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Large scale neural dynamics of rhythmic sensorimotor coordination and stability

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Large Scale Neural Dynamics of Rhythmic

Sensorimotor Coordination and Stability

By

Joseph W. Borrell

Accepted in Partial Completion

of the Requirements for the Degree

Master of Science

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MASTER'S THESIS

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Joseph W. Borrell

February 12, 2010

LARGE SCALE NEURAL DYNAMICS OF RHYTHMIC

SENSORIMOTOR COORDINATION AND STABILITY

A Thesis

Presented to

The Faculty of

Western Washington University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science

by

Joseph W. Borrell

January 2010

Abstract

Coordination Dynamics posits that the stability of coordinated patterns of movement may be a key variable for organizing neural activity underlying coordinated action. In support, recent findings suggest that premotor areas play an important role in maintaining pattern stability. The present EEG study investigates how changes in neural activation (assessed via event-related power) are affected both by rate and stability of coordination. Nineteen participants coordinated finger taps with an auditory metronome in either a synchronized or syncopated pattern presented at five different rates (1.00, 1.25, 1.50, 1.75, and 2.00 Hz). Premotor areas demonstrated increases in event-related synchronization (neural deactivation) within the alpha band following slow, synchronized movements. Stepwise increases in rate led to greater desynchronization (neural activation) throughout the entire duration of the movement cycle. During syncopation medial premotor regions remained desynchronized during movement. Moreover, medial premotor was more involved during synchronization with subsequent increases in movement rate. Counter to previous findings, medial premotor did not modulate changes in coordination stability. We suggested that medial premotor regions are involved in processes related to the coincidence of the finger tap and auditory tone. These findings support premotor cortex's role in motor inhibition, timing, and execution.

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Introduction

Sensorimotor coordination is a basic and fundamental ability that forms the foundation for a broad repertoire of complex behaviors. At its essence, coordination is defined as the spatial and temporal ordering between two coupled components. Consider the simple example of tapping your foot to the rhythm of a song, an act that requires the motor coordination of the muscles in the foot with the sensory perception of the auditory rhythm (or beat) of the song. Although seemingly simple, the required sensorimotor pattern is supported by large-scale neuronal circuits distributed across a number of cortical regions (Jantzen & Kelso, 2007). Research investigating the neural basis of sensorimotor coordination has attempted to understand how individual neural regions mediate putative component processes of coordination as well as how distributed brain regions work together to produce coordination patterns (Kelso, 1995). Potentially, these neuronal systems could be directly involved in various aspects of coordination such as sensorimotor planning, preparation, monitoring, and performance-error correction.

A key property of coordination is the ability to maintain functional patterns of coordination under constantly changing environmental conditions. For example, riding a bicycle requires coordination between the movement of the legs and arms, the action of the trunk muscles as well as visual and auditory input. This complex pattern unfolds effortlessly on ideal smooth surfaces such as an asphalt road but also adapts easily to environmental changes, for example a windy day or a gravel road, that threaten to disrupt the pattern. The processes and systems, at both the behavioral and neural level, by which we are able to effortlessly coordinate with objects and people in our environment across a broad range of ever-changing contexts remains unclear. This thesis investigates the neural mechanisms of coordination with particular

focus on systems that serve to maintain patterns of coordination under changes in the environment.

Sensorimotor Coordination

Coordination Dynamics is a theoretical and experimental framework for investigating processes underlying behavioral and neural coordination (e.g., Jantzen & Kelso, 2007; Kelso, 1995). Coordination Dynamics applies the language and tools of dynamics systems to the understanding of behavioral coordination by considering patterns of coordination as emerging from the weak coupling between the component parts that comprise the pattern (Kelso, 1995; Kelso, Scholz, & Schoner, 1988). Within this framework, the relative phase between coupled elements has emerged as a key variable for characterizing the interaction between components by providing a macroscopic description of coordination patterns and how they change over time (Haken, 1983). The resulting mathematical description of coordination (Haken, Kelso, & Bunz, 1985) has led to a number of theoretical predictions that have been supported experimentally (Kelso, 1995). Relative phase is defined as the time difference between the point of maximum finger flexion and the onset of the auditory beep divided by the interval between beeps. This normalized temporal difference is then projected onto a unit circle and expressed in degrees (or radians).

Rhythmic sensorimotor coordination is an important experimental model for testing the theoretical predictions of Coordination Dynamics and for connecting behavioral and neural levels of analysis (Jantzen & Kelso, 2007). Sensorimotor coordination requires the simple temporal ordering between finger flexion/extension and an external auditory stimulus such as a short beep. In this paradigmatic example, relative phase provides a macroscopic measure of how coordination patterns emerge from their interacting components.

Investigations using sensorimotor coordination have revealed the existence of two dominant coordination patterns (Kelso, Delcolle, & Schoner, 1990) (see Figure 1). Perfect synchronization (Figure 1A) occurs when the finger flexion and auditory beep are temporally coincident, resulting in a relative phase of 0°. Syncopation (Figure 1B) is defined when the finger flexion occurs at the midpoint between two consecutive auditory beeps, ideally producing relative phase of 180°. Although other patterns are possible, they typically require extensive learning and practice to establish (Zanone & Kelso, 1992). Synchronization and syncopation thus represent the basic intrinsic patterns generated when performing simple sensorimotor coordination.

Rate has proven to be an important control variable that reveals the dynamics of this simple coupled system (Jantzen & Kelso, 2007). At slow movement rates both the synchronized and syncopated pattern can be performed over time with little variability in relative phase. That is, they are both stable patterns. However, as the rate of coordination increases (i.e., increasing the rate of the auditory metronome) the syncopated pattern becomes more variable. Thus, the variability of our collective measure of the pattern (relative phase) increases. In the language of coordination dynamics, the pattern is said to become less stable. Eventually, the syncopated pattern reaches a critical rate (~2.00 Hz) at which spontaneous switches from syncopation to synchronization occur (Kelso, Delcolle, & Schoner, 1990). In contrast, the stability of the synchronized pattern is less affected by increases in coordination rate and switches from synchronization to syncopation are not observed. Thus the rate of coordination is said to be a control parameter (Haken, 1983) in the sense that it reveals the different states of the system and how they evolve.

Neural Mechanisms of Sensorimotor Coordination

The sensorimotor coordination paradigm provides experimental control over the stability of coordination patterns and thus a means to map key movement parameters onto brain function for the purpose of identifying the underlying neural circuitry. Using such an approach, brain imaging has begun to reveal the neural dynamics and processes underlying sensorimotor coordination. Functional magnetic resonance imaging (fMRI) provides a measure of neural activity with high spatial resolution (relative to other brain imaging techniques, e.g., MEG and EEG) by examining changes in blood-oxygen-level-dependent (BOLD) activity. Using fMRI, Mayville and colleagues (2002) examined the activity in neural networks underlying syncopated and synchronized patterns of sensorimotor coordination. Participants in this study conducted a rhythmic coordination task that involved squeezing an air pillow between their right index finger and thumb to an auditory metronome. Both patterns of coordination were examined at a single constant rate (1.25 Hz) and were executed with relatively little performance variability. Analyses of the fMRI revealed differences in neural activity between the two patterns. For the syncopated pattern, in comparison to the synchronized pattern, greater activation was found in a network composed of supplementary motor area (SMA), cerebellum, dorsolateral premotor cortex, and temporal cortices. No additional neural activation was found for the synchronized compared to syncopate condition. These findings imply that differences in pattern stability require a greater recruitment of neural networks to guide sensorimotor coordination. Mayville et al.'s (2002) findings provide potential support for the existence of a brain network that is sensitive to the stability of coordination patterns. Because only a single movement rate was examined, however, this study could not investigate the full range of pattern stability at the behavioral and neural level.

Expanding upon previous research, Meyer-Lindenberg et al. (2002) controlled the parameter of rate to infer the existence of a stability-modulated neural network in bimanual coordination. Similar to the goals and intent of sensorimotor coordination paradigms, bimanual coordination examines and tests theoretical predictions of Coordination Dynamics. However, instead of examining one's coordination with the environment (in the case of sensorimotor coordination), bimanual paradigms look at the coordination of homologous limbs and body parts (coordination with one's self). Due to these differences, bimanual literature uses the term "anti-phase" in place of the analogous "syncopation" in sensorimotor coordination paradigms (both occur at 180° relative phase) and "in-phase" instead of "synchronization" (both occurring at 0°).

 For their study, Meyer-Lindenberg et al. (2002) implemented transcranial magnetic stimulation (TMS) to determine the relationship between stability and cortical function. TMS uses electromagnetic induction to produce temporary and selective noninvasive lesions in brain regions of interest. These selective lesions are created through the electromagnetic depolarization of cortical pyramidal neurons (Kobayashi & Pascual-Leone, 2003). Pattern stability was manipulated using coordination rate conditions of 1.0, 1.5, 1.7, and 2.0 Hz, with participants performing a bimanual index finger movement task in either an "in-phase" or "anti-phase" pattern. TMS-induced disturbances to premotor cortex and SMA led to errors during performance of anti-phase coordination. Moreover, the amount of stimulation needed to disrupt coordination decreased as pattern variability increased, that is, only for increases in the rate of the anti-phase pattern. As the rate of the anti-phase pattern was increased, TMS-induced disruption over premotor regions resulted in a switch to the in-phase pattern. An increase in the amplitude of stimulation resulted in greater phase-errors and a switch to the in-phase pattern. Pattern switching was not encountered when primary motor cortex (M1) or brachial plexus was

stimulated using TMS indicating that switching did not result from simply disrupting the movement per se. Moreover, in-phase patterns were not susceptible to the TMS stimulation of premotor regions, regardless of coordination rate or stimulation strength. Taken together, these findings imply that lateral and medial premotor cortical regions are involved in maintaining patterns as they become unstable. Meyer-Lindenberg and colleagues suggest that neural feedback from motor regions is a delayed coupling parameter that provides the integration of multimodal information (visual and proprioceptive) to premotor cortex as a way to maintain pattern coordination and that TMS-induced disturbances in this coupling parameter result in instability and pattern transition phenomena. Moreover, Meyer-Lindenberg et al. suggest that the role of premotor and SMA is pivotal in motor feedback control, providing temporal information, preparation, and maintenance of "motor set" when movements become unstable. However, the temporal occurrence of these potential functions during a movement cycle was not examined.

In an fMRI study, Debaere et al (2004) found neural networks directly related to the stability of coordination patterns by manipulating the rate of movement (.9, 1.2, 1.5, and 1.8 Hz). Using a bimanual cyclical coordination task requiring flexion-extension of the wrist, Debaere et al. found that the anti-phase pattern led to greater activation of SMA, superior parietal cortex, and thalamic regions as stability decreased with increasing rate. A second network comprising of M1, globus pallidus, and cingulate motor cortex demonstrated neural activation related to the frequency of the movement performed regardless of the type of pattern performed. Similar to these findings, Ehrsson, Kuhtz-Buschbeck, and Forssberg (2002) found a network of non-primary frontoparietal areas, such as SMA, dorsal premotor cortex, and cingulate cortex related to a highly unstable non-synergistic task (i.e., thumb flexion accompanying the extension of all fingers) as opposed to a more stable synergistic task involving whole-hand flexion movements.

Activation of M1 was equal for both the synergistic and non-synergistic tasks and was related only to the individual movements being performed and not the synergy between them.

