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Understanding bimanual coordination across small time scales from an electrophysiological perspective

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Authors' contributions

LMRD and ESJ share first authorship; SPS and AD share last authorship. LMRD, ESJ and SPS developed the general framework for this review. All authors contributed to manuscript writing.

Highlights

- Comprehensive review of studies on bimanual coordination using EEG/MEG.

- Inter- and intra-hemispheric connectivity patterns characterize bimanual tasks.
- Connectivity patterns reveal modulations of inter-hemispheric inhibition.
- EEG/MEG measures as correlates of task demands, laterality, and instability.

Abstract (max 170 words)

Bimanual movement involves a variety of coordinated functions, ranging from elementary patterns that are performed automatically to complex patterns that require practice to be performed skillfully. The neural dynamics accompanying these coordination patterns are complex and rapid. By means of electro- and magneto-encephalographic approaches, it has been possible to examine these dynamics during bimanual coordination with excellent temporal resolution, which complements other neuroimaging modalities with superb spatial resolution. This review focuses on EEG/MEG studies that unravel the processes involved in movement planning and execution, motor learning, and executive functions involved in task switching and dual tasking. Evidence is presented for a spatio-temporal reorganization of the neural networks within and between hemispheres to meet increased task difficulty demands, induced or spontaneous switches in coordination mode, or training-induced neuroplastic modulation in coordination dynamics. Future theoretical developments will benefit from the integration of research techniques unraveling neural activity at different time scales. Ultimately this work will contribute to a better understanding of how the human brain orchestrates complex behavior via the implementation of inter- and intra-hemispheric coordination networks.

Keywords (max 12)

Electroencephalography (EEG), magnetoencephalography (MEG), bimanual coordination, functional connectivity, polyrhythms, motor learning, event-related potentials (ERPs), event-related (de)synchronization (ERD/ERS), coherence, phase synchronization.

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List of acronyms

ACC	Anterior cingulate cortex
BP	Bereitschaftspotential
CNV	Contingent negative variation
EEG	Electroencephalogram
EMG	Electromyogram
ERD/S	Event-related (de)synchronization
ERP	Event-related potentials
fMRI	Functional magnetic resonance imaging
M1	Primary motor cortex
MEG	Magnetoencephalogram
MP	Motor potential
MRCP	Motor-related cortical potential
NS	Negative slope
PET	Positron emission tomography
PMC	Pre-motor cortex
PMd	Pre-motor dorsal
PPC	Posterior-parietal cortex
pre-SMA	Pre-supplementary motor area
RAP	Reafferent potential
ROI	Region of interest
rTMS	Repetitive transcranial magnetic stimulation
S1	Primary somatosensory cortex
SMA	Supplementary motor area
TMS	Transcranial magnetic stimulation

Introduction

When typing a text, the fingers of both our hands are placed over the keyboard. Without looking at them, we move the fingers sequentially over small distances. Then letters, words, and eventually sentences appear on the screen. Next to semantic and syntactic processes, and the generation of coherent thoughts, a well-learned coordination pattern between both hands is in full operation in the brain. This goal-directed behavior requires the swift integration of perception, action, and cognition.

This is just an everyday example of the diversity of accurate upper limb movements performed with seemingly little to no effort. Prior to movement, spatial and temporal requirements need to be encoded in the central nervous system. Feedback from the senses allows for updating the codes to correct movement. What mechanisms are supporting this encoding for coordination of the upper limbs? A broad network of brain regions is linked to the coordination of both hands, including (but not limited to) the primary motor cortex (M1), pre-motor cortex (PMC), supplementary motor area (SMA), cingulate motor area, basal ganglia, and cerebellum (e.g. Jantzen et al., 2008; Swinnen and Wenderoth, 2004). More demanding tasks are associated with activations extending towards prefrontal, parietal, and temporal areas (e.g., Gross et al., 2002; Hardwick et al., 2012; Swinnen, 2002; Swinnen and Wenderoth, 2004). However, our knowledge on how these brain areas modulate their activity as a function of task demands and task features is still fragmentary. Degree and extent of brain activation is also determined by the skill level of the performer, as functional magnetic resonance imaging (fMRI) studies on training-induced plasticity have shown (Debaere et al., 2004b; Puttemans et al., 2005; Rémy et al., 2010; Ronsse et al., 2011). However, even though fMRI studies have generated considerable insights into the spatial distribution of brain activity, information about the temporal organization of brain activity (particularly at small time scales) can be obtained with electroencephalography (EEG) and magnetoencephalography (MEG).

The synchronized firing of neurons and neuronal populations is believed to add to the transmission of information at a short-range, i.e. within a single brain region, but also supports long-range communication between distant regions (Engel et al., 2001; van Wijk et al., 2012a).

Synchronization is typically described by common parameters of oscillations, like amplitude (spectral power), frequency, and phase, as well as by their bivariate counterparts, like cross-amplitude correlation (coherence) and relative phase, and more recently, the phase-amplitude coupling. The time scale of synchronization is often prescribed by the (frequency of) oscillation underlying it, which can be in the order of tens or hundreds of milliseconds. These time scales demand recording techniques with high temporal resolution. When studying whole brain activity, this calls for EEG/MEG. Other imaging methods which assess metabolic changes, such as fMRI and near-infrared spectroscopy (NIRS), are much less sensitive to these quick modulations.

EEG/MEG studies have addressed the planning and execution of bimanual movements, using different methodological approaches. There are various analysis strategies to extract information from EEG/MEG signals but, unfortunately, there is no consensus about their implementation. This might complicate the understanding for the naïve experimenter. The purpose of the current review is two-fold. First, we will provide a concise overview of behavioral studies on bimanual coordination and magneto- and electroencephalographic studies to better understand this area of research. This includes a sketch of the essentials of encephalographic recordings and the corresponding signal analyses that have been applied to bimanual protocols. Second, we discuss selected EEG/MEG literature on bimanual coordination, executive functions examined with bimanual paradigms, and motor learning. We clarify the terminology and offer a critical view at commonalities and disagreements across studies.

Both temporal and spatial parameters of movement constrain the movement repertoire of an individual limb and the range and coordinative stability in bimanual movements. Most EEG/MEG research on bimanual coordination has focused on the timing between the effectors (e.g. fingers or wrists), be that through relative phase (coordinative accuracy and stability) or other temporal measures. Therefore, we start with describing seminal temporal features of bimanual coordination from a behavioral perspective - for a more in depth review, see, e.g., Beek et al. (2002).

1. Temporal features in bimanual coordination

When looking at the temporal characteristics of movements, one often discriminates between discrete and rhythmic ones. Unfortunately, the border between discrete and rhythmic movements is not as well defined in motor control research as one may wish, because many researchers use these terms without proper formality. Reaching a target is considered a discrete movement, but reaching a key in the piano while performing a series of rhythmic tapping movements might not be that easy to label. Traditionally, three possibilities have been proposed (Howard et al., 2011; Huys et al., 2008; van Mourik and Beek, 2004): First, discrete movements are considered fundamental units of behavior, with rhythmic movements being strings of discrete movements; Second, rhythmic movements are fundamental units, with discrete movements being truncated rhythmic movements; and third, rhythmic and discrete movements are mutually exclusive classes. The distinction between these movement classes might be more important than appears at first sight as the neural generators may differ (Schaal et al., 2004).

In an attempt to introduce more mathematical formality to motor control research, Hogan and Sternad (2007) defined discrete movement as a movement preceded and succeeded by postures, in which posture refers to a bodily configuration defined by a period of no movement. By contrast, they considered rhythmic movements as a generic class of behaviors with several sub-types, ranging from strictly periodic to repetitive, corresponding to the degree of periodicity (Hogan and Sternad, 2007). For instance, finger tapping at low frequencies comprises a series of discrete movements whereas finger wiggling and circle drawing are rhythmic movements. A discrete movement becomes quasi-oscillatory (and therefore, rhythmic) with increasing frequency, which is the case for finger tapping at high frequencies (Huys et al., 2008; Repp, 2011).

Accordingly, and for the sake of simplicity, the trajectory of a rhythmic uni-dimensional movement in steady state (e.g. flexion/extension of a finger, a wrist, or forearm) can be approximated as a merely sinusoidal oscillation:

$$y(t) = A \cos(2\pi ft + \varphi)$$

Where A is the amplitude of movement, f is its frequency (i.e. how fast the limb moves), and φ is the (Fourier) phase of movement that may be identified via the point at the trajectory at which the movement starts. In the simplest case these parameters are considered constant. In the study of coordinative stability, however, amplitude and phase are modified to depend on time t . Assessing bimanual coordination then requires the study of two traces: $y_1(t)$ for the left hand and $y_2(t)$ for the right hand.

Seminal for studying stability of bimanual coordination are rhythmic isofrequency movements with both hands moving at the same frequency, i.e. $f_1 = f_2$. Then, the relative phase between the motions of the limbs, $\Delta\varphi = |\varphi_1 - \varphi_2|$, is a temporal parameter often used to characterize default coordination modes. Humans show a tendency towards the so-called in-phase coordination (i.e. $\Delta\varphi = 0^\circ$) that often concurs with a simultaneous activation of homologous muscles, or anti-phase (i.e. $\Delta\varphi = \pi$ or 180°), which concurs with alternated activation of homologous muscles (Beek et al., 2002; Kelso, 1984, 1995). In-phase and anti-phase coordination modes are relatively stable compared to intermediate phase patterns that are more difficult to perform and require extensive practice to learn (Kelso, 1984; Swinnen et al., 1997b; Treffner and Turvey, 1995; Zanone and Kelso, 1992). However, anti-phase coordination becomes unstable with increasing movement frequency, which may lead to spontaneous (unintended) transitions to in-phase coordination (Byblow et al., 1994; Carson et al., 2000; Carson et al., 1997; Haken et al., 1985; Kelso, 1984; Summers, 2002; Swinnen, 2002; Swinnen et al., 1997a; Temprado et al., 2003).

More complicated are non-isofrequency movements and/or coordination modes where the relative phase diverges from the preferred in- and anti-phase patterns, as it is the case when playing the drums. These movements often require some practice to be performed skillfully (Debaere et al., 2004b; deGuzman and Kelso, 1991; Kovacs and Shea, 2011; Lee et al., 1995; Puttemans et al., 2005; Remy et al., 2008; Ronsse et al., 2011; Serrien and Brown, 2003; Sisti et al., 2012; Swinnen et al., 1997a; Zanone and Kelso, 1992). Here we focus on polyrhythmic movements, with both hands moving at different frequency, $f_1 \neq f_2$, which obey a certain rational ratio with integer numbers

$f_1: f_2 = n:m$ ¹. There are different levels of difficulty for different frequency ratios. For instance, the ratios 2:3 or 3:5 are more difficult to perform than 1:2 or 1:3 (Deutsch, 1983; Peper et al., 1995a; Peper et al., 1995b; Summers et al., 1993). Similar to anti-phase to in-phase transitions in isofrequency movements, increasing the tempo of movement while trying to keep the same frequency ratio induces shifts to simpler finger tapping ratios in polyrhythmic movements (Haken et al., 1996; Peper et al., 1995a).

