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Review

MEG studies of sensorimotor rhythms: A review

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ABSTRACT

The human sensorimotor cortex demonstrates a variety of oscillatory activity that is strongly modulated by movement and somatosensory input. Studies using scalp EEG and intracranial electrical recordings have provided much of our current knowledge regarding the frequency and temporal specificity of these sensorimotor rhythms and their relationship to various movement parameters, however with limitations in identifying the underlying neural sources, and the variety of motor behaviors that can be studied, respectively. Magnetoencephalography (MEG) recordings, combined with spatial filtering source reconstruction methods, provide an ideal non-invasive method for the localization of sensorimotor rhythms and for describing their precise time course during a variety of motor tasks. This review describes the application of MEG to the study of oscillatory activity in the human sensorimotor cortex, including advances in localization techniques and recent contributions of MEG to our understanding of the functional role of these oscillations in both adult and developmental populations.

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Introduction

The human sensorimotor cortex demonstrates a variety of rhythmic brain activity that is strongly modulated by movement and somatosensory input. Transient increases and decreases in spectral

power recorded in the human EEG have been traditionally termed event-related synchronization (ERS) and desynchronization (ERD) respectively (Leocani et al., 1997; Pfurtscheller and Aranibar, 1977; Pfurtscheller et al., 1996). These phenomena have been shown to be elicited during and following preparation and performance of voluntary movements (Pfurtscheller and Lopes da Silva, 1999), passive movements (Cassim et al., 2001), and even during imagined movements (Pfurtscheller et al., 2005; Salenius et al., 1997; Schnitzler et

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al., 1997). Non-invasive scalp EEG and intracranial measurements using depth or electrocorticogram (ECoG) recordings have provided significant knowledge regarding the time course and putative neural generators of these sensorimotor rhythms in humans. Scalp EEG methods however, are limited in identifying the underlying neural sources with high spatial precision, and intracranial recordings are restricted to limited brain regions within patient populations. Advances in magnetoencephalography (MEG) recording technology and the development of more robust and accurate source modeling techniques with emphasis on time-domain signal processing have contributed novel information regarding the nature of cortical oscillations within motor and sensory structures of the brain, and will likely continue to play an important role in identifying the underlying mechanisms of

motor cortex oscillations and their functional role in motor control. With the introduction of multi-channel magnetometers that can record from the entire brain, MEG can be now used to construct detailed images of oscillatory brain activity in both adults and children with increasing accuracy and a greater range of movement paradigms. The following review provides an overview of the contributions of MEG to the non-invasive study of human sensorimotor rhythms.

Why MEG?

The development of MEG instrumentation has advanced immensely over the last three decades, providing multi-channel systems

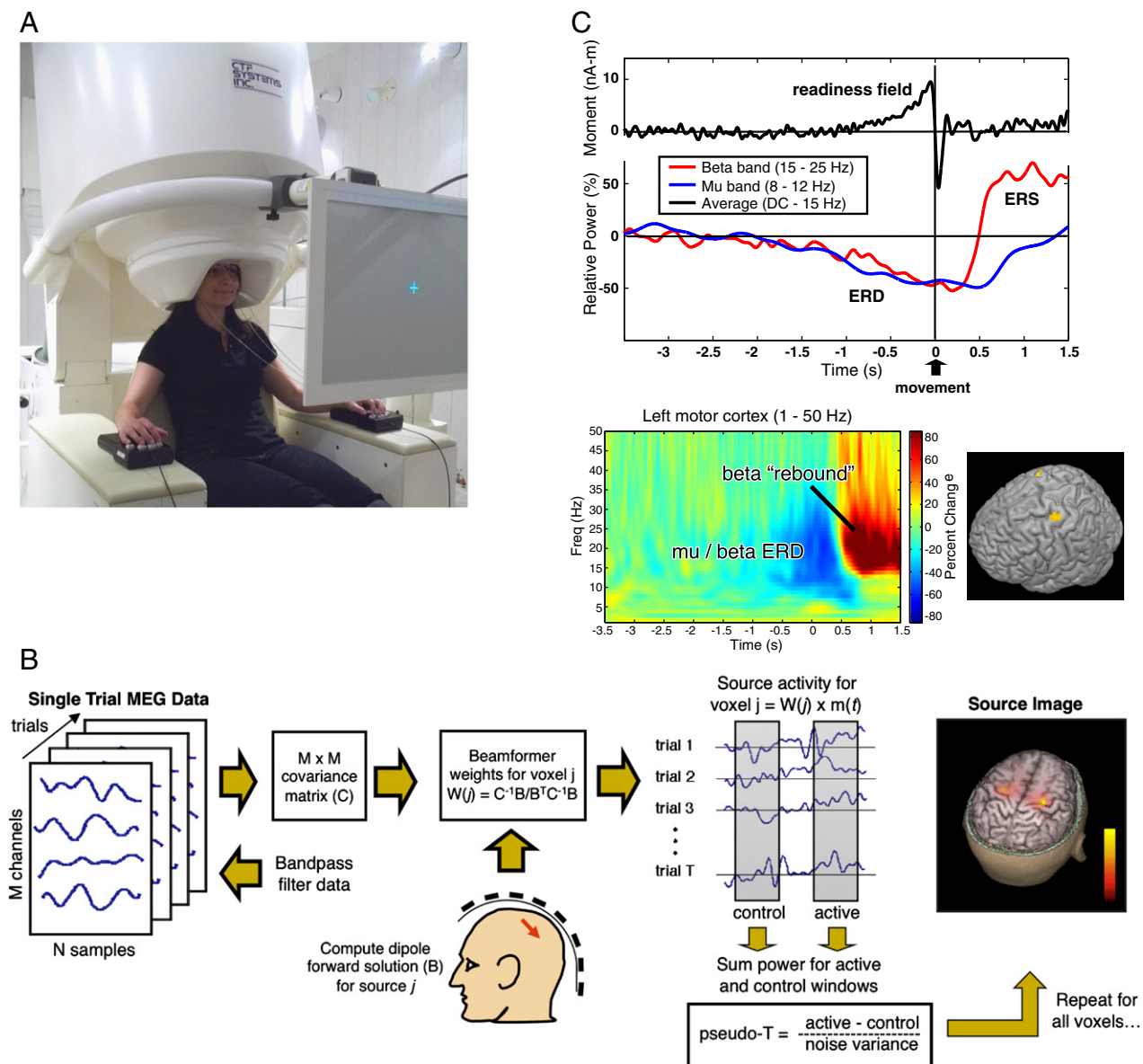


Fig. 1. (A) Subject seated in a 151-channel whole-head MEG system (CTF/MISL, Coquitlam, BC, Canada). (B) Synthetic Aperture Magnetometry (SAM) imaging method. The raw MEG data in the bandwidth of interest are used to derive adaptive spatial filters for each voxel using a minimum-variance beamformer algorithm. A pseudo-t metric (normalized to have unit noise gain) is computed for selected active and control time windows for each voxel throughout the brain volume, generating a 3-dimensional image of source power change, which can be superimposed on the subject's MRI. (C) MEG analysis of activity in the left (contralateral) motor cortex in a group of 9 subjects performing right index finger movements, time-locked to a button press. The waveforms show the time course of source activity ("virtual sensor") localized to a location in the precentral gyrus shown on a template MRI shown below. Red and blue traces indicate time of power change in the beta (15–25 Hz) and mu (8–12 Hz) frequency bands, respectively, showing beta band ERD prior to movement and beta band ERS ("rebound") beginning around 400 ms after the button press. A time-frequency plot of the same activity is shown below. The black trace shows the time-averaged source activity, demonstrating a slow DC shift (readiness field) preceding movement onset and movement-evoked fields following movement onset. Note that although mu band activity is present in this virtual sensor it would be maximally detected from a more posterior location in the postcentral gyrus.

