; Cassim et al., 2001; Cheyne et al. 2003; Muller et al., 2003; Gaetz and Cheyne, 2006; Houdayer et al., 2006; Jurkiewicz et al., 2006). In contrast, activity in the lower mu frequency range was weaker in the current study compared to that reported in most EEG (Pfurtscheller et al., 1996; Pfurtscheller and Lopes da Silva, 1999; Neuper and Purtscheller, 2001; Houdayer et al., 2006) and MEG studies (Salmelin and Hari, 1994; Salmelin et al., 1995; Hari and Salmelin, 1997; Cheyne et al. 2003; Gaetz and Cheyne, 2006), which may indicate basic mu reactivity to movement is more dependent on maturational processes that culminate in rolandic cortices during late adolescence. However, it is worth noting that oscillatory sensorimotor components in the beta range (i.e., ERD and PMBR) are typically stronger than mu components (Pfurtscheller and Lopes da Silva, 1999), which are occasionally difficult to resolve even in adult populations (e.g., Jurkiewicz et al., 2006). As for the beta responses, these adolescents showed contralateral dominance for both the pre-movement ERD and the PMBR. Within the primary sensorimotor areas, the contralateral postcentral gyrus exhibited the peak beta ERD response for each index finger, and the same was true for the PMBR focus and the precentral gyrus, both of which are consistent with the majority of past studies (Salmelin et al., 1995; Hari and Salmelin, 1997; Pfurtscheller and Lopes da Silva, 1999; Jurkiewicz et al., 2006). However, for each TFC per condition, we observed several additional areas of activity that have been reported much less commonly in adults. For example, to our knowledge, pre-movement beta activation of cerebellar cortices has not been previously reported, and in our study it was the strongest response in the right finger condition (right cerebellum) and was active in the left finger condition (bilateral cerebellum). We also found beta ERD activity in cortices of the SMA, which was the statistically strongest response for left and the second for right finger movements. Interestingly, the correlation analyses indicated

that beta ERD responses in the right SMA (left finger) were strongest in the youngest participants and tended to be less robust in the older adolescents. Likewise, pre-movement beta ERD activations in the ipsilateral cerebellar cortices (during left and right finger movements) were strongest in the children and became weaker in the adolescent participants. Although only correlational, these data suggest motor-related ERD activity in these regions decreases as individuals mature. Regions of bilateral cerebellar cortex also exhibited a PMBR during right finger movements, and a left inferior parietal area showed PMBR activity in the left finger condition. Compared to the limited MEG studies that have used volumetric imaging techniques on sensorimotor data, beta responses in our study were qualitatively larger contralateral to the behavioral event with, overall, more involvement from the ipsilateral primary sensorimotor cortices (Cheyne et al., 2003, 2006; Gaetz and Cheyne, 2006; Jurkiewicz et al., 2006). This additional activity in ipsilateral homologue areas may indicate transcallosal inhibitory processes do not fully develop until later adolescence, as previous studies have focused on adults and our group was comprised of children and young adolescents (mean age: 11.3 years). The trend toward weaker ERD responses in the ipsilateral postcentral gyrus of older participants during right finger movements is consistent with this view. The activation in non-primary cortices such as the SMA and cerebellum also suggests additional nodes may be needed to program somewhat elementary movements during the pre-adolescent years. It is well-recognized that bimanual coordination and auditory pacing motor tasks activate the SMA and the cerebellum in healthy adults (Newton et al., 2005; Pollock et al., 2005, 2008; Hanakawa et al., 2008), but these regions are not often found in experiments using simple unilateral movement paradigms (Salmelin et al., 1994, 1995; Cheyne et al., 2006; Jurkiewicz et al., 2006). Presumably, as the sensorimotor system more fully matures, these supra-primary regions (cerebellum and SMA) become less necessary for executing movements that do not require temporal coordination of complex muscular groups (e.g., multi-limb or -finger) and thus are gradually removed from the core network.

