

Neural Coordination Dynamics of Human Sensorimotor Behavior: A Review

Kelly J. Jantzen and J.A. Scott Kelso

Human Brain and Behavior Laboratory & Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, FL, 33431

1. Introduction

Coordination symbolizes one of the most fundamental, yet arguably least understood ability of living things. Humans effortlessly coordinate complex interactions between their bodies and the world in order to accomplish even the simplest of tasks. Coordination Dynamics, defined broadly as the science of coordination (see contributions, e.g. in Tschacher and Dauwalder 2003; Jirsa and Kelso 2004) describes, explains and predicts how patterns of coordination form, adapt, persist and change in natural systems. It uses the language, methods and tools of self-organizing dynamical systems (e.g. Haken 1983; Nicolis and Prigogine 1989) to provide a conceptual and theoretical framework for understanding coordination at multiple levels, from behavior to brain (Kelso 1995; Haken 1996; Kelso et al. 1999). A primary goal of coordination dynamics is to understand the laws, principles and mechanisms governing how patterns of behavior form in space and time; how these patterns are maintained; how they change in response to environmental or physiological demands; and how they are reorganized in an adaptive way, often allowing for the adoption of new patterns. “Understanding” means identifying both the essential variables and parameters that characterize dynamic patterns of coordination on a given level of description and the usually low-dimensional pattern dynamics that gives rise to a broad range of complex, dynamic behaviors. As a science of coordination that embraces both structure and function in living things, coordination dynamics deals essentially with *informationally* coupled self-organizing systems. That is, in coordination dynamics otherwise independent component subsystems are coupled by functionally meaningful information.

In studies of coordination dynamics, behavioral coordination has proven a fertile entry point into uncovering principles and mechanisms of human action (Kelso 1995; Jirsa and Kelso 2004). Within this conceptual and theoretical framework, coordination is defined in terms of collective or coordination variables that specify the spatiotemporal ordering between component parts. In the vicinity of critical points, emergent behavior has been shown to be governed by the low-dimensional dynamics of these collective variables (e.g., Haken, Kelso & Bunz, 1985). This low-dimensional dynamics is revealed by manipulating one or more control parameters whose role is simply to move the system through a series of state changes. Adopting this strategy in the case of human behavioral coordination

has revealed that the relative phase between component subsystems is a crucial collective variable and that the rate of coordination is a key control parameter (Kelso 1984; Haken et al. 1985). Thus, when rate is systematically increased, instabilities in coordination develop and spontaneous switches between patterns of coordination ensue. It is these transitions and the features that surround them that have established the self-organizing nature of human behavior (see Kelso, et al., 1987; Schönner and Kelso 1988 for early reviews).

A deeper understanding of human behavior and cognition rests on uncovering how the rich dynamics of human behavioral pattern formation is rooted in underlying brain processes. In this chapter we take the case of sensorimotor coordination as an entry point for determining the relation between the dynamics of human behavior and the dynamics of brain function. We begin with a brief description of levels of observation, including the kinds of measures that may help us to connect behavioral and neural levels (see also Fuchs et al. 1999; Jirsa et al. 1999; Kelso et al. 1999). We then go on to describe the experimental ‘workhorse’ paradigm used to study human behavioral pattern formation and the basic phenomena it reveals. This is followed by a brief overview of the theoretical and mathematical framework employed to explain these phenomena. Such concepts aid in identifying the key variables that govern coordination and hence provide experimental insight into its nature. Having identified key coordination variables, we then review the literature that has either directly or indirectly shown how patterns of human sensorimotor behavior may be mapped onto neural function. Finally, we conclude with some key questions that future research needs to address and how technological and analytical advances in functional neuroimaging may aid in finding the answers.

2. Levels of Observation

At the behavioral level we take as our entry point sensorimotor or perceptual motor coordination (Kelso et al. 1990). This can be broadly defined as coordinating one’s actions in space and time with environmental stimuli. Such stimuli can vary widely in scope ranging from a simple rhythmic stimulus presented over one or more perceptual modalities to multifaceted biologically relevant stimuli such as the actions of another person (e.g., DeGuzman, et al., 2005; Oullier, et al., 2003). Regardless, the idea is to identify key measures of the coordination between interacting elements and the dynamics governing this interaction. Much research over the last two decades has demonstrated that *relative phase* is a relevant collective or coordination variable that: a) captures (multiple) patterns of behavior of coupled systems; b) reveals specific features of the underlying dynamics of the coordinated system such as loss of stability; and c) demonstrates the existence of pattern switching. Operationally, relative phase is defined as the time difference between an environmental event (e.g., a simple tone beep, tactile vibration or visual flash), and the associated behavioral action (e.g., a simple finger flexion) divided by the stimulus period. Since we are dealing in the first instance with

rhythmic behavior, this normalized time difference is often expressed in radians or degrees by multiplying it by 2π or 360 respectively (see Jirsa & Kelso, 2005 for a more generic treatment).

At the neural level we concentrate on relatively macroscopic measures of brain function derived from electroencephalography (EEG), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI) and positron emission tomography (PET). These technologies supply a variety of measures of the activity of neural ensembles that, when combined with various analytic methods provide insight into the large scale functioning of the human brain. It should be noted that each of these recording tools provides unique information about large-scale patterns of neural activity and possesses advantages and disadvantages relative to one another. The latter will become clear as we proceed through forthcoming sections.

Current technologies restrict us to questions concerning how the rich dynamics of behavioral coordination originates from activity arising at the level of macroscopic brain function. Of course, this is not to say that other scales of observation are uninformative and do not provide additional insight into the questions addressed here. Neural activity unfolds over multiple spatial and temporal scales (e.g. cortical column, local field potential, single unit, ion channels, neurotransmitters, gene expression, etc.) that are likely to be important to understanding coordination at other levels. As for sensorimotor behavior, work at intermediate levels of observation suggests that biomechanical factors can play a role in modulating the intrinsic dynamics of human behavioral coordination (e.g. Ridderikhoff et al. 2004). For example, there appears to be a preference for recruitment of specific muscular synergies during coordination as revealed by the observation of transitions from extension on the beat to flexion on the beat (Carson et al. 1996; but see also Kelso, et al., 2001). This finding has been couched in terms of the modulation of central supraspinal mechanisms on spinal tendencies favoring the entrainment of flexors. Similarly, in wrist supination/pronation the most stable pattern (pronation or supination on the beat) is determined by the location of the axis of rotation with respect to the skeletal structure (Byblow et al. 1995; Carson and Riek 2000) suggesting that altering musculoskeletal constraints impacts the stability of performed coordination patterns. In short, although we concentrate here on understanding relative phase dynamics in terms of large scale neural activity we also recognize that the rich repertoire of both bimanual (Swinnen 2002) and unimanual coordination (Ridderikhoff et al. 2004) arises from a coalition of constraints (Kelso et al. 2001; Temprado and Swinnen 2005) that includes, but is not limited to the combined influence of supraspinal, musculoskeletal and environmental factors.

3. Behavioral Level: Stability and Instability

To illustrate the key ideas and features of coordination dynamics, we describe a simple experimental system that treats the problem of sensorimotor coordination

as a pattern forming process (Kelso et al. 1990). In the paradigmatic case, the temporal coupling is between a finger flexion/extension movement and a periodic auditory beep. The task requires participants to coordinate in one of two or more possible patterns. For the synchronized patterns movements are coordinated such that peak flexion of the movement occurs coincident with the metronome beat. Syncopation is accomplished by placing peak flexion directly in between two consecutive beats. In Kelso et al. (1990) the metronome was systematically increased in frequency from 1 Hz to 3.5 Hz in steps of 0.25 Hz. Instructions emphasized the importance of maintaining a 1:1 relationship between finger movement and metronome at all times, and if the pattern changed “not to intervene” or to intentionally restore the pattern (see also Kelso et al. 1988; Scholz and Kelso 1990). When finger flexion and metronome occur simultaneously in time the relative phase difference between them is 0° . Perfect syncopation is achieved when the relative phase difference is 180° .

A rich and reproducible set of behaviors flows from this paradigm. At low metronome rates a strong tendency exists toward frequency- and phase-locking in both conditions. That is, both patterns are performed in a stable manner with relative phase between finger and metronome close to 0 or 180 degrees. As the rate of the movement is parametrically increased, a spontaneous transition from syncopation to synchronization is observed at a critical frequency marking the change from a bistable regime (where both patterns are possible and may be said to coexist) to a monostable regime where synchronization predominates. In some cases further increases in rate result in the loss of entrainment between the finger and metronome resulting in phase wandering and various patterns of phase drift. Transitions between coordination patterns are typically preceded by an increase in the variability of the relative phase between sensory and motor events. Such fluctuation enhancement in the vicinity of transition points indicates a characteristic loss of stability typical of nonequilibrium pattern forming systems in nature (Haken, 1983). Indeed, the foregoing experiments and resultant theoretical modeling (Kelso, et al., 1990) have been taken to provide strong evidence that action-perception follows laws of general pattern forming processes (Turvey, 2004). The symmetry breaking property of the theory developed in the Kelso et al (1990) work has proven to be generalizable across different experimental paradigms, thereby providing a framework for understanding and investigating human behavior in a variety of contexts. For example, the same dynamical features such as loss of stability, critical slowing down and qualitative changes in the order parameter have been observed across different task contexts such as coordination between homologous limbs (Kelso 1984), non-homologous limbs (Kelso and Jeka 1992; Jeka and Kelso 1995; Swinnen et al. 1997), between persons and their environment (Kelso et al. 1990; Jirsa et al. 2000) and even in social coordination between people (Schmidt et al. 1998; 1999; Oullier, et al., 2003; Richardson et al., 2005). Similar principles govern perceptual grouping and coordination as nicely illustrated by the classic bistable properties of reversible figures such as the Necker cube (e.g. Kelso, et al., 1995), the visual perception of spatiotemporal inphase and antiphase moving stimuli (Hock et al. 1993; Bingham et al. 1999; Zaal et al., 2000) and speech categorization (Tuller et al. 1994; Case et al. 1995). For present

purposes, the key aspect of this essentially ‘nonlinear paradigm’ is that it provides a convenient entry point for investigating the dynamics of pattern formation and change at both behavioral and brain levels.