capable of accurately measuring magnetic brain activity with high sensitivity with advanced noise cancellation (Cheyne and Vrba, 2006). Modern MEG systems are capable of recording magnetic brain activity from hundreds of sensors distributed over the entire head from subjects during rest, or while performing cognitive or motor tasks in both seated and supine positions, with real-time detection of head motion (Fig. 1A). MEG measurements are considered to have a number of advantages over more traditional electrophysiological measurements of brain activity, such as the scalp EEG. One significant advantage is that propagation of magnetic fields through the head is less influenced by the varying conductivities of the overlying tissues in comparison to electrical potentials measured from the surface of the scalp, providing a less spatially distorted signal. In addition, the primary generators of magnetic brain signals are intracellular neuronal currents with relatively small contributions of volume currents, reducing the need for accurate estimates of the conductive properties of these tissues for the purpose of source modeling. For measurement of higher frequency brain activity, EEG signals are also more readily contaminated by muscle activity (Whitham et al., 2007), or even by spike potentials arising from involuntary eye muscle activity associated with microsaccades (Yuval-Greenberg et al., 2008). For these reasons, MEG can often provide a clearer separation of the generators of time varying brain signals. This can prove particularly useful for the analysis of interactions between different brain regions in the frequency domain. In particular, there is a growing interest in studying connectivity between different brain regions through phase or amplitude synchronization within specific frequency bands (Fries, 2005), including amplitude modulation of higher frequency oscillations by lower frequency rhythms (Canolty and Knight, 2010). However, when using EEG, these measures are highly susceptible to artificial or inflated estimates of phase synchrony due to volume conduction of activity from multiple synchronous sources, requiring the use of complex signal processing methods that reduce such false synchronization estimates (Nolte et al., 2004; Stam et al., 2007). Although crosstalk between neural sources will have some effect on MEG measurements at the level of the sensor array, coupling between widely separated brain regions has been demonstrated in the sensor data using MEG (Doesburg et al., 2010; Osipova et al., 2008). The further combination of these measures with source level analyses may provide a means to identify brain rhythmic activity from even closely spaced brain regions using non-invasive brain imaging methods. It should be acknowledged that MEG does suffer from some disadvantages in terms of poor sensitivity to activity in radially oriented cortex or very deep sources, as well as less availability and greater cost, and as such, scalp EEG will remain an important and complementary technique for the measurement of human oscillatory brain activity. Of course, intracranial EEG measures can avoid many of problems mentioned above and will continue to provide the most direct measure of oscillatory brain activity in humans, however, such studies are limited to the extent and location of the implanted electrode arrays or depth electrodes for the purpose of surgical planning in patients, who may also have altered brain rhythmicity due to their underlying neuropathology, as well as medication use which can have profound effects on background rhythmic brain activity.

Measuring oscillatory brain activity using MEG

With temporal sampling rates extending into the kilohertz range, MEG is inherently well suited for the non-invasive measurement of oscillatory brain activity—indeed the very first measurements of magnetic brain activity were of the occipital alpha rhythm (Cohen, 1972). Early MEG studies on the localization of rhythmic brain activity in motor areas involved sensor level analyses (Nagamine et al., 1996; Salmelin and Hari, 1994) or dipole modeling approaches applied in the frequency domain (Salmelin and Hamalainen, 1995). The equivalent current dipole or ECD is most well-known and most extensively

used model for brain source activity. It is based on the assumption that activation of a specific cortical region involves populations of functionally interconnected neurons within a relatively small area. When measured from a distance, this local population activity can be modeled by a vector sum or “equivalent” current dipole that represents the aggregate activity of these neurons. This approach has proven useful for modeling simple configurations of focal brain activity, yet is compromised by interaction between closely spaced sources, and may produce incorrect solutions due to unknown sources that are not included in the model. The introduction of source localization methods based on linear estimation techniques has improved the ability to derive directly continuous time-series of neural sources. A more recent technique introduced to the neuromagnetic source modeling literature is a spatial filtering approach based on the array processing technique known as beamforming. Beamforming is an array processing method used in radar and communications applications to improve the signal detection capability of multiple antenna arrays through the selective nulling of interference signals (Godara, 1997). This reduces the influence of unknown sources by removing spatial correlations in the data that do not correspond to source activity at the location of interest. Thus, beamforming techniques can be used as a method of scanning through source space to produce accurate three-dimensional volumetric images of source activity. This method was only recently adapted to the problem of EEG and MEG source reconstruction (Robinson and Vrba, 1999; Sekihara et al., 2001; Van Veen et al., 1997) taking advantage of the high dimensionality of signal-space afforded by multi-channel MEG systems. Adaptive beamforming does not require specifying the number of interference sources or their forward solutions making it ideal for MEG data, where both the number and location of brain and interference sources are unknown.

Various types of beamforming algorithms have been recently adapted to neuromagnetic measurements for localizing oscillatory brain activity. One such method, termed *synthetic aperture magnetometry* (SAM), introduced by Robinson and colleagues (Robinson and Vrba, 1999), estimates an optimal current direction at each voxel, based on the assumption that MEG signals are generated by intracellular currents flowing perpendicular to the cortical surface. Most importantly, the SAM beamformer uses single-trial data and provides a time series of source activity at each brain location, making the method ideal for time-frequency analysis. The SAM differential imaging approach is summarized in Fig. 1B. An alternative beamforming approach, termed Dynamic Imaging of Coherent Sources (DICS), was introduced by Gross et al. (2001), which computes spatial filters for multidirectional (vector) sources at each brain location in the frequency domain, with the added feature of being able to image the degree of coherence of the brain signal with a reference signal, such as the electromyogram or another brain source. Both methods can be used to construct 3-dimensional images of oscillatory neural activity by combining the output of arrays of spatial filters over the entire brain volume (by scanning over a predefined 3-dimensional grid) forming a volumetric image of changes in oscillatory power for selected time intervals and frequency bands. In addition, by summing power over the single trial epochs, these methods are ideal for the study of *induced* cortical oscillations, i.e., transient changes in source power that are induced by the occurrence of some action or stimulus event, but may not necessarily be precisely phase-locked to any point in time and therefore not enhanced by signal averaging. Since images are created volumetrically they can be transformed to standardized space for group averaging (Singh et al., 2003). Most importantly, these spatial filters provide a millisecond by millisecond time course of activity within each frequency band and can be used to generate time-frequency plots to visualize the time course of changes in source activity in the frequency domain.

The spatial filtering MEG approach has been successfully used to detect time-locked increases and decreases in the beta and mu

frequency bands in the vicinity of the central sulcus during somatosensory stimulation (Cheyne and Gaetz, 2003; Gaetz and Cheyne, 2006; Hirata et al., 2002) and voluntary hand movements (Jurkiewicz et al., 2006; Schnitzler et al., 2006; Taniguchi et al., 2000). Fig. 1C shows an example of source analysis of oscillatory activity in the motor cortex using SAM beamformer analysis of data from a group of 9 individuals performing self-paced right index finger movements, recorded with a 151-channel MEG system at the Toronto Hospital for Sick Children. The time-frequency plots show that changes in both mu and beta oscillatory activity begins as early as 1 to 2 s prior to voluntary movements, and continue well beyond the termination of movement, particularly in the beta band, which shows a strong and sudden transition from decreased power (ERD) to increased power (ERS) beginning 400 to 500 ms after movement termination. In contrast, the time-locked average (shown in black) shows a slowly increasing readiness field, beginning approximately 1 s prior to movement onset, constituting the magnetic equivalent of the readiness potential (Cheyne and Weinberg, 1989). This is followed by transient changes, likely associated with *movement-evoked field* components observed at the same latencies in the MEG sensors during movement execution over a period of about 300 ms after EMG onset (Cheyne et al., 1997; Kristeva et al., 1991). Interestingly, there are no concomitant changes in oscillatory power in the mu and beta band during these movement-evoked responses, and beta ERS begins well after this activity has completely subsided, suggesting that induced rhythms in the mu and beta band and evoked motor fields likely reflect different underlying generators and functional roles in movement preparation and control.

