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Spatiotemporal Dynamics of the Human Brain Associated with Transitions in Coordination Timing

by

Gene V. Wallenstein

A Dissertation Submitted to the Faculty of the College of Science in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

Florida Atlantic University Boca Raton, Florida December 1995 UMI Number: 9608954

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Gene V. Wallenstein

This dissertation was prepared under the direction of the candidate's dissertation advisors, Dr. J. A. Scott Kelso and Dr. Steven L. Bressler, Program in Complex Systems and Brain Sciences and has been approved by the members of his supervisory committee. It was submitted to the faculty of the College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Contemporary neuroscience is an interdisciplinary endeavor. As a field of study it has gone through many growing pains, particularly in the last decade, as new technologies and scientists from diverse areas have come to call it their home. As questions in this area have become more complex, integration among various fields has necessitated the development of Ph.D. programs designed to give young scientists the ability to maneuver in an increasingly daunting field of study. It may seem a rather reasonable notion to create interdisciplinary neuroscience programs, but their appearance seems to be a recent phenomenon. The Program in Complex Systems and Brain Sciences at the Center for Complex Systems, Florida Atlantic University is without question a leading facility for such study. Above all, it has given me insight into the many aspects, good and bad, of exploring neuroscientific questions. While I have indeed learned many things under the faculty's tutelage, without doubt the most precious gift has been the feeling that science is a worthy and noble pursuit.

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O sweet spontaneous earth

how often have the doting fingers of
prurient philosophers pinched and poked thee,
has the naughty thumb of science prodded thy beauty
how often have religions taken thee upon their scraggy knees
squeezing and buffeting thee that thou mightest conceive gods
but true to the incomparable couch of death thy
rhythmic lover thou answerest them only with

spring.

E.E. Cummings

ABSTRACT

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Recent studies have demonstrated that the strategy an individual uses to synchronize motor behavior (e.g. finger flexions) with externally delivered, periodic stimuli depends, in part, on the stimulus presentation rate (Mates, Muller, Radil, and Poppel, 1994; Engström, Kelse, and Holroyd, 1995). At rates slower than approximately 0.5 Hz, subjects typically exhibit a reactive-type coordination pattern where the response follows the stimulus by an order of magnitude consistent with typical response times (i.e. 150 - 250 milliseconds). At faster rates, however, subjects typically anticipate the impending stimulus in order to synchronize movement with it. In the present study, scalp electroencephalographic (EEG) signals (61 channels) were recorded during a sensorimotor task designed to investigate

transitions from one coordination mode to another. We found that subjects exhibited a spontaneous transition from reactive to anticipatory behavior as the stimulus presentation rate increased past some critical frequency. A spatiotemporal analysis of the EEG signals accompanying this task revealed: 1) a widespread frequency component in the EEG matching that of both the stimulus and movement; 2) peak spectral power density over central and antero-central regions in both men and women during reactive behavior; 3) an additional bilaterally distributed frontal component at the most anterior portion of the scalp in men during anticipatory behavior; 4) an additional left fronto-central component which extended posteriorly toward antero-central regions in women during anticipatory behavior; 5) fluctuation enhancement in both the EEG spectral power density and the time lag (τ) between the movement and stimulus accompanying the transition from reactive to anticipatory behavior; 6) that the spectral power density patterns obtained in the primary experimental condition (REACTIVE) were more similar in terms of their spatial distribution with a control condition in which subjects were asked to produce rhythmic movements without benefit of an external stimulus (MOTOR-ONLY) than with a control condition in which subjects passively watched a periodic visual stimulus (STIMULUS-ONLY); 7) that the spectral power density patterns obtained during reactive behavior in the primary experimental condition were more similar spatially to the MOTOR-ONLY condition than during anticipatory behavior; and finally 8)

that the spectral power density patterns obtained during the experimental condition are not completely accounted for in terms of purely motor- or stimulus-related components. These results are discussed within a common framework of pattern formation instigated by dynamic instabilities in the human brain and behavior.

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1. Introduction

Time and timing play a central role in the neuroscientific investigation of phenomena as seemingly diverse as learning and memory, sensorimotor integration, and speech production and perception. An organism's capacity to perceive and produce timed events is essential for its survival. For example, during complex movements involved in pattern perception and adaptive behavior (i.e. being able to see temporal patterns in nature and make adjustments to them), the ability to integrate different stimuli or to integrate stimuli with specific behaviors is an obvious necessity for the functioning of the organism. The study of timing on the behavioral and perceptual levels of observation has a long and rich history pursued mainly by researchers interested in how individuals associate particular "actions" with each other or actions with stimuli (be they external or internal) (see papers in Gibbon and Allan, 1984). The rather nebulous term, "actions", as used here is indicative of the many features examined in terms of behavior alone. For example, researchers studying temporal patterning during handwriting have postulated the motor programming unit of such behavior to reside at various scales including the agonist-antagonist phase cycle (Hollerbach, 1981), the letter (Teulings and Thomassen, 1979), and the word (Viviani and Terzuolo, 1980) to name a few. Stelmach et al. (1984) have suggested that the relative timing constraints between muscle groups involved in handwriting may be thought of as specifying a particular programming unit in a flexible manner such that the temporal patterning of these movements changes with task requirements.

The issue of temporal patterning and integration is also, of course, intrinsic to the study of other rhythmical movements such as with musical performance. In a review of both theoretical and experimental investigations, Shaffer (1984) comes to the conclusion that several factors contribute to successful timing during skilled musical performance: 1) a central time keeper or "clock" which is used as a point of reference by motor systems; 2) relative timing constraints which develop with practice among the specific muscle groups involved in playing a given instrument; 3) coupling between the central time keeper and motor subsystems such that various components can be timed relative to one another; and 4) the ability to assimilate external cues relative to the pace of the central time keeper. Regardless of whether or not the specific details of this theoretical framework are correct, they illustrate that a major concern in the psychological study of musical performance is with respect to temporal integration. The points raised by Shaffer (1984) also allude to the problem of characterizing temporal integration in terms of its point of origin. How and where do these timing constraints arise? Are they dictated by central mechanisms or are they best understood as emerging from peripheral constraints which may be biome-

chanical?

One way to study relative timing constraints in behavior is to explore conditions under which a pattern is stable (i.e. relaxes back to the original pattern if it is subjected to a small perturbation - see Chapter 3 for further details) and under which conditions it switches to another pattern. A growing body of work in sensorimotor integration, perception, and learning in humans has demonstrated instances where a single parameter may be varied resulting in spontaneous transitions from one pattern of coordination to another (see Kelso, 1995 for a review). One interesting aspect to these experiments is the fact that, typically, a given behavior will remain in a stable pattern over a broad range of parameter values (such as movement frequency) and then suddenly switch and remain in a new pattern over a large range of parameter values. Transitions from one behavioral pattern to another have been explained in various terms including 'energy expenditure' as in horses switching from one gait to another at points of maximal oxygen consumption (Hoyt and Taylor, 1981), 'biomechanical mechanisms' such as reducing peak force levels at transition points as horses switch gaits under a weighted load (Farley and Taylor, 1991), and a plethora of 'neural mechanistic explanations' under the vast array of central pattern generators (see Cohen, Rossignol and Grillner, 1988 for a review).

Such specific explanations for switching from one behavioral pattern to

another have relevance in many systems where a clear mechanism can be discerned, yet even in such instances, it is useful to show that the dynamics supporting the pattern have generality beyond the given task in question. There is a growing body of evidence which suggests that a broad class of qualitative changes from one coordinative mode to another are best understood in terms of phase transitions (Haken, 1983; Kelso, 1995). Indeed, phase transitions have been observed in a variety of systems and may provide a theoretical framework from which to understand pattern-formation and change independently of the particular physical composition of the system. For instance, Kelso, Delcolle and Schöner, (1990) instructed subjects to either coordinate peak finger flexions in between (syncopate) or at the same time (synchronize) with a series of auditory tones presented periodically. Spontaneous transitions from syncopated to synchronized movement coordination were observed as the rate of stimulus presentation was gradually increased past some critical value. No transitions were observed when the subjects began in the synchronization coordination mode, indicating bistable behavior (both syncopation and synchronization) before the transition point and monostability following it (Kelso, Delcolle and Schöner, 1990). Since there was no direct physical coupling between the individual performing the task and the stimuli, a biomechanical explanation of this transition is implausible. The behavioral results found by Kelso et al. (1990) led to a series of studies using non-invasive brain imaging techniques including magnetoencephalographic (MEG) and electroencephalographic (EEG) signal recording to investigate the neural correlates of the coordination transition (Kelso et al., 1991; 1992; Fuchs et al., 1992; Wallenstein et al., 1995a). A transition of approximately 180 degrees was found in the relative phase between the brain signals and auditory stimuli at the same time (on average) as the behavioral transition from syncopation to synchronization (Kelso et al., 1991; 1992; Wallenstein et al., 1995a). Moreover, when the brain signals observed during the task were aligned on a run-by-run basis at the transition point, an increase in the variance of the relative phase between these signals and the stimuli was apparent just prior to the transition, demonstrating fluctuation enhancement (Wallenstein et al., 1995a). Fluctuation enhancement (Wallenstein et al., 1995) and critical slowing down (Kelso et al., 1992; Fuchs et al., 1992) are key signatures of stability loss as a system undergoes a phase transition and will be dealt with more fully in Chapter 3. For our present discussion, the crucial point to note is that common dynamics were observed on both the behavioral and neural levels in terms of their phase relations and stability properties. Of course, these results can easily be expressed in terms of relative timing by remembering that the phase values are proportional to the temporal lag in between a response (whether it be behavioral or neural) and a stimulus.

The sudden shift of 180 degrees in both behavior and brain activity is really a transition in the timing of these signals relative to the stimuli.

Several investigators have also begun to look for evidence of temporal integration in the central nervous system by examining changes in motorrelated cortical potentials preceding rhythmical movements (Benecke et al., 1985; Lang et al., 1988; 1989, 1991; Wallenstein et al., 1995b). Wallenstein et al. (1995b) recorded scalp EEG signals during a temporal reproduction task in which subjects were initially paced by an auditory metronome at some constant frequency between 0.5 and 5.0 Hz. An examination of the reproduction errors associated with this task indicated that subjects exhibited preferred frequencies in which the required inter-response-interval (IRI) was reproduced most accurately (typically around 2.0 Hz). Of further interest is the observation that inter-hemispheric relative phase measures of the EEG were most consistent (least variance) in the same frequency range (Wallenstein et al., 1995b). Thus, a physiological signature from the central nervous system was found to correspond closely to the temporal accuracy of the movement sequence. One serious limitation of the above study, however, was lack of good spatial resolution (EEG signals were recorded from only 3 electrodes), restricting the ability to discern changes in the spatial topography of the EEG which might be associated with the behavioral results.

In an earlier study, Lang et al. (1990) demonstrated that when subjects were asked to produce bimanual finger flexions in 1:1 synchrony a slow, scalp-recorded readiness potential (RP) preceded the initiation of the motor sequence. They found that the RP had maximal amplitude over primary motor cortices when the fingers were synchronized. However, when subjects were required to produce more temporally complex ratios such as 2:3, additional activity was demonstrated at sites over the mesial frontocentral cortex which includes the supplementary motor area (Lang et al., 1990). One possible interpretation of these results is that the demand for temporally integrating disparate responses between the left and right hands is minimal during 1:1 synchrony since the two responses are coincident in time. However, during a ratio such as 2:3, finger flexions are occurring at different moments and must be timed precisely relative to one another. The increase in mesial frontal activity during this condition is consistent with a growing number of studies finding that the frontal lobe, in particular, the prefrontal cortex plays a critical role in the temporal integration or "binding" of successive stimuli and actions (e.g. Fuster, 1989).

It should be noted that the term "temporal binding" is used here to distinguish this problem from earlier stimulus-response based associationism models which have prevailed for the last 40 years. These include, but are not limited to, servo-mechanism models for real-time motor control, hierarchical

stimulus-response (S-R) bond models, as well as the so-called chain models used to build complex behaviors by "chaining" together smaller (S-R) components (see Suppes, 1969 for a critical review). Although these approaches have been instrumental in advancing our understanding of human behavior and suggesting further experimentation, they are limited because they often assume that the formation of complex behaviors can best be understood as a combination of smaller, simpler behaviors (Galanter, 1984). As was suggested from the neurophysiological data mentioned above, complex behavior might best be understood in terms of its developing temporal organization and the brain areas that become active during the continuous evolution of a coordinated act. Thus the problem can be stated as follows; how is the temporal organization of behavior related to spatiotemporal organization in the central nervous system? This question leads to additional issues, two of which will be addressed in the next chapters.

First, we explore the brain areas which are known to be involved in behaviors that require the internalization of a temporal rhythm is required. For example, as is shown in chapter 2, tasks which require little time estimation between a stimulus and response (i.e. reactive-type behaviors produced by responding as soon as possible following the stimulus cue), primarily involve central and antero-central motor areas in the generation of the movement. However, frontal brain areas are known to be involved if the task

has an intrinsic time estimation requirement (e.g. Goldman-Rakic, 1987), as when attempting to synchronize behaviorally with periodic stimuli by anticipating their arrival.

The second issue, which is dealt with in chapter 3, concerns the particular experimental paradigm best suited to examine the systematic evolution of one behavioral coordination mode to another. Namely, we suggest that a paradigm which explores the evolution of dynamical transitions from reactive behavior to anticipatory behavior may best enlighten which brain areas are most active during the continually changing temporal demands of the task and how the spatial topography and temporal properties of brain activity patterns is related to the different timing relationships in the behavior.

2. The Prefrontal Cortex and Temporal Integration

The prefrontal cortex is critically involved in the temporal organization of planned behaviors (Stuss and Benson, 1986; Goldman-Rakic, 1987). In this chapter, we outline the primary anatomical and neurophysiological support for this idea.

The prefrontal cortex is located at the anterior pole of the frontal lobe, and for sake of clarity, will be defined here as all frontocortical areas receiving projections from the dorsolateral nucleus of the thalamus (Kandel et al., 1991). This 'connectivity criterion' has often been used to emphasize the importance of studying the functionality of a given neural area within the context of its anatomical connections with other structures (Creutzfeldt, 1977). It should be noted, however, that even when using this criterion, establishing a single function for the area in question has been a rather elusive quest. In fact, as will be shown below, ablation studies have essentially ruled out mono-functionality of the area. Yet, a review of the literature reveals that the prefrontal cortex is critically involved in cognitive processes that generally fall under the description of temporally organizing purposive behavior.

2.1. Architectonic structure and neuroanatomy

The prefrontal cortex consists of the typical six layers of cells with a substantial granularization of layer IV (Kandel et al., 1991). Its primary subcortical afferents come from the mediodorsal nucleus (MDN) of the thalamus and appear to be topologically preserved (Goldman-Rakic and Porrino, 1985).