Beyond beta-frequency responses, we observed a high gamma ERS that coincided with the movement onset in these young participants. Cortices of the SMA, parietal regions, and the contralateral (right finger) or bilateral (left finger) precentral gyrus exhibited this high-frequency oscillatory response within a 250ms window surrounding movement onset. With regard to time and frequency specificity, Cheyne et al. (2008) described a similar gamma response in the contralateral precentral gyrus in their adult group. However, their data showed a strongly lateralized precentral gyrus response for left and right index finger movements, with no hint of SMA or parietal/postcentral gyrus involvement (Cheyne et al., 2008). Although given the negative correlations observed between the magnitude of gamma responses in the contralateral SMA and age, it is likely that this high-frequency oscillatory component dissipates during early adolescence. Such child/adult differences in SMA activity and lateralization in rolandic regions were also observed for beta responses, which again may just reflect a wider role for the SMA early in development and less matured callosal fibers between rolandic areas. As for cognitive-behavioral correlates, the spatiotemporal dynamics of the high-frequency gamma response suggest it is central to activation of columns of primary motor neurons. Essentially, for left and right finger movements, activation in the contralateral precentral gyrus was strongest near the “hand-knob” region, which is widely recognized as serving motor functions of the corresponding hand (Yousry et al., 1997). This activation extended into the adjacent central sulcus and postcentral gyrus in each condition, with a distinct cluster in the SMA that also exhibited synchrony within this frequency band. The time course of this oscillatory response also coalesces with the more commonly recognized beta frequency activations that precede (ERD) and follow (PMBR) the actual movement. While debate remains concerning the neural mechanisms reflected by these beta-band population responses (e.g., the idling hypothesis, active inhibition, and others; Pfurtscheller, 1992; Salmelin et al. 1995; Pfurtscheller et al., 1996; Pfurtscheller and Neuper, 1997; Cassim et al., 2001; Houdayer et al., 2006), their temporal dynamics are not consistent with a central role in the execution

signal. Basically, the beta ERD is a temporally sluggish response that precedes the movement by hundreds of milliseconds and does not reliably change until after the movement has terminated; the PMBR follows the movement so it cannot be a candidate. Thus, we propose this high-frequency ERS response may fill this gap and act as the rapid and temporally succinct signal that is presumably necessary to initialize activation in pertinent muscle fibers. The temporal dynamics would support such a role, and the anatomical correlates (i.e., contralateral precentral gyrus and SMA) match the regions where musculature efferents would be expected to originate (Yousry et al., 1997; Maldjian et al., 1999; Pollock et al., 2005, 2008; Hanakawa et al., 2008). Potentially, these areas synchronize to serve movement execution, and as a network contribute the real-time sensorimotor interactions (i.e., feedback) that are necessary for pre-programming, guiding, and correcting precise trajectory, amplitude, and related movement parameters.

Finally, these data are relevant to the current contention regarding the neural correlates of the PMBR response (e.g., Parkes et al., 2005; Jurkiewicz et al., 2006). Although the majority of studies had suggested a contralateral precentral focus for the PMBR (Salmelin et al., 1995; Hari and Salmelin, 1997; Pfurtscheller and Lopes da Silva, 1999), Parkes et al. found the response was more posterior within the postcentral sulcus in their combined EEG and fMRI study. In a follow-up MEG study, Jurkiewicz and colleagues (2006) reported the PMBR peak was centered on the hand knob region of the contralateral precentral gyrus. The current results also indicate the neural correlates of PMBR to be contralateral precentral gyrus, but our coordinates suggest a more anterior and inferior maxima within what is normally considered the premotor area. Interestingly, the coordinates reported for the PMBR response by Jurkiewicz et al. (2006) are virtually identical to those of our high-frequency ERS activity and that of Cheyne et al. (2008). Given this, it would have been particularly informative had Jurkiewicz et al. imaged this higher TFC in their study, or had Cheyne et al. imaged the PMBR activity. Nonetheless, this pattern, especially the premotor activity, could be a simple developmental effect as we also found clusters of PMBR activation in the cerebellum and postcentral gyrus in these children, which were not observed by Jurkiewicz and colleagues. As mentioned above, these additional neural areas may be involved in more basic movements (like those used here) in the maturing motor system, and be gradually eliminated from the core network as the system's development begins to asymptote. Another possible explanation for the PMBR location discrepancy between these studies and ours is that the finger movements across all three were slightly different, being abduction (Jurkiewicz et al., 2006), extension (Parkes et al., 2005), and knuckle flexion-extension (current study).