Sensorimotor oscillatory phenomena observed during motor tasks are also elicited by somatosensory or tactile stimulation alone (Bauer et al., 2006; Cheyne and Gaetz, 2003; Gaetz and Cheyne, 2006; Pfurtscheller et al., 2001) and neural populations in both primary motor and somatosensory cortex, located in the precentral and postcentral gyrus, respectively, likely act as local and somewhat independent generators of rhythmic activity within very similar frequency bands. From a neuroanatomical perspective, this should perhaps not be surprising given that postcentral parietal and somatosensory areas contribute up to 40% of the descending pyramidal tract (Rothwell, 1994) and there are also afferent inputs to precentral motor cortex (Lemon, 1979). Thus, even though MEG source imaging methods can identify separate oscillatory activity arising from these distinct sensorimotor regions, they should be viewed as part of a highly integrated system involving both descending motor output and proprioceptive and other haptic feedback involved in the ongoing control of movement. For brevity, the following sections will focus primarily on oscillatory activity associated with motor tasks, although many of these phenomena may be observed during somatosensory input that, in turn, may reflect activation of somatosensory feedback pathways that are also recruited during movement.

Sensorimotor rhythms

It has long been known that movements elicit frequency specific changes in the EEG (Chatrian et al., 1958; Gastaut, 1952; Jasper and Penfield, 1949) and changes in spectral power in the mu¹ (8–14 Hz) and beta (15–30 Hz) frequency bands can be observed during both voluntary (Leocani et al., 1997; Pfurtscheller and Aranibar, 1977) and passive movements (Cassim et al., 2001). The exact functional role of

¹ Note on terminology. Rhythmic activity in the alpha (8–14 Hz) range observed over the region of the Rolandic fissure is variably referred to as *central alpha* or *mu* band activity, although the latter refers more specifically to the mu rhythm originally described by Gastaut (1952). The mu rhythm is thought to be specific to the sensorimotor cortex with a more irregular waveshape and higher in frequency than the classic alpha rhythm observed over the occipital cortex. To avoid confusion, the term mu will be used throughout to refer to all activity in the 8 to 14 Hz range arising from motor areas.

sensorimotor mu and beta rhythms is not well understood. Sensorimotor cortex oscillations, particularly in the beta band, have been shown to be generated by local field potentials within the motor cortex of non-human primates (Kilavik et al., 2011; Murthy and Fetz, 1992; Sanes and Donoghue, 1993) and to be only loosely time-locked to specific phases of motor output, and therefore indicative of non-specific aspects of sensorimotor integration (Murthy and Fetz, 1996). One interpretation is that they are epiphenomenal and simply reflect background or 'idling' rhythmic activity in neuronal populations (Pfurtscheller et al., 1996) that are disrupted during movement, or enhanced during periods of cortical inhibition following movement (Chen et al., 1998). Alternatively, the rebounding of beta activity after movement onset has been suggested to reflect the processing of somatosensory feedback as it is elicited by passive movements and abolished by temporary deafferentation (Alegre et al., 2002; Cassim et al., 2001). The observation that beta-band rebound exhibits frequency specificity related to the body part being moved has led to speculation that the frequency of oscillation might reflect the extent of the cortical area activated, and in turn the dynamics of a local cortical oscillatory network (Pfurtscheller and Lopes da Silva, 1999). Others have speculated that these oscillations may reflect perceptual "binding" in the motor system analogous to that found for gamma band oscillations in the visual system (Marsden et al., 2000). Alternatively, sensorimotor oscillations have been suggested to reflect a type of *sensorimotor sampling* (MacKay, 1997) in which sensory input necessary for the guidance of movements can be more efficiently combined with synchronously firing neuronal populations involved in motor output. Others have speculated that sensorimotor oscillations may reflect a type of *recalibration* or interrogation of the 'system-state' after each movement (Riddle and Baker, 2006). The fact that *pre-movement* oscillatory activity arises from regions of the postcentral gyrus indicates that the primary somatosensory cortex (SI) is active during movement preparation in the absence of sensory input. As mentioned, a significant portion of the corticospinal tract originates in the postcentral gyrus, and these neurons project largely to the dorsal horn of the spinal cord where they are thought to be involved in the descending control of sensory inputs or even the 'gating' of proprioceptive input during movement (Lemon and Griffiths, 2005). This may explain why very similar oscillations can be produced in these brain regions by tactile stimulation alone. In this context, it should be considered that many studies of self-paced movements' movement tasks typically require orientation of the hand to a button or similar triggering device, and thus often involves to some degree integration of haptic information needed to perform the movement accurately from trial to trial. Thus, oscillatory activity in the motor cortex during such tasks may reflect the monitoring of various parameters of the motor system (hand position, muscle length), even prior to the onset of simple ballistic movements, and stresses the need to control for these parameters during any task involving motor responses. As will be discussed later, attention and other cognitive processes also play a role in the modulation of rhythmic activity in sensorimotor regions and similarly may reflect sensory gating mechanisms involved in motor preparation or anticipation of sensory input.

MEG studies of mu and beta oscillations

The first recordings of magnetic fields accompanying simple finger movements were reported by Deecke et al. (1982) who observed slow magnetic field changes (*readiness fields*) over sensorimotor areas of the brain preceding voluntary movements of the digits using a single-channel magnetometer. Sensorimotor rhythmic activity using MEG was first reported by Hari and colleagues (Tiisonen et al., 1989) using a 24-channel magnetometer, who demonstrated that these rhythms arose from regions of the sensorimotor cortex using dipole modeling of the narrow-band filtered signals. In a recent MEG study (Jurkiewicz et al., 2006) we used the SAM beamformer

algorithm to identify the cortical generators of changes in the mu and beta frequency bands during self-paced finger movements. Suppression of mu band (8–15 Hz) activity preceded movement onset, and localized bilaterally to regions of the postcentral gyrus (Fig. 2A). Power in the beta band (15–30 Hz) also decreased prior to movement onset but showed a marked sudden increase beginning approximately 300 to 400 ms after termination of EMG activity and lasting for over 500 ms. This *post-movement beta rebound* (PMBR) also localized to bilateral regions of the precentral gyrus, but with greater lateralization to the contralateral hemisphere. These findings corroborate earlier MEG studies, which demonstrated that dipole sources localized to mu and beta activity tended to localize to postcentral or precentral locations, respectively (Hari et al., 1997; Salmelin and Hari, 1994). In addition, PMBR appeared to be time-locked to the cessation, rather than the onset of movement and may constitute an *off-response* to the termination of sustained afferent or reafferent input to the primary motor cortex (Cassim et al., 2001). As noted, these oscillatory changes are often similar in frequency and location to that found during peripheral nerve stimulation (Hari et al., 1997) or tactile input (Cheyne et al., 2003; Gaetz and Cheyne, 2006).

Sensorimotor oscillations have been shown to have a somatotopic organization for different movements as well as frequency specificity (Pfurtscheller et al., 1997; Stancak et al., 2000) although it is unclear whether this reflects activation of different neural networks or the

spatial extent of the activated area (Pfurtscheller and Lopes da Silva, 1999). Using SAM beamformer analysis, we were able to demonstrate the somatotopic organization of PMBR for hand and foot movements (Fig. 2B), with a slightly higher mean frequency for foot dorsiflexions compared to finger movements (Cheyne and Gaetz, 2003). Although the somatotopy of sensorimotor cortex oscillations suggest the activation of neural populations corresponding to the involved muscle groups, it should be noted that the hand representation area of motor cortex is often co-activated with movements of other body parts (Gaetz and Cheyne, 2006), including overt speech movements (Saarinen et al., 2006). This meaning of this co-activation remains to be determined, but suggests that there are both specific and non-specific changes in motor cortex during movement, and that there may be cortical areas located in region of the hand representation area of the motor cortex that provides a more generalized function in motor control, perhaps related to its close proximity to dorsal premotor areas.