4. Theoretical Foundations

The theoretical model first proposed by Haken, Kelso and Bunz (1985), and its elementary extensions to include stochastic (Schöner et al. 1986) and symmetry breaking features (Kelso et al. 1990) form the foundation for the science of coordination and provide a basis for understanding the self-organizing dynamics of human behavioral and neural function (Kelso 1995; Haken 1996; Bressler and Kelso 2001). The original HKB formulation assumed, for simplicity’s sake, identical (homogeneous) elements. Here we provide a brief introduction to the computational model that accounts for the basic coordination phenomena in terms of the non-linear coupling between heterogeneous coordinating elements (Kelso et al. 1990). In this theoretical model, the coordination between finger flexion/extension movements and the environment is captured by the relative phase (ϕ) and represented by a nonlinear equation of motion that specifies the relative phase dynamics:

$$\dot{\phi} = \delta\omega - a \sin \phi - b \sin 2\phi + \sqrt{Q}\epsilon t$$

The parameter $\delta\omega$ accounts for inevitable differences between the individual coordinating elements, here different intrinsic oscillatory frequencies. The parameters a and b govern the strength of the coupling, the ratio (b/a) corresponding to a control parameter of rate or frequency in experiments. Thus, a decrease in the ratio signifies a decrease in the period or duration of coupled dynamical behavior. The final parameter ϵ , represents the presence of (delta correlated) noise fluctuations of strength Q .

For high values of the coupling ratio b/a (figure 1; left) the system exhibits bistability: two modes of behavioral coordination coexist for the same parameter set. Stable states of coordination, indicated by points where the negative slope of the function crosses the $\dot{\phi}$ axis (solid circles; open circles indicate unstable states) occur at relative phase relationships near 0 and 180 degrees. These values of the coordination or collective variable correspond to patterns of synchronization and syncopation respectively. As the ratio is decreased the system reaches a critical point and undergoes a switch from a bistable to a monostable regime where only the synchronized coordination pattern is stable. Note in the middle panel of figure 1 that only a single fixed point exists near 0 degrees and the negative going portion near syncopation no longer crosses the $\dot{\phi}$ axis. Further decreases in b/a result in destabilization of the inphase pattern corresponding to a complete lack of stable and unstable fixed points such that the function is lifted entirely off the axis (figure 1, right).

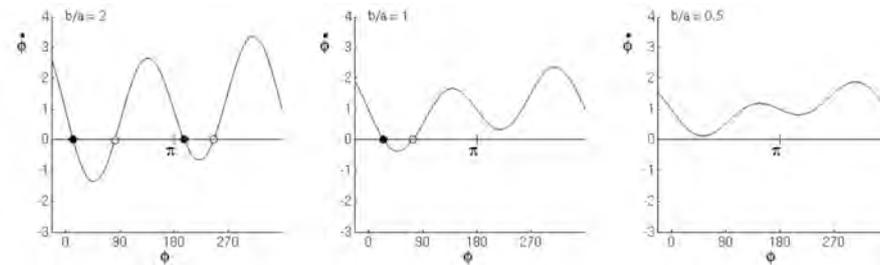


Figure 1. The theoretical model of Kelso et al. (1990) showing plots of the relative phase dynamics under conditions of high (left), medium (middle) and low (right) coupling strength with $\delta\omega$ set at a small value. As a result of symmetry breaking, notice the fixed points of relative phase are not exactly at 0 and 180 deg. On the left, the coordinative system is in a bistable regime where both inphase and antiphase coordination states exist (filled circles). Decreasing the coupling results in a switch to a monostable state where only inphase coordination is supported (middle). Further decreases in coupling, in combination the symmetry breaking term $\delta\omega$, abolish all stable states leaving only the remnants of attractors in the landscape or phase portrait.

The fact that the function retains its curvature is taken as evidence for remnants of attraction toward previously stable states. This effect is due to broken symmetry that arises as a result of intrinsic differences in the individual coordinating elements (embodied by the $\delta\omega$ parameter). Such *metastability* represents a more flexible form of self-organization where the component parts are free to express their individual behavior though still working together in loose association (Kelso, 1995; Friston, 1997). Systematically guiding the system through an appropriate parameter range exposes qualitatively different behavioral regimes and provides an entry point for studying neural mechanisms of pattern selection, formation, and change—in other words, decision-making. Some of the key questions that arise from this theoretical and experimental programme that aims to connect the dynamics of behavioral coordination with the dynamics of neural activity are:

1. How are intrinsic differences in stability between syncopated and synchronized patterns of sensorimotor coordination manifest at the level of brain function?
2. Since increases in movement rate for the syncopated pattern result in a decrease in coordinative stability whereas comparable decreases are not observed for synchronization, it is important to ask how are such changes in rate and stability manifested at the neural level?
3. Typical of informationally-based self-organizing dynamical systems (aka coordination dynamics), at a critical value of the control parameter of rate or frequency, spontaneous switches in pattern from synchronization to syncopation occur. Is a similar reorganization observed at the level of the brain? If so, what is the neuroanatomy and neurophysiology behind such pattern switching? *Putting our cards on the deck, we wish to emphasize that although switching is common in the self-organizing behavioral and neural systems described by coordination dynamics, this by no means implies the existence of “switches”*(cf. Martin, 2006).

In the following we review the imaging literature relevant to establishing connections between brain and behavioral dynamics in light of the foregoing questions. Because different technological and analytical approaches provide substantially different information about aspects of cortical and sub-cortical structure-function the remainder of this review is organized according to the methods used in acquiring or analyzing information from the brain.

5. Evoked Responses and the Search for Shared Dynamics

Early studies in the present framework employed sensorimotor coordination tasks as a means to uncover the link between the dynamics of behavior and the dynamics of the brain; connecting these levels by virtue of their shared dynamical properties (Kelso, 1981; Kelso et al. 1991; Fuchs et al. 1992; Kelso et al. 1992a; Kelso 1992). The high temporal resolution of electroencephalography and magnetoencephalography was exploited to quantify the relationship between behavioral patterns and spatiotemporal patterns of neural activity. Common features of the dynamics expressed at both levels of description were taken as evidence that similar principles of (self) organization govern pattern formation in brain and behavior. Of particular initial interest was the identification of qualitative changes in the pattern of neural activity that occurred simultaneously with transitions between coordination patterns.

In the first of these studies, a 37 channel SQUID (Superconducting Quantum Interference Device) sensor array was used to measure the spatiotemporal patterning of magnet fields generated by the intracellular dendritic current flow of large ensembles of cortical neurons located over left temporo-parietal cortex (2 cm. posterior to C3) during auditory-motor coordination (*viz.* Kelso et al. 1990). Unlike EEG signals that are subject to blurring at the various tissue boundaries, magnetic signals pass unimpeded through skull, scalp and cerebrospinal fluid providing a relatively undistorted measure of the neural sources underlying coordination patterns and pattern switching. The task was to syncopate right index finger flexion in time with an auditory stimulus that parametrically increased in rate from 1.0 Hz to 3.25 Hz in 0.25 Hz increments. Under instructions to maintain a 1:1 stimulus-response coordination, increases in rate resulted in a gradual loss of stability of and a transition from syncopation to synchronization at a critical frequency of 1.75-2.00 Hz.