The MDN relays neural information to the prefrontal cortex from the mesencephalic reticular formation (Guillery, 1959), the amygdala (Porrino et al., 1981), both the prepiriform (Powell et al., 1965) and inferotemporal (Whitlock and Nauta, 1956) cortices, and a large projection from the substantia nigra (Ilinsky et al., 1985). It should be noted that the prefrontal

cortex also receives projections from other thalamic nuclei. Typically, more caudal parts of the cortex receive projections from progressively more lateral thalamic neurons.

The prefrontal cortex also receives direct projections from the hypothalamus (Jacobson et al., 1978), the hippocampus and other limbic areas (see Ferino et al., 1987) and is extensively interconnected in reciprocal fashion with primary sensory areas of the neocortex which include parietal area 7 (somatic), temporal area 22 (audition), and inferotemporal area 21 (vision) (see Jones and Powell, 1970 for a review). In fact the prefrontal cortex sends fibers to virtually every area it is innervated by, with a topological connectivity that seems to remain consistent with afferentation. Exceptions to this reciprocity include the basal ganglia (Fuster, 1989), and both the ventral and intralaminar nuclei of the thalamus (Nauta, 1964; Rinvik, 1968), all of which have been implicated as effector motor mechanisms. These findings suggest a high degree of convergence in the prefrontal cortex from primary sensory cortices as well as several subcortical structures, indicating a multimodal, associative nature to the area.

2.2. Lesion studies

The hallmark paradigm of frontal ablation studies is the classic delayed response task in which a subject is presented with a stimulus (S1) that has information relevant to the production of a given behavior to be carried

out following an enforced delay period. The termination of the delay is typically signalled by a second stimulus (S2). Earlier this century, Jacobsen (1936) first described a behavioral deficit in lesioned rhesus monkeys trained in this task. Primates with bilateral lesions of the prefrontal cortex, particularly the dorsolateral convexity, fail to perform this task accurately if delays longer than a few seconds are utilized (Skeen and Masterton, 1982). Although early interpretations of these results pointed to deficits in short-term memory, additional studies have shown that frontal animals are capable of learning and retaining the initial cue for the delay period in question if the stimulus is made more salient (Blake, Meyer, and Meyer, 1966). Additional work has concentrated on evaluating which physical attributes and modalities are most critical in performing the delay task after frontal lesioning. The results of these studies suggest two important factors which contribute to the frontal animal's inability to perform this task; (1) a marked decrease in the capacity of the animal to ignore irrelevant stimuli; and (2) a severe difficulty in organizing temporal sequences of actions. Mishkin (1964) pointed out that frontal animals have a tendency to produce perseverative errors during the delay task. That is, previous trials have a high degree of interference with the current trial. Furthermore, these animals are easily distracted by additional cues bearing irrelevant information presented during the trial (Mishkin et al., 1969).

The second factor involves the frontally lesioned animal's inability to bridge temporal delays between successive stimuli and in temporally organizing behavior in general. Pribram et al. (1977) showed that frontally lesioned animals can indeed perform the delayed response task if the events of the task are organized such that the trial does not directly depend on time estimation. Additional studies have indicated that frontally lesioned animals can perform sequencing tasks where large temporal disparities (e.g. more than a few seconds between successive events) are not involved suggesting the deficit is related to the timing of behavioral events rather than their ordering per se (Passingham, 1985). Taken together these two factors, interference and the inability to temporally organize behavior, suggest that the prefrontal cortex plays a pivotal role in the integration and planning of motor sequences.

2.3. Single-unit and field potential studies

Since the development of chronic microelectrode recording techniques in behaving animals (circa early 1970s), a number of studies have examined the firing characteristics of single cells in the prefrontal cortex, particularly the sulcus principalis of the dorsolateral convexity, during the delayed response task (e.g. Kubota et al., 1974; Niki, 1974). In general, there are three broad classes of cells which can be classified more easily with respect to their functionality than morphology. (1) One type of cell which predominates

in the prefrontal cortex increases firing activity at the beginning of each trial, following S1, and responds primarily to the physical attributes of the stimulus cue (Niki, 1974). These units often begin firing within 75 to 125 milliseconds following the stimulus presentation and terminate shortly thereafter (Watanabe, 1986). They have been found to be sensitive to the modality and physical characteristics of the stimulus used to initiate the delayed response task (Watanabe, 1986). (2) A second class of cells in the dorsolateral convexity alter their firing properties in direct relation to the impending motor response associated with the task (Joseph and Barone, 1987). It is apparent that many cells within this class begin firing several seconds prior to the overt movement and systematically increase their firing frequency until several hundred milliseconds before the response (Fuster et al., 1982). As has been pointed out in a summary of this work, these cells have an anticipative characteristic to them and seem to participate in the preparation of "motor set" (Stuss and Benson, 1986). Increased firing by these cells usually precedes that observed in either the premotor or primary motor cortices. This suggests a general anterior to posterior sequence of unit firing in preparation for a motor response. (3) The third cell group, and perhaps most intriguing, are those that fire in a sustained fashion during the course of the delay period. These units maintain firing during the entire delay even if it is lengthened to one minute or longer (Fuster, 1973).

Increased cell activity typically begins a few hundred milliseconds following the presentation of S1 and is sustained until the appearance of S2, at which time the firing rate returns back to baseline levels (Fuster, 1973). It is likely that such cells, which are more prevalent in the prefrontal cortex than any other cerebral structure, function to integrate sensory-motor events across time. Fuster (1989) uses the term "cross temporal contingency" to further emphasize that the activation of these units is critically dependent on the time separation between the stimulus and movement.

The aforementioned observations have an interesting parallel in the realm of field potential recordings. Walter and colleagues (1964) were the first to recognize that a sustained negativity of approximately 20 to 40 microvolts can be recorded from the scalp during the period between the presentation of a "warning" stimulus (S1) bearing relevant information for the production of a motor response and a second "imperative" stimulus (S2), signalling response initiation. The resulting waveform was named "contingent negative variation" (CNV) to reflect the temporal contingency of the first and second stimuli. Systematic investigation of the CNV has determined that neither the modality nor other physical attributes of the stimulus has much influence on the overall structure and amplitude of the waveform (McCallum, 1978). Rather, the CNV seems more related to cognitive phenomena, typically described by labels such as "expectancy", "attention", and "mo-

tivation" to name a few (Rohrbaugh et al., 1977). It now appears that the CNV is composed of two distinct waveforms bearing different scalp topography and possibly different functional significance. The first component begins shortly after the warning stimulus and appears with maximal amplitude over anterior frontal areas (McCallum, 1978). This early component of the CNV is thought to be related to attention (McCallum, 1978). A second, later component is observable just prior to the imperative stimulus. This component, which typically has maximal amplitude over frontal areas as well as central locations presumed to overlie premotor and primary motor cortices, is related to the anticipation of the second stimulus cue and also varies with the planning and initiation of the movement itself (Brunia et al., 1993). Thus surface negativity develops over anterior frontal areas at the beginning of the delay period following the presentation of the warning stimulus and progresses toward posterior motor areas the closer in time one gets to the imperative stimulus.

Both negative components are thought to be generated by slow excitatory postsynaptic potential sinks at the apical dendrites of cortical pyramidal cells. This apical depolarization may be the result of the regulation of excitability in the cortex by subcortical structures, in particular the basal ganglia and reticular nucleus of the thalamus. The prefrontal cortex has been postulated to be activated by input from S1, and then to act on the

reticular nucleus to regulate cortical networks involved in S2-processing. This threshold regulation is thought to be reflected in the later CNV component (Birbaumer et al., 1990).

Although researchers are still trying to understand the relationship of single-unit activity during the delay task to the appearance of these slow field potentials, one interesting similarity is their dynamically changing to-pographical distribution observed during motor preparation. Recall that during the delay task single-cell firing activity begins in dorsolateral regions of the prefrontal cortex. It is approximately over these areas that the early component of the slow, surface negativity develops following the first stimulus cue. As the motor response becomes closer in time, single cell firing increases in posterior locations of the premotor and primary motor cortices, similar to the anterior-posterior progression of the surface negativity. Such observations have led some researchers to speculate that these slow cortical potentials reflect neural processes involved in cross-temporal sensorimotor integration (Stuss and Benson, 1986; Fuster, 1989).

2.4. Summary

The anterior aspect of the frontal lobe, known as the prefrontal cortex has been implicated in, among other things, the temporal integration and organization of behavior. Projections to and from this region suggest a substantial degree of 'convergence' from primary sensory areas as well as limbic and other subcortical structures. Lesions of the dorsolateral convexity of the prefrontal cortex produce deficits in certain behaviors as exemplified by the classic delayed response task. It appears that processes involved in temporally organizing movements are disrupted, such as attention, perhaps short-term memory, and most notably, the ability to control interference from both internal and external sources which compete with the successful completion of the task.

Recordings of single-unit activity and surface slow potentials thought to be generated from the dorsolateral portion of the prefrontal cortex suggest a role for this area in sensorimotor integration when a temporal contingency is introduced between successive stimuli and/or motor actions. During the delayed response task, an anterior to posterior recruitment of cell firing occurs during the period between the warning and imperative stimuli. It is believed that prefrontal activity of these cells is related to bridging the temporal gap during the delay period and integrating stimulus with response. Slow, surface negativity recorded during the delay period of this task bears a resemblance to the single-unit activity in that it too appears to have an anterior to posterior progression as the motor act approaches in time.

There are, of course, additional neural areas known to be critically involved in the timing of sequential motor acts. For instance, Ivry and Keele (1990) have shown that patients with lesions to the lateral cerebellum ex-

hibit deficits in both motor and perceptual timing tasks. This suggests that the lateral cerebellum, in conjunction with the basal ganglia, the sensory association cortex, and premotor cortical areas, plays a role in a complex feedback loop which may be critically involved in timing and time estimation.

3. The Synergetic Approach to Brain and Behavioral Coordination

As described in the preceding chapters, there is growing evidence that the relative timing demands placed on an organism when producing ordered motor behavior may be reflected in changes in spatiotemporal brain activity patterns. When an individual is required to react with a motor response as soon as possible following a stimulus cue so that the time estimation demands required to accomplish a specific task are minimal, central brain regions commonly associated with primary sensory and motor processing may be expected to become active. However, there is reason to believe that with the introduction of a rhythmical context and task requirement such that the timing between successive stimuli and responses must be estimated on a cycle-to-cycle basis, frontal areas may also be recruited. In order to investigate the evolution of one stable brain pattern to another and how these changes relate to the temporal aspects of motor coordination, a theoreti-

cal/experimental framework is needed which provides a means to express the commonalities between timing in the central nervous system and overt behavior. The language of Synergetics and tools from dynamical systems theory offer one possible window into understanding how observables from different physical levels and scales may operate with similar dynamics in terms of the patterns they form (Haken, 1983; Kelso, 1995).

Synergetics is concerned with understanding how the cooperation of a large number of individual components on one scale of observation contributes to the development of macroscopic patterns on another (Haken, 1983). For example, how is the behavior of interacting neurons related to the appearance of macroscopic fields such as exemplified in the MEG and EEG? As was alluded to in Chapter 2, the relationship between single-unit activity and field potentials of the frontal motor areas has been explored now for about two decades, albeit in the face of technological limitations. The ability to record from several single cells at a time allows for a closer comparison of how their interaction may contribute to the generation of macroscopic field potentials. However, even if contemporary procedures permitted the simultaneous recording of a large number of cells, a protocol would be neccessary to generalize the phenomena exhibited by these, say, hundreds of cells to a much larger number in the thousands (Nunez, 1981). Synergetics is a useful framework from which to pursue this issue in that

central to it are conceptual tools dealing with low-dimensional descriptors (known as order parameters or collective variables) of complex behavior. Order parameter values are used to classify the state of a system as it goes from one pattern of behavior to another. An external control parameter, manipulated by the experimenter, can often be found that allows one to observe all the possible patterns available to the system and the routes between them (Haken, 1983). Designing experimental situations that provide conditions under which a system may exhibit one stable pattern and then spontaneously switch into another stable pattern are central to the framework espoused here (Haken, 1983; Kelso, 1995). When a system produces stable behavior at one level of description, it implies that the macroscopic observables in question are changing more slowly than their constituent microscopic components. Thus, the idea is to employ experimental paradigms that allow the formation of stable patterns and focus on the dynamical mechanisms that govern the switching among such macroscopic states.

In systems, like the brain, where the relevant variables and control parameters are not known a priori, Kelso and his colleagues have articulated the following strategy (Kelso & Schöner, 1988; Schöner & Kelso, 1988; Kelso, 1995):

(1) Determine the essential quantities, also known as order parameters (collective variables), that serve as low-dimensional de-

scriptors of the system's behavior. These quantities are also utilized to demarcate one pattern exhibited by the system from another.

- (2) Identify the proper experimental variables known as control parameters, which can be used to move the system through its various states (patterns).
- (3) Probe the stability of the system's behavior in each state and determine if any transition (bifurcation) phenomena from one pattern to another are present.
- (4) Determine the order parameter dynamics and stability properties of patterns on other levels of observation (e.g. both behavior and EEG signals) and attempt to relate them via common dynamic mechanisms.
- (5) Model these relations using attractor dynamics describing the stable states and bifurcations of the order parameter(s) governing the patterns.

This approach has been used to study a wide variety of phenomena including speech production and perception (e.g. Tuller and Kelso, 1990), apparent motion in visual perception (e.g. Hock, Kelso, and Schöner, 1993), single and multilimb coordination (e.g. Jeka and Kelso, 1992), intentional

switching among different movement coordination patterns (e.g. Scholz and Kelso, 1990), multijoint coordination (e.g. Kelso, Buchanan, and Wallace, 1991), and motor learning (e.g. Zanone and Kelso, 1992) to name but a few. For instance, in earlier experiments by Kelso et al. (1981, 1984), subjects were instructed to produce bimanual finger abduction-adduction movements in the transverse plane. By using different starting positions with either the simultaneous activation of homologous muscle groups (inphase mode) or nonhomologous muscle groups (anti-phase mode), it was shown that the in-phase mode was more stable with respect to gradual increases in movement frequency (the control parameter). When subjects began in the anti-phase mode, an increase in the cycling frequency produced a spontaneous transition to the in-phase mode as some critical frequency was reached, while no transition was observed when the subjects began in the in-phase pattern (Kelso, 1981; Kelso, 1984; Haken, Kelso, and Bunz, 1985). Following the theoretical modeling of this work (Schöner, Haken, and Kelso, 1986), predictions with respect to increased fluctuations (Kelso, Scholz, and Schöner, 1986) and increases in the local relaxation time of the relative phase of the finger movements after they were perturbed from their on-going rhythm (Scholz, Kelso, and Schöner, 1987) were confirmed in the vicinity of the critical point, indicating the presence of two key signatures which typically accompany phase transition phenomena. Critical phenomena such as phase transitions are important signatures in physical systems because their appearance can lead to a better understanding of how spatial and temporal patterns form in nature. By examining the manner in which key observables lose and regain stability over a wide range of control parameter values, information can be attained with regard to how low-dimensional patterns develop and change. Although related features such as phase and frequency locking have been observed in the mammalian brain (Bressler, 1987a, b; Gray et al., 1989; Engel et al., 1991), the existence of phase transitions in the brain has only been considered recently (Kelso et al., 1991; 1992; Fuchs et al., 1992; Wallenstein et al., 1995a).