The foregoing bimanual coordination suggests that pattern stability is mediated by various cortical regions, such as SMA and premotor cortex. However, bimanual coordination is a specific system that examines the interaction between one's body parts (e.g., fingers, homologous and non-homologous limbs) without any consideration for the external environment. Previous behavioral investigations have found that sensorimotor and bimanual coordination demonstrate similar dynamics (Kelso, 1995; Kelso et al., 1988; Kelso et al., 1990). If bimanual and sensorimotor coordination are subject to similar underlying principles of stability, it can be theorized that both coordination patterns are subject to the same neuronal processes (Jantzen et al., 2007).

A recent fMRI study using a sensorimotor coordination paradigm examined the neural networks that underlie stability using fMRI (Jantzen, Steinberg, & Kelso, 2009). Participants were required to maintain a 1:1 right index finger flexion with each auditory metronome beep, in either a synchronized or syncopated pattern. Participants coordinated at five rates (.75 to 1.75 Hz, in .25 Hz increments) below the critical frequency at which spontaneous transitions between patterns typically occur. By controlling movement rate the researchers were able to directly manipulate pattern stability, similar to that of previous bimanual studies (Debaere, et al., 2004; Meyer-Lindenberg et al., 2002). Similar to previous findings, Jantzen et al. found that the relative phase of syncopated patterns became increasingly unstable as the rate of coordination increased. As pattern stability decreased, BOLD amplitude increased in a premotor-cerebellar circuit that included dorsal and ventral premotor cortex, SMA, pre-SMA, right anterior insula, and contralateral cerebellum (specifically in left dentate nucleus and left inferior semi-lunar lobe)

(see Figure 2). Activation of this network was not observed during synchronized movements, regardless of movement rate performed. These findings mirror previous bimanual coordination findings (e.g., Debaere et al., 2004; Meyer-Lindenberg et al., 2001) by showing a tight functional coupling between the stability of the pattern of coordination and the level of activity of premotor cortical areas.

Similar to previous research (Mayville et al., 2002; Meyer-Lindenberg et al., 2002), a rate-modulating network of right precentral gyrus and bilateral superior temporal gyri was found. However, unlike previous research, Jantzen et al. (2009) examined the connectivity of these two proposed rate and stability-modulating networks. Using structural equation modeling, differences in premotor coupling between synchronized and syncopated coordinative patterns were found. When rate was collapsed across all conditions, syncopated movements reflected stronger neural coupling between premotor cortex/SMA to primary motor cortex. Moreover, syncopated patterns demonstrated more connectivity between premotor cortex/SMA and SMA to primary motor cortex, as a function of increased rate.

These findings, along with previous research, have provided convincing evidence for two neural networks, one sensitive to pattern stability (SMA and premotor cortex) and one sensitive to rate (M1). However, little consideration has been given to the fine temporal dynamics of neuronal activation in these networks. The poor temporal resolution of fMRI prohibits examination of neuronal dynamics within the short temporal duration of a single sensorimotor movement. Unlike fMRI, electroencephalography (EEG) and magnetoencephalography (MEG) are tools that both provide superior temporal resolution (in milliseconds) with the capability of measuring the rich dynamics of neural activation within a single sensorimotor movement.

Event-Related Cortical Oscillations

EEG and MEG are both capable of examining cortical oscillatory activity related to functionally important processes of motor activity (e.g. preparation, initiation, assessment of performance) within a fine temporal scale (Silva & Pfurtscheller, 1999). Oscillatory phenomena among synchronously active neuronal populations have been examined through decreases and increases of event-related power in discrete functional bands. Event-related synchronization (ERS) occurs when neuronal populations are in a hyperpolarized state in which the transfer of cortical input is disengaged and becomes deactivated. In contrast, a decrease in the power of specific oscillatory bands (known as event-related desynchronization or ERD) indicates when the neuronal population enters an activated state. More specifically, it has been proposed that ERD indicates a change within neuronal ensembles from an idle state to an active processing state. For example, the synchronization of a sensorimotor finger tapping with an auditory stimulus is correlated with alpha and beta band decreases in oscillatory power over premotor and primary motor regions (Gerloff et al., 1998; Toma et al., 2002).

Moreover, ERD provides a quantitative and qualitative measure of cortical activity in terms of changes in oscillatory power within alpha (8 – 12 Hz) and beta bands (low: 15 – 20; high: 20 – 30) related to functionally distinct processes. For example, changes within the alpha band have been associated with the presence or absence of motor activity; and changes in beta band are typically associated with the type of pattern being performed (Chen, Ding, & Kelso, 2003). Rebounds of increased beta band power following movement have been recognized in the literature as post-movement beta rebounds (Silva & Pfurtscheller, 1999). These event-related rebounds in beta ERS activation are functionally associated with various aspects of motor control (e.g., planning, preparation, and performance assessment).

With respect to coordination, a number of studies (Mayville et al., 2001; Toma et al., 2002) have found that decreased pattern stability is associated with greater low and high beta ERD over premotor and motor regions. In an MEG experiment, Mayville et al. (2001) found that a syncopated pattern, in comparison to a synchronized pattern, resulted in greater ERD in low and high beta bands over premotor regions, SMA, and M1. Research has suggested (Silva & Pfurtscheller, 1999) that such prolonged ERD correlates with continued communication or recruitment of neural areas due to the increased demand for various processes (e.g., planning, preparation, performance monitoring).

Jantzen et al. (2001) used MEG to further illustrate the relationship between ERD and stability. Participants were trained to syncopate finger flexion with an auditory metronome at their respective critical frequency, that is, the frequency at which they spontaneously switched from syncopation to synchronization. During the pre-training stages of the experiment, syncopation resulted in greater alpha and beta ERD over premotor and SMA in comparison to synchronization. However, after training, syncopation became more stable than the earlier pre-training stages of the experiment. Moreover, syncopation resulted in less ERD, with little differences in power between syncopation and synchronization. Both the Mayville et al. (2001) and Jantzen et al. (2001) studies imply a relationship between cortical alpha and beta ERD and behavioral stability. These findings illustrate the usefulness of ERD in beta and alpha bands as a method of examining stability at the cortical level.

Extending these findings, Chen, Ding, and Kelso (2003) used MEG to determine task-related changes in event-related power for synchronizing and syncopating at a single rate (1.0 Hz). In comparison to a non-movement control condition, both synchronized and syncopated movement conditions were accompanied by increases in alpha ERD over bilateral M1. For

synchronized patterns, greater increases in beta event-related power were found. Moreover, greater decreases in beta event-related power were found for syncopated movements. These results imply that cortical beta band power reflects the difference in the type of pattern conducted. Alpha band power, on the other hand, was associated with making the movement. These findings provide support for a relationship between band-specific activation and features related to the task (e.g. movement, stability).

Previous MEG findings have provided spatiotemporal evidence of neuronal networks functionally related to sensorimotor coordination. Unfortunately none of these studies consider the fast time-scale dynamics of these networks with alterations and changes in important parameters such as performance rate and stability. Most of the aforementioned research examined neural activity condensed or averaged across single movement cycles. However, in a study by Toma et al. (2002) changes in large-scale neural dynamics were assessed within the rapid time scale of a single movement cycle. Toma et al. provided one of the first insights into the rich dynamics of neuronal networks by examining varying rates of sensorimotor coordination on the order of milliseconds. Participants in this study were required to synchronize right-hand thumb movements at rates varying from 0.5 to 4.0 Hz. At low movement rates cortical beta ERD was found prior to and shortly after the movement (see Figure 3). ERS (a "rebound" in activation) followed directly after the movement and persisted until the subsequent movement. At slow rates, interregional oscillations of neuronal activation and deactivation were localized over SMA and M1. Post-movement beta rebound, representing the idling and or resetting of motor cortices, occurred at movement rates below 2 Hz. As rate increased, beyond 2.0 Hz, no post-movement rebound was observed, resulting in continuous ERD over SMA and M1. In addition, motor and premotor regions become functionally coupled, possibly to maintain the

pattern due to increased demands on the coordination system. These changes in neuronal activation are compatible with previous research (Kelso, Delcolle, & Schoner, 1990) that found 2.0 Hz to be the rate at which transitions in behavioral patterns occur. More specifically, these findings reveal patterns of neuronal activation related to various functions required for sensorimotor coordination. Toma and colleagues suggest that post movement low beta (16-20 Hz) synchronization was indicative of higher cognitive functions related to motor control, initiation, preparation, planning, and performance assessment. Power decreases in the alpha band were interpreted by Toma et al. as being related to sensory function. Unlike previous research, the findings of Toma et al. illustrate the spatiotemporal evolution of cortical activation and deactivation that unfolds within a single movement cycle.

Several caveats from the Toma et al. (2002) study must be considered. First, this is the only study to demonstrate a pattern switch from synchronize to syncopate at the critical frequency (2.0 Hz). This contradictory finding could be attributed to their examination of muscular behavior using electromyography (EMG) as an index of motor coordination. Previous research has demonstrated EMG activity to be a misleading index of muscle force and contraction (Hultman & Sjoholm, 1983). Timing delays between the onset of EMG muscle activation and the actual extension/flexion of the thumb could also produce the observed switch from synchronize to syncopate. Second, while previous researchers have examined stability by including multiple patterns (e.g. syncopate, synchronize) Toma et al., (2002) only investigated the synchronized coordination pattern. An examination of only rhythmic synchronized coordination without a syncopation condition does not consider, nor manipulate, behavioral stability. Finally, Toma and colleagues examined rates of 0.5, 0.75, 1.0, 2.0, 3.0, and 4.0 Hz but did not consider neural activity or its relation to stability within the critical movement range

between 1.0 and 2.0 Hz. This functionally important range represents the regime in which patterns of behavior lose stability and spontaneously switch to new ones.

Ipsilateral Primary Motor Cortex (M1)

In addition to the stability-modulating regions described thus far, engagement of ipsilateral M1 has been found to play an important role in movements that have a high degree of difficulty (or complexity) (Verstynen et al., 2005). Previous studies examining motor complexity have also found increased ipsilateral M1 activation for movements of greater complexity (Catalan et al., 1998; Jurkiewicz et al., 2006). PET research has found greater regional cerebral blood flow in the ipsilateral M1 and medial prefrontal regions during complex self-paced finger movements than simple simultaneous finger movements (Shibasaki et al., 1993). Using fMRI, Verstynen et al. (2005) found greater ipsilateral activation for a sequential finger movement task and a finger chord formation task as opposed to a repetitive finger tapping task. Verstynen et al. have also suggested a combined neuronal network of ipsilateral M1 and medial premotor areas that are involved in the processing, planning, and timing of complex motor behaviors.

It has also been suggested that greater ipsilateral motor activation is needed when the demands of motor task require fine acuity and precise timing. A study by Chen et al. (1997) examined the motor performance of simple and complex piano sequences via repetitive TMS lesioning of contralateral and ipsilateral M1. TMS lesioning of ipsilateral M1 led to greater timing errors for the complex piano sequences. However, during the lesioning of contralateral M1 no disturbances in performance were observed for either task. Heightened ipsilateral motor activation has been observed when various motor regions have been compromised due to lesions, strokes, and injuries (Johansen-Berg et al., 2002). These studies typically find that patients with such neuropathology perform complex tasks with greater recruitment of ipsilateral motor regions

than healthy controls. Even for healthy individuals, in the case of this study, it can be assumed that when premotor regions and contralateral M1 are fully activated, additional neuronal regions are recruited to maintain the performance of a complex task. These studies imply a potential role for ipsilateral motor regions in maintaining motor programs that require dexterity, accuracy, and precision of movement.

The aforementioned studies typically employ and define complexity in an arbitrary manner by categorizing motor behaviors based on their perceived "difficulty." However, stability provides a way to directly manipulate the parameters of motor coordination that potentially underlie the notion of complexity. Previous research has not examined nor assessed the role of ipsilateral M1 with regard to changes in coordination stability.