This neurophysiological data may be summarized by three main findings. First, time-frequency analysis showed a frequency-dependent change in the temporal relationship between rate and the dominant frequency in the averaged MEG signal. At slow, pre-transition plateaus (<1.75 Hz) the frequency of the neural response was at the fundamental frequency of the stimulus/response. Following the transition, the spectral pattern's dominant Fourier component changed to twice the stimulus frequency (Fuchs et al. 1992), a finding interpreted in terms of a period

doubling bifurcation in forced nonlinear systems (see Kelso & Fuchs, 1995 for a possible model). The second finding was a qualitative change in the phase relations of the MEG sensors occurring coincident in time with the period doubling and with the behavioral transition. Relative phase was employed to capture, within a single quantity, both the spatiotemporal organization between the brain signals and the auditory stimulus as well as the finger position and the auditory stimulus. Particularly the anterior sensors demonstrated a phase shift of π at the point of the behavioral transition signifying a similar transition in relative phase for both brain and behavior (Kelso et al., 1991; 1992). Third, using principal component analysis, it was determined that a majority of the variance (97%) in the spatiotemporal signal could be accounted for by only four temporally evolving spatial patterns (Fuchs et al. 1992; Kelso et al. 1992). Theoretical modeling used coupled differential equations to capture the observed facts (Jirsa et al. 1994), two of the mode amplitudes acting as collective variables or order parameters to which lower amplitudes are “enslaved” (in the language of synergetics). These spatial modes demonstrated notable qualitative effects in the time and frequency domain in relation to the occurrence of the behavioral transition. Unfortunately, due to the limited coverage of the MEG sensor array, specific neuroanatomical substrates could not be determined. However, given the frontal concentration of activity, involvement of pre-motor and prefrontal regions was assumed (Kelso et al. 1992). Nevertheless, the key point is that when a complex system like the brain is placed in a behavioral context that requires pattern formation and switching, it appears to be governed by just a few order parameters. This supports the general view that the brain operates (or can be induced to operate) close to instability where only a few key quantities capture its behavior and the system is governed by low-dimensional dynamics (Haken, 1996; Kelso, 1992; 1995). Significantly, it was possible to derive these equations from a more microscopic approach in which neurons are defined in terms of their pulse rates and dendritic currents (Jirsa and Haken 1997; Jirsa et al. 1998). The latter of course are very relevant for the present discussion, since they give rise to the magnetic fields observed by MEG.

Subsequent work confirmed some of the findings in the Kelso et al. (1991; Kelso et al. 1992) MEG experiment while calling others into question. Daffertshofer and colleagues provided a replication of the original experiments using a 151 sensor MEG system that provided extended coverage and 36 EEG electrodes located primarily over bilateral motor areas (Daffertshofer et al. 2000). In line with the earlier studies, a phase shift of approximately π was observed simultaneously in both behavior and the EEG and MEG. This phase shift was broadly distributed across the MEG sensors suggesting a global reorganization of neural activity associated with the behavioral transition. In contrast to the analysis by Fuchs et al. (1992), no post-transition period doubling was observed leading to a suggestion that such a finding may have resulted from the specific method of analysis employed. Several arguments were subsequently made against this conclusion (Fuchs et al. 2000a) with a second MEG study definitively revealing the source of the observed period doubling (Fuchs et al. 2000b).

Further insight came in the form of EEG studies that provided homogeneous full head coverage to investigate spatial and temporal properties of activity arising

from the entire cortical surface during both synchronized and syncopated coordination (Wallenstein et al. 1995; Mayville et al. 1999). The inclusion of synchronization is important to control for the effect of movement frequency since synchronization does not change in stability or switch pattern when performed at the same rates as syncopation (Kelso et al. 1990). Large-scale reorganization of the dominant pattern of neural activity over contralateral sensorimotor cortex was observed coincident with transitions in coordination at the behavioral level (Wallenstein et al. 1995; Mayville et al. 1999). Importantly, this reorganization was associated with syncopation and not synchronization indicating that the reorganization was related to changes in pattern stability and not simply a product of changes in movement rate per se. Experimentally induced effects were confined to electrodes overlying contralateral central and parietal regions suggesting that dynamic changes in cortical function associated with behavioral change occurred principally in primary sensorimotor and premotor cortex.

In a definitive study, Fuchs and colleagues (Fuchs et al. 2000b) proposed an explanation for previous findings in terms of the interplay between auditory and motor evoked signals. In this work the syncopation paradigm was investigated using a 143 channel SQUID array allowing for the measurement of neuromagnetic signals from the entire cortex. As in previous studies, movements began at 1.0 Hz in a syncopated pattern of coordination and increased in rate by 0.25 Hz after every 10 cycles to a maximum of 2.75 Hz. Auditory (listening to tones presented with a randomized ISI from 2-4 seconds) and motor alone (self-paced movements separated by intervals of approximately 3s) conditions acted as controls.

Based on the spatiotemporal decomposition of the motor related response, the authors concluded that the π phase shift was due to the shifting in time of the motor response with respect to the auditory metronome. A shift of this kind reflects the tight time and velocity coupling between flexion of the index finger and the evoked magnetic response (Kelso et al. 1998). Comparison between the topographic patterns observed during coordination and those generated during control conditions indicated that at low movement rates the pattern of neural activity appeared to be dominated by auditory related activity while at higher rates a motor pattern was most prevalent. Principal component analysis was again used to decompose the signal into dominant spatial patterns and their temporal evolution. During pre-transition plateaus a majority of the variance was accounted for by a spatial mode that closely resembled the auditory control. Post-transition plateaus, on the other hand, were dominated by a clearly motor related mode. Projecting the data from each plateau onto a basis composed of the auditory- and motor-only controls demonstrated that the auditory related pattern (characterized by the N1m response) decreased in amplitude with increasing frequency while the motor component remained stable throughout (figure 2). Moreover, the period doubling reported previously (Fuchs et al. 1992) was shown to result directly from this interaction. Thus, at low movement rates the primarily monophasic auditory evoked response dominates the power spectrum resulting in a dominant frequency at the stimulus rate. As rate increases, the biphasic motor response becomes dominant resulting in the observed frequency doubling. From these data, we may conclude that the reorganizations observed in the brain dynamics are a reflection of the

change in the relationship between the brain signals underlying the generation of movement and those arising from auditory processing.

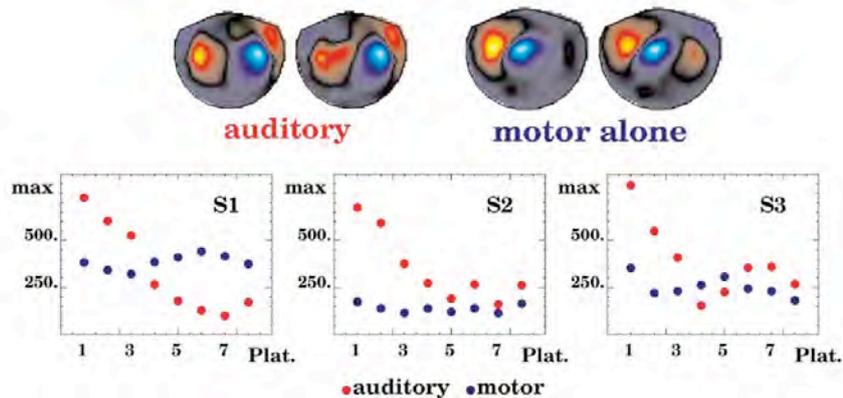


Figure 2. Shown are the relative strengths of the spatial modes corresponding to the auditory (red, top left) and motor (blue, top right) components of the sensorimotor task. As movement rate increases (left to right in bottom panels) the strength of the auditory component systematically decreases while the motor component remains fairly constant for all rates. The place where they overlap corresponds approximately to the behavioral transition. The three panels show data from different subjects. Adapted from Fuchs, Mayville, Cheyne, Weinberg, Deecke & Kelso (2000).

Frequency dependent decreases in the amplitude of the average auditory evoked response have been reported during sensorimotor synchronization (Mayville et al. 2001) and auditory perception in the absence of movement (Carver et al. 2002). The relationship between response amplitude and tone interval is well established for long intervals on the order of 1 or more seconds (Hari et al. 1982; Lu et al. 1992; Sams et al. 1993). Carver et al. (2002), investigated the auditory response at frequencies ranging between 0.8 and 8Hz (ISI=1250-125ms), a relevant parameter regime for sensorimotor coordination and rhythm perception and processing in general (Fraisse 1982). These authors reported both a cessation of the N1m and a transition from a transient to a steady state response at stimulus rates of approximately 2.0 Hz, a rate of demonstrable perceptual significance (Fraisse 1982; Drake and Botte 1993) as well as the typical rate at which transitions from syncopation to synchronization occur (Kelso et al. 1990). Such findings provoke questions as to whether behavioral transitions might be a consequence of a qualitative change in auditory processing (and perception) associated with the onset of a steady state response. Controversy exists as to whether steady state responses reflect summation of overlapping long latency responses, implying a shared functional anatomy, or whether responses occurring on these two timescales are represented by separate neural networks (Pantev et al. 1996; Gutschalk et al. 1999). Functional MRI and PET studies may offer some insight into this controversy (Pastor et al. 2002). In either case, dynamic changes in auditory processing could ultimately alter the nature of the auditory to motor coupling in a way that disrupts the syncopated pattern in favor of the synchronized one. The intrigu-

ing relationship between stimulus processing and behavioral dynamics may represent a potential line of inquiry that has received little attention thus far (e.g. Lagarde and Kelso 2006).

Finally, to better understand the rate-dependence of cortical motor-related processes, Mayville et al. (2005) investigated self-paced movements using a continuation paradigm. Twenty one different metronome pacing rates were included spanning the range of .5Hz to 2.5 Hz in steps of 0.1 Hz. After 20 pacing tones, the stimulus was turned off and participants continued moving at the designated rate. They show that the time course of the classic motor-evoked field (MEF) is tightly coupled to the behavioral response (as had previously been found by Kelso et al. 1998) and does not depend on rate per se. However, a second, weaker motor-related field, consistent with a readiness field, was observed to strongly decrease in amplitude at rates above 1Hz. Interestingly, this is exactly the rate at which subjects switch from a reactive mode of coordination, in which responses follow the stimulus and an anticipatory or predictive pattern in which responses begin before the metronome beat (Engstrom et al. 1996). The topology of this readiness field and its gradual accumulation of field amplitude prior to movement is consistent with a bilateral SMA source (Cheyne and Weinberg 1989; Erdler et al. 2001). Its decrease (by more than half when the rate exceeds 1.0Hz) may signify changes in the degree of motor processing necessary to move rhythmically at faster rates.