In conclusion, we have described the spatiotemporal dynamics of the full gamut of oscillatory responses in a group of typically-developing children. Our most interesting findings are likely the reduced lateralization in rolandic regions, and the additional brain areas (e.g., SMA and cerebellum) that serve elementary movements in the developing motor system. Beyond such findings, we observed the oscillatory dynamics serving basic unilateral finger movements during childhood and early adolescence are largely similar to those commonly found in MEG studies of adult participants. Essentially, both age groups exhibit a strong pre-movement beta ERD response with a rolandic peak in the contralateral postcentral gyrus, a PMBR response with maxima in the contralateral precentral gyrus, and slightly weaker pre- and post-movement mu rhythm responses. Although less evidence is available, it appears both age groups also exhibit high-frequency gamma activity that coincides with the movement onset and peaks in the hand region of the contralateral precentral gyrus (and/or SMA). In contrast to other mu and beta-band sensorimotor responses, the spatiotemporal dynamics of this gamma activity make it an excellent candidate for an oscillatory correlate of the movement "execution" signal (i.e., motor neuron to musculature efferents). Future studies should examine the developmental trajectory of the motor system, focusing on whether activity in cortices of the cerebellum and SMA decreases with maturation, and if so at what stage. Another avenue for future work would

be to evaluate the trajectory of gamma synchronicity; speculatively, one would expect much stronger high-frequency activity in the mature adult motor system, as these networks would have more established interconnections and other (e.g., weight-like) parameters for such synchronous interactivity.

Acknowledgments

This work was supported by grants from the National Institute of Mental Health (R01 MH63442, R01 MH081920), and the Developmental Psychobiology Research Group (DPRG) of the University of Colorado Health Sciences Center (UCHSC), Denver, CO, USA. Support for T.W.W. was also provided by USPHS grant T32 MH15442, “Development of Maladaptive Behavior” (UCHSC Institutional Postdoctoral Research Training Program), and grant F32 MH78359, “Sensorimotor Interactions in Childhood Schizophrenia.”