Special interest has been devoted to non-isofrequency patterns requiring continuous movements besides finger or wrist flexion/extension (Kovacs et al., 2010; Mechsner et al., 2001; Sisti et al., 2011; Walter et al., 1997). In a task where subjects learned to overcome temporal and spatial constraints by rotation of two dials with the hands, higher frequency ratios (3:1) required more training than lower relative frequencies (1:1, 2:1, 2:3) (Sisti et al., 2011). To explain their findings, Sisti et al. (2011) stressed the specific nature of the task: a circular and continuous movement without a salient event, and the use of a continuous cue defining speed. In particular, the associated timing of this movement is suspected to emerge from the intrinsic properties of the movement (i.e. emergent timing) rather than being cued by a discrete signal like in most polyrhythmic tapping studies (i.e. event timing).

Event and emergent timing are considered qualitatively different control processes. They have been proposed to maintain a consistent rate for the timing of both discrete and rhythmic movements (Ivry et al., 2002; Zelaznik et al., 2005). Event timing control involves a temporal representation of the target interval or posture between two events in discrete movements marked by salient events, such as finger tapping (Ivry et al., 2002). On the other hand, emergent timing does not require an explicit representation of the interval duration, but rather arises from the dynamics of trajectory control in rhythmic movements, such as circle drawing (Spencer et al., 2003; Turvey, 1977). Converging literature has reported the neural correlates underlying these two timing processes. Event timing was shown to rely on the cerebellum, as patients with cerebellar lesions failed to maintain temporal accuracy during discrete tasks, such as unimanual tapping, while performing equally to healthy subjects during circle drawing (Spencer et al., 2003). Alternatively, emergent timing may rely on inter-

¹ Note that the corresponding (generalized) relative phase in that case is given by $\Delta\varphi_{nm} = m\varphi_1 - n\varphi_2$.

hemispheric interactions through the corpus callosum. During bimanual finger tapping, callosotomy patients respected the temporal cue, but failed to do so when drawing circles (Kennerley et al., 2002; Ridderikhoff et al., 2005).

2. The use of EEG/MEG techniques in movement coordination

From behavioral research, we shift now towards encephalographic methods used to investigate the neural correlates of upper limb movement. Using electrodes placed on the scalp, EEG measures non-invasively the postsynaptic activity of thousands of pyramidal neurons. EEG detects coherent signals elicited by patches of cortical surface of a few square centimeters (Cooper et al., 1965). Due to the spatial alignment of these cortical neurons, their electrical potentials add up, which accounts for the measured voltages over the scalp (Nunez and Silberstein, 2000). The resulting mean electrical activity is attenuated and spreads across the head tissue, being detected by more than one electrode, a phenomenon referred to as volume conduction – see Michel and Murray (2012) for a recent review. Hence, not only the spatial alignment of neurons limits what can be measured by EEG, but also confounding activity from other populations that may contaminate the signal-of-interest. Put differently, activity generated by small neuronal populations cannot be discriminated, as it has lower amplitude than noise.

Changes in (pre- or post-) synaptic potentials typically come with dendritic currents that induce magnetic fields perpendicular to the current flow. By placing magnetometers outside the head, it is possible to measure fields oriented radially from the center of the head, i.e. MEG technology. Electric currents tangential to the scalp are the main source of these magnetic fields (Lau et al., 2008) – pyramidal cells generating these currents are primarily located in the sulci. Compared to EEG, magnetic fields are less attenuated by the variation in conductivity of the surrounding tissue; therefore, estimations of the biophysical parameters of the surrounding tissues can be less stringent (Cheyne, 2013). By the same token, however, the magnetic field is less damped than the electric potential rendering the aforementioned volume conduction a challenge for subsequent analyses (e.g., Nolte et al., 2004; Stam et al., 2007).

The following section presents several EEG/MEG methods and summarizes some major findings of neural markers for upper limb coordination. Traditionally, event-related potentials (ERPs)² have been investigated, which provide information on voltage changes at a millisecond scale. From this sole time domain description, we switch to the time-frequency domain to study the event-related (de)synchronization (ERD/S) in characteristic frequency bands of EEG/MEG, which reveals the involvement of neural oscillations in bimanual coordination and other tasks. In order to enhance the spatial resolution from EEG/MEG data, advanced mathematical models of source localization have been proposed, which are also briefly sketched. Finally, we present some methods to address one of the critical challenges in neuroscience referring to brain connectivity which has attracted increasing interest due to its potential to reveal basic insights into the mechanisms underlying various pathologies.

2.1 Event-Related Potentials

ERPs are voltage changes in response to a specific stimulus or event (Brandeis and Lehmann, 1986). They are time- and phase-locked to a certain event, i.e. the response has the same phase for every repetition of the stimulus. ERPs are considered EEG markers of cortical information processing generated by a stimulus (Kotchoubey, 2005). The event-related signal is extracted from ongoing brain activity by averaging the EEG across epochs which are time-locked to the stimulus onset. This requires the repetition of the same experiment several times to improve the signal-to-noise ratio, as it is assumed that the noise is randomly distributed across trials and that the response is stationary in a statistical sense, i.e. the statistical parameters of the signal do not change over time. Latencies and amplitudes of ERPs correlate with function and are modulated by the type of event, level of arousal, age, and pathologies (Gazzaniga et al., 2013; Leiser et al., 2011; Polich, 2007).

Movement-related cortical potentials (MRCPs) are elicited during preparation and execution of movement. The *self-initiated MRCP* consists of a series of potentials starting a couple of seconds before movement onset and lasting up to a few hundred milliseconds after movement onset (Cui and

² In the case of MEG one speaks of event-related fields (ERFs) instead of ERPs but for the sake of legibility we here restrict ourselves to the latter.

Deecke, 1999; Kornhuber and Deecke, 1965; Shibasaki et al., 1980). Approximately two seconds before movement onset, a bilateral negative potential is found over centro-parietal areas, called early Bereitschaftspotential (BP) (Deecke et al., 1976; Kornhuber and Deecke, 1990). This component is assumed to be generated in the pre-SMA, SMA, and lateral PMC. The early BP is followed by a steeper negativity, approximately 400 ms closer to movement onset, namely late BP or negative slope (NS). Late BP during hand movements is found over the contralateral central area to the moving limb, being generated in contralateral M1. At the movement onset, the negative wave (see Figure 1.A), called motor potential (MP), reaches a minimum over the contralateral-central area, presumably generated in M1. The response finalizes with a positive potential, named re-afferent potential (RAP) 300 ms after movement onset and is supposedly generated in the primary somatosensory cortex (Bötzel et al., 1997; Shibasaki and Hallett, 2006).

Insert Figure 1 about here

The MRCP generated by cued unimanual and bimanual movements is different from the self-initiated MRCP described above, as reported in a number of studies (Gerloff et al., 1998; Jankelowitz and Colebatch, 2002; Smith and Staines, 2006; Smith and Staines, 2010; Smith and Staines, 2012). *Cued MRCP* shows the same temporal pattern as spontaneous MRCP with a slow negativity of a couple of seconds before movement onset, a sharp negativity close to movement and positive deflection after movement. However, the neural sources differ. At the sensor level, additional activation over the fronto-central area (presumably over the SMA) in preparation of self-initiated movements compared to cued movements was reported (Gerloff et al., 1998). Similarly, EEG source localization showed that the early cued MRCP is generated in the contralateral premotor area, unlike the early BP in self-initiated movements which is generated in the SMA (Smith and Staines, 2012). Accordingly, an fMRI study reported involvement of the SMA in self-initiated movements and involvement of the dorsal and ventral premotor cortex in cued movements (Debaere et al., 2003), consistent with the distinction between internally- and externally-generated movements (Goldberg,

1985). Smith and Staines (2012) reported that late MRCP and RAP in cued movements are generated in the same areas as late BP and RAP in self-paced movements.

Next to the MRCP, the contingent negative variation (CNV) is another component of interest that is associated with the anticipation of movement in cued movements. CNV is also called the ‘expectancy’ wave as it is related to anticipation, attention, motor preparation, and task requirements (Jahanshahi and Hallet, 2003; Nagai et al., 2004). This component is elicited by a stimulus that contains information on the type of movement to be performed (pre-cue), followed by a waiting period, and finally, a second stimulus indicating the start of movement (response stimulus or go-cue). This cue is used as a temporal reference, and the waiting period between the pre-cue and the go-cue is the interval where CNV is elicited. This potential is centered on the scalp and broadly distributed (Cui et al., 2000). Unlike the cued MRCP, which is time-locked to movement onset, CNV is time-locked to the response stimulus and hence reflects higher-order processes related to anticipation in addition to motor preparation. Invasive recordings showed that the prefrontal cortex and the pre-motor dorsal (PMd) area generate CNV (Hamano et al., 1997; Ikeda et al., 1999). In particular, PMd is linked to action selection during motor preparation, as shown in studies on monkeys (Halsband and Passingham, 1985) and humans (Grafton et al., 1998). Furthermore, in a repetitive transcranial magnetic stimulation (rTMS) study, perturbation to PMd induced changes in CNV, confirming its link to motor preparation (Lu et al., 2012). The duration of the underlying process of CNV is still undefined, given that every study uses different time intervals between the pre-cue and response signal (Deiber et al., 2005).

2.2 Event-Related (De-) Synchronization

ERPs rely on the hypothesis that an electrical response follows a spatio-temporal pattern across the scalp that is phase-locked to the stimulus. In the absence of a stimulus or task, neural oscillations at different frequencies occur spontaneously. At the moment of the event, the phase of these oscillations may be reset, resulting in a spatio-temporal pattern that can be non-phase-locked to the stimulus. This information is lost in the averaging process of ERPs. Both phase-locked and non-phase-locked oscillations to the stimulus are visible with time-frequency analysis of individual trials (e.g., Bastiaansen et al., 2012) (see Figure 1.B). Event-related local increases in synchronization of

neuronal populations are seen by EEG/MEG as increases in power for a specific frequency band with respect to a baseline, and are named event-related synchronization (ERS); local decreases are called event-related desynchronization (ERD) and are associated to increases of neural activity (Pfurtscheller and Lopes da Silva, 1999). It has been proposed that ERS at lower frequencies (<40 Hz) is generated by a larger neuronal population than ERS at higher frequencies (Pfurtscheller, 2001). Synchronized activity generated by a larger neuronal population would indicate no differentiation of tasks and therefore no information processing within the neural population (Pfurtscheller and Lopes da Silva, 1999; van Wijk et al., 2012a).