Beta oscillations: pharmacological effects and neuropathology

MEG has been used to study the role of various neurotransmitter systems in the generation of sensorimotor and other cortical rhythms. Jensen et al. (2005) demonstrated that augmentation of beta band

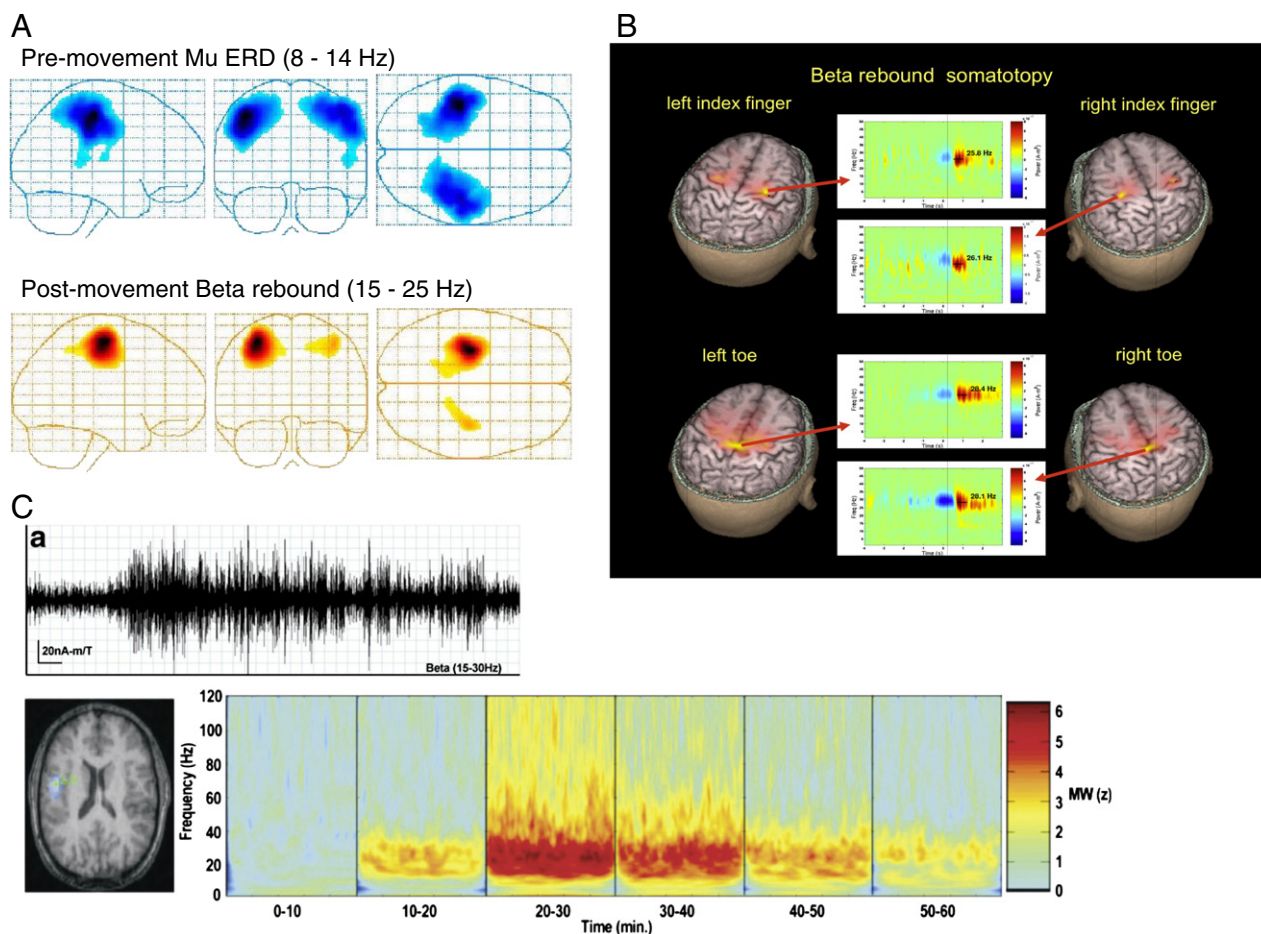


Fig. 2. (A) Group averaged SAM source images in 10 subjects performing right index finger movements, showing pre-movement mu band ERD (8–14 Hz, upper panel, blue shading) and post-movement beta band ERS or ‘rebound’ (15–25 Hz, lower panel, red shading). Adapted, with permission, from Jurkiewicz et al., 2006. (B) Somatotopy of beta rebound (single subject) showing beta ERS in bilateral hand motor areas for finger movements (upper panel) and more medial location of beta ERS for foot dorsiflexions (lower panel). Time-frequency plots show slightly higher frequency of ERS for foot movements compared to finger movements. (C) Spontaneous source activity in the motor cortex of a single subject over a one-hour period following administration of 5 mg of diazepam. Upper trace shows bandpass (15–30 Hz) filtered beamformer output. Time frequency plots below show integrated source power for selected time 10 min time windows showing power increase primarily in the beta frequency band during same procedure. Modified with permission from Hall et al., 2010, 2011.

activity by administration of a benzodiazepine, an agonist of the inhibitory neurotransmitter GABA, was localized to regions of the sensorimotor cortex with a concomitant shift in peak frequency, suggesting the direct involvement of GABAergic inhibitory interneurons in the generation of beta band oscillations. The influence of local GABA concentrations has recently been implicated in the generation of cortical rhythms in both visual and motor areas (Gaetz et al., 2011; Muthukumaraswamy et al., 2009). In recent studies by Hall and colleagues (Hall et al., 2010, 2011) it was shown that administration of 5 mg of diazepam resulted in marked enhancement of background beta oscillatory in the motor cortex lasting for 30 to 40 min (Fig. 2C). When taking into account these changes in baseline levels of beta activity it was found that task-related changes only in pre-movement beta suppression and not in post-movement beta ERS were modulated by administration of a GABA agonist. Thus, the role of specific neurotransmitter systems in the generation of beta synchronization in the motor cortex still remains unclear, and caution must be used in interpreting drug effects on task-related changes in oscillatory power due to changes in background activity. Nonetheless, these initial studies demonstrate the potential usefulness of combining MEG studies of cortical oscillations with pharmacological or other interventions in furthering our understanding of the underlying neurophysiological basis of sensorimotor rhythms and other brain activity (Singh, 2012).

There has been a long interest in the role of sensorimotor rhythms throughout the basal ganglia–cortical circuits in disorders of motor control such as Parkinson's disease (PD) and dystonia. For example, it has been suggested that excessively high beta band activity in basal ganglia structures may account for negative motor symptoms in both PD and dystonia (Amirnovin et al., 2004; Brown, 2003; Brown, 2007; Weinberger et al., 2009) and there is increasing evidence for the direct relationship between motor cortex and subcortical beta band oscillations (Brown, 2007; Tsang et al., 2012) suggesting that oscillatory activity in the beta band plays an important role in neural communication within these cortical–subcortical networks. This has led to theories that overall levels of beta oscillations act in an 'anti-kinetic fashion' promoting the maintenance of the current motor state (Engel and Fries, 2010; Gilbertson et al., 2005), and suppression of beta oscillations within these cortical–subcortical loops may have a general facilitatory effect on movement initiation (Jenkinson and Brown, 2011). Recent findings involving the use of direct (transcranial) electrical stimulation of the motor cortex have provided further support for a direct and frequency specific effect of cortex rhythmicity on motor control (Feurra et al., 2011; Joundi et al., 2012). MEG is known to be limited in its ability to image activity in deeper brain structures due to an exponential drop in signal strength with distance from the sensor array. This lower sensitivity, combined with the fact that the organization of neurons in subcortical structures such as the thalamus and basal ganglia may produce less coherent intracellular current flow due to the orientation of the neurons, raises questions as to the degree to which one can image subcortical activity using MEG. However, it can be shown that, in principle, such recordings may be possible with sufficient sampling (Attal et al., 2007) and the detection of oscillatory activity in the cerebellum using MEG has been reported in specific cases (Mohamed et al., 2011; Schnitzler et al., 2006; Wilson et al., 2010). Nonetheless MEG can provide detailed information regarding cortical oscillatory activity in these patient groups, particularly when combined with beamforming methods that can suppress artifacts due to stimulating devices or other non-cephalic sources of magnetic interference (Cheyne et al., 2007; Litvak et al., 2010; Wong and Gordon, 2009). For example, Litvak et al. (2011) were able to demonstrate resting state coherence in the beta band between the subthalamic nucleus and frontal brain regions in Parkinson's patients that could also be increased by dopaminergic medication. This suggests that use of MEG source imaging of cortical oscillations can provide important information regarding both the underlying etiology of motor disorders in

terms of the presence of pathological oscillations, as well as the effects of medications or other therapeutic interventions such as deep brain stimulation on this activity (Connolly et al., in press). MEG measures have also been recently combined with the use of transcranial magnetic stimulation and intracranial EEG to study changes in motor cortex function in epilepsy patients (Ibrahim et al., 2012; Makela et al., in press; Tarapore et al., 2012).