References

- Annett, M. Left, right, hand and brain: the right shift theory. Hillsdale: Lawrence Erlbaum Associates; 1985.
- Brovelli A, Lachaux JP, Kahane P, Boussaoud D. High gamma frequency oscillatory activity dissociates attention from intention in the human premotor cortex. *Neuroimage* 2005;28:154–164. [PubMed: 16023374]
- Cassim F, Monaca C, Szurhaj W, Bourriez JL, Defebvre L, Derambure P, Guieu JD. Does post-movement beta synchronization reflect an idling motor cortex? *NeuroReport* 2001;12:3859–3863. [PubMed: 11726809]
- Cheyne D, Bakhtazad L, Gaetz W. Spatiotemporal mapping of cortical activity accompanying voluntary movements using an event-related beamforming approach. *Human Brain Mapping* 2006;27:213–229. [PubMed: 16037985]
- Cheyne D, Bells S, Ferrari P, Gaetz W, Bostan AC. Self-paced movements induce high-frequency gamma oscillations in primary motor cortex. *Neuroimage* 2008;42:332–342. [PubMed: 18511304]
- Cheyne D, Gaetz W, Garnero L, Lachaux JP, Ducorps A, Schwartz D, Varela FJ. Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Cognitive Brain Research* 2003;17:599–611. [PubMed: 14561448]
- de Lange FP, Jensen O, Bauer M, Toni I. Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. *Frontiers of Human Neuroscience* 2008;2:7. doi: 10.3389/neuro.09.007.2008.
- Debaere F, Wenderoth N, Sunaert S, Van Hecke P, Swinnen SP. Cerebellar and premotor function in bimanual coordination: parametric neural responses to spatiotemporal complexity and cycling frequency. *NeuroImage* 2004;21:1416–1427. [PubMed: 15050567]
- Gaetz W, Cheyne D. Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *NeuroImage* 2006;30:899–908. [PubMed: 16326116]
- Geyer S, Matelli M, Luppino G, Zilles K. Functional neuroanatomy of the primate isocortical motor system. *Anatomy and Embryology* 2000;202:443–474. [PubMed: 11131014]
- Gross J, Kujala J, Hamalainen M, Timmermann L, Schnitzler A, Salmelin R. Dynamic imaging of coherent sources: studying neural interactions in the human brain. *Proc Natl Acad Sci USA* 2001;98:694–699. [PubMed: 11209067]
- Hari R, Salmelin R. Human cortical oscillations: A neuromagnetic view through the skull. *Trends in Neuroscience* 1997;20:44–49.
- Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G. Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proc Natl Acad Sci USA* 1998;95:15061–15065. [PubMed: 9844015]
- Hanakawa T, Dimyan MA, Hallett M. Motor planning, imagery, and execution in the distributed motor network: A time-course study with functional MRI. *Cerebral Cortex* 2008;18:2775–2788. [PubMed: 18359777]
- Hillebrand A, Singh KD, Holliday IE, Furlong PL, Barnes GR. A new approach to neuroimaging with magnetoencephalography. *Human Brain Mapping* 2005;25:199–211. [PubMed: 15846771]