Characteristic frequency bands or rhythms commonly involved in motor tasks in EEG studies are alpha or mu (8-12 Hz) and beta (12-30 Hz) over the central area, and gamma (>30 Hz) over the post-central and pre-frontal area. Alpha and beta ERD are most prominent for signals over the sensorimotor areas for imaginary movements (Neuper et al., 2005; Pfurtscheller et al., 2006), real hand movements (Pfurtscheller and Neuper, 1994; Stančák Jr. and Pfurtscheller, 1995) and observed movements (Rizzolatti et al., 2001). Mu ERD/S is thought to be generated by the interaction of thalamo-cortical relay neurons and reticular nucleus neurons (Lopes da Silva, 2006). On the other hand, beta oscillations are modulated by performance as demonstrated by its correlation to electromyogram (EMG) signals of the limbs (Kristeva et al., 2007; Salenius et al., 1997). Experimental work suggests that the beta rhythm is primarily visible in the sensorimotor cortex, though modeling work suggests its origin in cortico-thalamic loops (Aburn et al., 2012; Lopes da Silva, 2010; Moran et al., 2007; Salmelin and Hari, 1994). The relevance of the beta band during movements has been repeatedly emphasized across studies (Gross et al., 2005; Mima et al., 2000; Serrien and Brown, 2002; Serrien et al., 2003). Increasing frequency of movements reduces modulation of beta band over the centro-lateral area (Boonstra et al., 2006) and more specifically in M1 (Houweling et al., 2010a). The behavior of alpha/mu and beta rhythms differs at movement cessation, when muscles relax: beta ERS or beta 'rebound' appears over the central electrodes, whereas the mu rhythm remains attenuated (Neuper and Pfurtscheller, 2001). In a rhythmic movement at high frequency, cycles of beta ERD followed by ERS start to overlap, hindering performance (Houweling et al., 2010a).

Unlike alpha/mu and beta bands, ERS in the gamma band has been associated with an increase of cortical activity (Pfurtscheller et al., 1994; Steriade et al., 1996). Gamma ERS occurs 1 to 1.5 s before movement and lasts for the duration of the movement (Salenius et al., 1996). Similar to the relation between beta power and EMG, the gamma band over the post-central area, specifically at around 40 Hz, shows high coherence with muscle activity (Salenius et al., 1996). In a study using invasive recordings, the wide gamma band was divided into two parts: low gamma (35-50 Hz) and high gamma (75-100 Hz) (Crone et al., 1998). Low gamma ERS was elicited after movement onset and remained synchronized during movement. High gamma ERS began before movement and it regained baseline values before completion of movement. Compared to alpha and beta responses, gamma responses are more somatotopically specific. The gamma band has been linked to sensorimotor integration (Sanes and Donoghue, 1993) and has been proposed as the means by which the brain integrates diverse features of percepts (Senkowski et al., 2008).

2.3 Source estimation

Temporal and spectral features of electric or magnetic signals measured outside the head provide vast information about the activity of brain areas. However, the neural sources generating these signals are not directly available from EEG/MEG measurements and advanced methods are required to estimate the location of sources and the strength of their activity. Several configurations of neural sources could generate a similar distribution of electrical potentials over the scalp. That is, there is no unique solution to the problem of source localization, referred to as the “inverse problem” (see Figure 1.C). Assumptions about the physiology and the biophysics of the brain can help constraining estimates. First of all, a head model that defines the geometry and accounts for the conductivities of the different tissues (i.e. brain tissue, skull and scalp) is required. This allows for defining a so-called lead field that provides the possible transfer function from sources in the brain to sensors outside the brain. However, even with a properly defined lead field, source localization remains a challenge. A variety of methods have been proposed (for reviews, see Hillebrand and Barnes, 2005; Lopes da Silva, 2004; Michel et al., 2004; Wendel et al., 2009).

It is difficult to localize activity of deep brain structures by EEG/MEG given that the electrical signal is attenuated when being transmitted through the tissues, and that the magnetic field is reduced by the inverse of the squared distance. Computational and clinical studies state that EEG is more sensitive to deep brain structures than MEG (Ahlfors et al., 2010; Malmivuo, 2012; Wendel et al., 2009). However, there are MEG reports claiming activity to be originating in subcortical structures (Attal et al., 2012; Gross et al., 2002; Martin et al., 2006).

2.4 Connectivity

ERPs and ERD/S provide information about the electrical/magnetic activity occurring at a local spatial scale, within a brain region. More recently, the interaction between brain regions during a task or during rest has become a major focus of research. Synchronization of regions, i.e. long-range synchronization, might be the core of a dynamic organization in the nervous system (Fries, 2005). This long-range (or global) synchronization, often identified as functional coupling, can be obtained at the sensor level and the source level. The latter is primarily realized using MEG for studies on bimanual coordination (see Tables 1- 3).

Widely used measures in EEG/MEG studies are coherence and phase coherence (phase locking or phase synchronization) between signals at the sensor level. Coherence represents the correlation between two signals as a function of frequency (and time). Traditional approaches build on spectral analysis (coherence is the normalized modulus of the cross-spectrum between two signals) while phase coherence often employs the analytic form of the (band-pass filtered) signals, which yields a unique definition of the relative (Hilbert) phase as a function of time. This relative phase is then assessed through circular statistics (Mardia, 1972).

Most EEG studies on bimanual coordination opt for a region of interest (ROI) approach at the sensor level to estimate the coherence. The ROIs consist of pairs of electrodes in the left and right hemisphere (intra-hemispheric), pairs between left and right hemispheres (inter-hemispheric), and pairs in the central region (midline).

Theoretically, the coherence between two signals is not statistically independent from the spectral power of each signal, possibly inflating coherence values (Porges et al., 1980). However,

experimental findings have reported non-significant contributions of spectral modulations to changes in coherence, which suggests that this connectivity measure reflects synchronization at a large scale (Ford et al., 1986; Gross et al., 2005; Serrien and Brown, 2002; Serrien, 2008, 2009a, b, d).

Furthermore, there is no intrinsic relationship between global synchronization and ERD/S, as opposite responses due to a stimulus are possible at a large scale, although these synchronization measures cannot be distinguished on a small scale (up to one centimeter) (Fell and Axmacher, 2011). Caution should be taken as there is no standardized approach to the terminology used in neurophysiological studies with a tendency to equate neural activity (e.g. ERD/S) to functional connectivity (e.g. long-range synchronization or coherence) (Cohen and Gulbinaite, 2013).

Intra- and inter-hemispheric coherence is increased during movement compared to rest (Ford et al., 1986). Increases in beta coherence (and decreases in alpha power) were related to task difficulty in internally versus externally paced tasks (Gerloff et al., 1998), and in complex versus simple finger sequences (Manganotti et al., 1998). Note that decreases of alpha power indicate increased activity over the sensorimotor areas, whereas increases of beta coherence point to a rising flow of information between the hemispheres to execute a difficult task (Andres and Gerloff, 1999; Gerloff et al., 1998).

As stated above, connectivity analyses of estimated sources are more common in MEG studies. Relevant to bimanual coordination, two methods have been predominantly used. One method resembles the strategy of fMRI analysis, whereby connectivity measures can be calculated as interactions between regions with high task-related activity. Phase synchronization between the estimated sources is then defined by the variability between the phase time course of sources (Houweling et al., 2010a; Houweling et al., 2008b) – see, e.g., Boonstra et al. (2006) for estimates at the sensor level. The second method does not rely on sources with high activity levels to estimate the coupling, but on coherent sources to an external signal, usually the EMG signal of the effector of interest (Gross et al., 2001; Pollok et al., 2007).

Hand movements are accompanied by coherent activity at the alpha frequency in a broad network encompassing bilateral primary sensorimotor cortices (S1-M1) and PMC, contralateral PPC and thalamus, and ipsilateral cerebellum (Gross et al., 2005; Pollok et al., 2005a). Enhancement of phase synchronization in the beta band between bilateral M1s was observed during unimanual tasks

compared to rest but no significant differences were found (van Wijk et al., 2012a). Here we focus on cortico-cortical interactions. Studies on cortico-muscular interactions can be found elsewhere (e. g., Kristeva et al., 2007; Muthuraman et al., 2012; Salenius and Hari, 2003; van Wijk et al., 2012b).

The methods described in this section reflect the evolution of EEG/MEG analysis which goes hand in hand with better computational resources. From scalp to sources, and from neural activity to connectivity, these measures reflect the neural dynamics underlying bimanual coordination.

3. Dynamics of bimanual coordination measured with EEG/MEG

By combining behavioral and electrophysiological approaches, important insights into the neural control of bimanual movements have been obtained over the past decades. Among the studies on bimanual coordination, the stage of movement under study is closely related to the method applied. ERPs are mostly used to study preparatory and initial stages of movement, whereas ERD/S and connectivity analysis are mostly applied during movement execution. In the preparatory stage, an abstract intention is first defined, followed by a more detailed plan of *what* movement is executed, *when* and *whether* it should be executed, i.e. the ‘what, when, and whether’ components of intentional action (Brass and Haggard, 2008). This is followed by the initiation of movement that is often disregarded in the literature. During execution of movement, a continuous mechanism for control and error correction is involved to stabilize performance, according to the skill level of the performer (Ridderikhoff et al., 2008), which is of utmost importance for rhythmic movements.

Given the different mechanisms underlying behavior and the applied methods, EEG/MEG studies on planning and initiation of bimanual movements are discussed first, subsequently followed by studies of the execution phase of (ongoing) bimanual movements. An important consideration is that many EEG studies generally assume that the electrodes overlying a brain region measure activity directly below it, without estimating the sources, as seen in column “S”, which is absent in Table 1 and mostly empty in Tables 2 and 3. In order to differentiate results from sensor and source level analysis, the former will be referred to by the scalp areas and their corresponding brain regions, as described by the respective authors.

3.1 Movement planning and initiation

Several EEG/MEG studies have focused on motor preparation and initiation of unimanual movements from several seconds before movement onset to a couple of seconds after (Bötzel et al., 1997; De Vico Fallani et al., 2012; Jankelowitz and Colebatch, 2002; Shibasaki et al., 1980; Stancák Jr and Pfurtscheller, 1996; van Wijk et al., 2009). The same stages prior to movement onset have been largely overlooked for bimanual movements, and therefore the following summary of studies remains necessarily brief (see Table 1).

Insert Table 1 about here

Self-initiated bimanual movements are accompanied by larger BP and MP components than unimanual movements indicating the use of more neural resources to link both limbs (Kristeva et al., 1990; Urbano et al., 1998). BP in bimanual movements is not modulated by increasing the physical load exerted over the limbs, unlike unilateral movements in which load conditions elicit a larger BP than no-load (Kristeva et al., 1990). This difference might arguably illustrate bimanual modes to be of a ‘higher order’ than coding of unimanual or loading information. Moreover, larger amplitudes over the central region, especially over the midline might be misleading. Increased MP was found over the central area (presumably covering SMA) during bilateral movements (Urbano et al., 1998). Yet, the authors proposed that this could be due to the limitations of EEG to disentangle the signals coming from adjacent regions, such as the left and right SMA, especially if the analysis is restricted to the sensor space.