The present research exploits a behavioral paradigm in which a spontaneous change in the relative timing among the individual components of the system (in this instance, the stimulus and movement times) can be studied systematically so that the evolution of one stable pattern to another can be explored. By taking advantage of the natural tendency for a system to switch abruptly from, say, one timing relationship between a stimulus and response to another, it is possible to address the issue of whether the brain does so in a similar manner.

The more traditional experimental approach to relating brain and behavioral events has been to study only stable coordination patterns. Typically, the subject is required to produce a well-defined gesture and a variable

such as force, for example, is varied in discrete steps. The presentation of this variable is usually randomized such that a comparison of behavioral and neural events across different variable values in a continuous manner is impossible. Consequently, no information associated with the dynamical change in the variable is available for study. However, if a suitable control parameter can be found which promotes a dynamic instability from one stable coordination pattern to another, the evolution between patterns can be studied as well as their initial and terminal states. Considering this, it may be possible to characterize how the real-time development of patterns and the mechanisms of their change are related across levels (i.e. behavioral versus neural). Thus, with respect to the present experiment, the following questions may be asked: (1) do different brain areas become involved at the transition point when one behavioral timing pattern changes into another; (2) if there is a change in brain activity patterns, does the change occur on the same time scale (as abruptly) as that observed in the behavior; and (3) can we establish any relationships (such as stability properties) among the brain areas involved which share similar dynamics to the behavioral phenomena? In the next section, an experiment designed to explore these questions is outlined. It is principally concerned with understanding how demands for temporal integration in perception-action patterns are dealt with in the human brain.

4. Reaction - Anticipation Experiment

In order to study brain and behavioral patterns related to differing demands for temporal integration, it may be instrumental to consider two extreme scenarios (Engström, Kelso and Holroyd, 1995). First, "reactive behavior", in which a subject is asked to respond as soon as possible following the presentation of a stimulus requires little or no temporal integration because (1) there is no enforced delay between the stimulus and action, and hence no required control of timing relations, and (2) even if the experiment is such that stimuli are delivered periodically, there is no need to establish a rhythm between successive responses if one can react to each single stimulus one at a time. In this manner, stimulus-response pairings may be considered individual events without an externally or internally imposed rhythm.

However, now consider a scenario in which subjects are again instructed to respond as soon as possible following a stimulus, but the period between successive stimuli is shorter. It has been demonstrated that subjects have a tendency to produce reactive-type behaviors in response to periodic stimulation at relatively long inter-stimulus-intervals (ISIs) (e.g. longer than 2500 milliseconds), but tend to synchronize with stimuli presented with short ISIs (Mates et al., 1994; Engström et al., 1995). In fact, Mates et al. (1994) found that subjects produced movements slightly in advance of stimuli when asked to synchronize at ISIs shorter than approximately 2.4

seconds, but switched to a reactive-type behavior for ISIs longer than this value. They hypothesized that different factors may contribute to synchronization errors (SE) at different ISIs. It was thought that at relatively short ISIs (e.g. below 2000 msec), the limiting factors were primarily sensory and motoric while at longer ISIs (e.g. above 2000 msec) the main influences were central capacities such as temporal integration (Mates et al., 1994). That the particular behavior observed (reactive or anticipative type movements) depends on the ISI suggests that a single control parameter (ISI duration) can be manipulated to explore how one form of behavior may change into another (see Chapter 3). Utilizing this paradigm, Engström et al. (1995) found a spontaneous reaction-to-synchronization transition in motor coordination as the ISI was systematically decreased. This occurred even when subjects were instructed to produce only reactive behavior, that is, respond as soon as possible following the stimulus. This suggests that it may be possible to observe the neural correlates of how these behavioral patterns dynamically evolve from one timing pattern to another (Kelso et al., 1992; Fuchs et al., 1992).

In the present study we recorded whole-head EEGs during a behavioral task similar to that used by Engström et al. (1995). We hypothesized that central and antero-central brain regions may be most active during reactive coordination while frontal areas may predominate during anticipatory

behavior (section 2). Since we expected frontal involvement during anticipatory coordination, another hypothesis concerns sex-related differences in brain function. It is well known that differences exist in frontal brain morphology between men and women (Bear et al., 1986). Structurally, the right frontal area is wider and extends farther anteriorly than the left in most individuals, but this asymmetry is most pronounced in men (Bear et al., 1986). Moreover, recent neurophysiological studies have demonstrated some functional differences in frontal lobe involvement between the sexes. For example, a recent study showed significant differences in the distributions of magnetic resonance signal intensity in the frontal lobes of men and women during a simple phonological task in which subjects were asked to judge whether two nonsense words rhymed (Shaywitz et al., 1995). Thus, both functional and morphological differences exist in the frontal lobes of men and women. Consequently, we hypothesized that different patterns of frontal brain activity (e.g. location of maximal activity) may be exhibited by men and women during anticipatory coordination. Given the morphological differences, we also speculated that men and women may display similar left frontal brain activity patterns, but that men may exhibit an exaggerated right frontal component. For instance, this may manifest itself as greater spectral power density at right frontal locations in the EEG records of men. We now outline the procedure used to test these hypotheses.

5. Methods

5.1. Tasks

Five male and five female subjects participated in the study which consisted of a primary experimental condition and three control conditions. (1) REACTIVE (primary experimental condition) - Based on the earlier results of Engström et al. (1995) in which subjects were asked to respond following the stimulus presentation, but switched to a coordination pattern of anticipating the stimulus at some critical frequency, we asked each subject to depress an air cushion with their right index finger as soon as possible following the presentation of a brief LED flash. It was emphasized that subjects should try to make a single response for each stimulus presentation. (2) SYNCHRONIZE (control condition) - In order to compare the behavioral and brain data from the REACTIVE condition with a condition in which subjects were asked to synchronize their responses with the stimuli rather than respond following their appearance, each subject was asked to depress an air cushion with their right index finger such that peak flexion coincides in time with stimulus presentation at a constant rate of 2.5 Hz. This single frequency was used because earlier pilot data indicated that, in the REACTIVE condition, subjects displayed a pattern of anticipatory coordination at the fastest stimulus presentation rates. Thus, a comparison was made between similar behavioral distributions resulting from different instructions to the subject. (3) STIMULUS-ONLY (control condition) – In order to compare the degree of similarity between the REACTIVE condition and the pattern of brain activity resulting from the stimulus presentation, each subject was presented with a series of LED flashes at a base rate of 1.0 Hz and instructed to refrain from making any movements. (4) MOTOR-ONLY (control condition) – In order to compare the degree of similarity between the REACTIVE condition and the pattern of brain activity resulting from the movement, subjects were instructed to produce a series of self-paced finger flexions with their right index finger. No external stimuli were delivered.

Based on the earlier results of Engström et al. (1995) and pilot data, a range of frequency presentation rates was derived. The particular incrementation of stimulus presentation rates was developed to ensure that the time scale on which the coordination pattern changed from one mode to the other was faster than the time scale on which the control parameter changed. Consequently, in the REACTIVE condition, stimuli (red LED, 80 msec duration) were delivered periodically, beginning at a rate of 0.167 Hz. After 10 cycles, the stimulus rate increased to 0.2 Hz, then 0.25 Hz, 0.33 Hz, 0.5 Hz and then increased by 0.25 Hz increments until a final rate of 2.5 Hz. A series of 10 cycles in which the stimulus frequency remained

constant is referred to as a plateau and a run consists of thirteen plateaus.

5.2. Experimental procedure

For all conditions, subjects were seated in a chair with their right arm abducted approximately 30 degrees at the shoulder, and their forearm supported in a pronated position by the armrest. Movements were practically isometric and positioning of the right index finger was recorded as a continuous measure of changes in air pressure resulting from depressions of a small air cushion situated directly beneath the tip of the subject's finger. All of the experiments were performed with subjects seated in a sound-attenuating chamber (Industrial Acoustics Company).

Sixty runs were collected for each condition. In order to minimize eye movements, three seconds prior to each of the experimental runs, an LED flash warned subjects to visually fixate on the LED located approximately 100 cm directly in front of them. In all conditions, each run was separated by a minimum rest period of 10 seconds. After every 5 runs, the experiment was paused several minutes for additional rest.

5.3. Data acquisition

The EEG was recorded from a montage of 61 scalp locations (based on an expanded version of the 10/20 International System of Electrode Placement (Jasper, 1958)) according to the illustration shown in Figure 1.

Figure 1 represents a top-down view of the head with the subject's nose at the top. Each scalp electrode was referenced to the left mastoid for collection purposes, and later off-line to a balanced system of linked electrodes from the left and right sides of the scalp (left and right mastoids). Interelectrode impedance was reduced to less than 10 $K\Omega$. All the EEG signals were amplified (105) using Grass 12A5 amplifiers with high and low pass analogue filters set at 0.1 Hz and 100.0 Hz respectively, and sampled at a rate of 256.0 Hz (12 bit analog-to-digital conversion using 3 VAXlab ADQ32s). To monitor vertical and horizontal eye movements, the EOG was recorded by referencing the medial upper portion of the left orbital rim to the lateral lower portion of the right orbital rim. Recording of stimuli and movements was performed using the same sampling as indicated above, however, these channels were not amplified or filtered. Prior to statistical analysis, all EEG signals were visually inspected for eye, head, orofacial, or body movement artifacts and deleted from the records before further processing. Further details of this procedure can be found in Appendix 1. In order to compare recordings from different subjects, all electrode positions as well as the inion, nasion and both preauriculars were recorded 3-dimensionally (Pohemus 3-Space Isotrack) before each experimental session.

5.4. Data analysis

Behavioral performance

- (1) Means and standard deviations of the peak-to-peak movement amplitude were computed across runs for each subject, for each cycle of each plateau.
- (2) Fourier analysis was performed on the movement records of each subject, for each cycle of each plateau. The spectra obtained for each cycle from a given plateau (10 cycles = 10 spectra per plateau) were then averaged to determine the frequency of finger flexions for that plateau. Since cycle length decreased with increasing stimulus presentation rates, a variable window length was used in the calculation (Fuchs et al., 1992; Wallenstein et al., 1995a).
- (3) The time lag, τ , between the movement onset and stimulus was calculated for each cycle of each plateau. In order to determine whether τ was positive or negative, the movement and stimuli peaks were associated by the following process. First, the cycle length in between successive stimuli was calculated and divided by two. Second, each stimulus was paired with the movement peak residing in a window of half a cycle length on either side. For instance, at a stimulus presentation rate of 1.0 Hz, the length between stimuli is 1000 ms. This results in a 500 ms window on either side

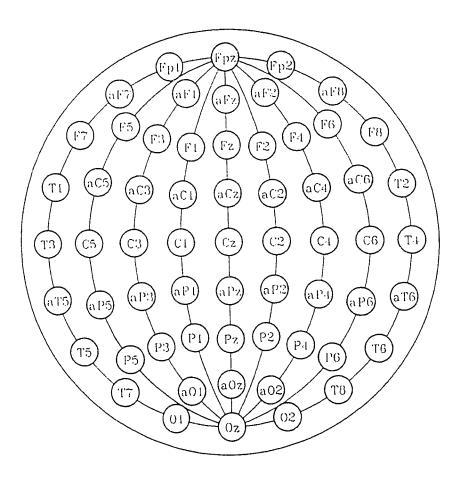


Figure 1: A projected top view of the electrode configuration. The subject's nose would appear just in front of Fpz.

of a given stimulus in which a response peak must fall in order to be paired with that stimulus. Positive values of τ indicated a movement lag relative to the stimulus.

(4) The transition: A visual inspection of single runs revealed that subjects typically exhibited positive time lags at relatively slow stimulus presentation rates, but displayed an abrupt change to near zero-time lags as the rate was systematically increased passed some critical value. For purposes of definition, two classes or "modes" of behavior were considered. In order to determine what range of time lag values belonged to each behavioral class, an inspection of the low stimulus frequency plateaus (plateaus 1 - 3) where positive time lags prevailed was performed. The range of variation in time lag values (mean = 298 ms; sd = 194 ms; minimum = 78 ms) was computed and used as a criterion for establishing boundaries of the behavioral modes. Using this range, "Reactive" behavior was defined as movements having a time lag (relative to the associated stimulus) more positive than 75 milliseconds. "Anticipatory" behavior was defined as movements having a time lag between -200 and 75 milliseconds. These definitions with respect to time lag leave no ambiguity in terms of categorizing the paired stimuli and movements. Using these definitions, the transition cycle from reactive to anticipative behavior was located in each run.

(5) Fluctuations in τ were computed after aligning the movement data at

the transition cycle and averaging across runs. The standard deviation of τ across runs was calculated for each cycle to determine how this value fluctuated before, during, and after the transition.

Electroencephalographic signals

- (1) Fourier analysis was performed on each cycle of each single run of the REACTIVE condition (by subject) EEG time-series. Spectral power density (SPD) was calculated at each frequency, f, by the formula: $spd(f) = Re(f)^2 + Im(f)^2$, where Re(f) and Im(f), are the amplitudes of the real and imaginary components of the Fourier transform. Window size and frequency resolution were defined in the exact manner as outlined above for the movement data.
- (2) Topographical spectral power density maps before, during, and after the transition were calculated by determining power at the frequency matching the stimulus presentation rate from the Fourier spectral cycle data and aligning each record at the transition cycle for each run and averaging these values across runs (by subject).
- (3) Fluctuations in spectral power density before, during, and after the transition were estimated by aligning each EEG spectral record (power at the frequency matching the stimulus presentation rate) at the transition cycle for each run and calculating the standard deviation across runs (by

subject).

- (4) Topographical spectral power density maps based on time lag (2 classes: reactive behavior and anticipatory behavior) and plateau were calculated by sorting all EEG records in terms of these two behavioral classes as outlined above under the motor performance section by cycle but within plateau. In this manner, a grouping of the EEG data was used that was dictated by the behavioral results. The spectral power at the frequency matching the stimulus presentation rate from each cycle was averaged across cycle within a given plateau and behavioral class. This resulted in a final distribution of spectral power density by 2 classes of time lag and 13 plateaus.
- (5) Topographical spectral power density maps associated with reactive and anticipatory behavior for the SYNCHRONIZE control condition were calculated using the same criteria as outlined above for the REACTIVE condition. Spectral power at the frequency matching the stimulus presentation rate (2.5 Hz) was used in constructing the maps. For sake of comparison with results from the REACTIVE condition, the data were split into the two behavioral categories (reactive versus anticipatory behavior) using the same range of values as indicated above.
- (6) Topographical spectral power density maps for the control conditions,

 MOTOR-ONLY and STIMULUS-ONLY were derived by calculating the

spectral power at the frequency matching the movement in the former and the stimulus presentation rate in the latter. These cycle data were then averaged (by subject).