The present study uses the high temporal resolution of EEG to examine event-related desynchronization (activation) of M1, SMA, and premotor cortex in the alpha and beta bands, as a function of both rate and stability. Participants coordinated a finger tap (extension/flexion) with an auditory metronome of tones, maintaining a 1:1 relationship between them. Expanding upon Toma et al., (2002), this study examined the stability of two distinct coordination patterns (synchronize and syncopate) performed at five different movement rates (1.00, 1.25, 1.50, 1.75, and 2.00 Hz) below the critical pattern-switching frequency (approximately 2.00 Hz). Exerting experimental control of both rate and stability provided the ability to fully investigate the neural activation related to each of these parameters.

Similar to findings by Toma et al. (2002), we expected to see decreases in post-movement beta rebound with increasing movement rate over premotor cortex, SMA, and M1. Based on the fMRI literature (e.g. DeBaere et al. 2004; Jantzen et al. 2009; Mayville et al. 2002) decreases in stability should be associated with greater ERD over SMA and premotor regions.

Although we have no predictions concerning the specific timing of when premotor cortical ERD will occur, the timing of the activation of the SMA with respect to movement onset can provide important clues as to the specific role SMA plays in stabilizing coordination. Finally, no study has previously examined ipsilateral M1 activity with changes in stability on a rapid temporal scale. This study will contribute insight into the role of ipsilateral M1 in helping to maintain patterns of coordination with changes in stability.

<div align="center">Method</div>

Participants

Nineteen subjects participated in this EEG study. However, nine participants total were excluded from further analyses. Five participants were excluded due to noise artifacts and four participants due to an inability to perform the coordination task. All participants were right-handed, as determined by self-reported responses to the Edinburgh handedness inventory (Oldfield, 1971) (Appendix A). This study was conducted in compliance with all human research standards outlined by the Institutional Review Board. Informed consent was obtained from each participant, prior to participating in this EEG study (Appendix B).

EEG Apparatus

A Biosemi "Pin-Type" active EEG system was used to record electrical activity of the brain. EEG data were recorded using 64 Ag/AgCl electrodes, equally distributed across the scalp according to the 10-10 placement system, with two reference electrodes – common mode sense (CMS) and driven right leg (DRL). Electrodes were mounted in place via an elastic scalp cap, with saline-based gel (Signa Gel) inserted into each electrode spot. EEG data were amplified and converted (from analog to digital) at a sampling rate of 512 Hz, and stored for further

analyses. All of the EEG data were collected and saved using vendor supplied software
(Actiview) operating on a PC.

Experimental Paradigm

Participants were instructed to coordinate finger flexion of their right index finger with an
auditory metronome of tones (440 Hz, 60 ms long). The auditory beep was presented using a
pair of headphones. Each participant coordinated at five different rates of 1.00, 1.25, 1.50, 1.75,
and 2.00 Hz. For half of the trials, participants were instructed to synchronize with the auditory
metronome, such that the peak finger flexion occurs coincident with the tone. For the other half
of the trials, participants were instructed to maintain a syncopated pattern, such that the peak
finger flexion occurred midway between two auditory tones. The combination of movement rate
and coordination pattern resulted in 10 experimental conditions. Overall, participants performed
a total of 150 trials for each of the 10 conditions broken down into three separate experimental
blocks. The order of each of the rates was counterbalanced randomly to control for possible
practice effects. Participants were further instructed to avoid alternative strategies (e.g.
synchronizing finger extension with the metronome beep for the syncopate task) that would
facilitate their performance.

Stimuli were presented using in-house presentation software written in visual basic on a
Windows XP operating system. On each trial block a visual prompt instructed the participant to
perform either the synchronized pattern ("on beat") or the syncopated pattern ("off beat").
Another prompt, "rest", informed the participant to stop and rest between blocks. Responses
were recorded as a key-press on a 10-button keypad. Behavioral data from the keypad generated
a timing signal that was stored together with the EEG data for further analyses.

Pre-Data Collection Protocol

Participants started the experiment by filling out and signing the informed consent form.

After this, a scalp cap and electrodes were placed and fitted onto their head. Measurements

between the inion and nasion, as well as the left and right preauricular points, were taken to

ensure proper and accurate placement of the electrodes, with electrode Cz placed directly

between these four points. Participants were then given verbal instructions on the experiment

and the coordination tasks to be performed. After this, the electrode offsets and raw electrode

activity were examined to ensure good contact with the scalp. Electrodes with an offset greater

than 20 or electrodes with obvious 60 Hz (or other) noise were removed and reapplied.

Behavioral Analysis

Coordination performance was quantified by the dependent variables relative phase and

stability. The relative phase was computed on each metronome-movement cycle according to the

following formula,

$$rp_i = \left(\frac{t_i - m_i}{\Delta t} \right) \bullet 2\pi$$

where *rp* is the relative phase on the *i*th movement cycle; t_i - m_i is the time difference between

the *i*th tone and the associated movement and Δt is the temporal interval between tones.

Multiplying by 2π expresses the resulting relative measure in radians on a unit circle. The

circular mean and standard deviation was computed on each trial block. The mean of the relative

phase was then computed across blocks to provide single performance measure for each

condition and subject. Similarly, the mean of the standard deviation of relative phase was also

computed across blocks for each subject and condition. The mean of the standard deviation of

relative phase provides an index of stability of coordination with more variable relative phase

indicating lower stability.

EEG Analysis

The majority of analysis was performed using EEGlab, a freely available MATLAB-based software package (Delorme & Makeig, 2004; available from http://sccn.ucsd.edu/eeglab/). All EEG data from the three experimental blocks were appended together and re-referenced to the average reference of all channels. After re-referencing, the data were filtered with a high band pass filter of 1 Hz and a low band pass filter of 50 Hz. Individual epochs of EEG were extracted from the larger time series within the range of −500 ms before to 500 ms after the movement as defined by the time of the button press. Trials contaminated by artifact were eliminated using EEGlab's default automatic rejection software (default setting: electrical potentials of 40 uV and above is rejected), as well as manual inspection by the experimenter. Finally the surface Laplacian was computed on each time point of the single trials to provide an estimate of the current source density. The current source density is the current flowing perpendicular to each surface electrode and provides an estimate of the dura potential (Nunez & Srinivasan, 2005) and thus a more focused view of the underlying cortical sources.

Time Frequency Analysis

Event-related power was computed at each electrode and experimental condition using established methods (e.g., Delorme & Makeig, 2004; Silva & Pfurtscheller, 1999). The time frequency analysis of event-related power examines spectral amplitude compared with an established baseline across a specified frequency range and distributed across a given time interval. The 1.00 Hz synchronized condition (the slowest rate) served as the baseline as it was the most stable condition and thus allowed for direct comparative analysis of other experimental conditions in terms of decreases in stability and increases in rate. The time frequency decomposition was carried out on each single trial using a sinusoidal wavelet transformation,

similar to that described in previous research (Makeig, 1993; Delorme & Makeig, 2004). The EEG waveform was decomposed into corresponding spectral components within the range of 8 to 50 Hz in successive 64 ms windows. The log spectral power from the baseline condition was averaged across the analysis window and subtracted from each condition. The average event-related power (ERP) for each condition was computed using the following formula:

$$ERP(f,t) = \frac{1}{n}\sum_{k=1}^{n}|F_k(f,t)|^2$$

where $F(f,t)$ is the spectral estimate of a particular trial (k) at frequency f and time t.

Spectral power was plotted in a time/frequency space with frequency ranging from 8 to 50 Hz (with 2 Hz resolution) plotted along the Y axis and time, ranging from -432 ms before to 432 ms after the movement (in 4 ms steps) plotted along the X axis. The amplitude of event-related power (in dB) was represented by a color pixel at a given frequency and time point, with blue representing a decrease from baseline or desynchronization and red representing an increase over baseline or synchronization (see Figures 6 and 7 for examples of time frequency plots).

Further analysis was performed to quantify changes in oscillatory power across experimental condition. First, power data were collapsed into discrete bands; alpha (8 – 12 Hz), low beta (14 -20), and high beta (22 – 30). Second, a 2 x 5 repeated measures analysis of variance (ANOVA) was computed at each time point and channel. Within a channel, false discovery rate with an experiment wide error rate of $p < 0.01$ was performed to correct for multiple comparisons.

Predictions

Behaviorally, we predicted that there should be a main effect of pattern such that synchronized patterns would be more stable than syncopated patterns. Moreover, with

increasing movement rate, we predicted an interaction such that pattern stability would decrease only for syncopate pattern, similar to previous findings (e.g. Jantzen et al., 2009; Kelso et al., 1988; Kelso et al., 1990).

Neurophysiologically, based on previous findings from Toma et al., (2002), electrode C3 (contralateral M1) and CP4 (ipsilateral M1) should reveal decreases in post movement beta with increasing rate resulting in a main effect of rate. Moreover, electrodes FCz (over SMA and pre-motor cortex) should demonstrate a Rate x Pattern interaction (stability), with greater ERD for the syncopate pattern than the synchronized pattern. Specifically, based on previous research (Gerloff et al., 1998; Toma et al., 2002) we predicted that all ERS and ERD activity in this study would be primarily found in alpha, low, and high-beta bands. We also expected to see greater engagement of ipsilateral motor cortex related to the complexity of the unstable syncopate conditions at higher rates.

<div align="center">Results</div>

Behavioral Data

The mean relative phase was assessed to determine whether the two patterns (synchronization and syncopation) were effectively performed (see Figure 4). Due to violations in spherecity (Mauchly's test, $p < .05$), all subsequent behavioral analyses are assessed using a Greenhouse-Geisser degrees of freedom correction. Overall, participants met the task performance requirements for both the synchronization ($M = -7.87°$, $SD = 26.49$) and syncopation patterns ($M = 179.96°$, $SD = 32.23$). As predicted, a 2 x 5 analysis of variance (ANOVA) using the factors Pattern and Rate revealed a significant main effect of Pattern, $F (1, 9) = 355.18$, $p < .0001$, *partial $\eta^2 = .99$*. There was no significant main effect of Rate, $F (1.35, 12.15) = 1.51$, $p = .22$, partial $\eta^2 = .02$, and no significant Rate x Pattern interaction, $F (1.42,$

12.78) = 1.63, p = .19, *partial η^2* = .18, indicating that behavior was consistent across all

movement rates.

      For measures of pattern stability the mean of the standard deviation of relative phase was

examined (see Figure 5) to confirm previous behavioral findings (Kelso et al., 1990). A 2 x 5

ANOVA with the factors Pattern and Rate revealed no significant main effect of Pattern between

synchronization (*M* = 25.73, *SD* = 8.67) and syncopation (*M* = 32.04, *SD* = 15.63), F (1, 9) =

2.98, p = .12, *partial η^2* = .25. However, there was a significant main effect of Rate F (1.48,

13.31) = 13.33, p = .001, *partial η^2* = .60, such that variability in performance increased with

increasing movement frequency, regardless of the type of pattern performed. A significant Rate

x Pattern interaction was found, F (1.88, 16.92) = 5.64, p = .0014, *partial η^2* = .39. This

interaction resulted because the increase in variability with increasing rate of coordination was

much greater for syncopation. These results confirm previous findings of an increased loss of

stability with increasing movement frequency for the syncopation task and not the

synchronization task.