Similarities between bilateral and unilateral movements have also been reported. In self-initiated movements, there was an increase of negative potential over central (SMA) and centro-lateral (M1-S1) areas after movement onset compared to preparation, presumably denoting the feedback loop between the central nervous system and the sensory afferents for both bilateral and unilateral movements (Urbano et al., 1998). Additionally, onset times of MRCs did not significantly differ between bilateral and unilateral self-initiated movements (Urbano et al., 1998).

Cued movements have been studied in the preparatory stage as well, but instead of concentrating on the MRCP, the early and late CNV are the indexes of interest in this case. The early CNV has been found over the fronto-central area and appears to be influenced by the amount of information given in the pre-cue interval (Deiber et al., 2005; Gómez et al., 2003). This indicates its relation to orienting attention, task-specific motor processing and the selection of motor action. In another study, however, early CNV was not modulated by the pre-cue (Cui et al., 2000). Elicited closer to the response stimulus, late CNV showed a centro-parietal distribution indicating its relation to central motor programming and sensory-related anticipatory attention for the second cue (Deiber et al., 2005), also found for unimanual movements (Gómez et al., 2003), as shown by its absence in a non-motor task (Cui et al., 2000). Discrepancies in the findings of early CNV might be due to the different choice of intervals to divide the subcomponents of CNV: the late CNV's interval in the study of Cui et al. (2000) is approximately one second before the onset of the second stimulus, whereas the same interval is used for both early and late CNV in the study of Deiber et al. (2005).

Additionally, CNV and MRCPs have been studied jointly for uni- and bimanual movements. For both modes, the amplitude of late CNV is similar, whereas MP over centro-lateral areas seems to be reduced in bilateral compared to unilateral tasks (Taniguchi et al., 2001). The authors propose that MP's reduction causes the delay of bilateral responses in reaction time tasks by concomitant excitatory and inhibitory processes occurring between both hemispheres through callosal connections. A mutual inhibition of the wrong response between the sensorimotor cortices could explain the reduction of the potential.

3.2 Movement execution

To address the dynamics during continuous movement execution we now dwell on the following aspects. First, modulations of oscillatory patterns with increasing task demands are described for uni- and bimanual movements. Second, arguments defending the absence of symmetric control and the importance of the dominant hemisphere during bimanual movements are presented.

Third, insights into the spatio-temporal reorganization of unilateral networks linked to bimanual movements are provided via the study of patterns of behavioral instability.

3.2.1 Effect of task demands via coordination mode

The neural dynamics related to different coordination modes have been addressed with protocols manipulating the task demands whereby conditions are arranged from the easiest to the most difficult in the following order: unimanual right, unimanual left, bimanual in-phase, and bimanual anti-phase (see Table 2). Task difficulty can also be altered via acceleration of tempo, which has been studied in polyrhythmic movements. A linear ERD in the primary motor cortices is observed up to a tempo threshold, after which this linear relationship disappears (Houweling et al., 2010a). The acceleration of tempo allows for investigating neurophysiological correlates of stable and unstable behavior, and will be discussed later.

Insert Table 2 about here

Although a gradual increase of neural resources involvement is generally expected with increasing demand as found in several fMRI studies (Aramaki et al., 2006b; Debaere et al., 2004a; Jäncke et al., 1998; Mayville et al., 2002; Tracy et al., 2001; Wenderoth et al., 2005), similar neural dynamics in different levels of task difficulty have also been found in EEG/MEG studies. Several EEG/MEG studies described bimanual movements as requiring more effort and energy than unimanual movements (a so-called coordination effort). It has been suggested that this difference may stem from increases of inter-hemispheric coherence in the beta band (Serrien, 2009b, d; Serrien et al., 2003), increases of coherence between cerebellum and contralateral PMC (Pollok et al., 2005b), or stronger suppression of average spectral power across alpha, beta, and gamma bands (Gross et al., 2005). Interestingly, unilateral left and bimanual movements showed a similar decrease in alpha power, which was higher than for unilateral right movements, contrary to the expected gradual increase with task demands or the similarity between unilateral left and right limb movements (Deiber et al., 2001).

By contrast, it has been argued that the natural tendency to move the upper limbs simultaneously overtakes unimanual movements (Daffertshofer et al., 2005; Holper et al., 2009; Serrien, 2008). In-phase movements (following the notation from Section 1, $\Delta\varphi = 0^\circ$) presented the lowest inter-hemispheric coherence in beta band compared to anti-phase ($\Delta\varphi = 180^\circ$) and unilateral movements, suggesting that bimanual in-phase coordination is the default mode associated with low effort, even lower than for unimanual tasks (Serrien, 2008). This line of thought is supported by TMS studies (Duque et al., 2005; Ferbert et al., 1992; Meyer-Lindenberg et al., 2002; Stinear and Byblow, 2002) and metabolic studies (Cuadrado et al., 1999; Holper et al., 2009)³.

Anti-phase movements are accompanied by an increased inter-hemispheric coherence in the beta band compared to in-phase movements suggesting an increase of neural communication for the former coordination mode (Serrien and Brown, 2002; Serrien et al., 2003). Decreases in this information exchange result in a deterioration of performance, as shown by reduction of inter-hemispheric connectivity with increasing movement frequency (Serrien and Brown, 2002). Additionally, increases in intra-hemispheric and midline connectivity in the beta band were found during the anti-phase mode (Serrien, 2008). In particular, midline connectivity was increased in the anti-phase coordination mode whereas in-phase and unilateral modes had similar values. Alternatively, the increasing frequency of movement was accompanied by higher lateral-midline connectivity during in-phase and anti-phase movements (Serrien and Brown, 2002).

This evidence shows that communication between the midline (presumably over the SMA) and the sensorimotor cortices is an expression of task demands, namely the type of coordination pattern and the speed at which it is performed. The importance of SMA involvement as a function of task complexity has been widely reported (Debaere et al., 2004a; Gross et al., 2005; Halsband et al., 1993; Lang et al., 1990; Pollok et al., 2007; Sadato et al., 1997; Serrien et al., 2002; Steyvers et al., 2003). Power analysis of beta at the source level has shown a higher decrease, which was associated with increased activity in SMA and left PMC during anti-phase movements in MEG studies (Gross et al., 2005; Pollok et al., 2007). Power decreases in the anti-phase coordination mode might be

³ References to studies using TMS, fMRI and other modalities are presented as a broad guide to the reader. A deeper analysis of these techniques is beyond the scope of this review.

explained by the same mechanism subserving syncopation in unimanual tasks. Syncopation consists of executing a movement in out-of-phase or off-beat to an external stimulus. Beta suppression was reported for unimanual tasks in syncopation (off-beat) to an external stimulus compared to synchronization (on-beat) (Chen et al., 2003; Mayville et al., 2001).

Contrary to the expected differentiation between in- and anti-phase movements, an MEG study reported similar average levels of overall power of the dominant M1 (i.e. left M1 for right-handed subjects) for both coordination modes (Gross et al., 2005), supporting fMRI findings (Aramaki et al., 2006b). On the contrary, the non-dominant (right) M1 was modulated by the task, with higher power during unimanual tasks and gradually decreasing with in-phase and anti-phase movements, indicating increased activity. In addition, differences in the left hemisphere for anti-phase movements were reported, specifically at narrow frequency bands: Decreased power (i.e. increased activation) during anti-phase movements compared to in-phase was found in the left PMC and SMA at 20 Hz, and in the left S1-M1 at 10Hz (Pollok et al., 2007). This lends support to the dominance of the left hemisphere during bimanual movements, as discussed in the next section.

Functional coupling in the alpha band between cerebellum, thalamus, PPC, PMC, S1-M1 and SMA has been reported during bimanual movements in MEG studies (Pollok et al., 2007; Pollok et al., 2005a; Pollok et al., 2005b), partially corroborating fMRI studies (Debaere et al., 2004a). Interestingly, the anterior cingulate cortex (ACC) has been considered part of the network involved in anti-phase movements but not in in-phase movements (Pollok et al., 2007). ACC has been extensively linked to attentional control (Carson and Kelso, 2004), error monitoring/detection (Bush et al., 2000), and particularly, to the execution of movements that deviate from the preferred mirror or in-phase patterns along the longitudinal axis (Wenderoth et al., 2005). Therefore anti-phase movements require involvement of higher-order processes in addition to basic motor control.

At subcortical level, Pollok et al. (2007) found decreased activity in the alpha band (increased power) of the left cerebellum during anti-phase finger tapping using MEG, contrary to fMRI studies that reported activity increases in the cerebellum during anti-phase compared to in-phase movements (Debaere et al., 2004a; Nair et al., 2003; Tracy et al., 2001). All the employed fMRI protocols consisted of continuous wrist cycling, which might involve different neural mechanisms (as discussed

in Section 1) and might require more trajectory control than finger tapping, necessitating larger involvement of the cerebellum. The activity decrease in the left cerebellum of the study by Pollok et al. (2007) in addition to an increase of right cerebellar activation during finger tapping in an fMRI study (Ullén et al., 2003) provides evidence for the dominance of the right cerebellum during bimanual movements, which is expected as the spino-cerebellar tracts do not decussate as compared to the spino-cortical tract. Stronger inter-cerebellar coherence was found during in-phase movements (Pollok et al., 2007), supporting the controversial proposition that subcortical structures are more relevant than cortical structures during in-phase movements (Ullén et al., 2003).

Some authors have taken task manipulations a step further by challenging visuomotor congruence. A study of Serrien (2009a) involved coordination of spatial features by simultaneously drawing different shapes with each hand and using a mirror to reverse visual cues with respect to the limb. As described above for difficult compared to simple tasks (bi- vs. unimanual, or anti- vs. in-phase), intra- and inter-hemispheric coherence values were higher for more complex task (reverse visual cues) than for easy task conditions (normal visual cues). This shows that connectivity patterns of higher coherence are not restricted to coding of limbs or to spatial and temporal control of online motor coordination performance, but encompass ‘higher-order’ processes of visuomotor integration as already expected from behavioral studies (Mechsner et al., 2001). Interestingly, in the study of Serrien (2009a) only intra-hemispheric connectivity in the beta band of the dominant hemisphere was gradually increased as a function of task complexity. This hints at an asymmetric hemispheric contribution to bimanual movement control, as discussed in more detail next.

3.2.2 Hemispheric asymmetry for bimanual coordination

Movement control is not symmetric across hemispheres (Wyke, 1971). Various studies have indicated the supremacy of the dominant (left) hemisphere during performance of bimanual movements in right-handed individuals (Table 2). Power suppressions (higher activity) in the alpha band were stronger in the dominant (left) S1-M1 than in the complementary non-dominant brain areas during bimanual movements (Pollok et al., 2005b). Also, higher activation in the beta and alpha bands in the left PMC and left S1-M1, respectively, was found during anti-phase movements (Pollok et al.,

2007). This supports previous findings of the left hemisphere's contribution in the production of bilateral movements in fMRI (Jäncke et al., 1998) and PET studies (Viviani et al., 1998).