(7) Topographical maps were compared for similarity both within and between conditions by calculating the correlation between any given pair, (x_i, y_i) ,

$$r^{2} = \left\{ \sum_{i=1}^{61} (x_{i} - X)(y_{i} - Y) / \left\{ SS_{x}SS_{y} \right\}^{1/2} \right\}^{2}$$
 (1)

where $SS_x = \sum_{i=1}^{61} (x_i - X)^2$, $SS_y = \sum_{i=1}^{61} (y_i - Y)^2$, and X and Y are the means (across all 61 channels) of the spectral power density from each map being compared. Statistical analyses of the correlations testing three types of null hypotheses were performed after transforming the r^2 values to Fisher Z values. Tests of no correlation, $r^2 = 0$, a perfect correlation, $r^2 = 1$, and a pairwise test for differences in the mean correlation (within condition) from each condition were performed.

(8) Groups of electrodes with maximal spectral power density were quantified by creating a grand distribution across electrodes and across the sorted conditions according to the procedures outlined in sections (2), (3), and (4) indicated above. The spectral power density values, x, at each electrode were then converted to a standard Z-score, where Z = (x - X)/S, X is the grand mean of all spectral power density values, and S is the standard deviation. A threshold Z-score of 2.576, corresponding to p < .005,

was used as a cut-off point such that electrodes having values larger than this were considered to have significant spectral power density.

Analyses of variance (ANOVA) were performed using BIOMED modules (BMDP P2V and P4V). Post-hoc analyses were performed using the conservative Scheffé test (BMDP).

6. Results

6.1. Coordination task performance

Fourier analysis revealed that in each plateau, the dominant frequency component of the movement was at the stimulus presentation rate. Sample time series of the movement and stimulus channel from a single run are presented in Figure 2a with particular concentration on a segment of the run showing the transition from reactive behavior (movement following stimulus) to anticipatory behavior (movement precedes stimulus). When using the procedure described in the last section to classify behavior according to time lag (reactive: > 75ms; anticipatory: -200ms < 74ms), the transition was found to be at the 18th cycle (between the 18th and 19th stimuli: stimulus presentation rate = 1.25 Hz) in this instance, as depicted in Figure 2a. Also shown are the single frequencies which exhibited maximum spectral power density from each plateau during the run (Figure 2b). These frequencies correspond to the stimulus presentation rate on

each plateau. From a visual inspection of these data, it is apparent that a 1:1 correspondence exists between each stimulus and peak in the movement channel indicating a finger flexion. However, at the transition cycle, the relationship goes from response lag to response lead. Thus the 18th stimuli is without a paired response in this case.

Each subject exhibited spontaneous transitions from a pattern of "reactive" behavior where positive values of τ predominated to a coordination pattern of "anticipatory" behavior where a mixture of positive and negative τ values (indicating movement lead relative to the stimulus) were observed as the stimulus presentation rate was increased. This transition from one coordination mode to another occurred at different cycles from subject to subject as well as within a given subject's data (see Section 4.2.3).

6.2. Behavior amplitude

A series of kinematic analyses was performed on the movement data. The peak-to-peak amplitude of the movement was calculated for each cycle. These values were then averaged for each cycle across runs within a given subject. A two-way ANOVA (subjects as cases), testing for differences in averaged movement amplitude (peak-to-peak) during the REACTIVE condition comparing sex (2) by cycle (130), revealed a significant main effect for cycle, F(129,520) = 1.96, p < .001. Posthoc analyses revealed that response amplitude decreased with increasing frequency across plateaus, but

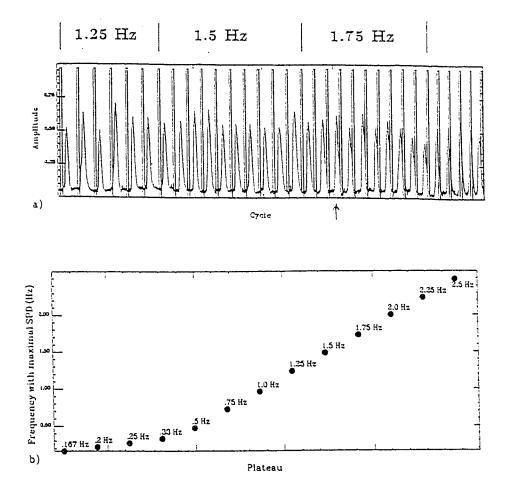


Figure 2: (a) An example times series of the movement and stimulus marker channels of a single run (unaveraged) taken from a representative subject (female). Shown is a "close-up" of the switch from reactive behavior (movement lagging stimulus) to anticipatory behavior (movement preceding stimulus). The transition was found to be at the 18th cycle (between the 18th and 19th stimuli: stimulus presentation rate = 1.25 Hz). (b) The movement frequency exhibiting maximal spectral power density (SPD) as a function of plateau, corresponding to the stimulus presentation rate in each plateau.

not within a given plateau, for both males and females. This effect is consistent with past observations employing a similar coordination paradigm (Wallenstein et al., 1995a).

6.3. Behavior time lag (τ)

In order to understand the timing relationship between successive stimuli and responses, an analysis of the time lag (τ) distributions for each plateau (by sex) was performed. The averaged (across subjects) density distributions of τ as a function of plateau are shown in Figure 3 for men (Figure 3a) and women (Figure 3b). Also shown are the distributions of time lag between the response relative to the stimulus preceding it and the stimulus following it for men (Figure 3c) and women (Figure 3d).

As the averages in Figures 3a and 3b suggest, subjects typically exhibited positive time lags (reactive behavior) at relatively slow stimulus frequencies and switched to a mixture of positive and negative (near zero mean) time lags (anticipatory behavior) as the stimuli were presented more rapidly (e.g. faster than 1.5 Hz - 1.75 Hz). This switching from a reactive to anticipatory timing mode was observed in each subject (see Appendix 1 for individual subject data) as the stimulus presentation rate was increased.

This mixture of reactive and anticipatory behavior in plateaus with faster stimulus presentation rates comes about from two primary sources. First, transitions occur at different times within a given run and a moderate

percentage of runs even contained continuous reactive behavior throughout the entire series (approximately 15 % for the men and 17 % for the women). Second, there was also the appearance of "flip-flop" behavior in which reactive coordination was exhibited for a number of cycles and replaced by anticipatory behavior for several cycles, then back to reactive behavior again. This type of behavior was exhibited in approximately 40.7 % of the runs for men and 39.7 % of the runs for women. An inspection of the runs where "flip-flop" behavior was exhibited indicated that 84 % of the post-transition cycles for men and 81 % for women displayed reactive coordination. Thus, when "flip-flop" behavior occurred, the tendency was to produce a majority of reactive behavior throughout the run.

A two-way ANOVA (subjects as cases), testing for differences in the timing of the movement relative to the stimulus, between sex (2) and plateau (13), resulted only in a significant main effect for plateau, F(12,52)=5.82, p<.001. This result taken together with a visual inspection of Figures 3a and 3b indicates that τ generally decreased toward zero with increasing plateau for both men and women.

This tendency for subjects to produce smaller time lags on average with increasing stimulus presentation rate indicates that the response time did not remain constant across plateau. A visual inspection of Figure 3 shows that as early as plateau 4 (0.33 Hz stimulus presentation rate), some re-

sponse times were in the 75 millisecond range (faster than a typical reaction time). The increase in the number of early response times at plateaus 5 and above gave the time lag distributions a greater symmetry as compared to the skewed distributions of the first four plateaus. These results suggest a degree of anticipation with respect to the impending stimulus beginning with plateau 4 and argue against the idea that the response time remained constant with increasing plateau.

6.4. Fluctuation enhancement in behavioral time lag (τ)

An analysis of the standard deviation of τ was performed in order to test for differences in fluctuations before, during, and after the transition cycle. Prior to analysis the transition cycle was located in each run according to the procedure outlined in Section 4.1.4. The response records were then aligned at the transition and the means and standard deviations of τ over runs were obtained for 10 cycles before and after the transition cycle. Only ten cycles were used because the averaged signals began to smear at cycles far from the transition. A two-way ANOVA testing for differences in the standard deviations of τ between sex (2) and cycle (21) resulted in a significant main effect for cycle, F(20,84)=3.08, p<.01. Posthoc analyses (pair-wise comparisons of each successive cycle) revealed a significant increase in the standard deviation in τ for both men and women only in the cycle preceding

Figure 3: Average time lag (τ) distributions (frequency of occurrence) as a function of plateau from (a) male and (b) female subjects. Plateaus where relatively slow stimulus frequencies were used (e.g. 0.167 Hz - 1.5 Hz) resulted in predominantly reactive-type behavior. As the stimulus frequency became faster, however, the mean of the distribution approached zero, indicative of anticipatory behavior. Also shown are the distributions of time lag between the response and the preceding stimulus (solid line) and the response relative to the stimulus following it (dashed line). Men are shown in (c) and women in (d)

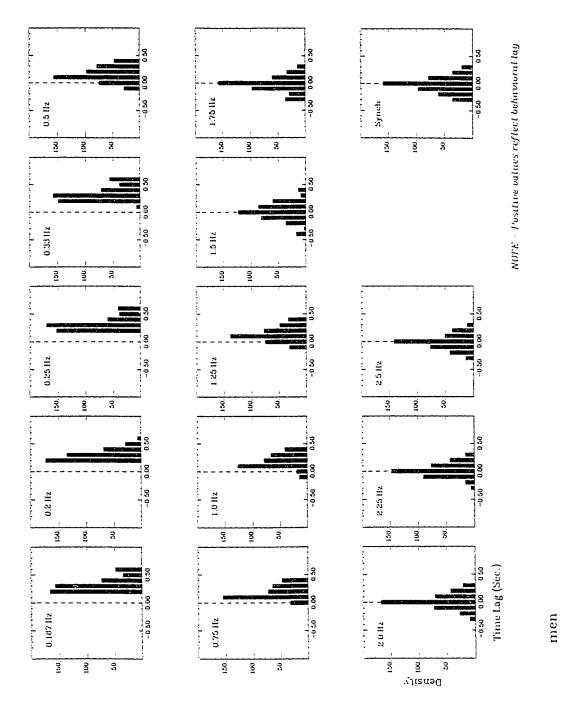


Figure 3 (a)

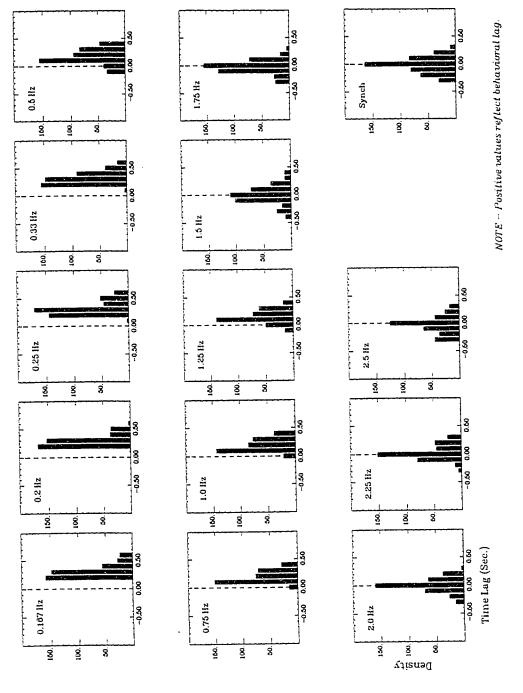


Figure 3 (b)

women

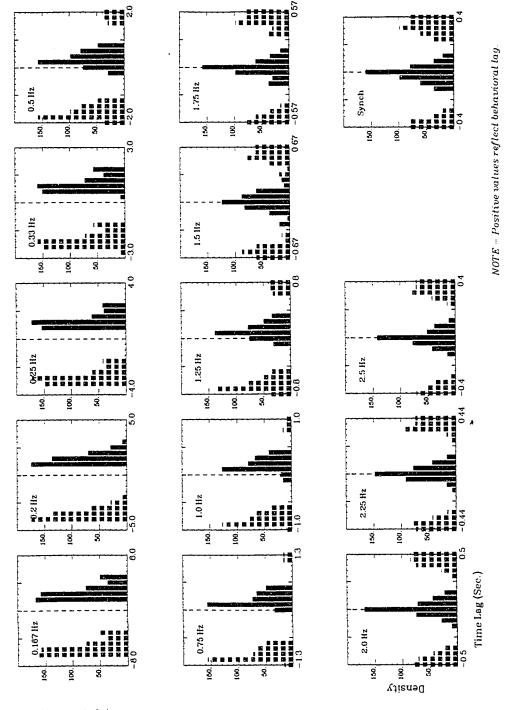


Figure 3 (c)

men

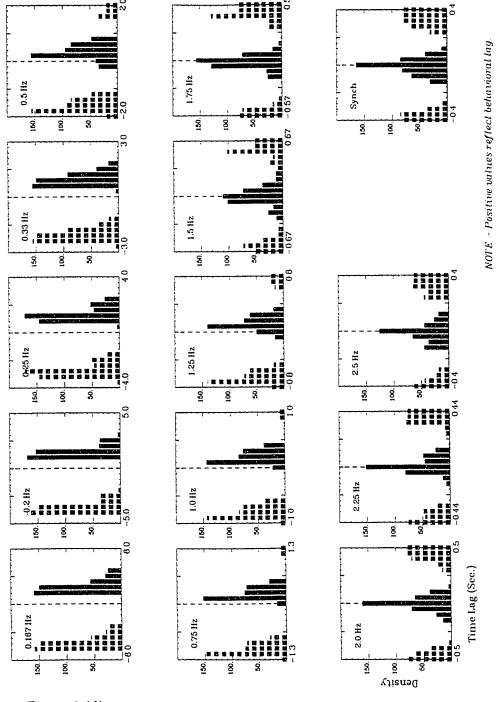


Figure 3 (d)

women

the transition cycle from reactive to anticipatory coordination (Figure 4 - although no sex effect was found in this analysis, both men and women are shown for comparison with the EEG data detailed in the following sections).

Trend analysis was also performed on these data. A comparison of the linear trend of the ten time lag standard deviation values (averaged across subjects and sex) before and after the transition cycle revealed a substantial difference in the slope of these values (pre-transition slope = 4.47, post-transition slope = .34). Taken together, these effects demonstrate fluctuation enhancement, a predicted feature in nonlinear systems, which is associated with instabilities (provided certain time scale assumptions are met - Section 3) as a change occurs from one mode of behavior to another (Haken, 1983; Kelso, 1995).

6.5. Frequency domain analysis of the EEG

Fourier analysis of the time series (by subject) indicated that the dominant energy component in the EEGs was typically at the same frequency as the stimuli. The grand averaged (across subjects) EEG time series are shown in Figure 5 for men (Figure 5a) and women (Figure 5b). An interesting point to note is the "smoother" appearance of the women's averages. Since the number of trials which comprised the averages was comparable for men and women (on a cycle basis), it may be that other factors such as skull size or resistivity are related to this effect.