Electroencephalography Data

      Figure 6 displays time frequency analysis plots for all 64 channels (distributed spatially

as they appear on the scalp cap), taken from the synchronize 1.00 Hz condition. As can be seen

from Figure 6, most of the neuronal activation (ERD shown in blue) and deactivation (ERS

shown in red) occurred in bilateral motor and medial premotor cortices. Because electrodes C3

(contralateral M1), CP4 (ipsilateral M1), and FCz (medial premotor cortex) revealed the most

distinctive and significant patterns of neuronal activity, we restricted our subsequent analysis to

these representative channels. Most of the overall neural activity observed in bilateral M1

occurred in the low and high beta range; for FCz, most of the neural activity was in the alpha

band. Analyses were performed using a 2 (Pattern) x 5 (Rate) ANOVA applied to every time

point for alpha, low-beta, and high-beta frequency bands.

For the 1.0 Hz synchronize condition, electrode C3 (see Figure 7a) showed low (β1) and

high beta (β2) ERD during and shortly after the movement and ERS between movements.

Quantification of changes in this ERS/ERD pattern across coordination pattern and rate are

shown for channel C3 in the first column of figure 8. Panels show power in the alpha (top), low

beta (middle) and high beta (bottom) bands for each rate condition (collapsed across pattern)

Time points showing a significant main effect of Rate (corrected $p < 0.001$) are highlighted in

light gray. There was a significant main effect of Rate in the alpha (390.62 ms after the

movement to -178.78 ms prior to the next movement), low beta (395.62 ms after the movement

to -175.78 ms prior to the next movement), and high beta bands (351.56 ms after the movement

to -253.90 ms prior to the next movement) for the time interval between successive movements.

Figure 9a shows that beta activation over C3 was related to stepwise increases in rate, regardless

of the type of pattern being performed, such that higher movement rates were associated with a

decrease in the amplitude of the post movement rebound. Similarly, ipsilateral M1, electrode

CP4 (Figure 8c), displayed post movement beta rebound of ERS in alpha (431.64 to 50.78 ms

prior to the next movement), low beta (416.02 ms after the movement to 93.75 ms prior the next

movement), and in high beta frequency bands (431.64 to 175.78 ms prior to the next movement).

As can been seen in Figures 8a and 8c, increases in rate gradually resulted in an increase in ERD

with continuous desynchronization in contralateral and ipsilateral M1 throughout the entire

movement cycle at the fastest rate (2.0 Hz).

For the synchronize 1.0 Hz condition, medial premotor areas, represented by electrode

FCz (see Figure 7b), displayed a pattern of alpha ERS shortly after the movement. Figure 8b

displays alpha band event-related power in FCz for all conditions across the duration of the movement cycle. Electrode FCz revealed ERS during the tap related to a Rate x Pattern interaction (dark gray highlights) in alpha (19.53 ms before movement to 287 ms after movement) (corrected $p < .001$). Figure 9b shows decreases in alpha band event-related power with increasing movement rate for synchronization but not syncopation. In contrast, alpha band power in FCz remained desynchronized across all coordination rates during syncopation. These findings are in contrast to our original predictions.

More in keeping with our predictions, activity in ipsilateral motor cortex related to stability was not observed (CP4, Figure 8c) (corrected $p < .05$) in alpha, low beta, and high beta frequency bands. A brief statistically significant interaction in the alpha band can be observed between movements (-280 to – 225 ms) in ipsilateral motor cortex (corrected $p < .05$). However, an examination of this interaction in the alpha band (see Figure 9c) reveals that this is not related to changes in stability. As can be observed in Figure 9c, a large difference in activation between syncopate and synchronize 2.00 Hz conditions accounts for this statistically significant interaction.

<div align="center">Discussion</div>

Behavioral Findings

Sensorimotor coordination provides an experimental entry point for understanding how we interact with the environment at both the level of behavior and brain. The present study examined this interaction through the stability of two different types of coordination patterns: synchronize and syncopate. The syncopate pattern was found to decrease in stability with increasing rate. In contrast, the synchronize pattern remained more stable regardless of increases in rate. These behavioral findings are compatible with previous reports and support the

theoretical approach of Coordination Dynamics (Jantzen & Kelso, 2007; Kelso et al., 1988; Kelso et al., 1990).

Neural Findings

Through the fine temporal resolution of EEG, we were able to examine the fast-paced dynamics of neuronal activity within a single movement cycle. We specifically investigated how spatiotemporal changes in event-related power of alpha and beta bands are affected both by the rate and stability of coordination. Most of the neural activity localized in primary motor cortex was observed in the low beta band. Similar to Toma et al. (2002), the present study found that stepwise increases in rate resulted in a monotonic decrease in post-movement beta rebound (increased activation) over contralateral M1 regardless of coordination pattern. This finding is compatible with previous fMRI research (e.g., Jantzen et al. 2009) and suggests that primary motor cortex is most strongly influenced by the rate of coordination. Post-movement beta rebound is theorized to represent the resetting or idling of motor cortex (Silva & Pfurtscheller, 1999). At slower rates the resetting and inhibition of motor cortex between movements may reflect that the sequence of movements is being planned and executed in a discrete manner, with the motor cortex resetting between each movement. However, as rate increases, activation of motor cortex remains continuous throughout the entire movement cycle with little to no post-movement beta rebound. The lack of post-movement rebound, resulting in continued neural engagement, could symbolize a transition from a discrete to a more continuous, or rhythmic, train of motor sequence.

Transitions from discrete to rhythmic motor sequences due to increases in movement frequency have been found in studies examining forearm movements (Nagasaki, 1991) and finger taps (Toma et al., 2002). Discrete motor sequences are defined by an interval between two

movements in which there is no motor activity (Hogan & Sternad, 2007). Such movements are identifiable by their distinct "start" and "stop" characteristics and usually classified as being more goal-oriented or target-oriented movements. Toma and colleagues suggest that rates around 1 Hz require neural deactivation of motor cortex (cortical idling or resetting) in order for subsequent movements to be executed in sequence. That is, the brain parses and controls each individual movement separately. For movements beyond this rate, cortical idling or resetting becomes increasingly attenuated and the brain is theorized to process the movements as a continuous/rhythmic train (for example see Zelaznik et al., 2005).

Predominantly all stability-related neural activity in medial premotor regions was found in the alpha frequency band. During and immediately following the tap, decreases in alpha band power over medial premotor regions were observed with increases in rate for synchronize. However, counter to what we predicted, no change in power was shown for syncopate regardless of the rate performed. It is also important to note that Toma and colleagues (2002) did not find similar alpha ERD. Syncopate remained completely desynchronized throughout the entire movement cycle. Alpha band activity over premotor regions has been suggested to be involved in the integration of relevant sensory information (e.g., the auditory tones of the metronome) in assisting coordination performance (Pineda, 2005). The occurrence of alpha ERS and ERD shortly after the tap could play a functional role in performance assessment between the finger tap and auditory tone. One potential explanation for these findings is that medial premotor areas are involved in processes related to the coincidence of the auditory tone with the movement. When the tone and movement are coincident with one another there is an increase of alpha ERS over medial premotor cortex. As the variability between tone and movement increases there is an increase of alpha ERD over these same cortical regions. This could help explain why

syncopate (which is always performed on the off-beat) shows similar alpha ERD regardless of the rate at which it is performed.

Medial premotor regions, especially SMA, have been suggested as playing a critical role in motor and perceptual timing. An fMRI study by Macar et al. (2004) found greater SMA activation involved during a motor timing task rather than a non-timing task which involved applying isometric pressure to a button. Previous research has found that repetitive TMS stimulation over SMA led to greater accuracy and fewer timing errors during the performance of a complex finger sequence task (Gerloff, et al. 1997). Halsband and colleagues (1993) examined patients with lesions to SMA/medial premotor cortex and found greater timing errors, in comparison to healthy controls, during the performance of a sequential finger task. The SMA is part of a fronto-striatal pathway that sends and receives projections to the basal ganglia via the thalamus. The SMA also projects to cortical regions such as prefrontal and parietal cortex. This aforementioned fronto-striatal network is suggested to be involved in various types of motor and perceptual timing tasks. Damage or dysfunction of this network, especially in the case of Parkinson's disease, have been known to result in deficits of motor and sensory timing (Malapani, et al. 1998).

Unlike previous findings that have found greater ipsilateral M1 activation with increased motor complexity, the present study does not support these claims. An interaction was observed in the alpha band in ipsilateral M1, between movements. However, this interaction was mainly due to a difference in power between syncopate and synchronize at the 2.0 Hz condition, and not stability. Overall, across all frequency bands in ipsilateral M1, there was no change in power related specifically to stability. Ipsilateral and contralateral M1, as previously mentioned, appear

to both be highly involved in maintaining the rate at which the task is performed, and not stability.

Unlike Toma and colleagues (2002), the present study found no supporting evidence that beta activity in medial premotor regions was modulated by rate. In contrast, the present study demonstrated a Rate x Pattern interaction in alpha ERS during the immediate post-tap period. The conflicting results for medial premotor regions between Toma et al. and the present study can possibly be attributed to differences in EEG analysis and methodology. Toma et al. found similar spatiotemporal patterns of neural activity for both medial prefrontal cortex and contralateral/ipsilateral M1. Toma et al. may have been measuring a similar source of neural activity between medial prefrontal and primary motor regions.

In their study, Toma and colleagues did not implement a method of spatial filter in their EEG analyses. Spatial filter methods, such as the surface Laplacian used in this study, provide spatially concise measures of cortical activity (Nunez & Srinivasan, 2005). The surface Laplacian analysis helps to increase electrode sensitivity to cortical sources in close proximity to each electrode, while filtering and suppressing sources of cortical activity related to current spreading. Without the use of a spatial filter, unwanted scalp potentials contribute and spread (via volume conduction) to affect multiple electrodes. Consequently, the lack of spatial filter results in a series of electrodes within close proximity that are essentially measuring the same source of activity. This ultimately results in a substantial loss of genuine localized neural sources that are drowned out due to the much larger overarching unfiltered source of activity. Previous researchers have found the surface Laplacian to improve spatial localization of activity within 2 to 3 cm from each electrode. Due to the spatial acuity of the surface Laplacian analysis, the

present study found distinctive spatiotemporal differences in neural activity across discrete brain regions, such as contralateral, ipsilateral M1, and medial premotor regions.

An additional source of the differences between this and Toma et al. (2002) is differences in the movement itself. Toma et al., examined thumb flexion/extension movements that were performed freely in the air without any sort of tactile reafference, while the present study examined finger taps directed towards a tactile surface. Tactile reafferences provide additional timing information for maintaining or improving temporal accuracy of motor movement during a repetitive tapping task (Drewing, Hennings, & Aschersleben, 2002). Tactile feedback has been shown to contribute to changes in event-related power in both alpha and beta band activity (Gaetz & Cheyne, 2006; Neuper & Pfurtscheller, 2001). The present study did not assess spatiotemporal properties of the finger tap's flexion/extension, making it impossible to determine changes in power related to tactile sensory feedback. Future research will need to consider possible effects tactile reafference could have on ERS/ERD activity during the performance of repetitive motor paradigms.

Another methodological difference between past and present studies was the use of directed finger taps to a key-press on a button-box. There is a possibility that this introduced a more goal-oriented approach to the motor task, in comparison to performing the finger taps freely and undirected to a tactile stimulus (e.g. in midair). When pressed, the key on the button-box also introduced additional auditory feedback that could have been used to assist or aid in coordination during the motor tasks. Future research examining motor coordination needs to take these into consideration.