Cortical patterns of connectivity are not symmetric either. Intra-hemispheric coherence of the dominant hemisphere in the beta band appears higher in bimanual and right hand movements compared to left hand movements in an EEG study (Serrien, 2008). Additionally, MEG studies have reported higher coherence between dominant (left) S1-M1 and PMC (Pollok et al., 2005b), and between dominant M1 and SMA (Gross et al., 2005) than the homologous pairs in the non-dominant hemisphere. We would like to note, however, that one EEG study (Deiber et al., 2001) and one TMS study (Foltys et al., 2001) failed to provide evidence for hemispheric asymmetry during bimanual movements.

Other studies have applied alternative methods to elucidate the direction of information flow between hemispheres, thereby attempting to resolve the question regarding hemispheric supremacy during bimanual movements. According to Serrien et al. (2003) directed coherence is increased in the beta band from the dominant to the non-dominant hemisphere in bimanual tasks, whereas the opposite direction appears suppressed compared to rest. Interestingly, when only the left hand was loaded with a weight, this suppression of non-dominant to dominant drive was more pronounced. This reduction was accompanied by performance deteriorations along with larger decreases of drive from the dominant to non-dominant hemisphere. The authors proposed that the performance might have been reduced in the load condition on the left hand due to changes in the sensorimotor system or due to the incapability of the non-dominant hemisphere to drive bimanual movements even when the weight properties were altered on the non-dominant limb. However, inconsistencies in the direction of information flow between dominant and non-dominant hemispheres were also reported by Pollok et al. (2005b) using MEG.

3.2.3 Temporal modulation or spatial reorganization of neural networks: hints from instability

There is a current discussion in the literature on the functioning of neural networks during unimanual movements and how they change during bimanual movements. At least two different views

on the neural networks involved in bimanual coordination prevail in the current literature that may be summarized as follows. The *recruitment hypothesis* (or spatial reorganization of the networks) accounts for bimanual coordination by the enrolment of additional brain areas beyond the ones supporting unimanual action (Heitger et al., 2012; Theorin and Johansson, 2007). Put differently, the spatial distribution of the neural activity is expanded during bimanual tasks. Alternatively, the *temporal modulation hypothesis* considers that the regions involved in unimanual coordination are temporally modulated (or follow a different temporal pattern) to perform bimanual tasks without spatial reorganization (Daffertshofer et al., 2005; Koeneke et al., 2004; Walsh et al., 2008).

Whereas fMRI studies have provided evidence for the recruitment hypothesis (Aramaki et al., 2006a; Aramaki et al., 2006b; Debaere et al., 2001; Debaere et al., 2004a; Ullén et al., 2003), several EEG/MEG studies do indeed support the temporal modulation hypothesis. To elucidate the spatiotemporal reorganization characterizing bimanual tasks, Banerjee et al. (2012) designed a method to reconstruct EEG scalp distributions in bimanual tasks from unimanual responses. Brain activity during stable bimanual coordination, as measured with MRCs, could be understood as temporal modulation of unimanual networks (Banerjee et al., 2012). Several MEG studies support this argument. Cortical oscillations at the movement frequency in a polyrhythmic task indicated that the bimanual network is indistinguishable from a mere superposition of left and right unimanual networks during stable performance (Daffertshofer et al., 2000). In that case estimated sources from unimanual movements served as a template for sources of polyrhythmic bimanual movements. Additionally, the network involved in in-phase bimanual movements (Pollok et al., 2005b) was similar to the network involved in unimanual movements in the alpha band (although from different subjects) (Pollok et al., 2005a). However, the skill level of the performer is a confounding factor in this type of analysis. At initial stages of coordinating both limbs, a wider cortical area is recruited for executing the task; whereas at later stages after sufficient practice, the spatial pattern of neural activity can be reduced due to neuronal reorganization, entailing a combination of both hypotheses.

Temporal modulation of unimanual networks might be key to understanding bimanual coordination. As such, recent MEG studies solely rely on the identity between superimposed unimanual networks and bimanual networks to explain instability of bimanual movements

(Daffertshofer et al., 2005; Daffertshofer et al., 2000; Houweling et al., 2010a; Houweling et al., 2010b). In fact, behavioral instability due to increments of frequency has been reported for polyrhythmic movements (Daffertshofer et al., 2005; Houweling et al., 2010a). At the moment of instability, bilateral M1s showed a decrease of power at the movement frequency of the contralateral hand, as well as in the beta band, which was followed by an increase of power in M1 ipsilateral to the hand leading the instability. Notably, an increase in the power of the M1 ipsilateral to the unstable hand was predominant. Additionally, beta ERD was higher during unstable performance than during stable performance. These results confirmed a model proposed by Daffertshofer et al. (2005) where bilateral M1 and PMC are modeled as oscillators and their inter- and intra-hemispheric interactions as coupling levels. During stable performance of polyrhythmic movements, oscillations in bilateral M1s and PMCs are phase-locked supporting inhibition of inter-hemispheric crosstalk. That is, in this state the interference between dissimilar movement frequencies is reduced. Instability occurs when inter-hemispheric crosstalk is not properly inhibited, phase locking is lost, and interference between bilateral motor cortices is large enough to destabilize performance. In fact, this model explains not only (the loss of) stability of polyrhythmic performance but also that of isofrequency anti-phase modes as well as unimanual movements when synchronized to an external beat.

Evidence for a combination of both hypotheses, i.e. spatial and temporal reorganization, during behavioral instability has been reported as well in an EEG study on bimanual tasks (Banerjee et al., 2012) and an MEG study on unimanual tasks (Mayville et al., 2001). In the first study, spatial reorganization was found at critical frequencies which caused instability and induced spontaneous switching from anti-phase to in-phase coordination modes (Banerjee et al., 2012). Likewise, spontaneous switching from syncopation to synchronization with increasing frequency during execution of unimanual movements in the presence of an auditory signal was accompanied by both spatial and temporal reorganization over the scalp in an MEG study (Mayville et al., 2001). In summary, whether spatial or temporal reorganization is found appears largely dependent on the method of acquisition. However, the skill level of the performer and the associated stability of the performed coordination modes might also play a role and this has not been directly addressed in these studies.

In summary, the present section on the neural dynamics of bimanual coordination has demonstrated how divergent the applied methods are as well as the obtained results. Nevertheless, converging evidence appears to suggest that bimanual movements often require more neural resources than unimanual movements, as shown by increased amplitudes of MRCPs during motor planning and stronger suppression of spectral power during motor execution. However, the level of practice might alter this pattern if the task is more demanding (e.g., during faster execution). Similarly, support has been provided for higher neural activity in SMA, left PMC, left S1-M1, ACC and right cerebellum in anti-phase compared to in-phase coordination patterns.

Bimanual coordination relies on communication between brain regions, for which the most critical white matter structure is the corpus callosum. Recent studies on the microstructural integrity of white matter pathways support this assumption (Gooijers et al., 2013; Gooijers and Swinnen, 2014). From a functional perspective, inter-hemispheric connectivity at both sensor and source level reflects the communication between hemispheres through the callosal pathways and a common control set by subcortical structures (e.g., the thalamus). Increases in inter-hemispheric connectivity (by means of coherence and phase synchronization) have been reported for bimanual compared to unimanual movements and for anti-phase compared to in-phase patterns. The relevance of this measure and the mechanism supporting it is of particular interest, as its reduction reflects performance deficits and its increment reflects variation in task demands.

As compared to inter-hemispheric connectivity, the interpretation of intra-hemispheric and midline connectivity may be less straightforward. For example, intra-hemispheric connectivity in the dominant hemisphere increases with task complexity, which possibly reflects the left hemispheric dominance that also holds for bimanual movements. However the ROI analysis typically includes electrodes placed over fronto-central, centro-lateral and centro-parietal areas in one hemisphere, precluding specificity. Connectivity analysis between specific lateral sites and the midline can provide more support for intra-hemispheric measures. In particular, the hemispheric dominance during bimanual movements is supported by connectivity increases between the left S1-M1 and PMC, and between the left M1 and SMA.

Regarding the networks supporting bimanual action, EEG/MEG studies provide primary evidence for the temporal modulation of unimanual networks, whereas fMRI approaches primarily report about the spatial distribution of brain activity and activity modulations including additional recruitment of areas as a function of task conditions. This conceptual difference between EEG/MEG and fMRI studies is due to the time resolution inherent to each acquisition method but also to differences in experimental conditions (such as the skill level of the performer, task difficulty, etc). Even though fMRI has a superb spatial resolution, temporal resolution is in the order of seconds. This might hinder the registration of the quick temporal modulations of unilateral networks, whereas EEG/MEG data allows for inspection at a millisecond scale. However, advanced methods for data analysis which improve spatial resolution of EEG/MEG recordings have elucidated patterns of spatio-temporal reorganization within the temporal occurrence of behavioral instability at fast tempos for polyrhythms and anti-phase movements, which is presumable caused by failure of inter-hemispheric inhibition. The best approach would be to use both EEG/MEG and fMRI in order to disentangle the involvement of regions at different time scales.

4. Executive functions examined with bimanual coordination paradigms

The study of bimanual movements is not only meaningful to reveal a better understanding of the principles underlying interlimb coordination but can also be instrumental to examine executive functions, such as task switching, inhibition, and multiple task integration, as discussed next.

4.1 Intended task switching

Unlike the previous studies that looked into spontaneous switching between coordination modes at increasing cycling frequencies, changes between coordination modes can also be voluntarily produced in cued switching paradigms to study higher-order processes related to response switching, as part of executive functioning (see Table 3).

Insert Table 3 about here

Intended switching between coordination modes has shown a decrease in alpha power in the centro-parietal regions (Deiber et al., 2001; Tallet et al., 2009; Tallet et al., 2010). This is also present in unimanual paradigms with intended switching between hands (Serrien and Sovijärvi-Spapé, 2013). This indicates that alpha power is more related to attentional processes associated with switching rather than the specific encoding of a new coordination mode. Additionally, an overall increase of inter- and intra-hemispheric coherence in the beta band has been observed in a sequence of alternating coordination modes compared to a condition where a single coordination mode is maintained (Serrien, 2009b). Similar results in centro-parietal areas were reported by Lorist et al. (2009) and Sohn et al. (2000) in cognitive dual tasks. Two reasons for this increase were proposed by Serrien (2009b). First, a process encompassing an increment in neural communication might be in action in order to overrule interference from past neural activity into current activity. Second, the coherence increases might be related to an increase in the attentional demand (Serrien, 2009b).