6. Oscillatory Activity and Coherence

There is currently considerable interest in understanding cognitive and motor functions in terms of large scale neural integration mediated by synchronous activity across different frequency bands (e.g., Chen, et al., 2003; Varela et al. 2001; Gross et al. 2002; Brovelli et al. 2004; Babiloni et al. 2005; Gross et al. 2005). This interest reflects the hypothesis that synchronous oscillations may support the coordination of activity across distributed specialized cortical and subcortical regions and thereby form the foundation for complex neural representations and cognition (Basar, 2005; Bressler and Kelso 2001; Crick and Koch 2003; Singer 1994; 2001). Dynamic changes in the synchronous activity of the brain are reflected in large scale EEG and MEG recordings of human neural function (Nunez 1995) and are typically characterized as relative decreases or increases in power within specific frequency bands (Neuper and Pfurtscheller 2001). Decreases in band power are thought to reflect event-related desynchronization (ERD) within localized neuronal ensembles indicative of a change from an idling to a processing state (Lopes da Silva and Pfurtscheller 1999; Pfurtscheller and Andrew 1999). Conversely, event related synchronization (ERS) is thought to indicate an inhibitory or deactivated state in which the localized neural area is not involved in cortical processing (Lopes da Silva and Pfurtscheller 1999; Neuper and Pfurtscheller 2001). Regional changes in the power of oscillatory brain activity is complemented by the analysis of coherence in oscillations between distributed brain areas; a measure used to characterize the degree of functional coupling between

brain regions (Singer 1993;1994; Gerloff et al. 1998). In this section we will draw from research that investigates, both directly and indirectly, the relationship of oscillatory power and coherence in the brain to behavioral coordination and stability.

6.1. Desynchronization, Coherence and the Stability of Coordination.

A growing number of studies have investigated the spatiotemporal pattern of movement-related oscillatory power and coherence associated with unimanual sensorimotor synchronization (e.g. Pollok et al. 2005). Sensorimotor synchronization between finger movements of the dominant hand and external sensory stimuli is accompanied by a decrease in oscillatory power in both alpha and beta bands over bilateral sensorimotor/premotor and medial premotor cortical areas (Gerloff et al. 1998; Manganotti et al. 1998; Deiber et al. 2001; Toma et al. 2002). Localized decreases in power have been reported in conjunction with an increase in interregional coherence, particularly between sensors approximately overlying contralateral sensorimotor cortex and medial premotor regions such as supplementary motor area (Gerloff et al. 1998; Manganotti et al. 1998; Toma et al. 2002). Such findings are thought to reflect a task-related increase in functional coupling between neural areas and underscore the importance of integration within a motor-premotor circuit for coordination.

Whereas frontal and parietal areas play an accepted role in the control of action (Rizzolatti et al. 1998), the specific relationship between activity in these regions and measures of behavioral dynamics such as stability and pattern switching is less established. However, there is growing evidence that such a relationship may exist. For example, moving from simple to more complex sequences of finger movement results in increased coherence in alpha and beta bands between contralateral sensorimotor and medial premotor sites (Manganotti et al. 1998). This increased coherence is accompanied by a decrease in low (8-10 Hz) (Manganotti et al. 1998) and high (10-12 Hz) (Hummel et al. 2003) alpha power over bilateral sensorimotor and parietal regions. Additional evidence suggests that the level of desynchronization in alpha and beta bands during coordination is related to the stability of the pattern (Jantzen et al. 2001; Mayville et al. 2001; Chen et al. 2003). Using MEG, Mayville and colleagues (2001) investigated differences in power in several frequency bands while participants produced syncopated and synchronized coordination at rates that increased systematically from 1.0 to 2.75 Hz. Syncopation was associated with significantly less power in the low (15-20Hz) and high (20-30Hz) beta bands over contralateral and central sensorimotor sensor sites. Greater desynchronization within these bands suggests greater neural engagement and higher processing demands during the less stable syncopation task. Taken together these findings lay the foundation for an hypothesis concerning the relationship between coordinative stability and neural function: less stable patterns of movement may be associated with both increased engagement in localized brain regions (indicated by increased event-related desynchronization) and concomitant

increases in the functional coupling between motor and premotor areas (suggested by the increase in coherence in the EEG and MEG).

Studies that investigate how movement-related changes in power and coherence are influenced by practice further support the connection between brain activity and the stability of behavior. Behavioral studies already show that the intrinsic stability of a coordination pattern can be altered through practice. Learning increases both the stability of a previously unstable pattern (Zanone and Kelso 1992; Zanone and Kelso 1997) and the availability of attentional resources (Zanone et al. 2001; Monno et al. 2002; Temprado et al. 2002; Temprado and Laurent 2004). In an MEG experiment, Jantzen, Steinberg and Kelso (2001) trained participants to syncopate at their individual critical frequencies (frequency at which transitions from syncopation to synchronization typically occur). Initially, syncopation resulted in a significant reduction in alpha and beta power at sensors overlying bilateral sensorimotor and premotor areas when compared to synchronization. Training successfully increased the stability of syncopation thereby shifting the critical frequency and delaying transitions to synchronization. Behavioral improvement was accompanied by a reduction or elimination in power differences between syncopation and synchronization suggesting that alpha and beta power may reflect the stability of the performed pattern. Interestingly this reduction was observed not only at the practiced rate but also at lower rates suggesting that stability improvements generalize to all movement rates.

Learning-dependent modulation of task related coherence has also been reported in subjects who practiced a task in which two independent unimanual finger sequences had to be combined in order to form a new bimanual antiphase coordination pattern (Andres et al. 1999; Gerloff and Andres 2002). Early in learning significant coherence in alpha (8-12.9 Hz) and beta (13-30.9 Hz) bands was observed between right and left sensorimotor areas and between these regions and mesial premotor cortex (SMA) (Andres et al. 1999). Such interregional functional coupling was greatly reduced at a later learning stage when performance was also found to be significantly more stable.

Although provocative, research findings suggesting that oscillatory power and coherence in motor and premotor areas are influenced by stability and changes in stability as a result of learning are still quite preliminary. So far, they allow one to infer a relationship between changes in neural activity and changes in stability in the case of learning a single coordination pattern only. Learning, however, has been shown to alter the dynamics of the entire system by either increasing or decreasing the accuracy and stability of coordination across a broad repertoire of patterns beyond those explicitly practiced (Zanone and Kelso 1991; Schönér et al. 1992; Zanone and Kelso 1992; Kelso 1995). Moreover, the nature of the change due to learning arises from the cooperative or competitive interplay between the pattern to be learned and pre-existing tendencies or “intrinsic dynamics” (Zanone and Kelso 1992). Understanding the neural basis of this interplay may provide greater insight into how stability and changes in stability are represented by the ongoing activity within and between a network of brain areas that minimally includes M1 and SMA (a broader network will be described in section 7).

6.2. Rate Dependence of Oscillatory Power and Coupling

Important insight into how localized oscillatory power and functional coupling is moderated by different rates of coordination is provided in a recent study (Toma et al. 2002). The brain dynamics was assessed on a rapid time scale to allow for a quantification of changes in power and coherence over the course of a single movement cycle. Such work complements the majority of research in this area in which power and coherence measures are integrated over a longer time scale that typically includes multiple movement cycles. Thumb movements were synchronized with an auditory tone presented at 0.5, 0.75, 1, 2, 3 and 4 Hz. At slow movement rates (1 Hz and below), a transient pattern of power changes in both alpha and beta bands was observed over bilateral primary sensorimotor cortex and SMA. Desynchronization was evident just prior to and following the onset of EMG activity. This was followed by a relative increase in synchronized activity reflecting post movement rebound (Lopes da Silva and Pfurtscheller 1999). Cortical desynchronization was accompanied by a transient increase in coherence that quickly returned to or dropped below baseline levels prior to the start of the next movement cycle. This temporal progression of activity suggests that at low rates (where coordination is known to be multistable) successive coordinated movements are characterized by a phasic pattern of localized activation and deactivation accompanied by interregional coupling and decoupling. At rates of 2Hz and above, a different temporal pattern of activity emerges: activity in alpha and beta bands remains desynchronized with respect to baseline for the entire movement cycle. Moreover, the functional coupling between motor and premotor regions remains elevated during the entire movement cycle.

The importance of the Toma et al (2002) study lies in uncovering the temporal evolution of neural interactions over the course of a single action-perception cycle and how such interactions change under increases in the control parameter of rate. The results show that during synchronization a qualitative change in the transient pattern of desynchronization and interareal coupling occurs at about the same frequency at which spontaneously switches between coordination states are observed ($\approx 2\text{Hz}$). The inclusion of additional, intrinsically less stable patterns such as syncopation in future work would allow for a better determination of the specific role that changes in motor-premotor coupling play in mediating stability and switching between patterns. The results of such studies may also offer an explanation for the intrinsic differences between coordination patterns in terms of altered coupling within specific neural circuits.