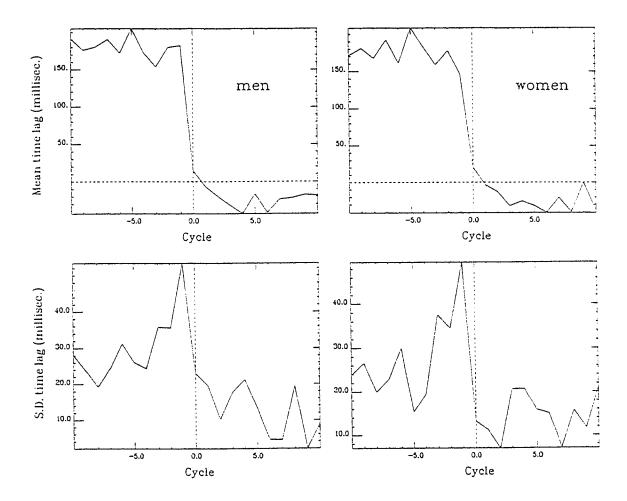


Figure 4: The grand means and standard deviations (aligned at the transition cycle) of τ (milliseconds) for (a) men and (b) women. The transition cycle was located in each run by the procedure described in Section 4.1.4. Shown are 10 cycles before and after the transition.

Figures 5c (men) and 5d (women) show the power spectra calculated for each cycle of every single run, then averaged within plateau. The finding that the dominant frequency in the EEG coincides with the stimulus (and movement) rate is consistent with past observations of rhythmical sensorimotor tasks (e.g. Kelso et al., 1992; Fuchs et al., 1992; Wallenstein et al., 1995). Since the largest spectral peak matched the frequency of stimulus presentation in any given plateau, additional analyses were performed using the power at these frequencies to see if there were topographical changes could be related to timing changes in movement coordination.

6.6. Spectral power density of the EEG by plateau and behavioral mode

Prior to statistical analysis, all EEGs were sorted into the two behavioral modes based on time lag (τ) as described in Section 4.1.4. The spectral power was then calculated for each cycle and averaged within plateaus and behavioral mode (by subject). For purposes of statistical comparison, only plateaus where both reactive and anticipatory behavior took place were used in the analysis (i.e. plateaus 8 - 13). These averages (the number of cycles that went into these averages is provided in Appendix 4) are illustrated in Figure 6, which shows the topographical maps of spectral power density for both men (Figure 6a) and women (Figure 6b) as a function of plateau and behavioral mode. In order to quantify which groups of electrodes ex-

Figure 5: The grand averaged (across subjects) EEG time series for (a) men and (b) women. Each graph is on a separate microvolt scale range in order to provide better visual resolution. The vertical lines indicate plateau boundaries where the stimulus presentation rate was changed. Also shown are power spectra calculated for each cycle of every single-run and averaged within plateau for (c) men and (d) women.

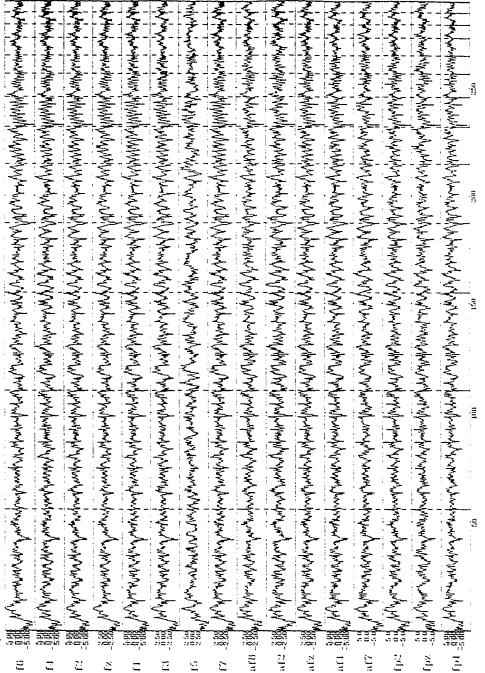


Figure 5 (a)

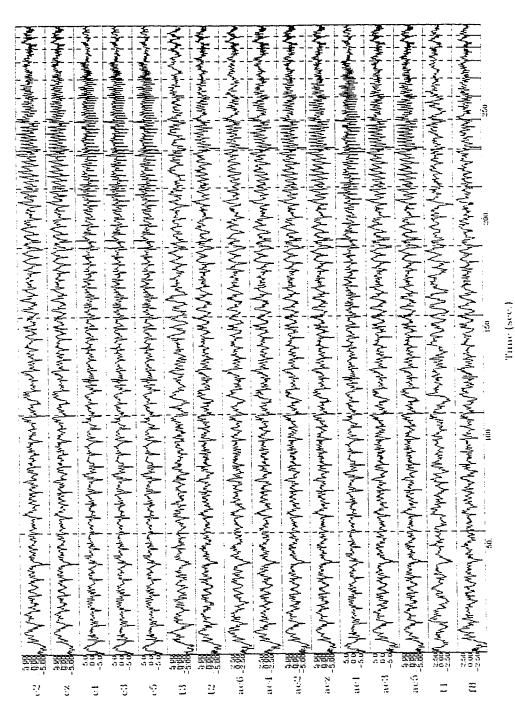


Figure 5 (a) - continued

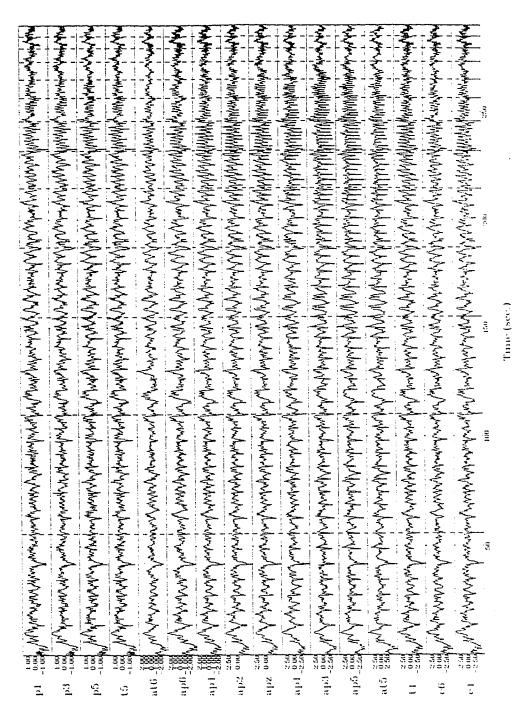


Figure 5 (a) - continued

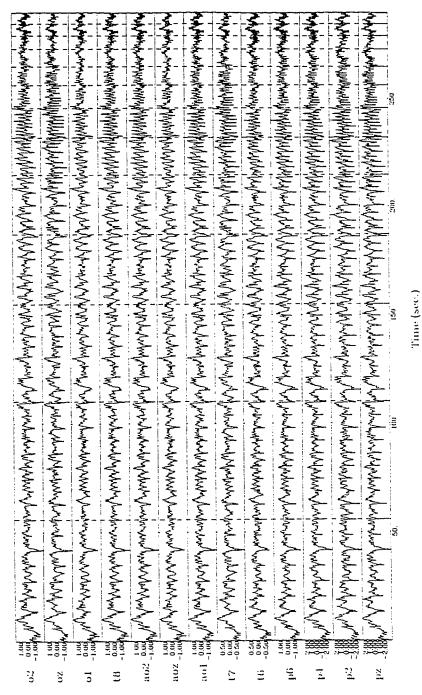
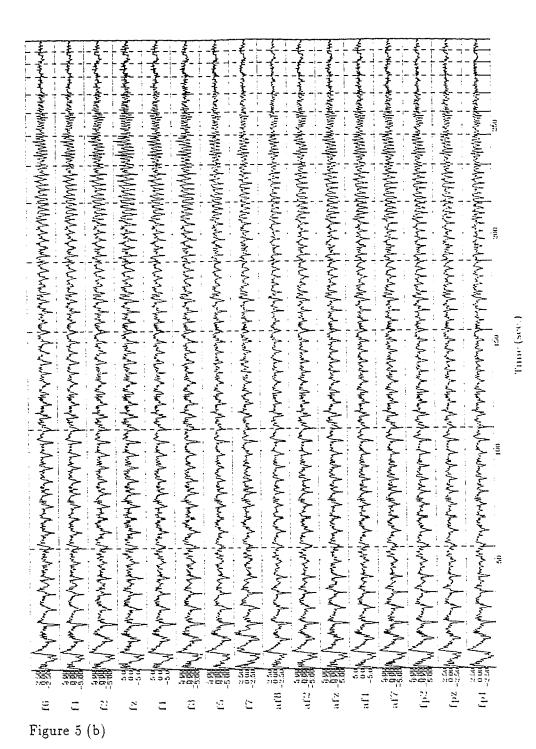


Figure 5 (a) - continued



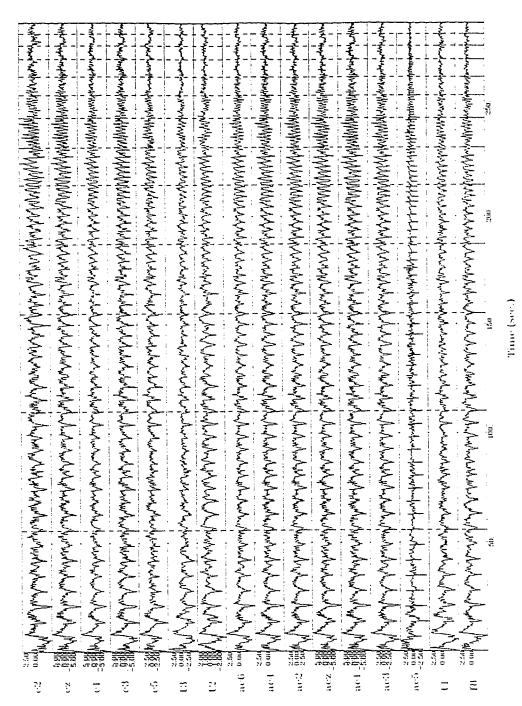


Figure 5 (b) - continued

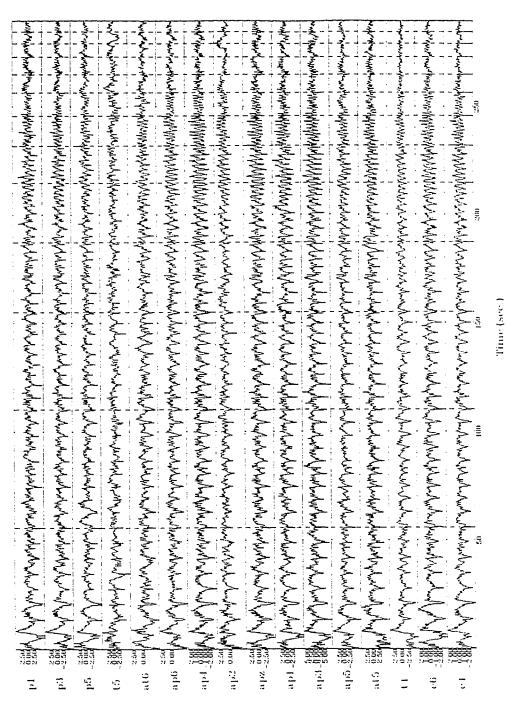


Figure 5 (b) - continued

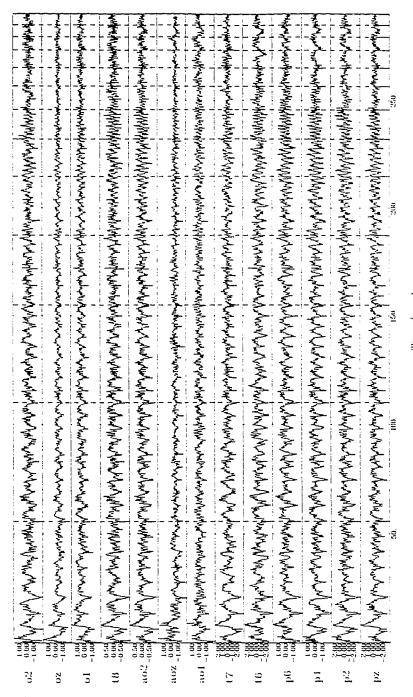


Figure 5 (b) - continued

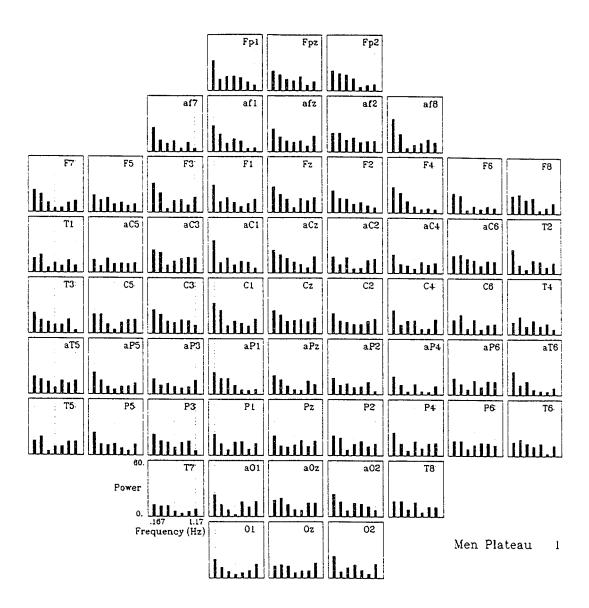


Figure 5 (c)