Besides the changes in power and coherence that are common to the switching of coordination modes, there are changes that are particular to each type of movement. In the literature, the primary focus has been on switching from bi- to unimanual movements (and vice versa) and switching from anti- to in-phase bimanual movements (and vice versa). The former leads to increases in beta inter-hemispheric coherence, reflecting the effect of past on present activity, as inhibiting a bimanual pattern would require more neural effort in order to update and switch to a unimanual task (Serrien, 2009b). The opposite switch, i.e. from uni- to bimanual movements, is not accompanied by significant changes in coherence levels (Serrien, 2009b). Tallet et al. (2009) also reported asymmetric coherence patterns during switching from bimanual to unilateral right movements. Coherence between the dominant hemisphere and the midline (presumably over SMA) was increased during the switching maneuver, whereas a decrease was found between the non-dominant hemisphere and the midline. Tallet et al. (2009) proposed this asymmetry to reflect a reinstatement of communication in the dominant hemisphere to continue movement of the right hand, and disruption of communication, or inhibition, in the non-dominant hemisphere to stop movement of the left hand.

Intended switching from the anti- to in-phase coordination mode was accompanied by an increase in beta power over the fronto-central region, whereas no significant changes were found at the coherence level (Tallet et al., 2010). ERD/S studies have reported increases of beta power after termination of movement, indicating a decrease in neural activity (Pfurtscheller and Lopes da Silva, 1999). If this is extrapolated to a switch from difficult (anti-phase) to easy (in-phase) movements, an increase of beta power would be related to the reduction of neural effort to perform the new task. The opposite switch, i.e. from in- to anti-phase movements, is linked to an increase in alpha and beta coherence between sensorimotor cortices and the midline, which implies more engagement of relevant neural regions for a more complex movement (Tallet et al., 2009; Tallet et al., 2010). This is supported by behavioral findings, where switching from in- to anti-phase is considered more difficult than the opposite (Serrien and Swinnen, 1999). The lack of significant changes in the anti- to in-phase switch compared to the in- to anti-phase switch might reside in the bidirectional inter-hemispheric inhibition taking place alternatively in anti-phase movements. This mode entails the division by two of the movement cycle's period set by the metronome, which is not necessary in in-phase movements (Repp, 2008; Tallet et al., 2009; Tallet et al., 2010).

4.2 Task integration during multitasking

Daily activities often require different tasks to be performed simultaneously, such as walking and talking, counting, or listening to others. Stabilizing a bimanual pattern, while there is interference from another task, involves a multitasking cost in the central nervous system with a potential decline in performance of the bimanual movement. An important factor that mediates resource distribution for simultaneous tasks that can be selectively directed is attention (Monno et al., 2002). In order to measure the capacity for resource allocation and automatic attentional switching, an ERP elicited at around 300 ms after stimulus onset named P3b has been used. Specifically, a reduction of P3b was shown in a dual task which encompassed identification of a novel visual stimulus in a sequence of common stimuli while performing anti-phase movements with the forearms (Matthews et al., 2006). The coordination pattern was kept stable during the single motor and the dual-task conditions with

motor priority. However, the dual task induced a P3b reduction over the centro-parietal area, which confirms the relation of P3b to attentional priority and provides an argument to consider P3b as an index of attentional cost (Matthews et al., 2006; Monno et al., 2002). P3b is presumably generated by temporo-parietal regions and the ACC (Kok, 2001). The latter has been reported to be part of the neural network for anti-phase movements but not for in-phase movements (Pollok et al., 2007), as discussed previously in Section 3.2.1.

In another study evaluating the effects of dual tasking in uni- and bimanual tasks (task 1) during verbal counting (task 2), coherence was examined (Serrien, 2009d). Inter-hemispheric and midline connectivity increased in the dual- compared to single-task condition during unimanual movements. In contrast, coherence did not significantly change for the dual- compared to single-task condition during bimanual movements, and the values were similar to the dual-task unimanual condition. In this regard, the lack of strengthening of functional connectivity in the dual- compared to single-task condition was associated with detriments in motor performance. It is likely that these similar connectivity levels are due to competition for resources, as the dual task employed (verbal counting), seems to recruit a distributed neural network (Dehaene et al., 2003; Stanesco-Cosson et al., 2000) including motor-related areas (Andres et al., 2007; Brown et al., 2005; Franz et al., 1992). Hence, the sensorimotor processes involved in the dual task may have interfered with the primary motor task.

In summary, protocols examining executive functions via bimanual movements, including task switching and dual tasking, have been used in association with EEG/MEG recordings. Regarding the former, decreases in the alpha power have been linked to the switching maneuver, regardless of the direction of the switch (e.g., in- to anti-phase, or vice versa), suggesting elevated attention demands. To date, there is no conclusive evidence that characterizes the neural dynamics during switches towards specific coordination modes. Regarding the integration of dual tasks, only two studies are relevant and provide an initial view of the cost in the central nervous system associated with simultaneously performing a bimanual task and another type of task, suggesting a limited capacity of

attentional resources. However, further research is required in order to confirm the reliability of measures that may reflect the dual-task cost.

5. **Bimanual learning and neural plasticity**

Coordination patterns that deviate from the intrinsic in-phase and anti-phase coordination modes, such as multifrequency patterns and/or modes with less intrinsic relative phase relations require practice to be performed with high accuracy and consistency. Various feedback techniques are available to support the acquisition of such coordination skills and to promote integration of the subtasks into a gestalt (Swinnen and Wenderoth, 2004). Training-induced bimanual skill improvement is associated with changes in neural activation as demonstrated by fMRI studies (Beets et al., 2014; Debaere et al., 2004b; Puttemans et al., 2005; Remy et al., 2008; Ronsse et al., 2011). Accordingly, studies using EEG/MEG techniques have identified a bimanual learning network that is modulated by practice-induced changes, including the bilateral SM1, SMA, PMd, PPC and cingulate motor area (Gerloff and Andres, 2002). These practice-induced changes in neural representations are characterized by specific patterns of brain oscillations (Hikosaka et al., 2002), as EEG/MEG studies show (see Table 4).

Insert Table 4 about here

ERPs and connectivity measures have been used to investigate cortical modulations and functional coupling between brain regions, respectively, in response to bimanual movement training. Most EEG/MEG studies focused on short-term motor learning (30 minutes of practice). However, such protocols only reflect the effects of short-term repetitive practice, rather than long-term learning and retention - for an exception, see Wright et al. (2012). It is well established that short-term motor learning can modulate cortical excitability (Classen et al., 1998; Kleim et al., 2004), whereas motor map reorganization and synapse formation presumably occur at later stages, following motor skill acquisition and performance gains (Kleim *et al.*, 2004). Accordingly, fundamentally different neural processes may underlie short- versus long-term training-induced neuroplasticity.

MRCPs have been used to investigate cortical changes in response to short-term movement training (Hill, 2009; Staines et al., 2002). Smith and Staines (2006) showed that the training of a novel visuomotor task during 30 minutes, which involved wrist flexion/extension and subsequent transfer to unimanual movements, was associated with enhancements of motor preparatory activity, in accordance with previous ERP and metabolic studies (Petersen et al., 1998; Staines et al., 2002). Especially, improvements in unimanual performance following bimanual training were associated with amplitude increases of the early MRCP associated with motor preparation, but not the CNV, associated with anticipation of the cue. Additionally, performance improvement during the latter portion of bimanual training was associated with amplitude increases of the early MRCP and amplitude decreases of the RAP. The authors concluded that the negative relationship between training-induced improvements in motor performance and the amplitude of cortical markers for motor performance was associated with transfer effects to a unimanual task, indicating that short-term training can change the level of motor preparation and sensory feedback processing in healthy subjects. In a subsequent study, Smith and Staines (2010) investigated in- versus anti-phase bimanual movement training. To this end, they developed three types of cued movement training with a total duration of 30 minutes: in-phase bimanual, anti-phase bimanual and repetitive unimanual. Again, these were assessed for transfer to unimanual movements. Results showed that a significant training-related increase in preparatory activation correlated with a behavioral enhancement following in-phase bimanual training, but not after anti-phase bimanual or unimanual training.

To overcome the limitations associated with short-term training, Wright et al. (2012) developed a more ecologically valid paradigm that included a five-week training program about learning to play the guitar. After training, the amplitude of NS and MP components of the MRCP were reduced and were correlated with motor improvements, whereas the early BP did not show significant changes. These findings appear contradictory to those from Smith and Staines (2006; 2010), and highlight the importance of long-term learning. They suggest that, as an individual becomes more competent in a motor skill, less neural resources are required during motor planning, resulting in the observed MRCP changes.

Regarding inter-regional functional coupling, lesion studies provide strong evidence for the importance of inter-hemispheric connections between premotor and sensorimotor regions in bimanual activities (Geffen et al., 1994; Leonard et al., 1988; Sperry, 1968). Alpha, beta, and gamma bands have been shown to be most sensitive to motor modulations induced by training, reflecting different underlying systems (Pfurtscheller et al., 1996; Salmelin and Hari, 1994). Along this line, Andres and co-workers (1999) investigated the functional coupling and regional activation of human sensorimotor regions during short-term bimanual skill learning. Coherence and spectral power were estimated in alpha and low beta bands during the fusion of two overlearned unimanual finger tapping sequences into one bimanual sequence before and after a 30-minute training period. They reported inter-hemispheric coherence increases during the early bimanual learning phase that returned, to values similar to the unimanual control conditions following bimanual training. In general, spectral power appeared to be less affected by training, supporting the differential physiological meaning of the two measures. These results are supported by extensive evidence reporting that initial coherence increases might reflect a greater initial need for active integration when bimanual sequences are not yet established as motor routines, with subsequent evolution of connectivity values towards baseline levels reflecting a more efficient system after training (Debaere et al., 2004b; Puttemans et al., 2005; Serrien and Brown, 2003).

Additionally, Andres and coworkers suggested that modulations of inter-hemispheric coupling as a result of bimanual learning might be relayed through the corpus callosum, since partial callosotomy leads to a decrease in inter-hemispheric coherence (Brazdil et al., 1997; Gerloff and Andres, 2002). More specifically, patients with lesions of the corpus callosum show deficits in the acquisition of novel bimanual sequences, but not in the execution of previously learned bimanual sequences. Serrien and Brown (2003) argued that the inter-hemispheric modulations observed by Andres et al. (1999) reflected the optimization of task performance rather than learning a new bimanual task, since participants were able to perform the bimanual sequence correctly from the beginning of the recording.