In a recent fMRI study, Jantzen et al. (2009) found that BOLD activation over SMA and premotor cortex increased in response to decreases in coordination stability. In conjunction with

Jantzen et al., we predicted that medial premotor regions would show similar increases in ERD activation with decreased stability. However, this pattern of activation related to a loss in stability was not observed. These dissimilar findings may be attributed to differences in brain imaging apparatus. fMRI measures hemodynamic responses as a surrogate for neuronal activity whereas EEG directly measures neuronal electrode activity from the scalp. Moreover, the temporal resolution of these imaging apparatuses differs considerably. EEG provides up to 1 ms temporal resolution, while current fMRI techniques provides a temporal resolution of 2 s maximum (Norris, 2006). In the case of the Jantzen et al. (2009) study, fMRI is incapable of examining the fast-scale dynamics of neuronal activity observed here in this study with EEG. Nonetheless, EEG and fMRI provide different and important information regarding how neuronal networks are involved in modulating and controlling coordination.

In summary, the present study observed spatiotemporal differences in oscillatory power between primary motor cortex and medial premotor regions related to the rate and stability of coordination. We found similar low and high beta neural activity in bilateral M1 as Toma and colleagues (2002). However, our findings show ERS activity in medial premotor regions shortly after the movement, potentially related to the coincidence of timing between the finger tap and metronome beep. Future research should further explore this proposed coincidence timer and its involvement in coordination. The potential role of this timer and coordination could have applications to deficits typically observed in neurological disorders such as Parkinson's disease. EEG with its excellent temporal resolution can determine the mechanisms that underlie rate-dependent changes in bilateral M1 that are typically observed with PET and fMRI. This research is important in understanding how the brain organizes and maintains complex patterns of behavioral coordination.

References

Catalan, M. J., Honda, M., Weeks, R. A., Cohen, L. G., & Hallett, M. (1998). The functional neuroanatomy of simple and complex sequential finger movements: A PET study. *Brain, 121*, 253-264.

Chen, D. F., Ding, M., & Kelso, J. A. S. (2003). Task-related power and coherence changes in neuromagnetic activity during visuomotor coordination. *Experimental Brain Research, 148*, 105-166.

Chen, R., Gerloff, C., Hallett, M., & Cohen, L. G. (1997). Involvement of the ipsilateral motor cortex in finger movements of different complexities. *Annals of Neurology, 41*, 247-254.

Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., & Swinnen, S. P. (2004). Cerebellar and premotor function in bimanual coordination: Parametric neural responses to spatiotemporal complexity and cycling frequency. *Neuroimage*, *21*, 1416-1427.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics. *Journal Neuroscience Methods*, *134*, 9-21.

Drewing, K., Hennings, M., & Aschersleben, G. (2002). The contribution of tactile reafference to temporal regularity during bimanual finger tapping. *Psychological Research, 66*, 60-70.

Ehrsson, H. H., Kuhtz-Buschbeck, J. P., & Forssberg, H. (2002). Brain regions controlling nonsynergistic versus synergistic movement of the digits: A functional magnetic resonance imaging study. *Journal of Neuroscience*, *22*, 5074-5080.

Gaetz, W., & Cheyne, D. O. (2006). Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *NeuroImage, 30*, 899-908.

Gerloff, C., Corwell, B., Chen, R., Hallett, M., & Cohen, L. G. (1997). Stimulation over the human supplementary motor area interferes with the organization of future elements in complex motor sequences. *Brain, 120*, 1587-1602.

Gerloff, C., Richard, J., Hadley, J., Schulman, A. E., Honda, M., & Hallet, M. (1998). Functional coupling and regional activation of human cortical motor areas during simple, internally paced and externally paced finger movements. *Brain, 121*, 1513-1531.

Haken, H. (1983). Advanced synergetics: Instability hierarchies of self-organizing systems and devices. Berlin: Springer-Verlag.

Haken H., Kelso, J. A. S., & Bunz, H. (1985). A theoretical-model of phase-transitions in human hand movements. *Biological Cybernetics. 51*, 347–356

Halsband, U., Ito, N., Tanji, J., & Freund, H. J. (1993). The role of premotor cortex and the supplementary motor area in the temporal control of movement in man. *Brain, 116*, 243-246.

Hogan, N., & Sternad, D. (2007). On rhythmic and discrete movements: Reflections, definitions and implications for motor control. *Experimental Brain Research*, *181*, 13-30.

Hultman, E., & Sjoholm, H. (1983). Electromyogram, force and relaxation time during and after continuous electrical stimulation of human skeletal muscle in situ. *Journal of Physiology, 339*, 33-40.

Jantzen, K. J., Fuchs, A., Mayville, J. M., Deecke, L., & Kelso, J. A. S. (2001). Neuromagnetic activity in alpha and beta bands reflect learning-induced increases in coordinative stability. *Clinical Neurophysiology, 112*, 1685-1697.

Jantzen, K. J., & Kelso, J. A. S. (2007). Neural coordination dynamics of human sensorimotor behavior: A review. In V.K Jirsa & R. MacIntosh (Eds.) *Handbook of Brain Connectivity*. Springer: Heidelberg.

Jantzen, K. J., Oullier, O., Marshall, M., Steinberg, F. L., & Kelso, J. A. S. (2007). A parametric fMRI investigation of context effects in sensorimotor timing and coordination. *Neuropsychologia, 45*, 673–684.

Jantzen, K. J., Steinberg, F. L., & Kelso, J. A. S. (2009). Coordination dynamics of large-scale neural circuitry underlying rhythmic sensorimotor behavior. Journal of Cognitive Neuroscience, 21, 2420-2433.

Johansen-Berg, H., Rushworth, M. F. S., Bogdanovic, M. D., Kischka, U., Wimalaratna, S., & Matthews, P. M. (2002). The role of ipsilateral premotor cortex in hand movement after stroke. *PNAS, 99*, 14518-14523.

Jurkiewicz, M. T., Gaetz, W. C., Bostan, A. C., & Cheyne, D. (2006). Post-movement beta rebound is generated in motor cortex: Evidence from neuromagnetic recordings. *NeuroImage, 32*, 1281-1289.

Kelso, J. A. S. (1995). Dynamic patterns: The self-organization of brain and behavior. MIT Press, Cambridge.

Kelso, J. A. S., Delcolle, J. D., & Schoner, G. (1990). Action-perception as a pattern-formation process. *Attention and Performance*, 139-169.

Kelso, J. A. S., Scholz, J. P., & Schoner, G. (1988). Dynamics governs switching among patterns of coordination in biological movement. *Physics Letters A, 134*, 8-12.

Kobayashi, M., & Pascual-Leone, A. (2003). Transcranial magnetic stimulation in neurology. *Lancet Neurology*, *2*, 145–156.

Macar, F., Anton, J. L., Bonnet, M., & Vidal, F. (2004). Timing functions of the supplementary motor area: An event-related fMRI study. *Cognitive Brain Research, 21*, 206-215.

Makeig, S. (1993). Auditory event-related dynamics of the EEG spectrum and effects of exposure to tones. *Electroencephalography clinical Neurophysiology, 86*, 283-293.

Malapani, C., Ratkin, B., Levy, R., Meck, W. H., Deweer, B., Dubois, B., et al. (1998). Coupled temporal memories in Parkinson's disease: A dopamine-related dysfunction. *Journal of Cognitive Neuroscience, 10*, 316-331.

Mayville, J. M., Fuchs, A., Ding, M., Cheyne, D., Deecke, L., & Kelso, J. A. S. (2001). Event-related changes in neuromagnetic activity associated with syncopated and synchronization timing tasks. *Human Brain Mapping, 14*(2), 65-80.

Mayville, J. M., Jantzen, K. J., Fuchs, A., Steinberg, F. L., & Kelso, J. A. S. (2002). Cortical and subcortical networks underlying syncopated and synchronized coordination revealed using fMRI. *Human Brain Mapping, 17*, 214-229

Meyer-Lindenberg, A., Ziemann, U., Hajak, G., Cohen, L., & Berman, K. F. (2002). Transitions between dynamical states of differing stability in the human brain. *PNAS, 99*, 10948-10953.

Nagasaki, H. (1991). Asymmetrical trajectory formation in cyclic forearm movements in man. *Experimental Brain Research, 87*, 653-661.

Neuper, C., & Pfurtscheller, G. (2001). Event-related dynamics of cortical rhythms: Frequency-specific features and functional correlates. *International Journal of Psychophysiology, 43*, 41-58.

Norris, D. G. (2006). Principles of magnetic resonance assessment of brain function. *Journal of Magnetic Resonance Imaging, 23*, 794 – 807.

Nunez, P. L., & Srinivasan, R. (2005). *Electric Fields of the Brain: The Neurophysics of EEG.* Oxford University Press Inc., New York.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97-113.

Pineda, J. A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing." *Brain Research Reviews, 50*, 57-68.

Shibasaki, H., Sadato, N., Lyshkow, H., Yonekura, Y., Honda, M., Nagamine, T., et al. (1993). Both primary motor cortex and supplementary motor area play an important role in complex finger movement. *Brain, 116*, 1387-1398.

Silva, F. H., & Pfurtscheller, G. (1999). Basic concepts on EEG synchronization and desynchronization. In: Pfurtscheller, G., & Silva F. H. (Eds). Event-related Desynchronization, vol. 6. Elsevier, Amsterdam.

Toma, K., Mima, T., Matsuoka, T., Gerloff, C., Ohnishi, T., Koshy, B., et al. (2002). Movement rate effect on activation and function coupling of motor cortical areas. *Journal of Neurophysiology, 88*, 3377-3385.

Verstynen, T., Diedrichsen, J., Albert, N., Aparicio, P., & Ivry, R. B. (2005). Ipsilateral motor cortex activity during unimanual hand movements relates to task complexity. *Journal of Neurophysiology, 93*, 1209-1222.

Zanone, P. G., & Kelso, J.A.S. (1992). Evolution of behavioral attractors with learning - Nonequilibrium phase-transitions. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 403–421.

Zelaznik, H. N., Spencer, R. M., Ivry, R. B., Baria, A., Bloom, M., Dolanksy, L., et al. (2005).