6.3. Differential Roles for Alpha and Beta Oscillations

Previous work has suggested a functionally distinct role for movement related alpha and beta desynchronization. For discrete self paced movements, beta or mu desynchronization (20 Hz) has been associated with activity of the primary motor cortex (i.e. precentral gyrus) and alpha desynchronization (10 Hz) with activity of

somatosensory cortex (Salmelin et al. 1995). Definitive evidence determining whether alpha and beta desynchronization reflect dissociable processes during sensorimotor coordination is still lacking, however. For example, an increase in desynchronization during performance of the less stable syncopated pattern of coordination is observed in both alpha and beta bands (Jantzen et al. 2001; Mayville et al. 2001). Moreover, the spatial distribution of this desynchronization is similar for both bands suggesting that alpha and beta desynchrony may reflect a single underlying process. Although Toma and colleagues (Toma et al. 2002) reported rate related changes in oscillatory power and coupling in both alpha and beta bands, their experimental effects were clearly more pronounced in the beta band. In contrast, Pollok et al. (2005) reported that coherence between distributed brain regions involved in auditory-motor synchronization was mediated primarily within the alpha range with relatively little beta contribution. However, because only synchronization was investigated in the latter study, the possibility that beta desynchronization increases when performing less stable patterns of coordination could not be assessed.

Recent MEG work by Chen, Ding and Kelso (2003) suggests different functional roles for alpha and beta bands. Subjects performed a combination of four conditions that allowed for a distinction between patterns of activity related to kinematic (flexion/extension) and relative timing (syncopation/synchronization) demands. Alpha activity was associated with the presence or absence of movement with similar desynchronization observed across all conditions. In contrast, beta activity distinguished *between* patterns of coordination: synchronization conditions revealed an increase in task related power in left sensorimotor and frontal regions whereas syncopation resulted in beta power decreases in contralateral sensorimotor areas. These findings suggest that alpha reflects neural processes associated with making finger flexion-extension movements while beta reflects more abstract or cognitive demands associated with the organization of different coordination patterns. Such an hypothesis is supported by a recent EEG study from Deiber and colleagues (Deiber et al. 2005). These authors employed a bimanual coordination task and assessed cortical activity following a precue that specified information concerning the coordination pattern (“abstract” feature), the fingers to move (“concrete” feature) or both. Conditions that allowed for preplanning of the pattern demonstrated the greatest beta (15-25Hz) desynchronization. Since such desynchronization was observed prior to movement onset, it may reflect processes related to the organization of the coordination pattern more so than those occurring during the movement itself.

Taken together, these results show that the neural activity manifest by a change in oscillatory (alpha and beta) power is related to the organization of coordinated action. Both bands reflect differences in stability between coordination patterns and track learning induced changes of intrinsically unstable patterns. Such neural activity may be related to the organization of abstract features of coordination at the level of the stability of the spatiotemporal pattern produced as opposed to the activation of the fingers *per se*. Although EEG lacks a high degree of spatial specificity, the spatial distribution of beta ERD implicates bilateral sensorimotor, premotor and supplementary motor areas in this process suggesting that

these regions form a network critical to the organization of coordinated action. Although methods to extend and improve spatial resolution and localization accuracy of EEG and MEG are under development (see section 8.0), the inherent limitations of these two measurement techniques restrict their effectiveness for investigating and identifying multiple distributed neural sources, particularly those in the mid-brain and cerebellum. As a consequence, subsequent research has turned to functional imaging approaches such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) to identify and characterize the distributed neural networks supporting sensorimotor coordination. We turn to a consideration of these next.

7. Brain Networks Underlying Patterns of Coordination revealed using fMRI and PET

A first objective is to identify the basic cortical and subcortical networks that support sensorimotor coordination and to determine whether these networks differ for different behavioral patterns. Using fMRI, Mayville and colleagues (Mayville et al. 2002) sought to determine whether different brain networks underlie the two dominant coordination modes, synchronization and syncopation. During coordination conditions participants were required to either syncopate or synchronize with an auditory metronome presented at a constant rate of 1.25 Hz. At this slow rate both synchronization and syncopation can be performed in a stable fashion. Controls included a listening condition in which participants heard the metronome but did not move, and a motor only condition during which self-paced movements were made in the absence of an auditory metronome. All experimental conditions were presented in a standard block design of alternating periods of task and rest during which no stimuli were presented and participants remained still.

A contrast between coordination modes revealed a large-scale brain network that was more active for the intrinsically less stable syncopated coordination pattern. Syncopation was associated with either increased or additional activity in bilateral dorsal premotor cortex, supplementary motor area, insula, bilateral cerebellum and bilateral basal ganglia and thalamus. No areas demonstrated greater activity during synchronization compared to syncopation. Individual subject results suggested that activity in primary sensorimotor cortex, SMA and ipsilateral cerebellum was common to both coordination modes since the majority of participants showed activity in these areas during both tasks. However, activity in the SMA and cerebellum was greater for syncopation. In contrast, activity in lateral premotor cortex, basal ganglia and contralateral cerebellum was observed in only a small subset of subjects during synchronization. The Mayville et al (2002) results confirm previous EEG and MEG findings that found coordination dependent modulation of activity over premotor areas (e.g. Fuchs et al., 1992, 2000b). In addition, they target a broader set of cortical and subcortical regions for the less stable coordination pattern.

Follow-up fMRI studies have replicated and extended the foregoing findings, consistently identifying syncopation dependent increases in blood oxygen (BOLD) in a network that includes SMA, dorsal premotor cortex, basal ganglia, insula and cerebellum (Jantzen et al. 2002; 2004; 2005; Oullier et al. 2005). This work has demonstrated that the BOLD differences identified by Mayville et al. (2002) are not strictly related to differences in sensory and motor demands of the two patterns, but instead may be related to higher-level cognitive processes associated with the formation of the required coordination pattern. In one of these studies, the importance of explicit motor output and the resulting sensory feedback in determining coordination dependent differences between synchronization and syncopation was assessed using an imagination paradigm (Oullier et al. 2005). The primary finding was that compared to synchronization, syncopation resulted in significantly greater BOLD signal amplitude in SMA, premotor cortex, thalamus and contralateral cerebellum regardless of whether coordination was actually performed or only imagined (*i.e.* in the absence of any movements). This finding may be taken as evidence that activity in these brain areas is related to processes critical for organizing the pattern of coordination regardless of whether it is actually performed or not. Activity in primary motor cortex and ipsilateral cerebellum, on the other hand, was much greater for actual performance conditions, as might be expected given their proposed role in purely sensory and motor aspects of coordination.

7.1 Parametric approaches connecting rate, stability and BOLD.

The foregoing studies employed fMRI to investigate the brain networks underlying synchronized and syncopated patterns of coordination when performed at a single, slow rate. Results revealed a distributed network of areas that are more active in response to syncopation when compared to synchronization. But what is the role of this brain network? How can activity within this network be related to the pattern dynamics of behavioral coordination expressed through the collective variable (relative phase) and its stability? The beauty of the ‘nonlinear paradigm’ is that stability can be experimentally manipulated by parametrically controlling the rate of movement for different coordination patterns. Thus, increasing rate during synchronization has little or no effect on the stability of coordination whereas similar increases during syncopation result in a gradual decrease in stability, eventually leading to large scale switching between patterns. It would seem, therefore, that a critical link for tying together behavioral pattern formation and brain activity is to determine how activity within and between specific brain networks is altered by systematic parametric variation in coordination rate (and hence stability).

7.1.1 Rate

The majority of studies investigating the relationship between measures of neural function and changes in the rate of movement or stimulus presentation has emphasized the dissociation between brain areas that are task dependent (i.e., demonstrate similar increases in activity regardless of rate) and areas that are rate dependent. There is widespread agreement for a positive linear relationship between rate and level of activity observed in primary visual (Fox and Raichle 1984), auditory (Price et al. 1992; Binder et al. 1994; Rees et al. 1997) and sensorimotor (Sabatini et al. 1993; Rao et al. 1996; Jenkins et al. 1997; Sadato et al. 1997; Jancke et al. 1998; Kawashima et al. 1999) regions. In this latter group of studies, activity in primary somatosensory and motor regions (*i.e.* pre and post central gyrus) has been shown to increase in a monotonic (and in most cases linear) way with systematic increases in the rate of sensorimotor synchronization. However, reports are mixed when considering rate dependence across broader sensory and motor networks that include premotor, insular and cerebellar regions. Inspection of the literature reveals that such discrepancies likely stem from experimental factors and may be attributed primarily to differences in the nature of the motor tasks employed and, to a lesser degree, differences in the range of rates investigated.