Gamma band oscillations in motor cortex

Although the majority of neuroimaging studies have focused on the more widely known lower frequency rhythms in the alpha/mu or beta frequency bands, there has been increasing interest in the presence of higher frequency (> 30 Hz) gamma oscillatory activity within the human motor system. Although gamma band activity has been more frequently implicated in perceptual binding of multiple inputs within sensory systems (Engel and Singer, 2001) it is now apparent that movements can also elicit a very specific form of transient, narrow-band oscillatory activity in the 70 to 90 Hz range. It should be noted here that the term *gamma band* is often used very generally to refer to neural activity extending from 30 Hz up to 100 Hz or higher, leading to some confusion in the literature when referring to movement-related gamma band activity. Gamma activity in the lower frequency range, particularly around 40 Hz, has been associated with a variety of higher order cognitive functions (Tallon-Baudry and Bertrand, 1999). This activity tends to be more spatially distributed, and may be apparent only with integration over large time and frequency windows (Pesaran et al., 2002). Gamma band activity in motor cortex in the low (30 to 60 Hz) range has been reported during movement in intracerebral depth electrode recordings (Szurhaj et al., 2006) and ECoG recordings from motor and premotor areas (Brovelli et al., 2005; Miller et al., 2007; Pfurtscheller et al., 2003) as well as in MEG (Schoffelen et al., 2005; Tecchio et al., 2008; Waldert et al., 2008). However, for clarity this activity should be distinguished from the much more transient and narrow-band 70 to 90 Hz gamma oscillations observed within the primary motor cortex.

Crone et al. (1998) reported increased gamma activity in the electrocorticogram (ECoG) in awake patients performing sustained muscle contractions, noting that high-frequency (75–100 Hz) oscillations showed greater somatotopic organization and tended to be more time-locked to movement onset than lower frequency mu and beta rhythms. Pfurtscheller et al. (2003) have also shown highly focal gamma band oscillations in ECoG recordings overlying the contralateral primary motor cortex in the 70 to 90 Hz range (see Fig. 3C). Thus, invasive recordings in humans have confirmed the presence of gamma oscillations in cortical motor areas. As mentioned, EEG studies of high gamma activity can be hampered by muscle activity and other high-frequency artifacts, although more recently movement-related gamma activity has been reliably demonstrated in scalp EEG recordings (Ball et al., 2008; Darvas et al., 2010). In a recent study, we were able to demonstrate high-gamma band activity in the contralateral motor cortex during self-paced movements across a group of subjects for movements of different body parts (Cheyne et al., 2008). As shown in Fig. 3A, these consist of brief bursts of very narrow band induced oscillations, beginning roughly at movement onset and lasting 100 to 300 ms with a peak frequency in the 70 to 80 Hz range for finger movements. Unlike high-frequency oscillations (HFOs) associated with highly time-locked somatosensory stimulation, which are also detectable with MEG (Hashimoto, 2000), these gamma bursts are not phase-locked to any discernible event, such as movement onset, and are thus not visible in the narrow-band averaged response. In contrast to lower frequency sensorimotor rhythms, motor gamma activity appears to be strictly lateralized to the contralateral motor cortex and also more somatotopically organized showing homuncular distribution for movements of the upper and lower limbs (Fig. 3B), consistent with the focal distribution found in the ECoG (Crone et

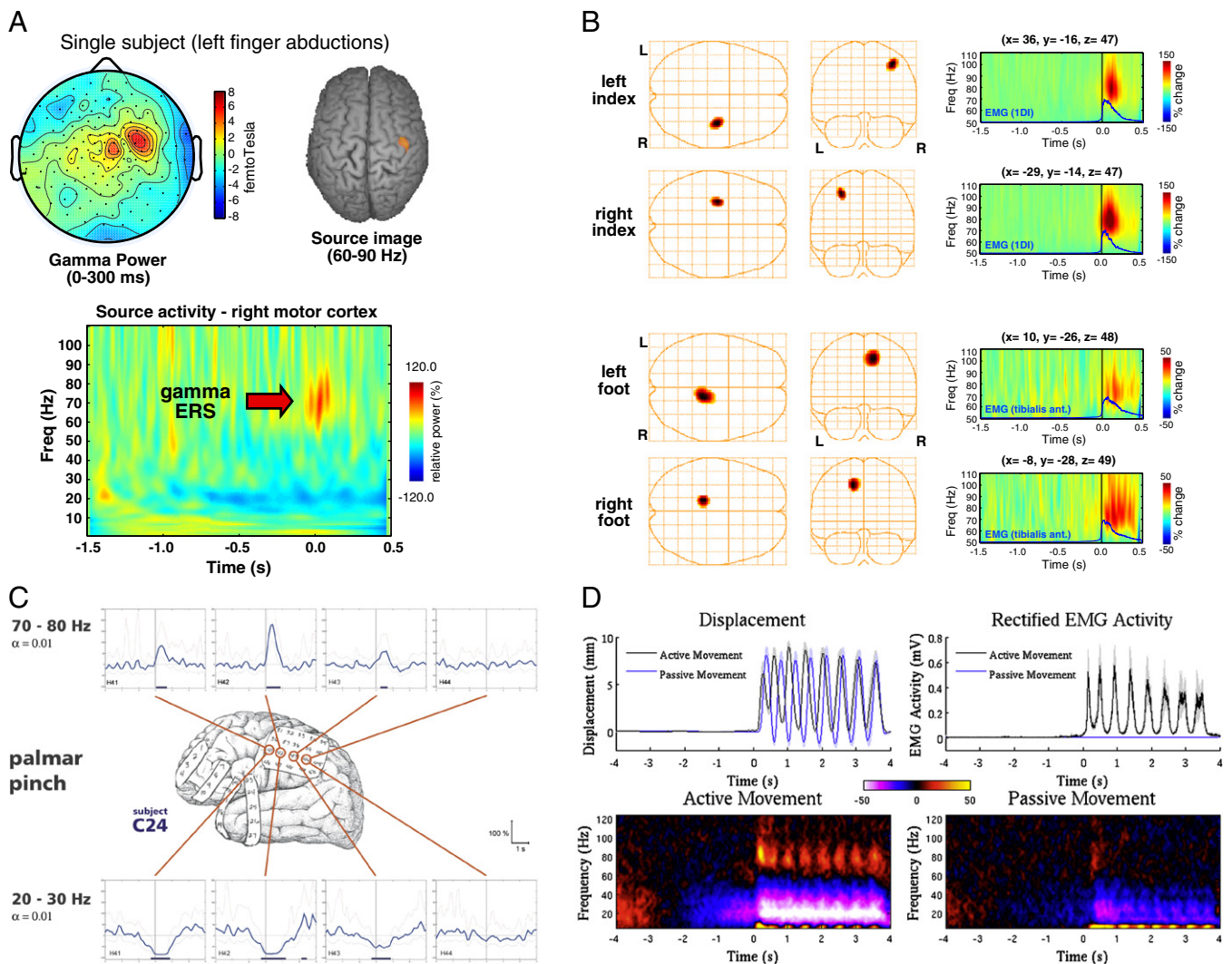


Fig. 3. (A) Gamma band responses during left finger abductions in a single subject. Topography of gamma source power (upper left) shows a dipolar field pattern over the motor cortex. SAM source localization of gamma power increase from a source in the right motor cortex, shown on the template MRI (right). Time-frequency plot shows brief burst of gamma band activity around 70 Hz immediately following EMG onset ($t = 0$ s). (B) Group source images of high gamma activity in 9 right-handed subjects showing somatotopic organization for both left and right index finger abductions and foot dorsiflexions. Group averaged time-frequency plots (right) show robust burst of gamma activity with slightly lower peak frequency for foot movements. Rectified EMG activity is overlaid (blue traces) showing that gamma activity peaks shortly after EMG onset. Adapted from Cheyne et al., 2008, with permission. (C) Electroencephalogram recordings of gamma and beta band activity overlying the motor cortex in an epilepsy patient showing similar time-course of 70–80 Hz activity restricted to the electrode overlying the precentral gyrus (adapted, with permission, from Pfurtscheller et al., 2003). (D) Gamma band activity in motor cortex during repetitive active and passive movements. Finger displacement and associated rectified EMG activity is shown in upper plots. The corresponding source activity is shown below. Note gamma activity shows bursts corresponding to individual movements, while beta band activity shows sustained activity. This activity dissipates for passive movements at the same rate. Adapted, with permission, from Muthukumaraswamy, 2010.