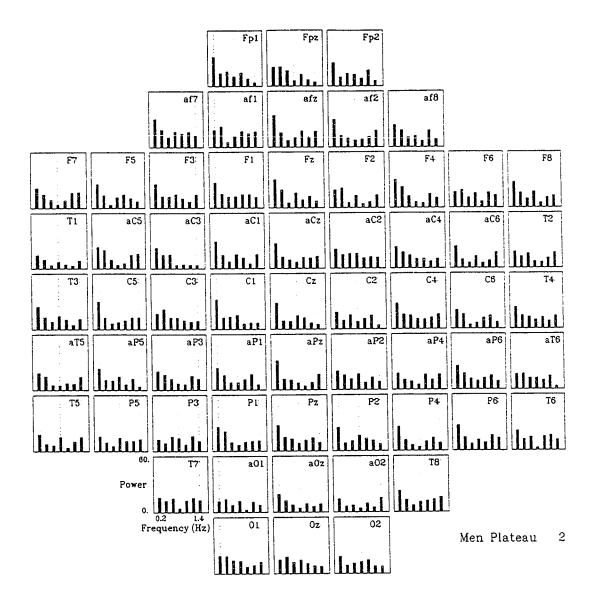


Figure 5 (c) - continued

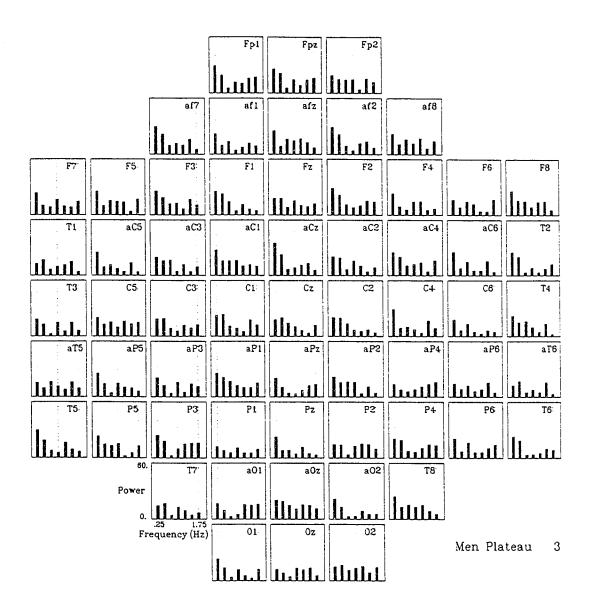


Figure 5 (c) - continued

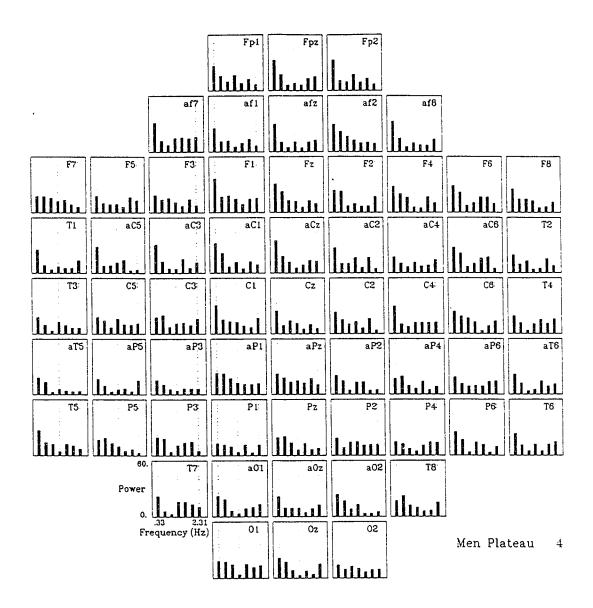


Figure 5 (c) - continued

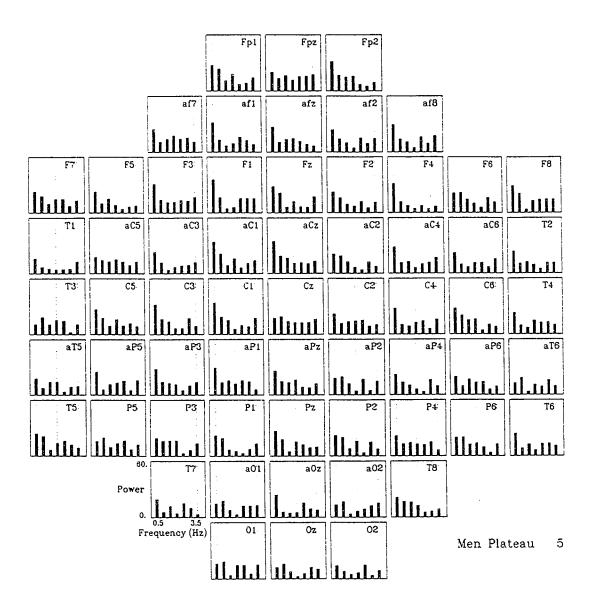


Figure 5 (c) - continued

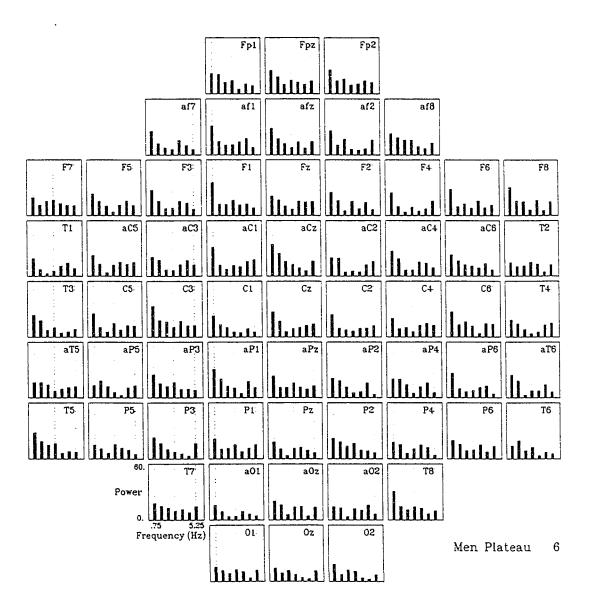


Figure 5 (c) - continued

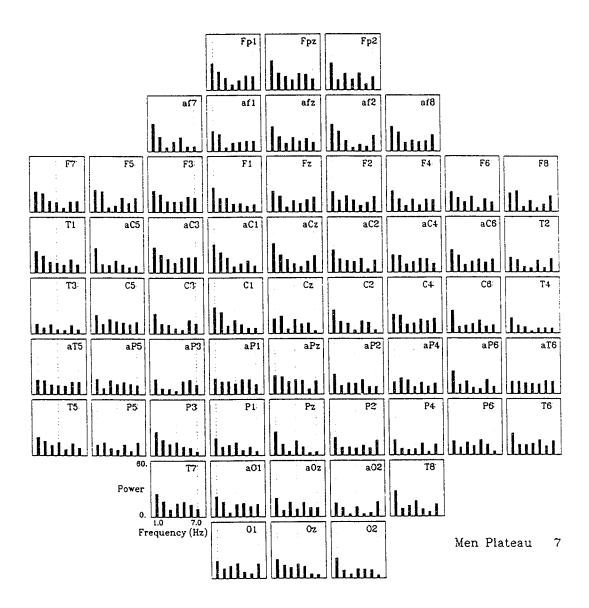


Figure 5 (c) - continued

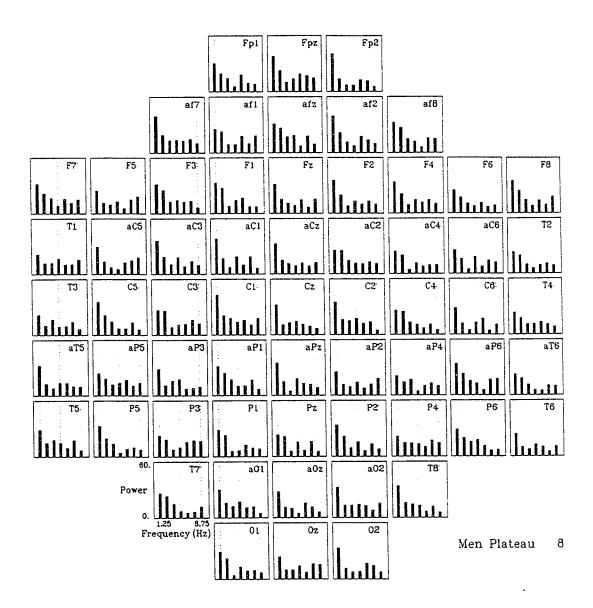


Figure 5 (c) - continued

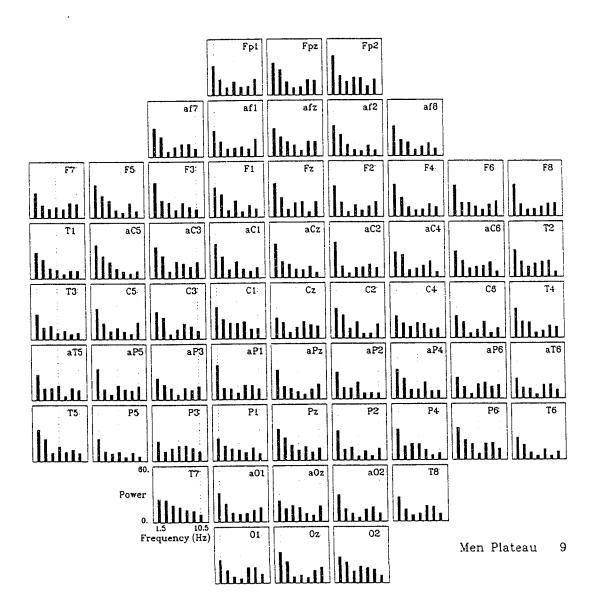


Figure 5 (c) - continued

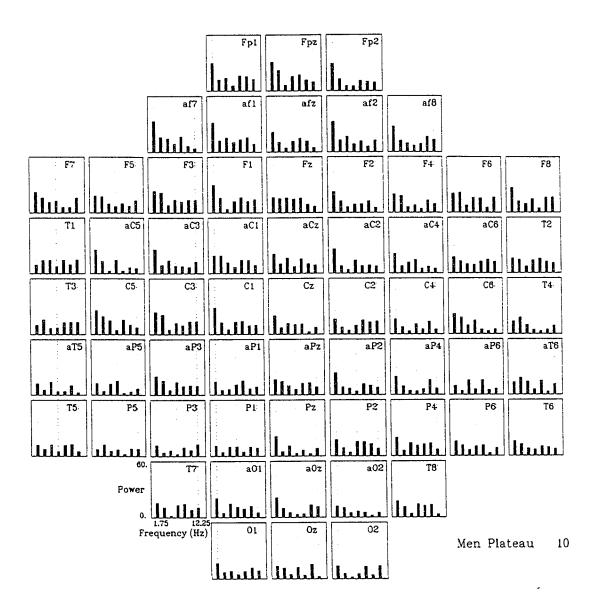


Figure 5 (c) - continued

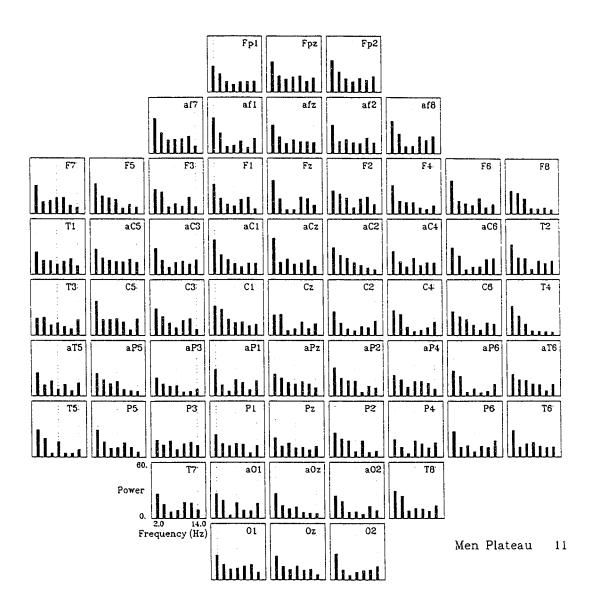


Figure 5 (c) - continued

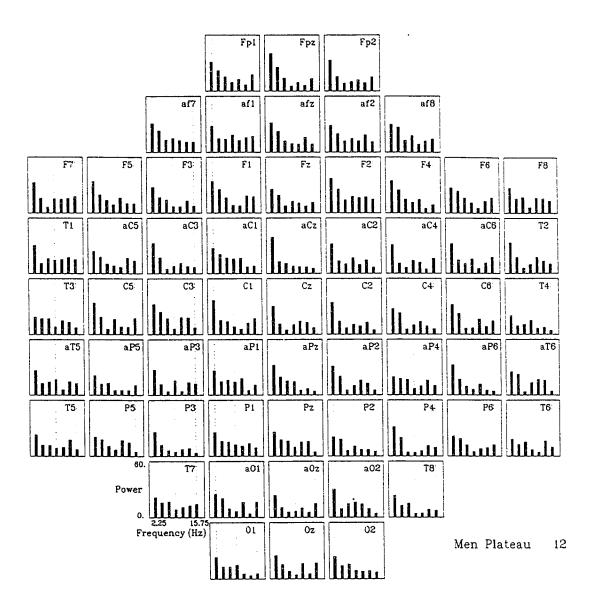


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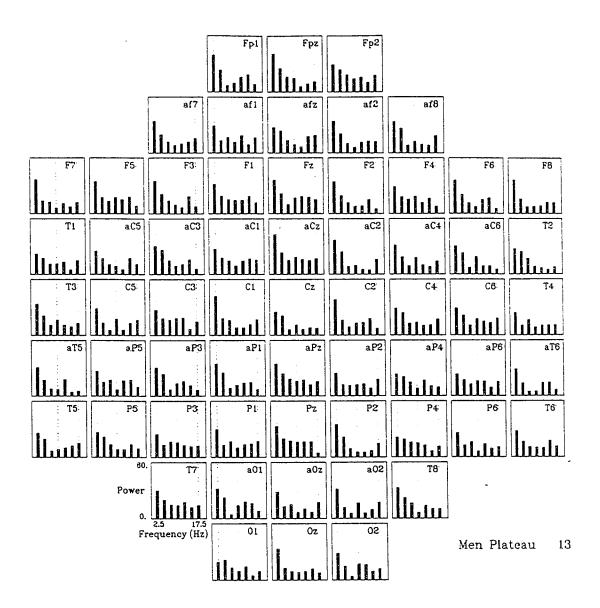


Figure 5 (c) - continued

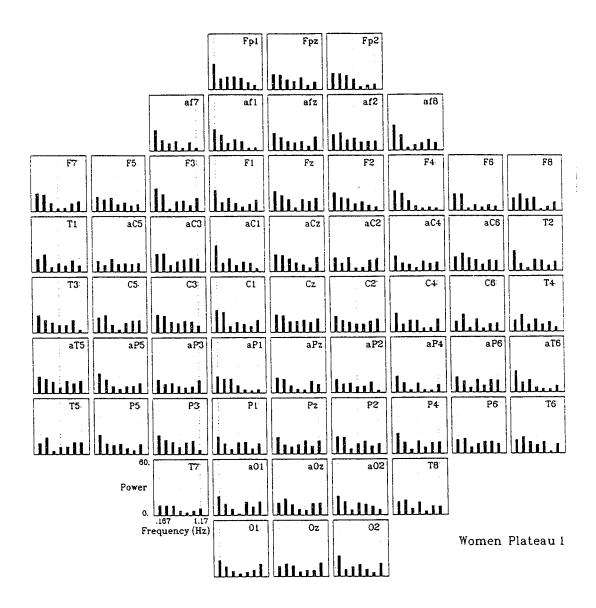


Figure 5 (d)