Timing variability in circle drawing and tapping: Probing the relationship between event
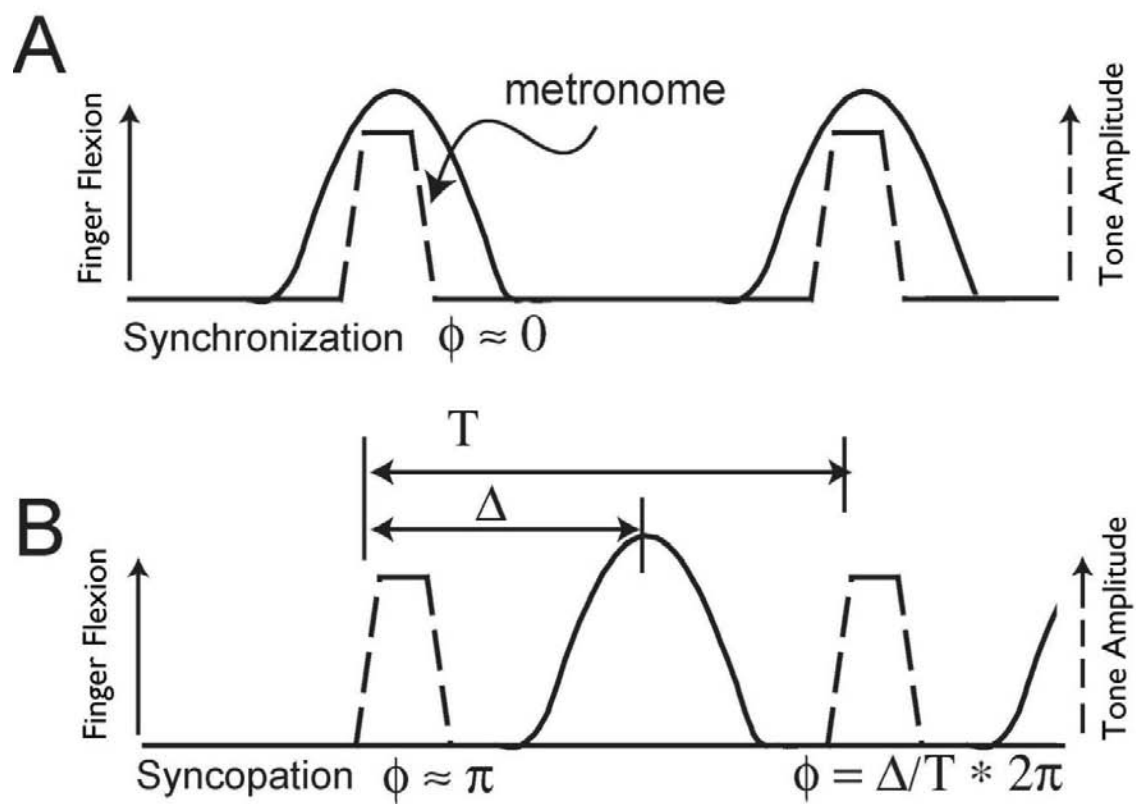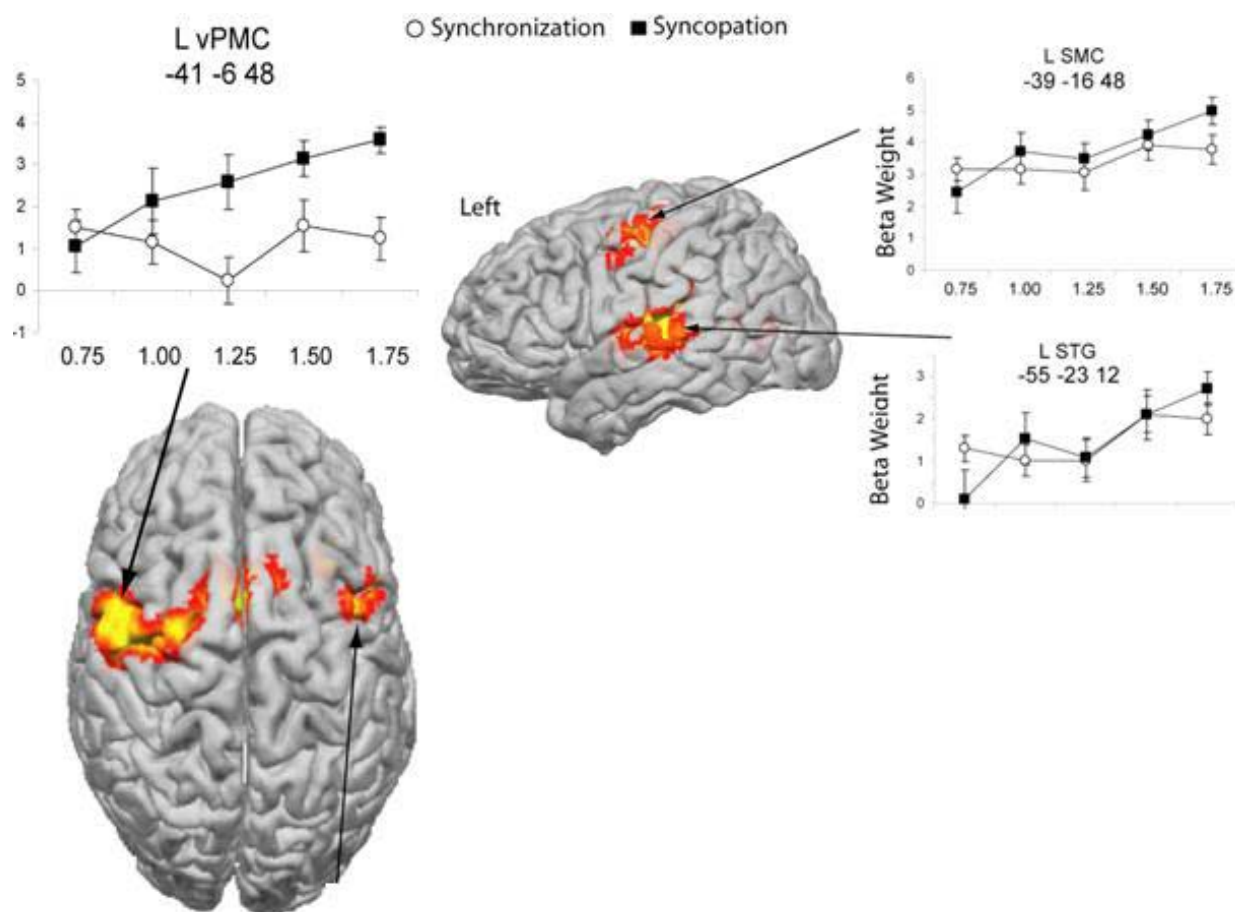
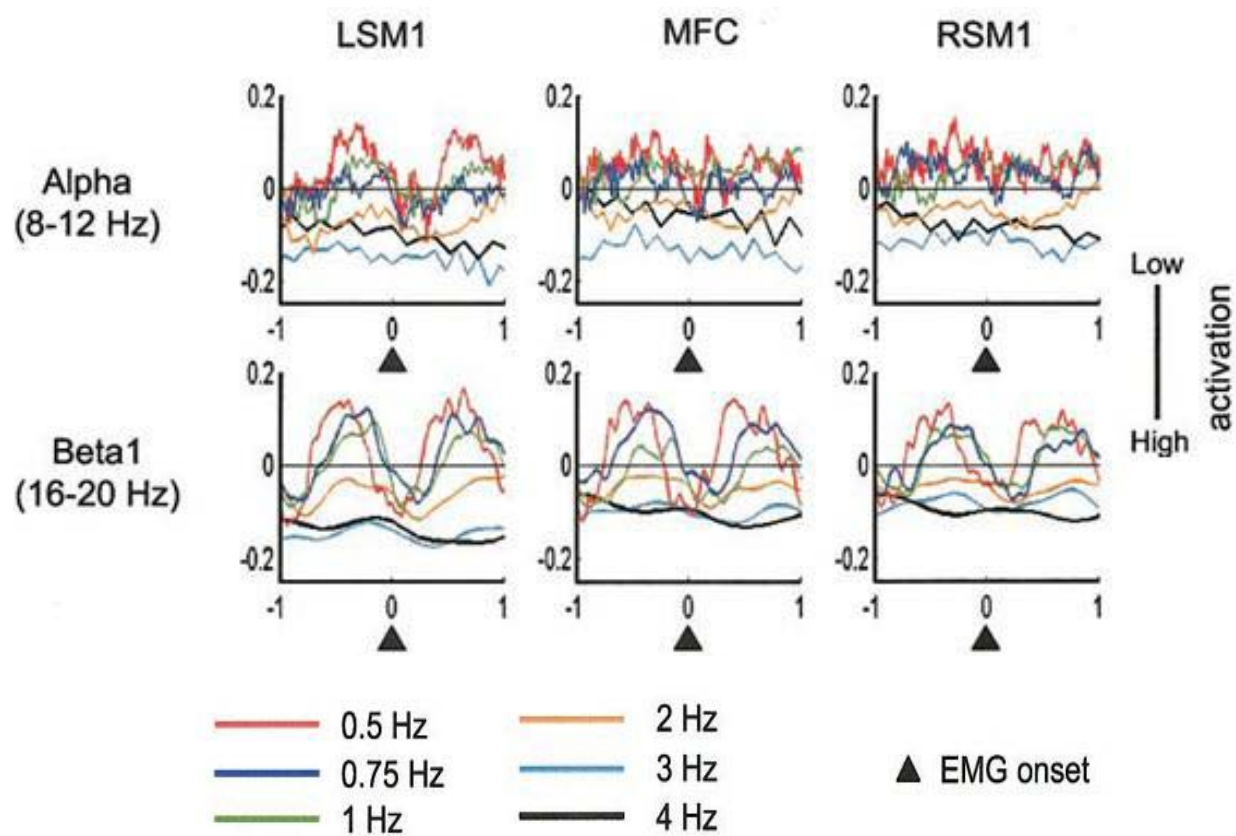