al., 1998; Pfurtscheller et al., 2003). These *motor cortex gamma* oscillations have been replicated in other MEG studies (Dalal et al., 2008; Tecchio et al., 2008). Muthukumaraswamy (2010) carried out a detailed MEG study of the effects of various movement parameters on motor cortex gamma, confirming that this activity was observed for both cued and voluntary movements and closely time-locked to active movement, but not simply related to somatosensory feedback, as individual gamma bursts were observed during sequential movements, but not during passive movements of the finger at the same rate (Fig. 3D).

The functional role of high gamma oscillations in motor cortex during movement is unknown. It is clear that these oscillations are markedly similar in frequency and latency to those observed in various subcortical structures during movement execution, including the subthalamic nucleus (Alegre et al., 2005; Amirnovin et al., 2004; Lalo et al., 2008) and globus pallidus (Tsang et al., 2012). Thus, high gamma activity in MI during movement onset appears to be

widespread throughout the basal ganglia and thalamocortical networks, including the subthalamic nucleus, which receives direct input from the motor cortex (Brown, 2003). This led us to speculate that gamma bursts in motor cortex observed in the MEG may reflect disinhibition of movement via the indirect pathway of the basal ganglia cortical loop – i.e., “releasing of the brake” to initiate individual movements (Cheyne et al., 2008). This facilitative effect of high gamma activity on movement is supported by a recent report on the ability of direct stimulation of motor cortex at gamma frequencies to reduce reaction times (Joundi et al., 2012), opposite to the effect found for stimulation at beta frequencies. We also noted in our MEG study that there was a marked similarity in gamma oscillations observed in the left and right motor cortices for movements of the same body part within each subject. For example, subjects that had very large amplitude and time-locked gamma bursts for left-sided index finger movements had similarly robust gamma activity for right-sided finger movements and often with identical peak

frequency. We suggested that this might be taken as evidence of a common underlying generator or network for MI gamma oscillations in different hemispheres for left and right-sided movements, rather than local, independent oscillatory networks in MI, and suggestive of a common subcortical driver of these rhythms. Similarly, gamma oscillations showed a lower mean gamma frequency for foot movements in comparison to upper limb movements, possibly reflecting different oscillatory networks for upper and lower limb movements that are independent of side of movement. However, further studies are needed to establish the causal links between cortical and subcortical high gamma band activity.

In summary, high frequency gamma oscillations observed in the MEG during movement onset appear to be elicited during all types of movement in the absence of any specific cognitive or perceptual process. One would therefore predict the presence of high frequency gamma activity in MEG or EEG recordings overlying primary motor areas, particularly in the 70 to 80 Hz range, during any task that involves ongoing movement or manual responses. Similarly, small movements elicited during seizure activity may also be associated with high gamma activity in motor areas that might be confused with abnormal high frequency oscillations in the gamma range. Thus, care should be taken not to confuse movement evoked high frequency gamma activity with high frequency oscillations that may be more typically related to cognitive or other neural processes.

Corticomuscular coherence

The previous sections described changes in the amplitude or power of sensorimotor rhythmic activity during various aspects of motor control. However, it is well-known that oscillations in motor cortex, particularly in the beta frequency band, can demonstrate coherence with electromyographic activity in the periphery during sustained motor contractions, suggesting a possible role in direct corticospinal drive to the muscle. Using a single channel magnetometer, Conway et al. (1995) made the fundamental observation of increased coherence between the surface electromyogram activity in a contracting muscle and MEG recordings made over the contralateral motor areas. Subsequently, there has been an extensive amount of research on MEG–EMG or *corticomuscular* coherence (CMC) and the functional relationship between spontaneous cortical rhythms and EMG activity during movement (Baker et al., 1999). Changes in the frequency of coherence varies with the strength of muscular contraction (Brown et al., 1998) and MEG studies have shown changes in CMC frequency in patients with Parkinson's disease (Salenius et al., 2002; Timmermann et al., 2003).

Patterns of corticomuscular coherence are usually observed during extended periods of muscular contraction. This is in part due to the fact that relatively long sampling periods are required to compute reliable estimates of coherence. Hence the relationship of CMC to specific phases of discrete voluntary movements is unknown. Recent MEG studies have shown that CMC was related to task-specific aspects of movement (Kilner et al., 2000) and was abolished during the phasic part of movement relative to a hold phase suggesting that it may be related to dynamic adjustments of force. Using the DICS beamformer, Gross et al. (2005) demonstrated increased CMC in multiple cortical areas during movement. Increases in coherence between EEG recordings over motor cortex and the EMG has been shown for transient movements in the beta band and coincident with periods of beta ERS (Feige et al., 2000). Periods of increased CMC have also been shown to correlate with the level of attention to motor performance (Kristeva-Feige et al., 2002) or readiness to respond in a reaction time task (Schoffelen et al., 2005) indicating a role in higher-order aspect of motor control. In addition to coherence in the beta band, CMC can be observed at higher gamma band frequencies, particularly during dynamic movements (Omlor et al., 2007). It should be noted that CMC in the 40 Hz range is also observed during

sustained isometric contractions, also known as the “Piper” rhythm (Brown et al., 1998), although it has recently been shown that this activity does not show the same time course as 70–80 Hz motor cortex gamma, which subsides rapidly during sustained contractions, demonstrating that these oscillations are not simple harmonics of each other (Muthukumaraswamy, 2011).

Sensorimotor oscillations and cognitive processes

It is well known that sensorimotor rhythms are strongly modulated during simple voluntary movements. However, these rhythms are also modulated during a variety of cognitive tasks involving cued motor responses, particularly tasks that involve selective responding or inhibitory control. In most cued tasks, suppression of mu and beta power typically begins *following* presentation of the imperative “go” cue. Interestingly, this activity, particularly in the beta band, has been shown to exhibit a faster return to baseline on inhibited or withheld trials in go/no-go tasks (Swann et al., 2009; Zhang et al., 2008) suggesting that beta suppression may index the timing of motor preparation in such tasks. However, EEG studies have shown the onset of beta suppression over motor areas can precede imperative cues to respond when they are predictable (Alegre et al., 2003). Studies have shown increased beta suppression when the response hand or movement parameters are known in advance of a go cue (Doyle et al., 2005; Tzagarakis et al., 2010; van Wijk et al., 2009) or when speed is emphasized over accurate responses (Pastotter et al., 2012). In recent MEG study by Tzagarakis et al. (2010) subjects were pre-cued as to the number of possible targets to which a directed hand movement had to be made. The target location was indicated 1 to 1.5 s later as a go cue. By time-locking changes in beta activity over motor areas to the pre-cue or to the go cue it was shown that beta band suppression followed onset of the pre-cue and reached the same level of decreased power at movement onset for all conditions, however, the level of beta suppression during the post-cue interval decreased with the number of targets, i.e., with increasing uncertainty of the upcoming movement, suggesting that beta suppression may index the degree to which the process of selection of a motor response amongst a number of alternatives has been completed (Fig. 4A). This is similar to the finding reported by Donner et al. (2009) in which beta suppression became increasingly lateralized over a pre-movement period during a perceptual discrimination, indicating that a left or right hand response would be made, suggesting that the degree of beta suppression was directly related to the decision process.