Serrien and Brown (2003) conducted a study to investigate cortico-cortical coupling during the acquisition of a completely new task by means of coherence between cortical areas. Participants

performed bimanual cyclical wrist flexion/extension movements at a 2:1 ratio over a 30-min acquisition period. Coherence was evaluated in the alpha, beta and gamma frequency bands. Results showed both an initial increase and subsequent decrease in coherence between the primary sensorimotor regions and over the midline area in the alpha and beta bands, in accordance with Andres and collaborators (1999). However, a novel finding was an early increase in inter-hemispheric coupling in the gamma band between prefrontal regions. Altogether, this suggests that the strength of cortico-cortical connectivity is adaptively modified across regions and frequencies while learning a complex bimanual pattern. Additionally, the authors observed that learning a highly demanding bimanual task involves the suppression of pre-existing preferred isofrequency coordination modes, particularly the in-phase and anti-phase modes (Serrien and Swinnen, 1997; Swinnen et al., 1997b; Swinnen et al., 1993). These pre-existing preferred coordination modes not only influence, but are also influenced by the to-be-learned bimanual task (Serrien, 2009c) with two main factors showing the highest impact on this reciprocal influence, i.e., the number of tasks or task variations practiced and the order in which the tasks are trained. Interactions between new and intrinsic dynamics were evaluated by Serrien (2009c) in a bimanual finger tapping task with a 2:1 ratio according to two training schedules over 10 minutes: continuous (consecutive trials), and interrupted (non-consecutive trials with intermediate 1:1 in-phase performance). In-phase and anti-phase modes were probed before and after training. Results showed that both continuous and interrupted practice improved motor performance, but to a smaller extent in the latter case. Inter-hemispheric, intra-hemispheric and midline connectivity decreased during continuous practice, whereas inter-hemispheric connectivity increased with interrupted practice. It was concluded that the particular practice schedule affects motor learning, with a stronger impact from pre-existing preferred coordination modes to the to-be-learned bimanual task than vice versa.

The MEG literature has primarily focused on cortical modulations of event-related activity during the short-term acquisition of new bimanual polyrhythm tasks involving force production while recording both MEG and EMG signals. Boonstra et al. (2007) used a bimanual 3:5 polyrhythm task with a duration of 37 minutes, approximately, and investigated the motor-related power in order to identify learning-specific spectral changes in cortical activity of bilateral M1. The authors observed

improved performance of the polyrhythm with practice and the accompanying event-related beta modulation was enhanced, particularly, in the contralateral motor cortex of the more-difficult-to-adjust end-effector, here, the slow finger. The authors concluded that (1) motor learning is associated with a change in neural activity in cortical motor areas that differs across hemispheres, and (2) initial stages of motor learning require additional mental effort since the motor skill is not yet automated, supporting previous research (Halsband and Lange, 2006). Along the same lines, Houweling and co-workers (2010a; 2008a; 2008b; 2010b) transferred a bimanual polyrhythm task training paradigm developed by Mechsner et al. (2001) to the MEG environment to investigate the functional coupling of oscillatory activities during motor learning of about 30 minutes. They looked at cortico-cortical and cortico-spinal synchronization in the alpha, beta and gamma bands based on pre/post learning differences (Houweling et al., 2008b). Results revealed event-related (de-) synchronization of beta activity in bilateral cortical motor areas and alpha modulations in the cerebellum. The latter increased after learning and, simultaneously, the bilateral M1 coupling increased around the movement frequency reflecting improved motor timing. Furthermore, the inter-hemispheric gamma synchronization between primary motor areas decreased, reflecting reduced attentional demands after learning. These findings pointed to a functional role for inter-hemispheric synchronization in the establishment of motor coordination patterns.

In summary, the EEG/MEG literature on motor learning has primarily focused on ERPs and functional connectivity of inter-hemispheric sensorimotor regions during short-term motor learning. Regarding ERP studies, MRCP components have been classically investigated during bimanual movement training, showing both amplitude increases and decreases in the early and late components of the MRCP, respectively, that were associated with improvements in motor performance. Only one study to date has shown decreases in the early components of MRCP that were associated with long-term motor learning, which is not in line with the abovementioned findings. Inter-regional functional connectivity studies on alpha, beta and gamma bands have shown an early increase followed by a decrease in connectivity, across several motor areas. Taken together, these findings reflect that motor learning is associated with a change in neural activity and connectivity. Specifically, initial increases

in both ERP amplitudes and functional coupling may indicate the necessity of greater neural resources when bimanual sequences are not yet established as motor routines, with subsequent regress towards baseline levels, reflecting a more economic neural system after training. Importantly, further research is required to solve discrepancies between short- and long-term practice results, and to investigate the neural reorganization that only occurs at later stages of motor skill acquisition.

6. Future research

Despite the considerable insights into the neural mechanisms supporting motor control in general and bimanual coordination in particular, as gained by the different imaging modalities, many questions still await to be answered. Here we discuss different methodological and scientific avenues that are yet to be explored to enhance our understanding of bimanual coordination.

Regarding the techniques for data acquisition, the use of multimodal approaches might provide insights from different physiological perspectives: magnetic/electric and metabolic. The characteristic low spatial resolution of EEG/MEG recordings can be complemented by the simultaneous use of fMRI. In particular, this strategy has not been fully exploited in the area of motor research. Some studies have started to implement this strategy with motor imagery tasks (Burianová et al., 2013; Formaggio et al., 2010). Given the particular strengths of each method, multimodal approaches might also help to interconnect different levels that have been studied separately or only by pairwise combinations so far: structure (brain grey and white matter), function (brain activity), and connectivity. Only a few studies have investigated the correlations between EEG measures and structural measures from diffusion MRI for visual and sensory stimuli, resting state and cognitive tasks – for a review, see Sui et al. (2013). However, no study so far has examined the relationship between both structural and functional measures from EEG/MEG in relation to bimanual coordination. Bimanual movements heavily rely on the integrity of the corpus callosum, as shown in callosotomy patients (Kennerley et al., 2002; Preilowski, 1972; Ridderikhoff et al., 2005). Therefore, future research linking structural measures of the corpus callosum to the functional connectivity during movement is greatly relevant to understand bimanual coordination in a comprehensive manner.

Regarding the experimental tasks, most studies have made use of movements that are presumably related to event timing (see section 1), such as finger tapping or flexion/extension of fingers or wrists. Little is known about the underlying neural dynamics of continuous movements without a salient event. Furthermore, isofrequency movements dominate current EEG/MEG literature. Phase deviations from the preferred in- and anti-phase coordination modes have been a focus of study in fMRI work. Also, the few available polyrhythmic studies have not challenged task allocation assignments for each limb in relation to hand dominance so far, as the fast rhythm is always performed by the dominant hand. More recently, polyrhythmic movements whereby the non-dominant hand performs the faster of the 2 rhythms, have been explored in an fMRI study (Beets et al., 2014).

With respect to learning-related questions, an important issue to clarify is the difference between learning and performance. Most EEG/MEG studies have focused on initial stages of motor learning, or short-term learning, of simple tasks dependent on online feedback with either visual or auditory cues. Further research is required to resolve discrepancies between short- and long-term practice results, and to investigate the processes of neural reorganization that occur at later stages of motor skill acquisition. The next step is to distinguish true learning characterized by more permanent changes from temporary performance effects that are assisted with cues or augmented feedback sources which have been repeatedly reported in motor-related research (Kantak and Winstein, 2012; Salmoni et al., 1984; Swinnen, 1996). Additionally, cross sectional approaches comparing novices with experts during production of bimanual tasks will be helpful to obtain a deeper understanding of skilled performance.

Another consideration is the statistical power of studies. As seen in column “n” of Tables 1-4, most EEG/MEG studies have studied ten or less participants, and in some cases the sample size has been reduced during the processing stage due to high noise levels or outliers. The statistical power of studies has become an important matter of concern not only in EEG/MEG experiments, but in the whole field of neuroscience (Button et al., 2013; Guo et al., 2013). Sample size calculations prior to the start of the study and bigger sample sizes are necessary to lend stronger credibility to the obtained results.

Finally, an exciting avenue for data analysis is investigating other connectivity measures, such as the band-limited power (e.g., Betti et al., 2013), or cross-frequency couplings (de Lange et al., 2008; Sakowitz et al., 2005). The oscillatory nature of neurons allows information flow through neural entrainment (or synchronization) either at a local or a global level. A step further into the complex network of neural interactions is to examine the amplitude and phase couplings between frequency bands. Long-range interactions through beta-gamma coupling between left M1 and occipito-parietal cortex during motor imagery have been reported, challenging the line of thought explaining mental processes as being of a sequential and hierarchical nature (de Lange et al., 2008). Furthermore, synchronized activity across frequency bands has been shown to be involved in multisensory integration (Sakowitz et al., 2005), which is key for motor planning and execution.

Summary

This review presented a brief description of the vast knowledge on behavioral principles of bimanual coordination, and how these are reflected in neural dynamics with a high temporal resolution. Generally, bimanual movements require more neural resources (stronger spectral suppression and inter-hemispheric connectivity) than unimanual movements, similarly to anti-compared to in-phase modes. Behavioral instability during bimanual movements due to increased tempos is accompanied by spatio-temporal reorganization of the neural networks. There is strong evidence that the dominant hemisphere is more active than the non-dominant one during bimanual movements, reflected by stronger alpha and beta suppressions and higher intra-hemispheric connectivity. The dominant hemisphere probably exerts control over the non-dominant limb via ipsilateral projections and/or transcallosal communication. Additionally, bimanual movements have been used as a window to look into cognitive control functions via task-switching and dual-task protocols, using coherence measures and the P3b component. Importantly, EEG/MEG literature shows that motor learning is associated with a change in cortical modulations and functional coupling. Finally, scientists interested in this field should be aware of both the history of behavioral research on

motor skills and the advances in the field of neuroscience to design meaningful studies. This paper represents an attempt to contribute to that awareness.

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Table 1. Summary of studies on planning of bimanual tasks. N: Sample size; E: ERP; Sp: Spectral analysis.

Table 2. Summary of studies on execution of uni- and bimanual tasks. N: Sample size; Tech: Technique; E: ERP; Sp: Spectral analysis; C: Connectivity analysis; S: Source estimation.

Table 3. Summary of studies on cognitive functions using bimanual paradigms. N: Sample size; Tech: Technique; E: ERP; Sp: Spectral analysis; C: Connectivity analysis; S: Source estimation.

Table 4. Summary of learning studies using unimanual and bimanual paradigms. N: Sample size; Tech: Technique; E: ERP; Sp: Spectral analysis; C: Connectivity analysis; S: Source estimation; RT: reaction time.

Figure 1. Methods of analysis of EEG signals. A. MRCP associated with right finger movements on electrodes C1, Cz and C2 (over the central line of the scalp). Modified from Shibasaki and Hallett

(2006). B. Comparative illustration of the ERP showing phase-locked activity with respect to a reference time point $t = 0$, and both phase and non-phase locked activity on the right side visible with time-frequency analysis. From Bastiaansen et al. (2012). C. Measured signals on the scalp can be used to estimate the underlying sources of activity via the solution of the inverse problem which is undetermined. For this, a model of how signals are spread across the tissue is required, i.e. the forward problem.

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Tables

Table 1. Summary of studies on planning of bimanual tasks. N: Sample size; E: ERP; Sp: Spectral analysis.