- Hoechstetter K, Bornfleth H, Weckesser D, Ille N, Berg P, Scherg M. BESA source coherence: a new method to study cortical oscillatory coupling. *Brain Topography* 2004;16:233–238. [PubMed: 15379219]
- Houdayer E, Labyt E, Cassim F, Bourriez J, Derambure P. Relationship between event-related beta synchronization and afferent inputs: Analysis of finger movement and peripheral nerve stimulations. *Clinical Neurophysiology* 2006;117:628–636. [PubMed: 16427358]
- Jenkins IH, Jahanshahi M, Jueptner M, Passingham RE, Brooks DJ. Self-initiated versus externally triggered movements II. The effect of movement predictability on regional cerebral blood flow. *Brain* 2000;123:1216–1228. [PubMed: 10825359]
- Jurkiewicz MT, Gaetz WC, Bostan AC, Cheyne D. Post-movement beta rebound is generated in motor cortex: Evidence from neuromagnetic recordings. *NeuroImage* 2006;32:1281–1289. [PubMed: 16863693]
- Koelewijn T, van Schie HT, Bekkering H, Oostenveld R, Jensen O. Motor-cortical beta oscillations are modulated by correctness of observed action. *Neuroimage* 2008;40:767–775. [PubMed: 18234516]
- Koenke S, Lutz K, Wustenberg T, Jancke L. Bimanual versus unimanual coordination: what makes the difference? *NeuroImage* 2004;22:1336–1350. [PubMed: 15219606]
- Maldjian JA, Gottschalk A, Patel RS, Detre JA, Alsop DC. The sensory somatotopic map of the human hand demonstrated at 4 Tesla. *NeuroImage* 1999;10:55–62. [PubMed: 10385581]
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fmri data sets. *Neuroimage* 2003;19:1233–1239. [PubMed: 12880848]
- Maldjian JA, Laurienti PJ, Burdette JH. Precentral gyrus discrepancy in electronic versions of the talairach atlas. *Neuroimage* 2004;21:450–455. [PubMed: 14741682]
- Miller KJ, Leuthardt EC, Schalk G, Rao RP, Anderson NR, Moran DW, Miller JW, Ojemann JG. Spectral changes in cortical surface potentials during motor movement. *Journal of Neuroscience* 2007;27:2424–2432. [PubMed: 17329441]
- Muller GR, Neuper C, Rupp R, Keinrath C, Gerner HJ, Pfurtscheller G. Event-related beta EEG changes during wrist movements induced by functional electrical stimulation of forearm muscles in man. *Neuroscience Letters* 2003;340:143–147. [PubMed: 12668257]
- Nachev P, Kennard C, Husain M. Functional role of the supplementary and pre-supplementary motor areas. *Nature Reviews Neuroscience* 2008;9:856–869.
- Neuper C, Pfurtscheller G. Evidence for distinct beta resonance frequencies in human EEG related to specific sensorimotor cortical areas. *Clinical Neurophysiology* 2001;112:2084–2097. [PubMed: 11682347]
- Newton JM, Sunderland A, Gowland PA. fMRI signal decreases in ipsilateral primary motor cortex during unilateral hand movement are related to duration and side of movement. *NeuroImage* 2005;24:1080–1087. [PubMed: 15670685]
- Papp N, Ktonas P. Critical evaluation of complex demodulation techniques for the quantification of bioelectrical activity. *Biomedical Sciences Instrumentation* 1977;13:135–143. [PubMed: 871500]
- Parkes LM, Bastiaansen MCM, Norris DG. Combining EEG and fMRI to investigate the post-movement beta rebound. *NeuroImage* 2006;29:685–696. [PubMed: 16242346]
- Passingham, RE. Functional organisation of the motor system. In: Frackowiak, RSJ.; Friston, KJ.; Frith, CD.; Dolan, RJ.; Mazziotta, JC., editors. *Human Brain Function*. San Diego: Academic Press; 1997. p. 243-274.
- Passingham, RE.; Chen, YC.; Thaler, D. Supplementary motor cortex and self-initiated movement. In: Ito, M., editor. *Neural Programming*. Tokyo: Karger; 1989. p. 13-24.
- Pfurtscheller G. Event-related synchronization (ERS): An electrophysiological correlate of cortical areas at rest. *Electroencephalography and Clinical Neurophysiology* 1992;83:62–69. [PubMed: 1376667]
- Pfurtscheller G, Graimann B, Huggins JE, Levine SP, Schuh LA. Spatiotemporal patterns of beta desynchronization and gamma synchronization in corticographic data during self-paced movement. *Clinical Neurophysiology* 2003;114:1226–1236. [PubMed: 12842719]
- Pfurtscheller G, Lopes da Silva FH. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology* 1999;110:1842–1857. [PubMed: 10576479]