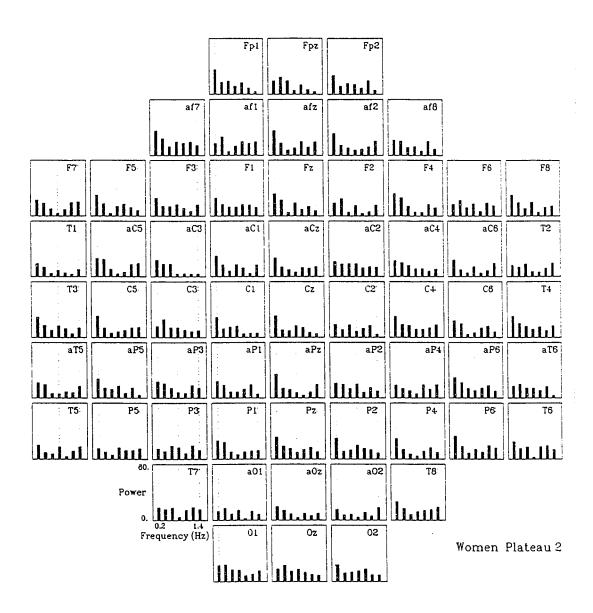


Figure 5 (d) - continued

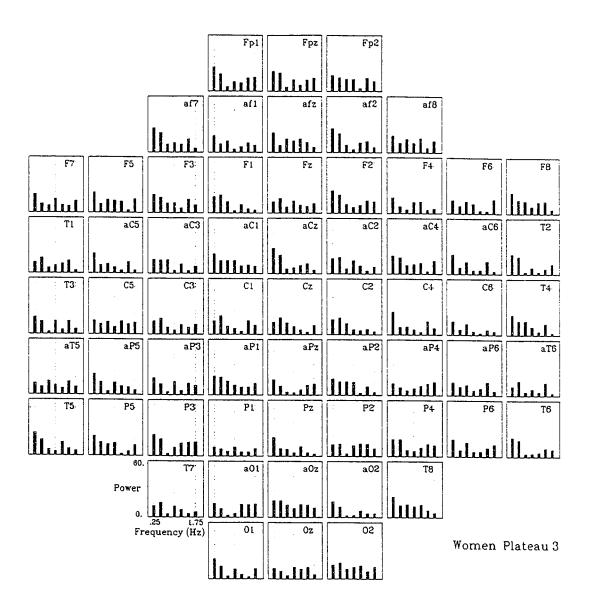


Figure 5 (d) - continued

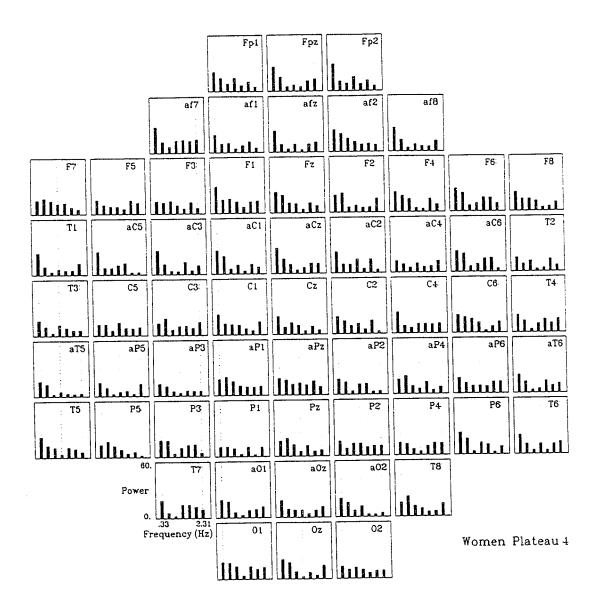


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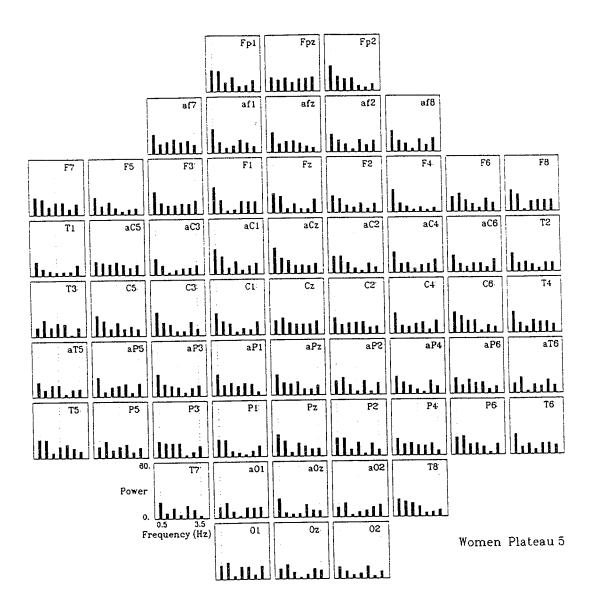


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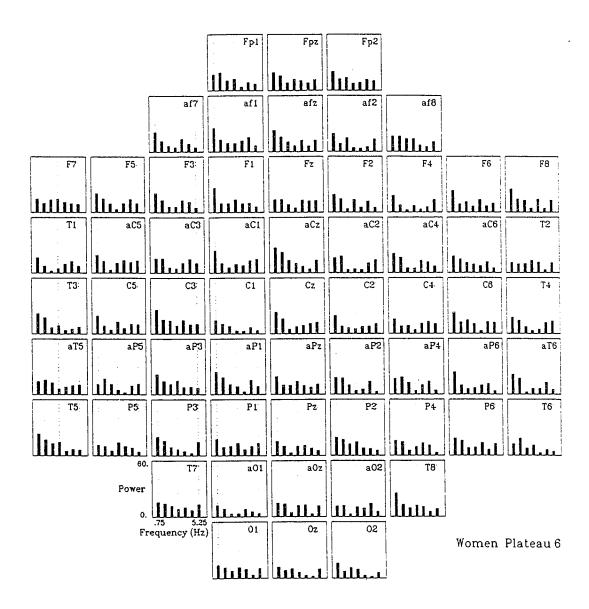


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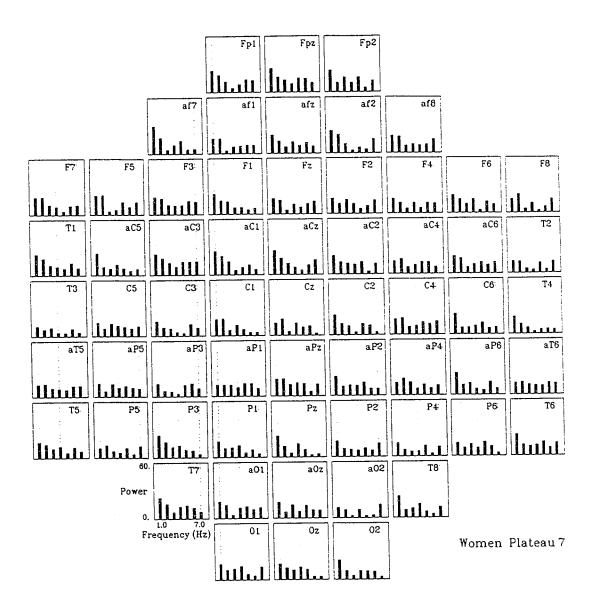


Figure 5 (d) - continued

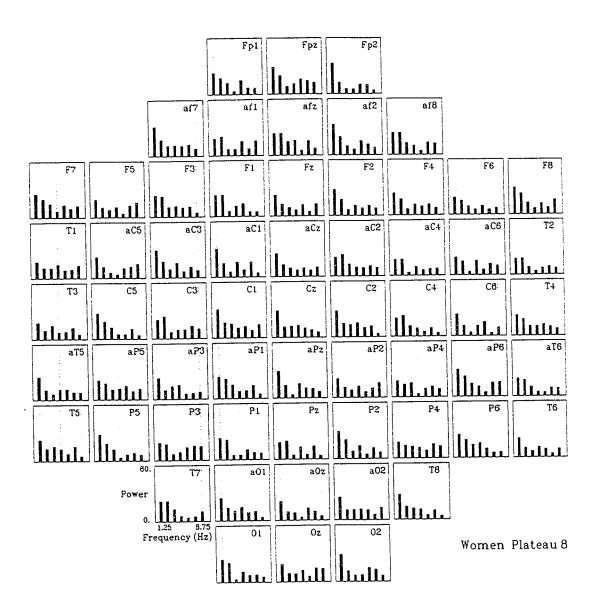


Figure 5 (d) - continued

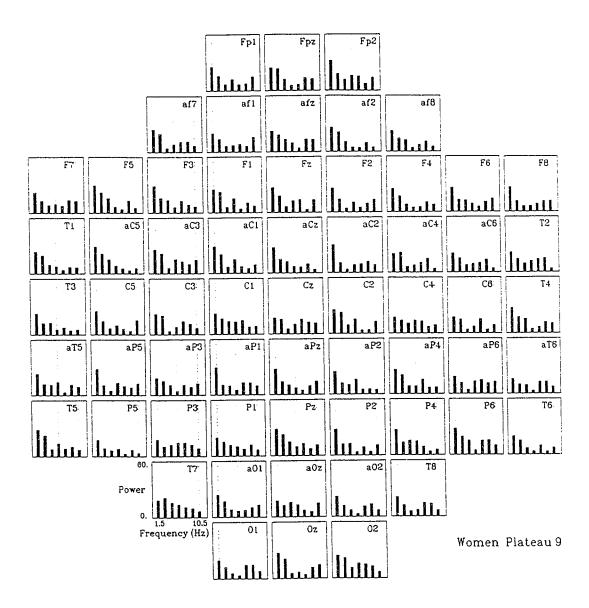


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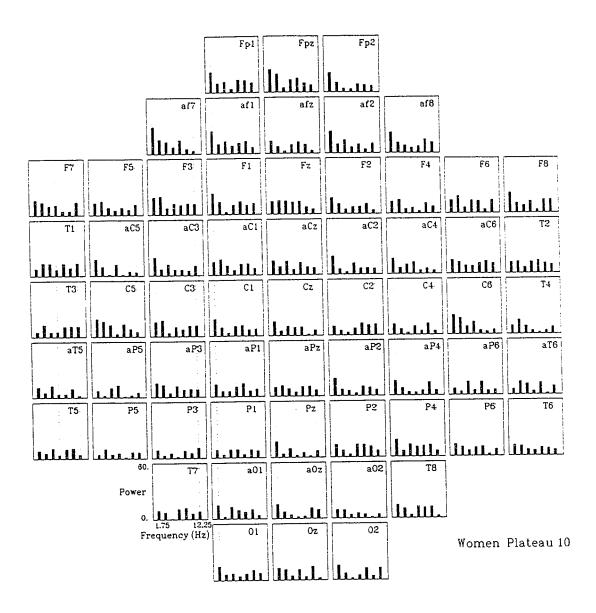


Figure 5 (d) - continued

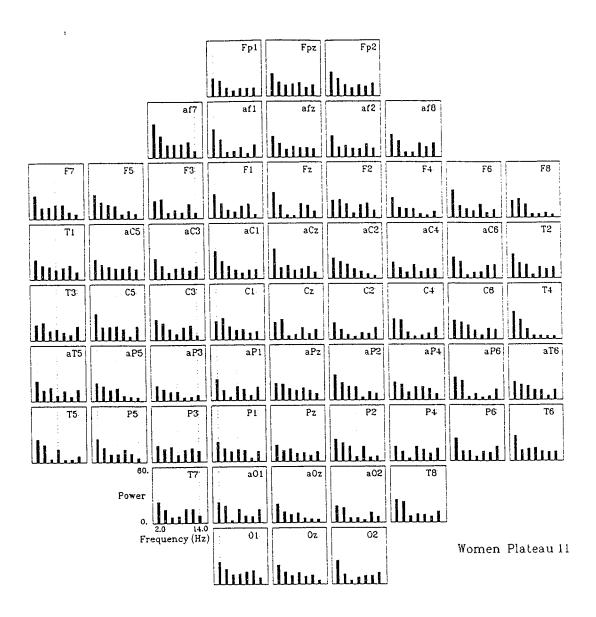


Figure 5 (d) - continued

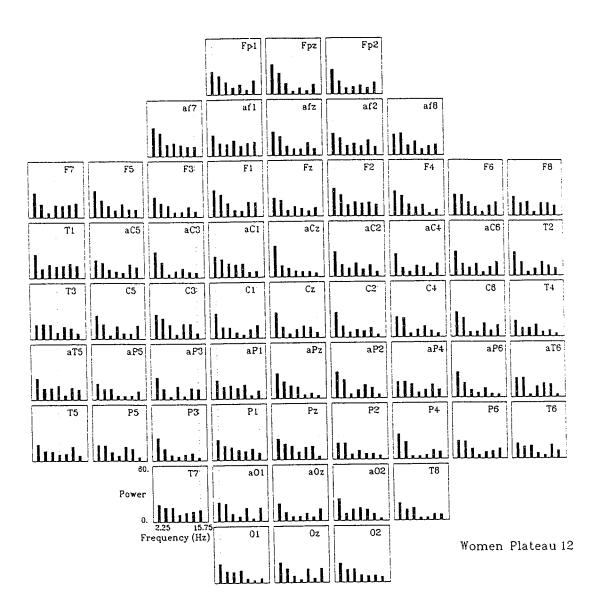


Figure 5 (d) - continued

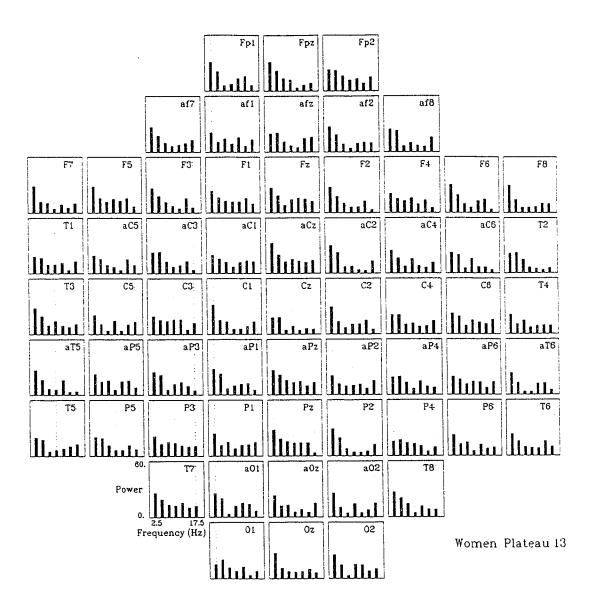


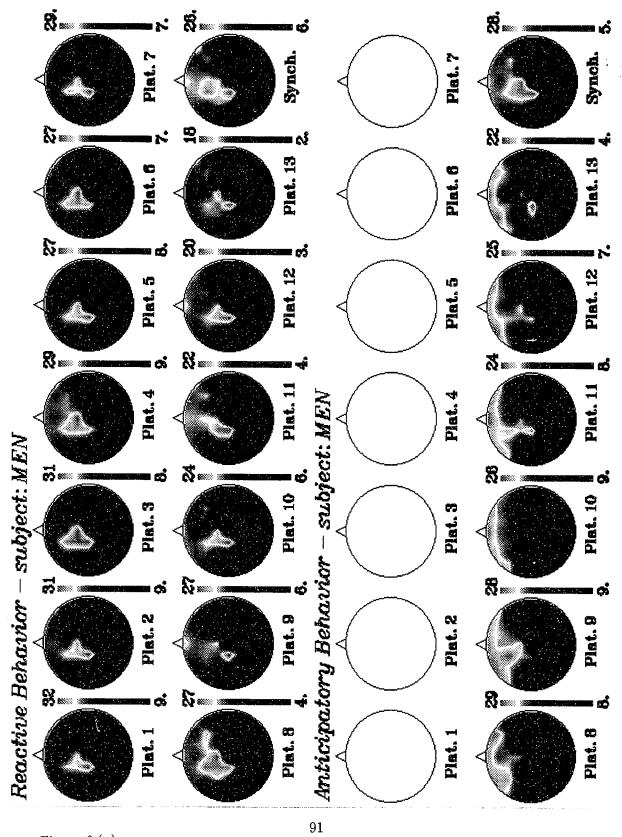
Figure 5 (d) - continued

hibited significant spectral power density, a grand distribution (across subjects, plateaus, behavioral mode, and electrodes) was created from the data shown in Figures 6a and 6b. Each value of spectral power density was then converted to a standard Z-score (Section 4.1.4). Electrodes having a Z-score exceeding a threshold corresponding to p < .005 were considered to exhibit significant spectral power density. Using this criterion, both men and women show a broad antero-central peak in significant spectral power density during reactive behavior situated primarily at recording electrodes. aC3, aC1, C3, and C1. During the anticipatory coordination mode an additional significant frontal component appeared which was bilateral and broadly distributed in prefrontal regions in both men and women. Maximal spectral power density during anticipatory movements was found to be situated at recording electrodes, Fp1, Fpz, Fp2, aF7, and aF8, for both men and women.