In studies employing relatively simple movement paradigms, rate dependent activity has been restricted to primary perceptual-motor areas and their dominant pathways. For instance, Jancke and colleagues (Jancke et al. 1998) measured BOLD signal changes in response to simple button presses synchronized with a visual stimulus presented at rates from 0.5 to 5.0 Hz in 0.5 Hz increments. Activity was positively correlated with movement rate in contralateral sensorimotor cortex and posterior parietal cortex, both of which are likely related to motor and sensory (dorsal visual stream) processing. In a study of self-paced finger tapping, with movements performed at $\frac{1}{4}$, $\frac{1}{2}$, 1, 2 and 4 times the subject's preferred rate, related CBF increases were confined to contralateral primary sensorimotor cortex (Kawashima et al. 1999). Although SMA, parietal, and cingulate cortex were all activated during the task, their level of activity did not scale with rate. These data tend to support the notion that activity in primary input-output regions is modulated by the basic motoric demands associated with increasing the number of movements per unit of time, whereas activity in other areas is associated with processes that are not directly altered by rate. Interestingly, in the Kawashima et al. (1999) work, the non-rate dependent areas demonstrated increased blood flow for all rates other than the preferred frequency, regardless of whether movements were faster or slower. Such a finding suggests that activity in such areas may be more responsive to movement features such as difficulty, stability or variability as opposed to rate *per se*.

In contrast to simple motor tasks, more elaborate movements or movements performed at fast rates (>4.0 Hz) reveal a rate dependency expressed over a much broader network of functional areas (Sabatini et al. 1993; Jenkins et al. 1997; Jancke et al. 1998; Riecker et al. 2003). For instance, when finger to thumb opposition movements are performed in place of simple finger tapping, a rate depend-

ency is observed in SMC as well as in SMA and bilateral cerebellum (Sabatini et al. 1993). Jenkins and coworkers (1997) employed a coordination task in which participants were free to make joystick movements in any chosen direction. These multi-faceted movements (requiring coordination across multiple joints) were paced with an auditory signal presented at rates between 0.2 and 1.0 Hz. This paradigm was associated with a positive linear relationship between rate and cerebral blood flow (CBF) within SMC, SMA, cerebellum, premotor cortex, insula and primary auditory cortex.

At higher movement rates two different relationships are found depending on the functional area under question. Reicker et al., (2003) had participants perform synchronized tapping at rates from 2.0 Hz to 6.0 Hz, frequencies typically at or above the rates at which syncopation can be stably performed (Kelso et al. 1990) and that approach the biomechanical limit for producing rhythmic movements. Linear rate related increases in BOLD were observed in contralateral SMC, SMA proper, pre-SMA and left thalamus. A step-wise increase from low (<4.0 Hz) to high (>4.0Hz) rates was also observed in two areas of the ipsilateral cerebellum. This increase occurred at the same frequency at which activity in SMC appeared to reach an asymptote suggesting a qualitative change in processing and production at these high movement rates.

Taken together these data support two important conclusions concerning the role of movement rate in modulating neural activity. First, the combined evidence from a large number of studies strongly supports the conclusion that activity in primary sensorimotor cortex is modulated by the speed at which movements are performed, at least up to rates below those at which biomechanical influences are felt. Second activity in non-primary motor areas including lateral premotor cortex, SMA, cerebellum and the insula are not influenced by movement rate per se, but likely reflect changes in more abstract task features such as difficulty or complexity that arise from the combined influence of task demands and movement rate.

7.1.2. Behavioral Complexity

More recently there has been an explicit attempt to understand the specific link between the complexity of motor behavior and levels of brain activity. Such studies serve to further dissociate brain regions that respond differentially to parameters such as rate, force, complexity and so forth (Wexler et al. 1997). It is necessary to clarify here that although the term “complexity” has been used to imply a specific conceptual, theoretical or mathematical approach to understanding human action in terms of emergence, pattern formation, self organization and the like (e.g. Coveney and Highfield 1995; Kelso 1995) and also in terms of neural complexity (e.g. Sporns, 2004; Tononi, et al., 1998), in the literature cited in this section, “complexity” is employed in a more colloquial way to refer to the categorization of movements according to the difficulty people have producing them. Consequently, the specific features manipulated in altering the complexity of a movement vary across the literature according to how complexity is conceived. Complexity has often been explored by employing tasks that involve the spatio-

temporal ordering of specific sequences of finger movements of the same hand (Harrington et al. 2000) or of movements of the two hands (Tracy et al. 2001; Meyer-Lindenberg et al. 2002; Ullen and Bengtsson 2003; Debaere et al. 2004). In the unimanual case, manipulation of complexity has been achieved by increasing the number of movements performed (Catalan et al. 1998), by altering the relative timing between movements (Dhamala et al. 2002; Lewis et al. 2004) or by adjusting the ordering between fingers with less sequential orderings being considered more complex (Haaland et al. 2000). Varying complexity on a number of arbitrary dimensions has resulted in a broad interpretation of the functional role of the brain areas involved.

Initial studies explored the role of predictability in accounting for activity in premotor networks. Predictability of a motor sequence has been associated with increased activity in a network of brain regions (VanOostende et al. 1997; Dasonville et al. 1998) that overlap with those sensitive to rate (Sabatini et al. 1993; Jenkins et al. 1997; Jancke et al. 1998; Riecker et al. 2003) and those distinguishing between coordination patterns (Mayville et al. 2002). When compared to predictable cued finger sequences such as repetitively moving fingers in a fixed order, random and therefore unpredictable movements were associated with increased BOLD activity in premotor cortex, SMA, pre-SMA and parietal cortex (VanOostende et al. 1997; Dasonville et al. 1998). These empirical results have been interpreted in terms of a link between activity in frontal and parietal regions and cognitive operations associated with decreased predictability (i.e. greater demands on planning, decision making and memory). However, in terms of the ordering between fingers, the predictable condition always required a simple sequential pattern whereas the unpredictable condition required transitions between non-adjacent fingers.

An alternative explanation is that activity in premotor and parietal regions was influenced by changing the spatiotemporal pattern to be produced in the two conditions. Ordered movements that produce simple patterns where fingers are moved in increasing or decreasing order (e.g. 2345) are less complex than patterns requiring coordination between non-adjacent fingers (3425). This alternative view has been supported by subsequent EEG work that independently varied predictability of a sequence and sequence order (Hummel et al. 2003). These authors showed that task related power decreases, a measure of cortical engagement thought to reflect local neural resources (Lopes da Silva and Pfurtscheller 1999), were modulated by the complexity of the spatiotemporal pattern produced, but were similar across conditions that varied in predictability and memory load.

In keeping with the foregoing research is a study in which movement patterns were reformulated in terms of muscular synergies in which synergistic movements occur when fingers flex together in a synchronized (in-phase) fashion and non-synergistic movements involve alternating flexion of digits in a syncopated (anti-phase) fashion (Ehrsson et al. 2002). Nonsynergistic movements were associated with greater activity in SMA, cingulate motor area (CMA), bilateral dorsal premotor cortex, intraparietal sulcus and lateral cerebellum. This pattern of neural activity is remarkably similar to the one resulting from comparisons between synchronized and syncopated coordination (Mayville et al. 2002) where behavior is

defined in terms of relative phase and the pattern of muscle recruitment remains the same throughout. It is no secret that one of the hallmarks of synergies is 'invariant' or stable timing relations among component elements across parametric change (Kelso 1986; 1997).

The relative importance of the coordination between fingers as opposed to predictability, rate or memory has been further supported by a group of fMRI studies in which motor sequences were over-learned prior to the onset of scanning. Catalan et al. (1998) increased complexity by increasing the number of fingers used to perform a sequence and by altering the movement order and length of the sequence to be performed. Their PET results showed that increasing complexity was associated with increases in CBF in SMA, premotor cortex, cerebellum, bilateral parietal cortex and precuneus. A similar approach in which finger sequence length and complexity were defined with respect to the order of fingers moved was employed in PET (Boecker et al. 1998) and fMRI (Haslinger et al. 2002) studies. All movements were well practiced and movement rate, force and the overall number of movements performed were maintained across conditions. The fMRI results revealed clusters of complexity related BOLD activity in bilateral parietal cortex, left premotor cortex and the dentate nucleus in the right cerebellar hemisphere (Haslinger et al. 2002), further implicating the cerebellum in this complexity related network. The PET results suggest a role for central midline structures, showing a relationship between increased complexity and greater activity in the SMA, pre-SMA, and bilateral basal ganglia (Boecker et al. 1998). Taken together, this body of work supports the hypothesis that frontal motor networks and possibly cerebellum play an important role in mediating coordination in functional tasks of increasing complexity.

A further distinction has been offered by Harrington et al. (2000) who sought to directly differentiate the role of physical (surface) features of the sequence task and more cognitive or abstract aspects. Of relevance to the current review is that activity in dorsal premotor cortex, middle frontal gyrus, supra marginal gyrus and left insula was associated with the number of transitions between fingers, independent of the number of fingers used to generate the sequence (3 vs. 2). Such a finding suggests that these brain areas mediate processes central for guiding the coordination between fingers, that is, for generating the required spatiotemporal pattern. In contrast, a network comprised of superior parietal lobe and contralateral cerebellum was found to be active exclusively in response to changes in the number of fingers employed. However, two curious findings emerged from this important study. First, complexity did not modulate activity in SMA, a region commonly reported to be responsive to changes in complexity (Harrington et al. 2000). Second, in contrast to most of the literature, a negative relationship was found between BOLD amplitude and complexity in a majority of the regions identified. The Harrington et al work provides important methodological and conceptual advances for understanding complexity in terms of specific motor demands and task dimensions, specifically the spatial and temporal relation between individual movements. However, their somewhat discrepant results underscore the need for further investigation of this relationship with particular focus on how specific task features are represented at the neural level.