In a recent MEG study (Cheyne et al., 2012), we observed task-related changes in beta suppression during cued motor responses to a rapidly presented stream of digits, where subjects were required to respond to an infrequent target digit by switching response hands. Somewhat unexpectedly, bilateral suppression of beta oscillations in motor cortex began prior to presentation of the switch cue, indicating anticipatory preparation of both left and right responses. Moreover, reduced early suppression contralateral to the switch hand was predictive of switch errors, suggesting that early motor preparation was critical for successful switching (see Fig. 4B). These findings support the hypothesis that beta band suppression may reflect a state of *motor readiness* to respond, and that this preparation becomes automated in speeded response tasks that may enhance the ability to respond rapidly to cues for multiple responses, at the expense of biasing response selection.

It should be noted that many of the forgoing studies involve paradigms in which modulation of sensorimotor rhythms were elicited by appearance of a pre-movement cue, which may be related to internal selection of different motor outputs, as well as the need to suppress prepotent responses that may be induced by differing response probabilities. However, beta suppression following choice response cues occurs even on trials in which no motor response is ultimately

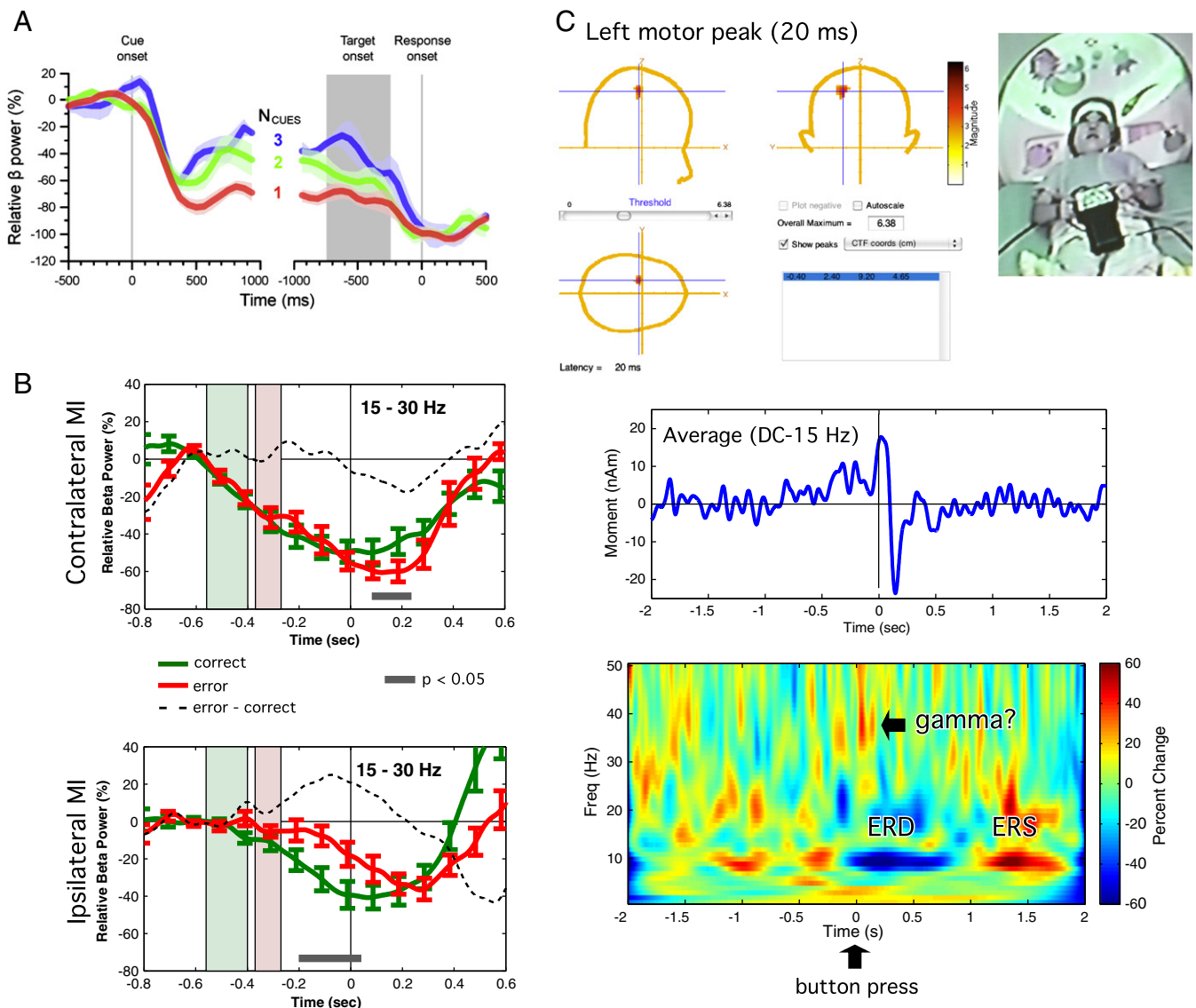


Fig. 4. (A) Time course of beta band power from MEG sensors located over the contralateral motor cortex in a group of subjects making movements to 1–3 different spatial targets, time-locked to cue onset (left), and movement onset (right) following the target onset (ISI = 1 to 1.5 s). Gray rectangle indicates range of target onset times. Red, green and blue traces indicate whether 1, 2 or 3 potential targets were presented. See text for details. Reproduced, with permission, from Tzagarakis et al., 2010. (B) Change in beta band power in the contralateral (left) and ipsilateral (right) motor cortex in 12 subjects performing a speeded response-switching task for correct trials (green traces), error trials (red traces) and their difference (dotted traces). Green and red rectangles indicate range of stimulus onset times for correct and error trials, respectively. Periods of significant differences between correct and error trials indicated by gray bars. Adapted from Cheyne et al., 2012, with permission. (C) MEG activity during a motor task in children using a customized MEG system for pre-school aged children (Yokogawa Electric Corp). Top right: 4 year-old subject in MEG system performing a motor task. Top left: Source localization of motor activity in MEG coordinate system for 3–1/2 year old boy. Time course of source activity is shown below: Upper plot: time-locked average of 95 movements (DC–15 Hz) showing pre-movement (readiness field) beginning 1 s prior to button press. Lower plot: time–frequency activity from the same location showing slightly delayed mu and beta band suppression (ERD) followed by an increase in power (ERS). A weak burst of gamma activity at movement onset can be observed around 35 to 40 Hz.

made. Recalling that motor imagery, action observation, or even directed spatial attention can modulate sensorimotor rhythms, beta band suppression to choice-response cues emphasizes the need to distinguish the role of sensorimotor rhythms in motor preparation per se, as opposed to processing of sensory information or other cognitive processes that may activate these neural populations. A recent MEG study by Fujioka et al. (2012) demonstrated that amplitude of sensorimotor beta oscillations could be passively entrained by periodic auditory stimulation, suggesting that the motor system is passively recruited during the perception of rhythm without any associated motor response. Although it remains to be determined if these beta modulations play a causal role in processing sensory input, or simply reflect a predilection of the sensorimotor system to become rhythmically entrained, there is increasing evidence that

task-related changes in beta oscillations in the motor system may play a more general role in cognitive processes, such as the predictive timing of sensory input (Arnal and Giraud, 2012), in addition to their role in anticipatory motor planning and response selection.