Author	N	Technique	Task	Pattern	Analysis		Main Findings
					E	Sp	
Kristeva et al. (1990)	8	EEG	Flexion/extension index finger	In-phase	x	-	No effect of inertial loading in BP amplitude in bimanual, unlike unimanual Larger BP amplitudes in bimanual compared to unimanual BP and N(0-100ms with respect to movement onset) amplitudes were larger in non-dominant hemisphere
Urbano et al. (1998)	4	EEG	flexion/extension middle finger	in-phase	x	-	Negativity over contralateral-central and mid frontocentral during motor preparation, initiation and execution showed no difference in latency for bi- and unimanual movements Amplitude over contralateral-central area was not statistically different between bilateral and unilateral Amplitude over mid frontocentral area showed higher activation during execution in bilateral
Cui et al. (2000)	16	EEG	sequence of index and little finger pressing thumb	in-phase	x	-	Later CNV topography varied with motor complexity, indicating that exact preparation for a motor process was performed Maximum amplitude of NP (negativity of performance, during execution) over central area, supposedly supplementary and cingulate areas, bilateral M1s Early CNV over frontal areas; late CNV over central areas
Taniguchi et al. (2001)	12	EEG	button pressing	in-phase	x	-	Decreased motor potential (over C3 and C4) in bilateral compared to unilateral
Deiber et al. (2005)	12	EEG	flexion/extension of index and/or little finger	in & anti-phase	x	x	Initial 500ms of CNV accompanied by alpha and beta ERD Initial CNV was influenced by precue given in S1

Table 2. Summary of studies on execution of uni- and bimanual tasks. N: Sample size; Tech: Technique; E: ERP; Sp: Spectral analysis; C: Connectivity analysis; S: Source estimation.

Study	N	Tech	Task	Pattern	Analysis				Main Findings
					E	Sp	C	S	
Banerjee et al. (2012)	12	EEG	Flexion-extension index finger	In & anti-phase	x	-	-	-	Bimanual coordination is generated by temporal modulation of unimanual tasks, similarly for in-phase and anti-phase Instability at high frequency of anti-phase movement is explained by recruitment of additional networks Stable bimanual in- and anti-phase performance rely on similar recruited networks
Daffertshofer et al. (2000)	3	MEG	Finger tapping	Polyrhythm	-	x	x	-	Bimanual cortical patterns can be explained by superposition of unimanual cortical patterns Areas of phase-locking do not necessarily coincide with areas of higher spectral power Model of polyrhythm movement based of two non-linearly coupled self-sustained oscillators
Daffertshofer et al. (2005)	1	MEG	Finger tapping	Polyrhythm	-	x	x	-	Contralateral motor cortices showed activity at movement frequencies of each hand during stable performance Increase of power in ipsilateral areas to the unstable hand during unstable behavior
Ford et al. (1986)	14	EEG	Fist clenching	In-phase	-	-	x	-	Higher inter and intra-hemispheric coherence in alpha band during uni- and bimanual movements
Gross et al. (2005)	10	MEG	Wrist flexion/extension	In & anti-phase	-	-	x	x	Bimanual movements showed higher activity than unimanual for alpha, beta and gamma across the whole brain Anti-phase movements showed higher activity than in-phase for alpha, beta and gamma across the whole brain Activity of non-dominant M1 was modulated by task from unimanual to in-phase and anti-phase
Houweling et al. (2010b)	13	MEG	Flexion-extension/finger tapping	Polyrhythm	-	x	x	x	Increase of power at movement frequency of fast hand in ipsilateral M1 during instability Beta power was reduced with increasing movement frequency
Pollok et al. (2005b)	7	MEG	Index flexion/extension	In-phase	-	-	x	x	Functional coupling in cortex (thalamus, PPC, PMC, S1-M1, SMA) in alpha band during bimanual execution Higher activity in dominant (left) S1-M1 during bimanual movement
Pollok et al. (2007)	14	MEG	Finger tapping	In & anti-phase	-	-	x	x	Increased activity in ACC and SMA during anti-phase movement Decreased power (increased activation) at 10 and 20Hz in left S1-M1, and in PMC & SMA, respectively Increased alpha power (decreased activity) in left cerebellum during anti-phase movement
Serrien and Brown (2002)	6	EEG	Wrist flexion/extension	In & anti-phase	-	x	x	-	Decrease of interhemispheric coherence in beta band along with performance deterioration with increasing tempo Performance and interhemispheric coherence were more reduced in anti-phase compared to in-phase movements Increased connectivity between sensorimotor cortices and midline with increasing tempo
Serrien et al. (2003)	6	EEG	Flexion/extension of wrists	In & anti-phase	-	x	x	-	Dominant hemisphere controlled communication with non-dominant in bimanual and unilateral right movements Increased coherence during anti-phase compared to in-phase movements Deterioration of performance with load accompanied by decrease of inter-hemispheric coherence in beta
Serrien (2008)	10	EEG	Finger tapping	In & anti-phase	-	x	x	-	Increased intra-hemispheric coherence in beta in left hemisphere for unilateral right and bimanual movements Higher intra- and inter-hemispheric and midline coherence in beta band in anti-phase coordination mode Lowest inter-hemispheric coherence in beta band in in-phase compared to anti-phase and unilateral movements
Serrien (2009a)	9	EEG	Drawing	Other	-	-	x	-	Intra-hemispheric coherence in beta band was increased as a function of task complexity in dominant hemisphere Inter and intra-hemispheric coherence in beta band was increased in complex tasks in non-dominant hemisphere

Table 3. Summary of studies on cognitive functions using bimanual paradigms. N:Sample size; Tech: Technique; E: ERP; Sp: Spectral analysis; C: Connectivity analysis; S: Source estimation.

	Study	N	Tech	Task	Pattern	Analysis				Main findings
						E	Sp	C	S	
Dual task	Matthews et al. (2006)	16	EEG	Pronation-supination of forearm	anti-phase	x	-	-	-	Reduction in P3b for dual task motor priority compared to simple motor task
	Serrien (2009d)	9	EEG	finger tapping	in-phase	-	-	x	-	Similar levels of inter-hemispheric and midline connectivity in beta band for single and dual bimanual task Higher level of intra-hemispheric connectivity in beta band during single bimanual task than dual
Cued switching	Deiber et al. (2001)	10	EEG	index and middle finger press button	in & anti-phase	-	x	-	-	Alpha ERD did not differentiate bimanual in-phase and anti-phase sequences Alpha decreased over central and mesial regions during steady state of uni- and bimanual sequences Alpha decreased more for left and bimanual sequences than for unilateral right
	Tallet et al. (2010)	7	EEG	finger tapping (index)	in & anti-phase	-	x	x	-	Decrease of alpha for anti- to in-phase and in- to anti-phase switching Increase of beta inter-hemispheric coherence and lateral-midline pairs during in- to anti-phase switching Increase of beta over fronto-central region during anti- to in-phase switching
	Serrien (2009b)	8	EEG	finger tapping (index)	in-phase	-	x	x	-	Increased beta inter and intra-hemispheric coherence in a series of movement compared to execution of a single type of movement Higher inter-hemispheric coherence in beta band during switch from bimanual to unimanual movements No significant differences during switch from unimanual to bimanual movements
	Tallet et al. (2009)	11	EEG	finger tapping (index)	in & anti-phase	-	x	x	-	Reduction of alpha over sensorimotor and mesio parietal areas in tasks involving motor inhibition and switching Increment of beta coherence over sensorimotor areas during switching from in-phase to anti-phase Right lateral-midline connectivity decreased and left lateral-midline connectivity increased in in-phase to unimanual right movement

Table 4. Summary of learning studies using unimanual and bimanual paradigms. N: Sample size; Tech: Technique; E: ERP; Sp: Spectral analysis; C: Connectivity analysis; S: Source estimation; RT: reaction time.

Study	N	Tech	Task	Pattern	Analysis				Main Findings
					E	Sp	C	S	
Andres et al. (1999)	18	EEG	Finger tapping	In & anti-phase	-	x	x	-	Increased interhemispheric coherence in bimanual movements at early learning stages Decreased interhemispheric coherence in bimanual movements after later learning stages, similar to unimanual control
Boonstra et al. (2007)	9	MEG	Flexion-extension fingers	Polyrhythm	-	x	x	x	Event-related modulation of beta power in the contralateral motor cortex was inversely related to force output. The degree of beta modulation for the motor cortex increased during the experiment and was positively correlated with motor performance of the slow hand
Houweling et al. (2008a)	9	MEG	Flexion-extension/finger tapping	Polyrhythm	-	x	x	x	Improved timing of the slow hand correlated with an increase in power in contralateral M1 Power spectral densities of bilateral M1s revealed both fast and slow frequency components Beta activity was modulated at the frequency of the slow hand and the degree of modulation increased during motor learning
Houweling et al. (2008b)	9	MEG	Flexion-extension/finger tapping	Polyrhythm	-	x	x	x	Event-related (de-)synchronization of beta-activity in bilateral cortical motor areas and alpha-modulations in the cerebellum The alpha-modulation increased after learning and the bilateral M1 coupling increased around the movement frequency Inter-hemispheric gamma-synchronization between primary motor areas decreased
Houweling et al. (2010b)	9	MEG	Flexion-extension/finger tapping	Polyrhythm	x	x	x	-	Cortico-spinal synchronization in the beta band correlated with learning Intermittent phase locking episodes between beta oscillations in contralateral M1s and the corresponding EMG The strength of the locking correlated with amplitude modulation and increased with improved performance
Serrien (2009c)	16	EEG	Finger tapping	Polyrhythm, in & anti-phase	-	x	x	-	Continuous practice resulted in improved performance with reduced coherence across the motor network Interrupted practice resulted also in improved performance (less than continuous) with no reductions in intrahemispheric and midline connectivity and increases in interhemispheric connectivity
Serrien and Brown (2003)	6	EEG	Flexion-extension wrist	Polyrhythm	-	x	x	-	Practice associated with a decrease in coherence between primary sensorimotor regions and over the midline area in the alpha and beta bands, respectively, along with an increase in functional interhemispheric coupling between the prefrontal areas in the gamma band
Smith and Staines (2006)	10	EEG	Flexion-extension wrist	In & anti-phase	x	-	-	-	Late MRP amplitude did not change, but there was a trend of the early MRP amplitude to increase Decreased RTs correlated with an increased early MRP amplitude in unimanual movements before and after training Accuracy and early MRP amplitude increased and a positive re-afferent potential decreased in bimanual movements
Smith and Staines (2012)	10	EEG	Flexion-extension wrist	In & anti-phase	x	-	-	-	Increase in preparatory activation correlated with behavioural enhancement after cued in-phase training No modulations in response to cued anti-phase training or repetitive unimanual movement
Wright et al. (2012)	10	EEG	Play the guitar	Other	x	-	-	-	Training-related decreases in the amplitude of the later pre-movement components of the MRCP (NS' and MP)