7.1.3. Stability

Research linking parameters such as rate and concepts such as complexity to changes in activity within (and across) functional networks of the brain is provocative because it suggests that brain areas supporting basic sensory and motor aspects of coordination (*i.e.* primary sensory and motor areas) might be distinguished from those involved in processing more abstract demands (*i.e.* SMA, premotor cortex and cerebellum). Such research has important implications for understanding coordinated behavior and leads us to an exciting hypothesis regarding the neural circuitry underlying syncopation and synchronization, namely that the basic neural circuitry for processing sensory and motor elements of a task may be separable from the neural circuitry responsible for mediating the coordination between component elements. The former network may be expected to reflect of changes in rate and not be sensitive to intrinsic differences in stability between coordination patterns. In contrast, the network of areas identified by Mayville et al. (2002) and others may underlie the stability of coordinated behavior regardless of the particular sensory and motor elements involved.

Within the Coordination Dynamics framework, relative phase (with its multi- and metastable properties) provides a low dimensional description of the collective spatiotemporal ordering between coordinating elements. This has led some to hypothesize that changes in stability reflected in the parameter of relative phase may be reflected in networks that differentiate between inphase and antiphase modes of coordination (Meyer-Lindenberg et al. 2002). This hypothesis leads to the prediction that activity in networks concerned with the relative phase between components should track the variability (inverse of stability) of this parameter. Since decreases in stability with increasing movement rate are observed during antiphase and not inphase coordination, increases in neural activity within this network should be observed only for the former pattern. However, areas active in response to changes in movement rate should respond similarly regardless of pattern.

To address these predictions recent studies have investigated the relationship between large scale measures of brain function and the stability of bimanual coordination using PET, TMS (Meyer-Lindenberg et al. 2002) and fMRI (Debaere et al. 2004). In the former work cerebral blood flow was measured while performing in-phase and antiphase movements at four movement rates (1.0 1.5, 1.7, 2.0 Hz) below the critical frequency (Meyer-Lindenberg et al. 2002). Moving at increasingly higher rates resulted in a significant reduction in stability only for antiphase movements, a finding compatible with well-known studies of bimanual coordination and theoretical predictions thereof. Increases in measures of cerebral blood flow concomitant with increasing instability were observed in bilateral dorsal premotor cortex, SMA and cingulate as well as the left frontal operculum, ipsilateral cerebellum and left supramarginal gyrus. Activity in contralateral sensorimotor cortex, on the other hand, demonstrated a linear increase in CBF for both patterns indicating sensitivity to changes in rate regardless of pattern stability

Comparable changes in BOLD were reported when movements were made either inphase, anti-phase or in a 90 degree pattern (Debaere et al. 2004). For the

latter performance was measured in terms of relative phase error. Error may not provide an optimal index of stability since, when averaged over a relatively long period of time, even unstable coordination patterns can appear to have little or no error in phase. Nonetheless, a monotonic decrease in performance with increasing cycling frequency was observed for the antiphase and 90 degree patterns but not for the inphase pattern. As expected, both dorsal premotor cortex and cerebellum demonstrated an interaction between movement rate and coordination pattern, showing a BOLD increase for the out of phase and 90 degree patterns and not for the in-phase pattern.

We recently performed a similar parametric study to investigate the mapping between BOLD amplitude, movement frequency and stability of unimanual sensorimotor coordination patterns (Jantzen et al., submitted). Participants coordinated right hand finger flexion with an auditory metronome in either a synchronized or syncopated pattern at five different movement rates (0.75, 1.0, 1.25, 1.50, 1.75 Hz), all below the critical frequency at which spontaneous transitions from syncopation to synchronization are known to occur. Changes in stability-related brain regions induced by parametric manipulation of coordination frequency should be mirrored as systematic increases in BOLD signal intensity during syncopation but not during synchronization since stability remains relatively unaffected for the latter. Theoretical considerations (see Section 4) further predict that regions sensitive to systematic increases in rate or frequency should exhibit monotonic increases in signal intensity independent of the coordination pattern performed.

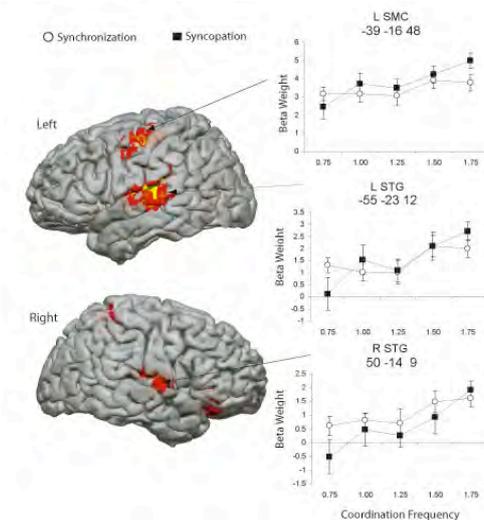


Figure 4. Cortical regions exhibiting a main effect of movement rate/coordination frequency are plotted in color on a template brain rendered in 3 dimensions and viewed from the left (top) and right (bottom) lateral views. The between subject mean of the regression coefficients (beta weight) for each experimental condition is plotted as a function of the required coordination frequency. BOLD amplitude patterns were very similar for both synchronization (open circles) and syncopation (closed squares) suggesting that these brain areas are related to basic sensory and motor demands regardless of mode of coordination. The brain areas identified as well as the Talairach coordinates are presented in each plot. Error bars are set to \pm standard error.

The results provide neurophysiological evidence for the existence of two separate but interacting brain networks underlying basic patterns of perceptual-motor coordination. BOLD amplitude in contralateral SMC and bilateral primary

auditory areas increased linearly with increases in movement rate for both syncopated and synchronized coordination (figure 4). This pattern of activity is consistent with a modality dependent processing role focused primarily on the elementary sensory and motor demands of the task. In contrast, a second network consisting of pre-SMA, bilateral premotor, ipsilateral cerebellum and right insula, exhibited activity that mirrored behavioral stability. In keeping with our theoretical framework, BOLD amplitude in this network of brain areas increased linearly with decreases in the stability of the syncopated pattern (figure 5). No such increases were observed during synchronization since this pattern was observed to remain stable across movement rate.

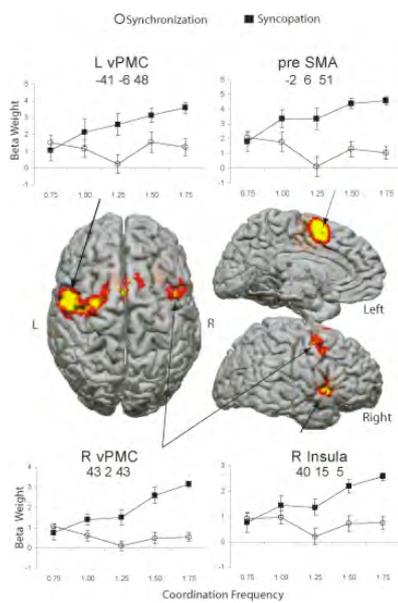


Figure 5. Regions exhibiting an interaction between movement rate/coordination frequency and sensorimotor pattern are plotted in color on a template brain rendered in 3 dimensions. Views are of the dorsal surface of the brain viewed from the top, and the left medial and right lateral surface of the brain both viewed sagittally. Plotting conventions are as in Figure 4. Here a clear dissociation between synchronization and syncopation is observed in medial and lateral premotor areas as well as in the right insula. The pattern of BOLD activity closely follows the pattern of behavioral variability, a measure of stability, by increasing monotonically with increasing rate during syncopation but not during synchronization. Thus, these areas respond in relation to differences in pattern stability as opposed to movement rate per se. vPMC: ventral premotor cortex., preSMA pre supplementary motor area.

The parametric approach of coordination dynamics thus allows for the differentiation between brain networks related to a) dynamic features of coordination that represent the global organization of the behavioral pattern, in particular stability and b) those related to more elementary modality dependent sensory and motor features. Studies using Transcranial Magnetic Stimulation (TMS) have provided further support for a link between the stability of coordination patterns and activity in cerebellar-frontal networks (Meyer-Lindenberg et al. 2002; Serrien et al. 2002; Steyvers et al. 2003). TMS was used to transiently disrupt SMA and lateral premotor cortex during performance of bimanual coordination. Applying TMS to these regions during antiphase coordination resulted in increased phasing errors between the hands (Meyer-Lindenberg et al. 2002; Serrien et al. 2002; Steyvers et al. 2003) and induced behavioral transitions from anti-phase to in-phase coordination (Meyer-Lindenberg et al. 2002). No like alterations in behavior were observed when TMS was applied during inphase coordination. Moreover, the magnitude of the TMS perturbation needed to provoke a behavioral transition

decreased as behavioral instability increased (Meyer-Lindenberg et al. 2002). Similar TMS disturbances applied to primary motor cortex did not affect the pattern of coordination indicating that the results were not due to a simple perturbation of the efferent signal (Meyer-Lindenberg et al. 2002). Overall the foregoing results suggest the following hypothesis: Activity across a network that minimally includes SMA, lateral premotor cortex and cerebellum is linked to the degree of behavioral stability. Depending on how close the brain is to an instability, disruption of this network may result in the destabilization and eventual dismantling of a less stable pattern in favor of a more stable one.