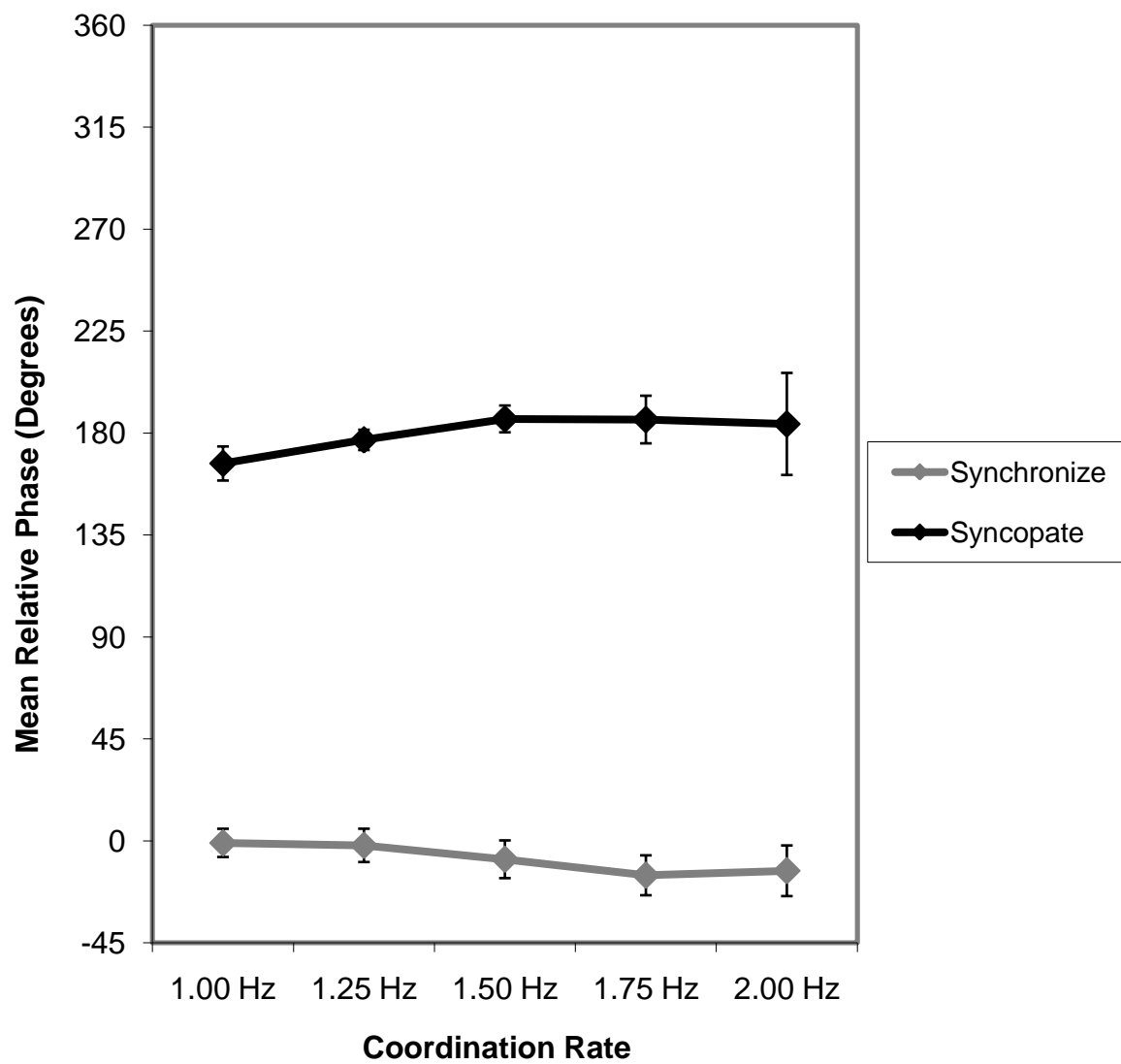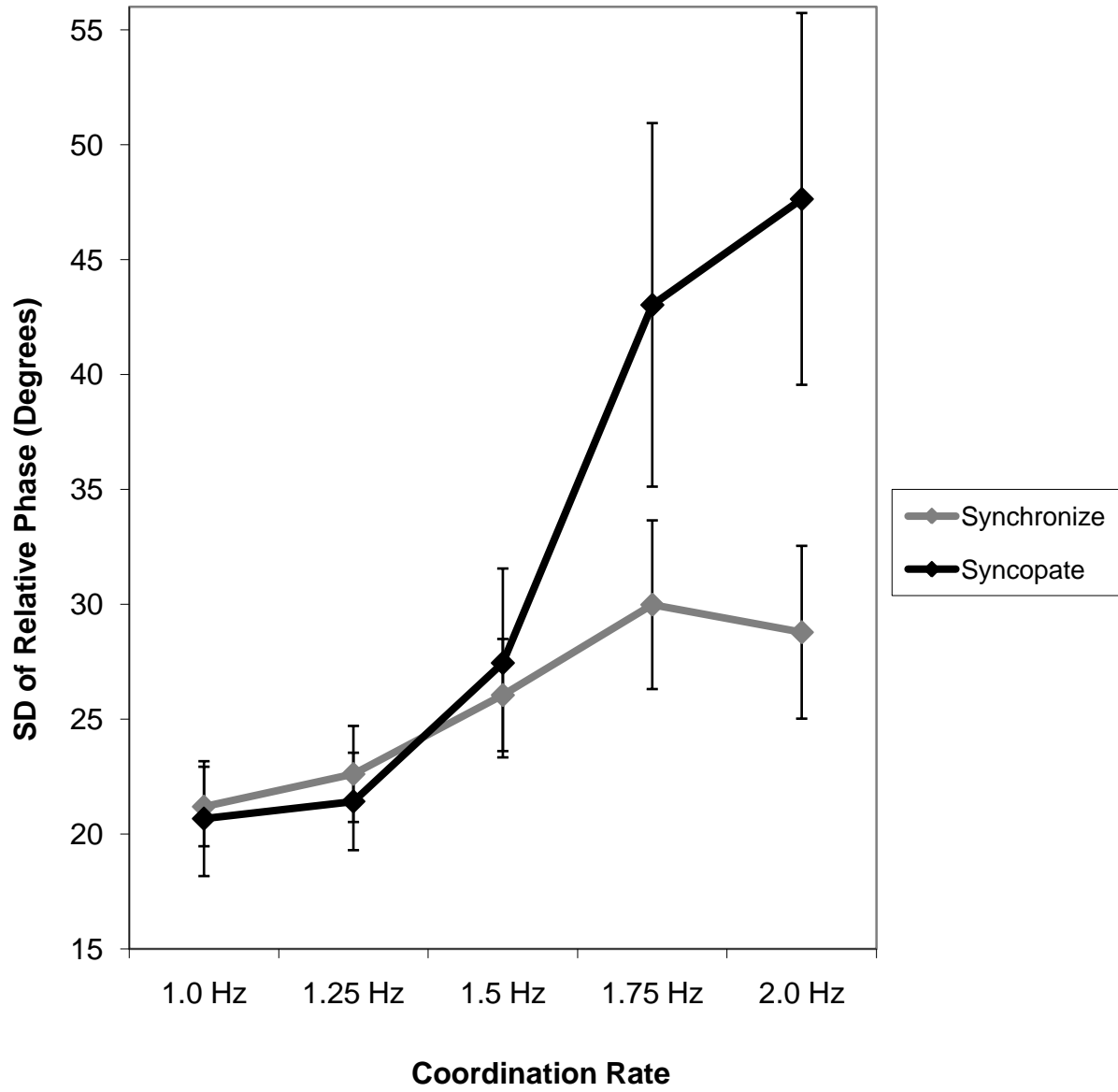and emergent timing. *Journal of Motor Behavior, 37*, 395-403.
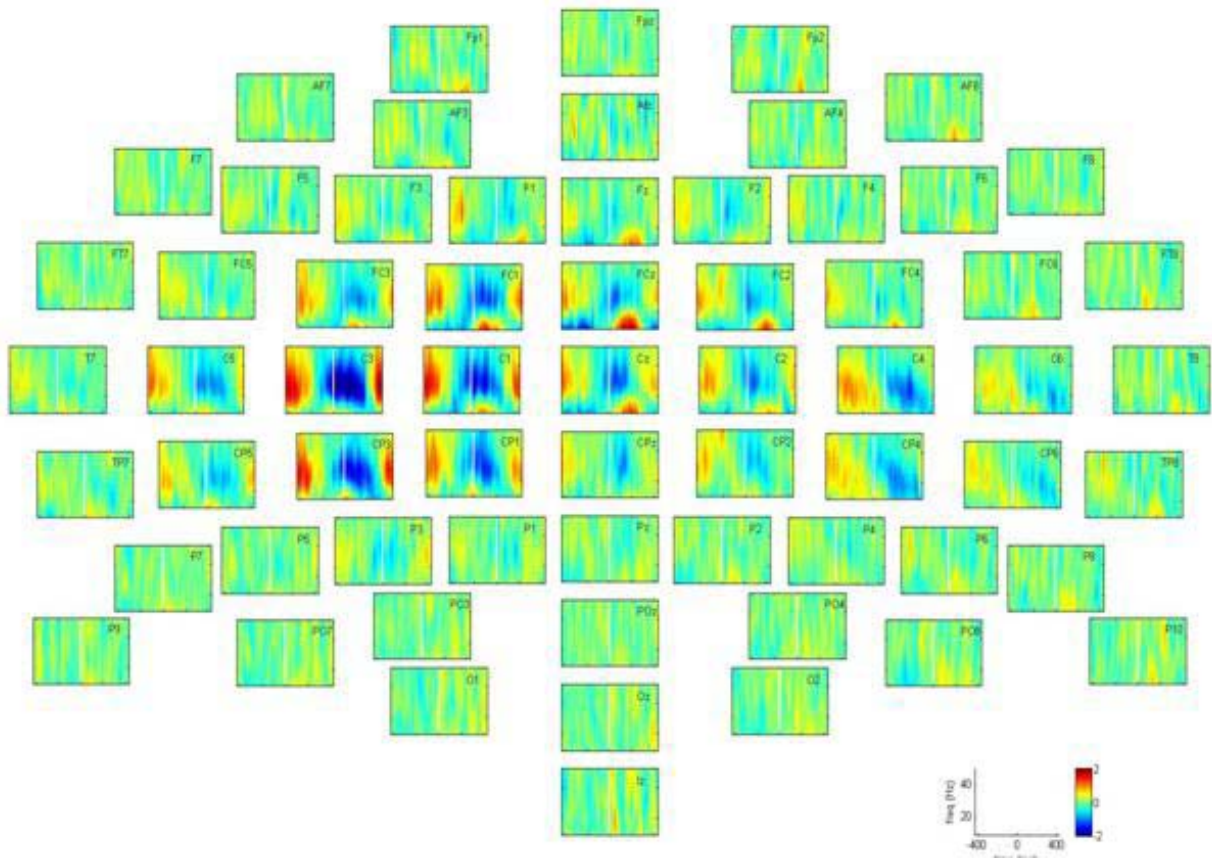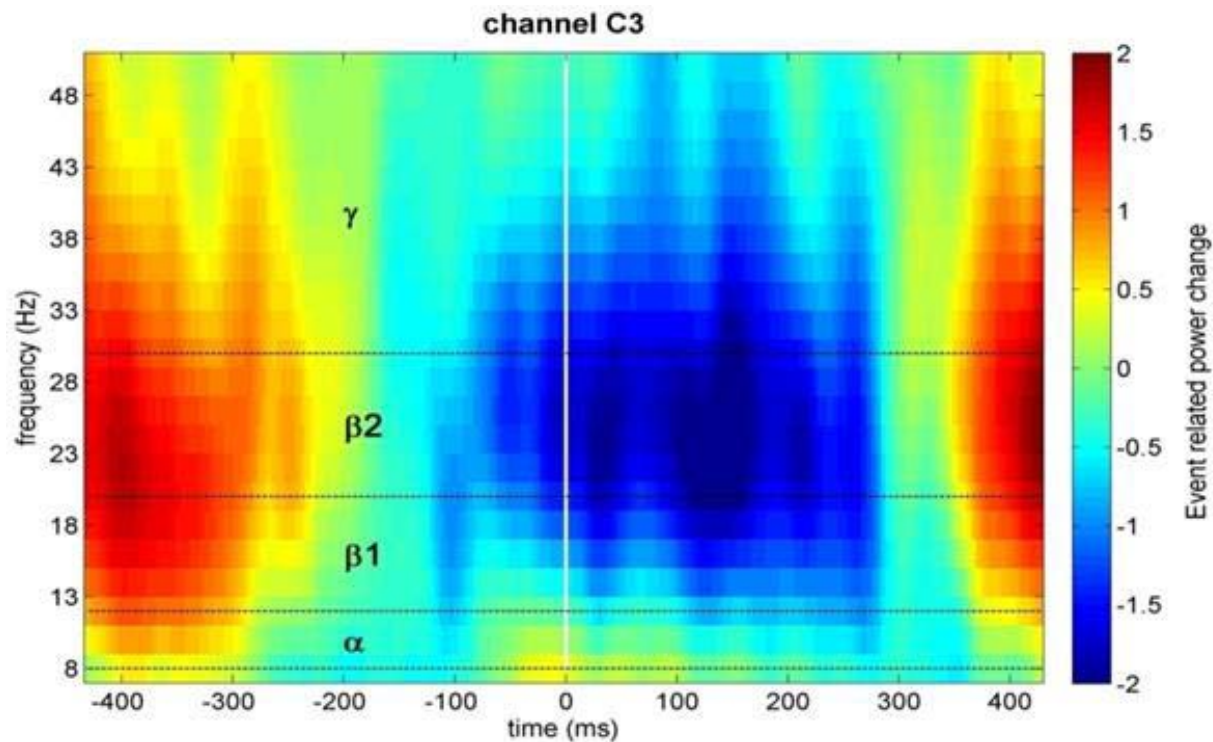
Figure 1.