- Pfurtscheller G, Neuper C. Motor imagery activates primary sensorimotor area in humans. *Neuroscience Letters* 1997;239:65–68. [PubMed: 9469657]
- Pfurtscheller G, Neuper C, Brunner C, Lopes da Silva FH. Beta rebound after different types of motor imagery in man. *Neuroscience Letters* 2005;378:156–159. [PubMed: 15781150]
- Pfurtscheller G, Stancak A Jr, Neuper C. Post-movement beta synchronization A correlate of an idling motor area? *Electroencephalography and Clinical Neurophysiology* 1996;98:281–293. [PubMed: 8641150]
- Pineda JA. The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing”. *Brain Research Reviews* 2005;50:57–68. [PubMed: 15925412]
- Pollock B, Gross J, Kamp D, Schnitzler A. Evidence for anticipatory motor control within a cerebello-diencephalic-parietal network. *Journal of Cognitive Neuroscience* 2008;20:828–840. [PubMed: 18201129]
- Pollock B, Gross J, Muller K, Aschersleben G, Schnitzler A. The cerebral oscillatory network associated with auditorily paced finger movements. *NeuroImage* 2005;24:646–655. [PubMed: 15652300]
- Rizzolatti G, Luppino G. The cortical motor system. *Neuron* 2001;31:889–901. [PubMed: 11580891]
- Salmelin R, Hari R. Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience* 1994;60:537–550. [PubMed: 8072694]
- Salmelin R, Hamalainen M, Kajola M, Hari R. Functional segregation of movement-related rhythmic activity in the human brain. *NeuroImage* 1995;2:237–243. [PubMed: 9343608]
- Schoffelen JM, Oostenveld R, Fries P. Neuronal coherence as a mechanism of effective corticospinal interaction. *Science* 2005;308:111–113. [PubMed: 15802603]
- Swinnen SP. Intermanual coordination: from behavioural principles to neural-network interactions. *Nature Reviews Neuroscience* 2002;3:348–359.
- Szurhaj W, Labyt E, Bourriez JL, Kahane P, Chauvel P, Mauguire F, Derambure P. Relationship between intracerebral gamma oscillations and slow potentials in the human sensorimotor cortex. *European Journal of Neuroscience* 2006;24:947–954. [PubMed: 16930422]
- Talairach, J.; Tournoux, P. Co-planar stereotaxic atlas of the human brain. Stuttgart, Germany: Thieme Medical Publishers; 1988.
- Tecchio F, Zappasodi F, Porcaro C, Barbati G, Assenza G, Salustri C, Rossini PM. High-gamma band activity of primary hand cortical areas: A sensorimotor feedback efficiency index. *Neuroimage* 2008;40:256–264. [PubMed: 18178106]
- Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, et al. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 2002;15:273–289. [PubMed: 11771995]
- van Veen BD, van Drongelen W, Yuchtman M, Suzuki A. Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Transactions on Biomedical Engineering* 1997;44:867–880. [PubMed: 9282479]
- Waldert S, Preissl H, Demandt E, Braun C, Birbaumer N, Aertsen A, Mehring C. Hand movement direction decoded from MEG and EEG. *Journal of Neuroscience* 2008;28:1000–1008. [PubMed: 18216207]
- Ween JE. Functional imaging of stroke recovery: An ecological review from a neural network perspective with an emphasis on motor systems. *Journal of Neuroimaging* 2008;18:227–236. [PubMed: 18466275]
- Yousry TA, Schmid UD, Alkadhi H, Schmidt D, Peraud A, Buettner A, Winkler P. Localization of the motor hand area to a knob on the precentral gyrus: A new landmark. *Brain* 1997;120:141–157. [PubMed: 9055804]

Figure 1.

Experimental Design. Participants fixated on the cross hair as the red dot moved clockwise toward the blue dots, displacing each green dot in turn. Participants were instructed to make one flexion-extension movement each time the red dot was within the blue area (but only one movement per revolution).

Figure 2. Surface Rendering of Masked MNI Brain. Ventral (left) and dorsal (right) views of brain regions that were included in the mask. Cyan = cerebellum (ventral view), yellow = left precentral gyrus, magenta = left postcentral gyrus, blue = left SMA, green = right precentral gyrus, cyan = right postcentral gyrus (dorsal view), red = right SMA.

Figure 3.

Time-Frequency Representation of Gamma ERS. Participants exhibited strong high-frequency gamma ERS activity that coincided with the movement onset and fully dissipated prior to movement termination. A representative time-frequency plot from a MEG sensor near the left sensorimotor strip, referenced to the pre-movement baseline period (−3.0 s to −2.2 s), during right index finger movement is shown above. To focus on the gamma ERS response, the pertinent frequency range (70–90 Hz) is shown on the ordinate with the respective time (−1.0 to 1.0 s) appearing on the abscissa (movement onset = 0 s). Scale to the right illustrates that increases in power (ERS) are shown in red and decreases in power (ERD) are shown in blue, as a percentage of the power at the respective frequency within the baseline period.

Figure 4.

Activation per Time-Frequency Component for Right Finger Movements. (A) Pre-movement beta ERD activity was observed in bilateral SMA, right cerebellum (Figure 5), and centered on the left postcentral gyrus. Weaker ERD activity was also found in the central sulcus and precentral gyri. (B) High-frequency ERS responses (74–86 Hz) that coincided with the movement onset peaked near the “hand knob” region of the left precentral gyrus, with an additional cluster of activity in bilateral SMA. (C) Post-movement beta ERS (i.e., PMBR) activation was strongest in anterior and inferior aspects of the left precentral gyrus, in what are likely premotor cortices. Significant PMBR responses were also observed in bilateral cerebellar cortices (not shown). Images are shown in neurological (right = right) convention (threshold: $p < .01$, FDR-corrected).