7.2. The generic nature of coordination dynamics and stability dependent networks

The research reviewed here supports the notion that key collective variables or order parameters that capture coordinated behavior at the behavioral level are also critical for representing coordinated action at the level of the brain. New findings illustrate how such pattern formation and change is mediated by the integrated activity of cortical and subcortical networks. An important feature of relative phase dynamics is that it provides an effector- and modality-independent description of the emergence of coordination patterns. This begs the question: Is there an effector or modality independent representation of this quantity at the level of the brain? While the present review has been focused on sensorimotor coordination, it appears that highly similar brain networks support coordination whether coordinating with oneself or with the external environment. The existence of such stability dependent networks leads inevitably to the proposal that common neural substrates may support behavioral coordination regardless of the coordinating elements themselves.

Considered as a whole, the imaging work underscores the importance of the SMA and premotor cortices in mediating coordinative stability independent of the specific elements being coordinated. There is growing evidence for stability dependent networks regardless of whether the patterns of behavior refer to the fingers of a single hand (Ehrsson et al. 2002; Nair et al. 2003), between oneself and the environment (Jantzen et al. 2002; Mayville et al. 2002; Jantzen et al. 2004; Jantzen et al. 2005; Oullier et al. 2005), between homologous (Sadato et al. 1997; Immisch et al. 2001; Meyer-Lindenberg et al. 2002; Ullen and Bengtsson 2003; Debaere et al. 2004) and non-homologous limbs (Debaere et al. 2003). Stability dependent networks are engaged even when coordination is imagined (Nair et al. 2003; Oullier et al. 2005). Such evidence speaks compellingly for the tenet that, like behavior itself, the coordination dynamics of the human brain can be captured by informationally relevant quantities such as the relative phase among interacting coordinating elements (Kelso 1994; Deiber et al. 2005). The specific neural representation of the coordinating elements or agents will vary in task and modality dependent ways. In the examples described here, activity of primary sensory and motor areas is related to the elements being coordinated independent of the pattern

of coordination. However, an emerging insight is that other brain regions form a network that can be differentiated from modality specific areas by virtue of their relationship to the underlying dynamics.

8. Summary and future directions

In the last 20 years or so, sensorimotor coordination has proven itself a cardinal example of self-organizing, pattern forming processes and, by virtue of that fact, has provided an ideal experimental platform for studying the dynamics of brain and behavior. In this chapter we have reviewed literature relevant to forming a conceptual and theoretical link between dynamic aspects of behavioral coordination and spatio-temporal properties of brain function. Taking the theoretical perspective that coordination in complex biological systems is fundamentally a result of self-organizing dynamics, we have discussed research that describes how interactions among coordinating elements is mediated at the level of the brain and how such brain activity may underlie specific dynamic features of behavioral coordination such as loss of stability and switching between patterns. Evoked potential studies of auditory-motor coordination have highlighted the possible role of the dynamic interplay between auditory and motor related activity in the brain. Transitions between behavioral patterns occur at approximately the same frequency as the onset of auditory steady state evoked responses. This intriguing finding has received little subsequent inquiry and additional investigations are required to firmly establish the role of primary perceptual areas in mediating rate-dependent coordination stability and switching.

A relationship between the stability of the coordination pattern and activity within a fronto-cerebellar network has also been established based on converging evidence from multiple imaging studies. Activity in a network that includes SMA, lateral premotor cortex, insula and cerebellum appears to be related to the stability of the relative phase dynamics, suggesting a role for this network in organizing and monitoring the global relationship between coordinated elements. This network (a) is more active for less stable coordination patterns; (b) reflects changes in stability induced through learning; and (c) reflects changes in stability induced through manipulation of control parameters. This stability related network has been distinguished from primary sensory and motor processing areas that respond to changes in the rate of coordination but do not appear to be sensitive to alterations of pattern stability. Although detailed information about the interaction between areas that form these networks is still lacking, initial work suggests that less stable patterns are associated with increased coherence between SMA and M1.

A schematic representation of the rate and stability related networks and the putative connections between them is provided in figure 6. The critical next steps in understanding the relationship between cortical and subcortical networks underlying dynamic properties of coordination will focus on the pattern of neural coupling between individual brain areas and how that pattern relates to coordination.

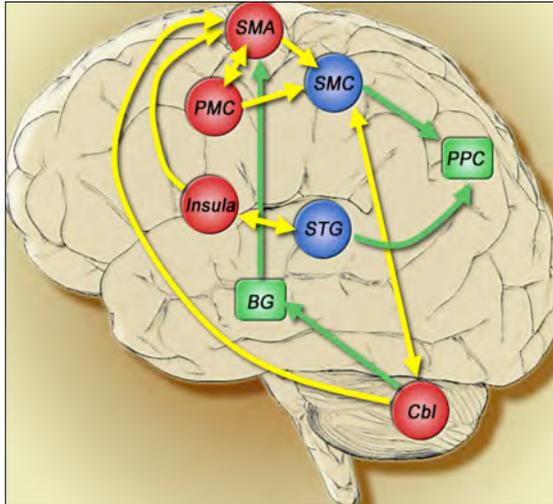


Figure 6. A schematic representation of brain circuits supporting sensorimotor coordination and the putative functional connections between them (yellow and green arrows). Blue and red areas demonstrate rate and stability dependent activity respectively. Green areas have been inconsistently observed in the literature and therefore their importance for rhythmic coordination is less established. SMA: supplementary motor area, SMC: sensorimotor cortex, PMC: premotor cortex, PPC: posterior parietal cortex, STG: superior temporal gyrus, Cbl: Cerebellum.

What are the dynamics of the two networks and how do they interact? It is now widely accepted that cognition and behavior emerge from the dynamic interplay between the dual tendencies of segregation, in the form of localized activity within functionally specific neural regions, and integration as realized by interregional communication between regions (see Bressler & McInosh 2007; Sporns & Tononi 2007). While the work represented in this chapter has made significant strides in identifying specific brain regions and patterns of brain activity corresponding to patterns of human behavior, much more research is needed to understand the networks themselves in terms of detailed structure, connectivity and dynamics— both in normal and clinical populations.

Advances in understanding neural dynamics and how this dynamics maps onto behavior will be aided by new analysis techniques that provide enhanced temporal and spatial resolution (Gross et al. 2001; Jirsa et al. 2002; Astolfi et al. 2005; Babiloni et al. 2005) and allow for a characterization of the directed influence between interconnected brain regions (Beggs, Clukas & Chen 2007; Breakspear & Jirsa 2007; Horwitz & Husain 2007; Stephan & Friston 2007). Spatial filtering techniques such as the variety of beamformer methods (Darvas & Leahy 2007; Fuchs 2007) provide a means to move toward brain-based measures of neural activity that possess both high spatial (mm) and temporal (ms) resolution. The promise of such approaches for combining results from multiple imaging modalities is demonstrated by the spatial overlap between desynchronization in beta band oscillations localized on the surface of the cortex and BOLD based imaging results

generated during simple motor (Taniguchi et al. 2000), as well as language and motion detection tasks (Singh et al. 2002). Initial investigations have begun to investigate network properties supporting simple internally and externally paced movements (Gross et al. 2002; Tass et al. 2003; Babiloni et al. 2005; Pollok et al. 2005). Also, some advances have been made toward understanding how the coupling between a restricted network of brain areas changes as a function of different coordination patterns (Gross et al. 2005).

Questions critical to understanding the relationship between behavior and the spatiotemporal dynamics of the brain that are now open to new analytical approaches include:

- What is the nature of the functional interaction between brain areas forming hypothesized stability and modality dependent networks? How are neural interactions facilitated within and between these networks (see figure 6)?
- How are interactions within and between networks supporting different behavioral patterns altered by systematic changes in coordination pattern, rate and stability? Are losses in stability accompanied by a decrease/increase of coupling between brain areas forming these two networks? Alternatively, is coupling between brain areas altered by learning, intention or attention induced increases in stability of coordination?
- Can different functional networks be defined based on the oscillation frequencies of participating areas (*e.g.* alpha vs. beta vs. gamma), and if so how do these networks interact in space and time?
- What happens to established brain networks around critical points where stability is lost and new patterns adopted? Are the neural processes that underlie switches from syncopation to synchronization generalizable across different instances of behavioral pattern switching and decision-making?
- Does the brain contain generic networks for supporting dynamic properties of behavior, such as stability? Can a similar network be identified across multiple forms of coordination (*e.g.* multisensory, interpersonal, interlimb) independent of the coordinating elements (visual, auditory, somatic, etc) involved? Although there is some evidence that such is the case, this question has never been addressed exhaustively across experimental tasks particularly at the level of large scale brain networks.
- How is behavioral coordination achieved under conditions in which key connections or nodes of the network are damaged or disrupted as in traumatic brain injury, Parkinson's Disease, stroke, cortical or cerebellar lesions, etc.

Clearly the foregoing list of questions is far from inclusive, representing but a small sample of how recent advances in analytical approaches to neuroimaging data may be applied in the study of coordination. The questions posed are meant to provoke further research into establishing a direct connection between the theoretical and mathematical formulations of behavioral dynamics and measures of

brain function on the one hand, and to understand how the rich dynamics of human behavior arise from the large-scale interaction among distributed brain areas that share a degree of specialization on the other.

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