Figure 2.

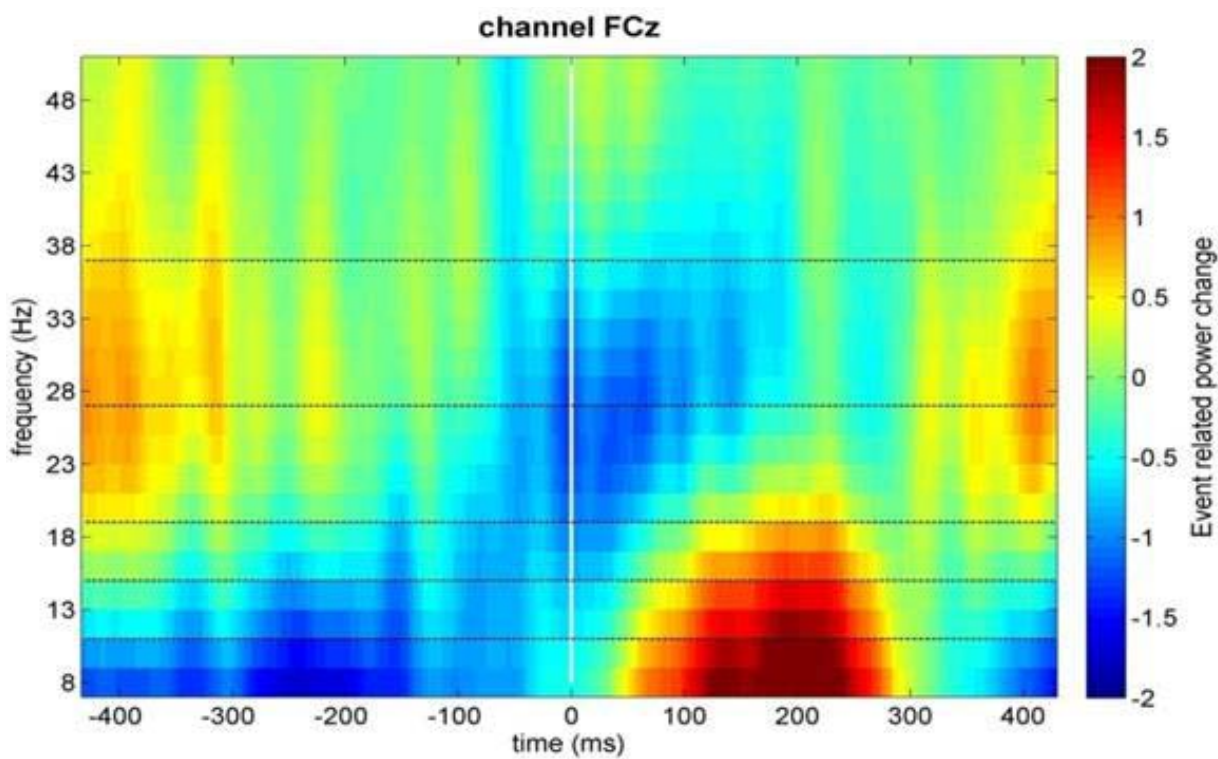Figure 3.

Figure 4.

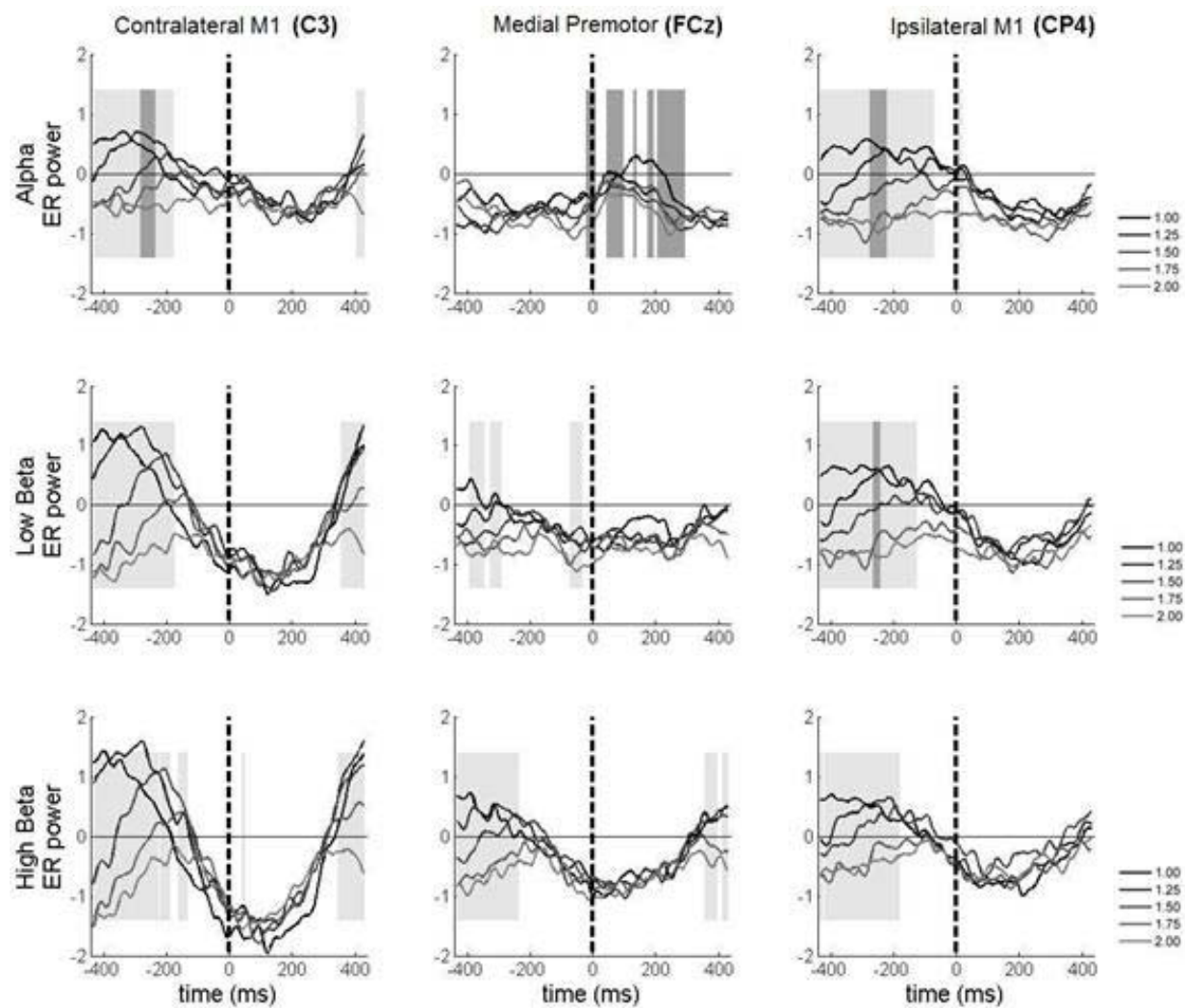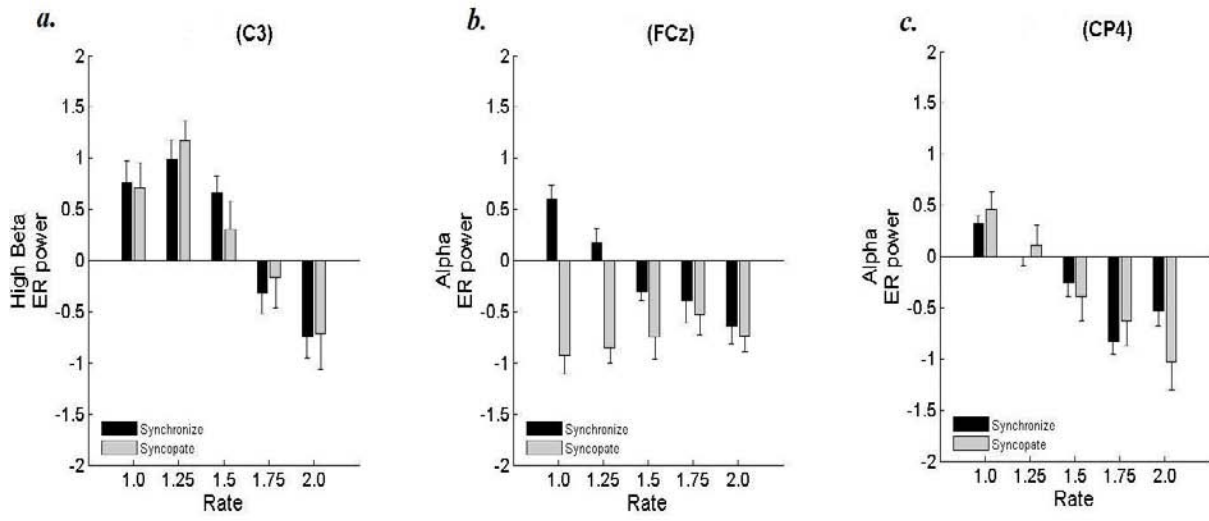Figure 5.

Figure 6.

Figure 7.

a.

b.

Figure 8.

Figure 9.

Appendix A

Consent Form

Purpose and Benefit:

Researchers have been interested in the link between brain activity and coordinated movements to better understand how the brain coordinates actions in time with many events in the environment to produce very complex behaviors like dancing and riding a bike. The purpose of this experiment is to examine the brain processes associated with the performance of different coordinated patterns of behavior. The results of this study will advance our understanding of how patterns of behavior are represented in the brain ad may lead to a greater understanding and treatment of movement disorders.

I UNDERSTAND THAT:

1) This experiment will involve the filling out of a questionnaire (to determine hand preference) and performance of a series of simple motor tasks in which finger movements are made in time with the presentation of a sound or image. My participation in the experimental procedure will involve approximately 45 minutes.

2) The electrical activity of my brain will be recorded during the experiment through a set of electrodes placed in a cap and fitted onto my head. A water-soluble conductive gel will be placed on my scalp under each electrode. At the end of the experiment the position of each electrode on my head will be measured. My participation in the setup and clean up of the electrodes will involve approximately 30 minutes.

3) Although recording of the electrical activity of my brain is a non-invasive procedure, there is a small risk that I may feel discomfort from the cap or the conductive gel. There is also a small risk of experiencing fatigue during the experiment. In either event I can stop the experiment whenever necessary. I may benefit from the experience of participating in a cognitive neuroscience experiment.

4) My participation is voluntary; I may choose to withdraw from participation at any time without penalty.

5) All information is confidential. My signed consent form will be kept in a locked cabinet separate from the brain recordings and movement data. My name will not be associated with any of my data at any time.

6) My signature on this form does not waive my legal rights of protection.

7) This experiment is conducted under the supervision of Dr. Jantzen. Any questions that you have about the experiment or your participation may be directed to him at 650-4046.

If you have any questions about your participation or your rights as a research participant, you can contact Geri Walker WWU Human Protections Administrator (HPA), (360) 650-3220, geri.walker@wwu.edu. If during or after participation in this study you suffer from any adverse effects as a result of participation, please notify the researcher directing the study or the WWU Human Protections Administrator.
****

I have read the above description, am at least 18 years of age, and agree to participate in this study.

_____   _____
Participant Signature   Date

_____
Participant's PRINTED NAME

NOTE: Please sign both copies of the form and retain the "Participant" copy.

Appendix B

Handedness Questionnaire

Participant Name:

Experiment Name:

When performing the following activities…	Which hand do you prefer			Do you ever use the other hand?	
Writing:	NONE	LEFT	RIGHT	YES	NO
Drawing:	NONE	LEFT	RIGHT	YES	NO
Throwing:	NONE	LEFT	RIGHT	YES	NO
Using Scissors:	NONE	LEFT	RIGHT	YES	NO
Using a Toothbrush:	NONE	LEFT	RIGHT	YES	NO
Using a Knife (without a fork):	NONE	LEFT	RIGHT	YES	NO
Using a Spoon:	NONE	LEFT	RIGHT	YES	NO
Using a Broom (upper hand):	NONE	LEFT	RIGHT	YES	NO
Striking a Match:	NONE	LEFT	RIGHT	YES	NO
Opening a Box (lid):	NONE	LEFT	RIGHT	YES	NO

Totals: _____ _____ _____   _____ _____

Handedness Score: _____