Figure 5. Pre-Movement Beta ERD Activation in Cerebellar Cortices. Beta ERD activation for right finger movements was strongest in ipsilateral cerebellar cortices, with a local maxima in the inferior portion of right cerebellum crus II. Lines in sagittal image (far right) indicate the placement of shown axial slices in the volume. Images are in neurological convention (threshold: $p < .01$, FDR-corrected).

Figure 6. Activation Peaks per Time-Frequency Component and Condition. Red arrows indicate pre-movement beta ERD peaks, green arrows indicate peaks of the PMBR, and the maximas of the high-frequency ERS responses are shown with blue arrows. (A) Right finger movements: from left to right, red ovals indicate pre-movement beta ERD peak in left postcentral gyrus, PMBR peak in the left premotor area, right SMA peak (beta ERD), and the high-frequency ERS peaks in left precentral gyrus and SMA. (B) Left finger movements: red ovals show the PMBR peak in the right premotor area, the SMA peak for the pre-movement beta ERD (posterior blob), the SMA and right precentral gyrus peaks for the high-frequency ERS response, and the right central sulcus/postcentral gyrus peak for the pre-movement beta ERD. Lines in sagittal images (far right) indicate the placement of axial slices shown per row. Images are in neurological convention.

Figure 7. High-Frequency ERS Activation for Left Finger Movements. Analogous to results obtained for the right finger (see Figure 4B), high-frequency (74–86 Hz) ERS activity coinciding with onset of left finger movement peaked in the right precentral gyrus on the “hand knob,” with a separate cluster of activation in the right SMA. Images are shown in neurological convention (threshold: $p < .01$, FDR-corrected).

Table 1

Peak Activation Coordinates per TFC and Condition

Anatomical Label	MNI Coordinates (x,y,z)			T Score	
Left Finger					
Pre-movement beta ERD	R supp motor area	14	-23	50	9.89
	R postcentral gyrus	32	-29	55	6.07
	R cerebellum crus I	54	-68	-27	4.55
	L cerebellum IV-V	-18	-36	-18	4.22
High-frequency ERS	R supp motor area	14	-18	50	7.00
	R precentral gyrus	36	-18	54	6.91
	L inferior parietal	-27	-45	54	4.67
	L precentral gyrus	-45	-5	59	3.75
Post-movement beta ERS	R precentral gyrus	32	-5	50	4.99
	R postcentral gyrus	68	-9	27	4.95
	L postcentral gyrus	-50	-9	54	4.94
	L inferior parietal	-59	-18	45	4.67
Right Finger					
Pre-movement beta ERD	R cerebellum crus II	50	-72	-41	6.89
	R supp motor area	5	14	50	5.85
	L postcentral gyrus	-36	-32	41	5.55
	R precentral gyrus	32	5	32	4.36
	L precentral gyrus	-45	9	32	4.00
R postcentral gyrus	45	-36	68	3.68	
High-frequency ERS	L precentral gyrus	-27	-14	54	6.13
	L postcentral gyrus	-18	-41	81	6.05
	L supp motor area	-9	-9	54	4.90
Post-movement beta ERS	L precentral gyrus	-54	9	45	6.43
	L precentral gyrus	-45	0	23	4.25
	L cerebellum IV-V	-9	-41	-5	4.16

Anatomical Label	MNI Coordinates (x,y,z)	T Score
R cerebellum IV-V	9 -45 -5	4.03
L cerebellum VI	-27 -59 -18	4.02
R cerebellum crus I	41 -54 -32	3.98

Note: all maxima (T values) are significant at $p < 0.01$ (FDR-corrected), roman numerals indicate the cerebellar lobule involved