Attention and sensorimotor rhythms

The effect of attention on sensorimotor rhythms has been demonstrated in selective attention tasks using MEG, largely in the mu or alpha band, although changes in the gamma band have also been reported (Bauer et al., 2006), and more predominantly in somatosensory cortex. A number of MEG studies have shown decreases in mu band power in SI contralateral to the attended hand during a variety of somatosensory stimulation tasks (Bauer et al., 2012; Dockstader

et al., 2010; Jones et al., 2010; Popovich et al., 2010; van Ede et al., 2011). These changes are presumed to be more related to somatosensory processing (Pineda, 2005) than motor processes, although it raises the question of whether beta band changes prior to movements in some selective response tasks may reflect shifts in directed spatial attention to the moving hand. However, a recent EEG study demonstrated that lateralization of beta band amplitude was influenced more by the side of movement than the side of directed spatial attention (Doyle et al., 2005). Recent computational modeling studies by Jones and colleagues (Jones et al., 2009, 2010) have proposed possible neural mechanisms underlying the effects of attention on mu rhythm amplitude in sensorimotor cortex, based on the relative timing of feedforward and feedback inputs from thalamus and other cortical regions. Their model also accounts for relative levels of mu and beta oscillations within the same brain region, as well as correlations between background mu rhythm and the amplitude of sensory evoked responses (Jones et al., 2009). An alternative hypothesis is that sensorimotor oscillations in the mu frequency band reflects the role of cortical activity within the alpha frequency range which acts as a global brain mechanism for shifting neural processing to task-relevant brain regions (Jensen and Mazaheri, 2010; Womelsdorf and Fries, 2006). It has also been proposed however, that slightly different mu or alpha band rhythms may exist within the sensorimotor cortex that may differentiate more general attentional mechanisms from the engagement of motor networks (Pfurtscheller et al., 2000) and similar frequency specificity has been proposed for beta oscillations during cue expectancy versus motor preparation (Kilavik et al., 2011).

Changes in mu band activity can also be seen during both motor imagery (Mellinger et al., 2007; Neuper et al., 2006) and action observation (Cheyne et al., 2003; Hari et al., 1998; Virji-Babul et al., 2008, 2010), suggesting that the mu rhythmicity in somatosensory cortex can be modulated by a variety of cognitive processes in the absence of either sensory input or motor execution, and may also signal the engagement of mirror-neuron systems (Hari et al., 2000; Virji-Babul et al., 2008). Although the functional relationship between movement-related rhythms and modulations of mu activity in the absence of overt movement needs to be clarified, clearly the sensorimotor mu rhythm appears to have a functional role in attention and other mental processes related to anticipation of sensory events, or even motor learning, and likely involves interactions between the sensorimotor system and other brain networks.

Sensorimotor oscillations and brain development

As described in the foregoing sections, significant progress has been made in our understanding of the functional mechanisms and behavioral significance of oscillatory activity of the human sensorimotor system, with an increasing contribution of MEG imaging techniques. However, to date there are relatively few studies of how these processes change with development. This is in part due to the technical challenges associated with neuroimaging studies in young children, due to increased head movements, poorer visual fixation, and the difficulty in getting young children to perform complex motor tasks. Functional MRI studies in very young children in particular are hampered by the low tolerance for even small head movements and the intimidating environment of the MRI scanner for very young children. EEG studies in children in certain age groups can also pose issues of compliance due to the time-consuming and somewhat invasive process of electrode application, although the introduction of electrode cap technology eliminating the need to abrade the skin makes EEG recordings possible even in infants (Tucker, 1993). For example, recent EEG studies have shown decreases in the mu band during both overt motor activity and action observation, indicating that modulation of the mu rhythm exists in infants as young as 9 months of age (Marshall et al., 2011; Southgate et al., 2009).

In the case of MEG, the main obstacle for developmental studies is the fixed size of the helmet-shaped sensor array, which is designed to accommodate adult-sized heads. However, MEG may have some advantages over other imaging modalities, as the lack of need to apply electrodes reduces setup times, the recording environment is quiet and much less intimidating than an MRI scanner, and small amounts of head movement can be tolerated. Nonetheless, there are relatively few MEG studies of motor activity in children to date, and these have mostly involved older children or adolescents. Wilson et al. (2010) examined MEG activity during flexion-extension movements in ten children and adolescents ranging in age from 8 to 15 years. Movements were timed to the position of a rotating target to avoid sensory responses to cue onset. Similar to adult studies, beamformer spatial filtering revealed typical ERD and ERS patterns in the beta band within the primary motor cortex, as well as high (80 Hz) gamma band activity in contralateral motor cortex. They also noted additional activation of the supplementary motor area and ipsilateral cerebellum, leading the authors to speculate that a more widespread network is activated during movements in children, although the small number of subjects and large age range in this study makes it difficult to relate these differences to a specific stage of neural development. Huo et al. (2011) studied a larger cohort of 60 children ranging from 6 to 17 years of age and reported high gamma ERS in motor cortex over a broad frequency range (65–150 Hz). They also reported more frequent ipsilateral gamma ERS in the younger children, although they used an alternating left/right response task which might have partly contributed to the ipsilateral activation. MEG recordings of cued finger movements in children 4 to 6 years of age were reported by Gaetz et al. (2010) who compared sensorimotor oscillations in these children with adolescents and adults. Both beta and gamma band changes were observed in the two younger groups, however beta band changes, particularly beta rebound during the post-movement period, was markedly reduced in the children.

MEG studies of motor function in young children may be of particular interest as many of the neural systems that underlie cognitive and other brain functions undergo dramatic changes in the first few years of life. Although motor cortex regions mature at relatively rapid rates relative to other brain regions (Giedd et al., 1999; Huttenlocher, 1979), there is evidence that various parts of the motor system, including inhibitory connections between hemispheres continue to develop in early life. Transcranial magnetic stimulation (TMS) studies have shown that motor evoked potentials (MEPs) can be elicited only after two years of age following myelination of the descending corticospinal tract, however ipsilateral MEPs are also observed in children prior to the age of 10, which are presumably suppressed in adults once transcallosal inhibitory pathways are fully developed (Nezu et al., 1997). This may underlie similar age-related changes in the development of fine motor skills, along with the disappearance of mirror movements at around the same age (Mayston et al., 1999). ERP studies (Chisholm and Karrer, 1988) have shown changes in the topography and polarity of the readiness potential with age, with early pre-movement activity emerging after the age of 6 years as positive potential, and developing into the negative slow shift observed in adults only after 9 or 10 years of age (Chiarenza et al., 1995).

Although MEG measurements in younger children are technically challenging, studies of motor cortex function during development may provide an ideal avenue for the investigation of brain development. In particular, the study of early brain development in children under the age of 6 or 7 years of age is largely lacking in cognitive neuroimaging, due to the limitations of neuroimaging techniques such as fMRI, resulting in a developmental 'gap' in our knowledge of brain development (Poldrack, 2010). Towards this goal, we recently initiated a study of movement related brain activity in children 3 to 5 years of age with colleagues at Macquarie University in Sydney. We used an MEG system customized for pre-school children (Johnson et al.,

2010) to measure brain activity during a videogame-like task where children pressed a response button with their left or right hand in a quasi-regular fashion to shoot objects (cookies or wands) at cartoon images that slowly appeared on a computer screen at random intervals. Movement-related fields in sensorimotor regions, including mu and beta band modulations, as well as contralateral high gamma oscillations were observed in all children, providing evidence that these sensorimotor rhythms are present at an early age. An example is shown for a 3 1/2 year old boy in Fig. 4C, demonstrating mu, beta and gamma band changes during movement. However, the observed patterns of oscillatory activity in these younger children differ from the typical adult pattern, with a delayed and greater dominance of mu band relative to beta band modulation. In addition, contralateral high gamma band ERS was observed at movement onset, but often at a lower frequency than that typically observed in adults. These preliminary results suggest that cortical motor networks demonstrate development changes in preferred oscillation frequencies, possibly due to changes in cortico-subcortical or intracortical connectivity. Although more studies need to be done, and will be enhanced by the further development of specialized MEG instrumentation for recordings in young children, these examples demonstrate the usefulness of MEG source localization methods for the non-invasive measurement of motor cortex oscillations in during motor and cognitive tasks, particularly in developmental populations.

Summary

MEG studies of sensorimotor cortex oscillations have advanced over the last three decades and remain a rapidly growing area of research. With the increasing prevalence of advanced MEG instrumentation in both research and clinical settings, this area of research will continue to expand, with the increasing application of MEG measurements to the study of both normal and pathological oscillatory brain activity in humans. The increasing interest in the role of neural synchrony in communication within distributed neuronal networks will also provide new and important analysis tools with which to study rhythmic brain activity and the role it plays in sensorimotor integration. As a highly non-invasive method, MEG also provides a means with which to study the maturation of motor systems in early human development, which can potentially provide exciting new clues regarding the neurogenesis and functional role of cortical motor rhythms.

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