In order to determine if changes in the spatial distribution of EEG spectral power density could be found in relation to changes in sensorimotor timing, an analysis comparing sex by plateau by behavioral mode (reactive versus anticipatory) by electrode location was performed. A four-way ANOVA comparing sex (2) by behavioral mode (2) by plateau (6) by electrode location (61) resulted in a weak four-way interaction, F(300, 5856) = 1.21, p < .05. In order to understand this interaction, several posthoc

analyses were performed. As a first step, the data were initially treated separately by sex. A three-way ANOVA was performed comparing for differences as a function of behavioral mode (2) by plateau (6) and electrode location (61). This resulted in a significant three-way interaction for men, F(300, 2928) = 1.29, p < .01, and a weaker significant three-way interaction for women, F(300, 2928) = 1.114, p < .04. Additional posthoc analyses were employed to unpack these interactions. Tests of simple effects due to behavioral mode (Scheffé) revealed that significantly (p < .01) larger values of spectral power density appeared during anticipatory compared to reactive behavior at several frontal electrodes (Table 1). This was observed for both men and women. These differences are illustrated in topographical form in Figure 7 as a function of plateau and sex (red-colored areas are significantly different). Both men and women exhibited significantly (p < .01) large spectral power density during anticipative compared to reactive behaviors at a number of frontal and antero-central recording sites. Men showed a broad region of significant differences which included central, antero-central and frontal recording locations, while women exhibited significant differences predominantly at frontal, right frontal and left antero-central sites (Table 1).

Figure 6: The topographical maps of spectral power density (grand average across subjects) for (a) men and (b) women as a function of plateau and time lag (reactive versus anticipatory behavior). The same maps are reproduced on a uniform scale in c and d.



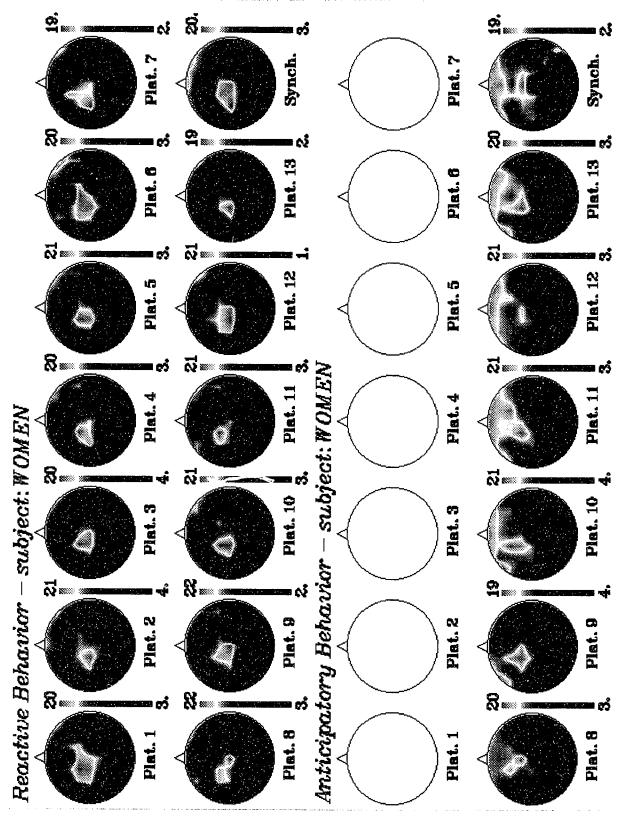
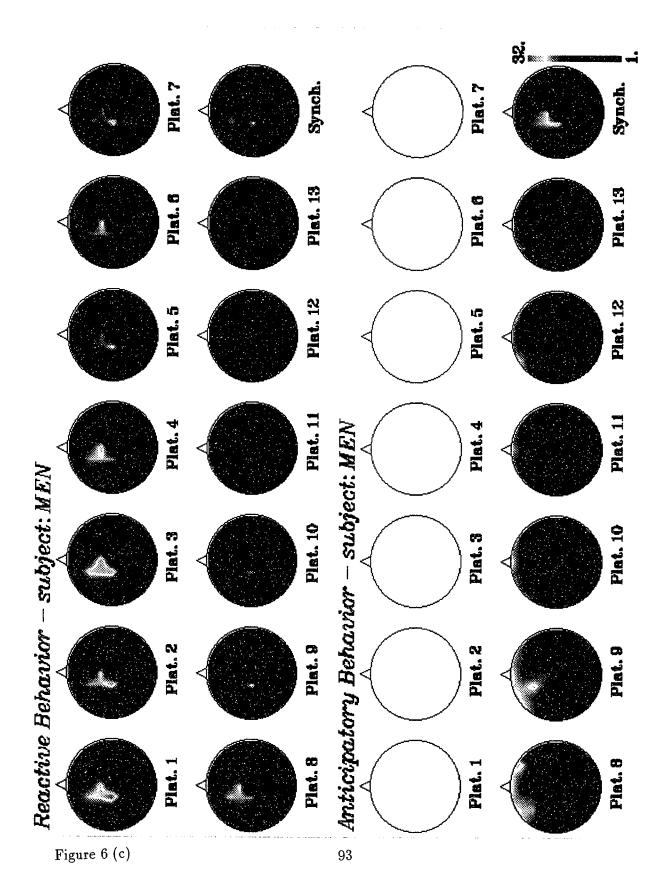


Figure 6 (b)



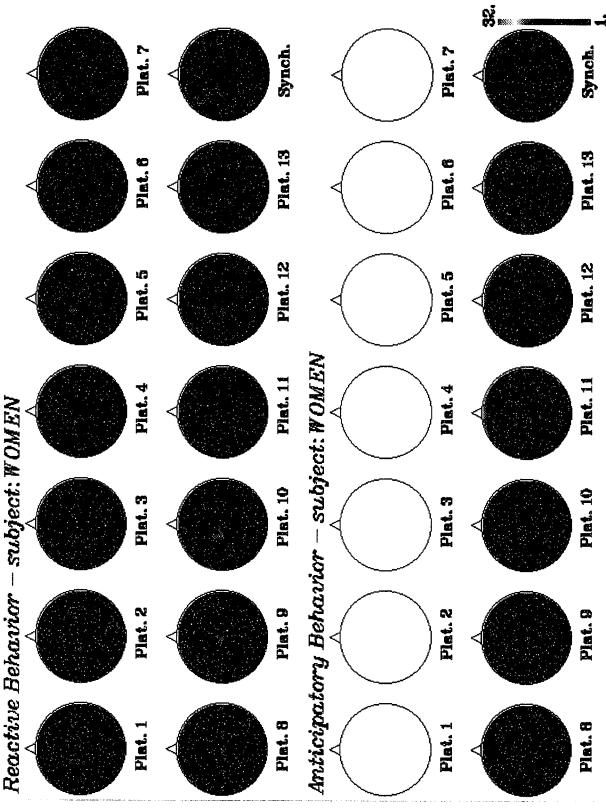


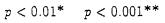
Figure 6 (d)

Further posthoc analyses were employed to investigate differences as a function of sex and behavioral mode. Prior to statistical analysis, the data were averaged across plateau. A three-way ANOVA comparing sex (2) by behavioral mode (2) by electrode location (61) resulted in a significant three-way interaction, F(60,976) = 1.49, p < .01. Tests of simple effects due to sex (Scheffé) revealed that significantly (p < .01) different values of spectral power density appeared for men and women at several antero-central and frontal electrodes depending on the behavioral mode (Table 2).

6.7. Spectral power density of the EEG before, during, and after the transition from reactive to anticipatory behavior

The frequency domain analysis of the preceding sections indicated that significantly different spatial patterns of spectral power density arose for reactive versus anticipatory behavior for both men and women. In order to gain a better understanding of which brain regions were differentially involved as one behavioral pattern dynamically changed to another, the spectral power density values obtained from each cycle of each run were aligned at the transition and averaged across runs (see Section 4.1.4 for details). Figure 8a shows the distributions of stimulus frequencies at which the transition cycle occurred for men and women. The averages (see Appendix 4 for the total number of cycles in each topographical map) are presented

Men:	Women:	
Fp1, 12.3*	Fp1, 13.8*	
Fpz, 12.6*	Fpz, 14.9**	
Fp2, 11.9*	Fp2, 14.8**	
aF7, 13.7*	aF7, 14.5*	
aF1, 14.9**	aF1, 12.9*	
aFz, 12.7*	aFz, 13.2*	
aF2, 12.2*	aF2, 14.8**	
aF8, 11.4*	aF8, 12.9*	
F7, 11.7*	F7, 11.3*	
F5, 11.9*		
	F2, 12.3*	
	F4, 11.9*	
	F6, 12.1*	



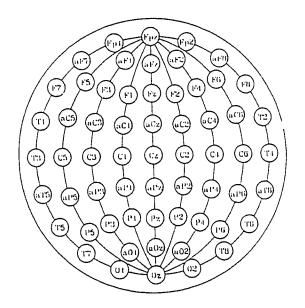


Table 1: F-values from posthoc analysis (Scheffé) testing for differences in EEG spectral power density due to behavioral mode revealed that significantly (p < .01; d.f. = 1, 8) larger values of spectral power density appeared during anticipatory compared to reactive behavior at these electrodes.

in topographical form in Figure 8 for both men (Figure 8b) and women (Figure 8c).

Figure 7: Recording sites where significantly different spectral power density values were observed during reactive versus anticipatory behavior are colored red. The patterns of significant differences are shown as a function of plateau for both men and women.

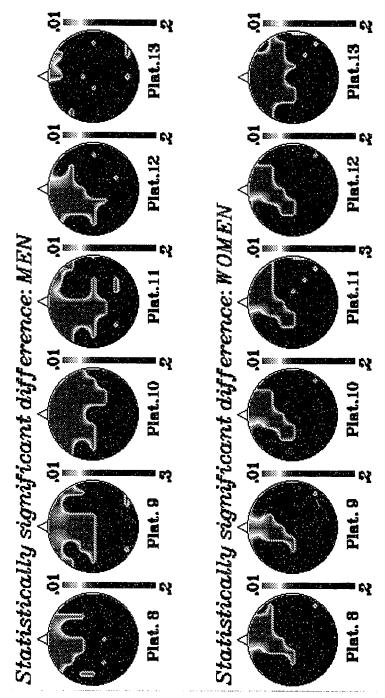
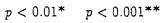


Figure 7

As in the previous section, in order to quantify which groups of electrodes exhibited maximal spectral power density, a grand distribution (across subjects, cycles, and electrodes) was created from the data shown in Figures 8a and 8b. Each value of spectral power density was then converted to a standard Z-score (Section 4.1.4). Electrodes having a Z-score exceeding a threshold corresponding to p < .005 were considered to exhibit significant spectral power density. Using this criterion, men exhibited significant spectral power density at the central recording locations, aC1 and aCz, during reactive behavior (pre-transition) and over a broad region of frontal, antero-central, and central electrode locations including, F7, aF7, aC3, Fp2, and aF8, during anticipatory behavior (post-transition). Women exhibited significant spectral power density at the central and left anterocentral recording locations, F3, aC3, aC1, and Cz, during reactive behavior. Following the transition to anticipatory behavior, women exhibited significant spectral power density as these same sites with additional maxima at the fronto-central electrode locations aF1 and aFz.

In order to compare the topographical patterns of spectral power density before and after the transition, the data from the 5 cycles before the transition cycle were averaged together to form a pre-transition pattern. The same process was performed on the 5 cycles following the transition to derive a post-transition pattern. A three-way ANOVA comparing sex (2) by

Reactive:	Anticipatory:
Fpz, 11.3*	
	aFz, 11.4*
	F5, 11.8*
	F3, 12.1*
	F1, 12.4*
	F4, 11.9*
	aC1, 12.0*
aCz, 12.4*	
C1, 12.1*	1
Cz, 13.2*	



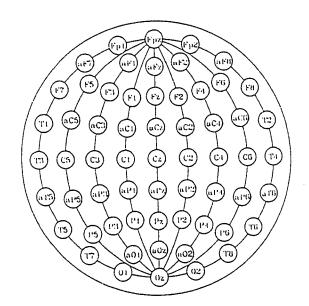
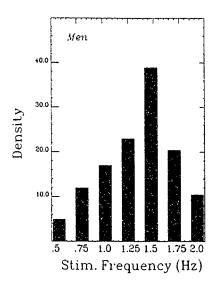


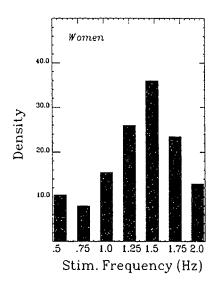
Table 2: F-values from posthoc analysis (Scheffé) testing for differences in EEG spectral power density due to sex revealed that significantly (p < .01; d.f. = 1, 8) different values of spectral power density appeared for men and women at these electrodes depending on the behavioral mode.

behavioral mode (2: pre- versus post-transition) by electrode location (61) resulted in a significant three-way interaction, F(60,976) = 1.53, p < .01. In order to understand this interaction, several posthoc analyses were performed. A test of simple effects (Scheffé) due to behavioral mode revealed significant (p < .01) differences in spectral power density at several left antero-central and frontal electrode locations for men and fronto-central electrode locations for women. These locations are reported in Table 3. The results indicate that spectral energy at frequencies matching the stimulus presentation rate (and movement) changed significantly at these electrode locations as the movement coordination switched from reactive to anticipatory behavior.

A test of simple effects (Scheffé) due to sex indicated significant (p < .01) differences in spectral power density at several left antero-central electrode locations in the pre-transition patterns and several frontal locations in the post-transition patterns. These results are reported by electrode location and behavioral mode in Table 4 and indicate that men and women show significantly different spectral energy at frequencies matching the stimulus presentation rate both before and after the transition from reactive to anticipatory coordination.

Figure 8: (a) The distributions of stimulus frequencies at which the transition cycle occurred for men and women. The topographical maps of spectral power density (grand average across subjects) for (b) men and (c) women aligned at the transition cycle (Tc: 0). Five cycles before and after the transition cycle are shown. The same maps are reproduced on a uniform scale in d and e.





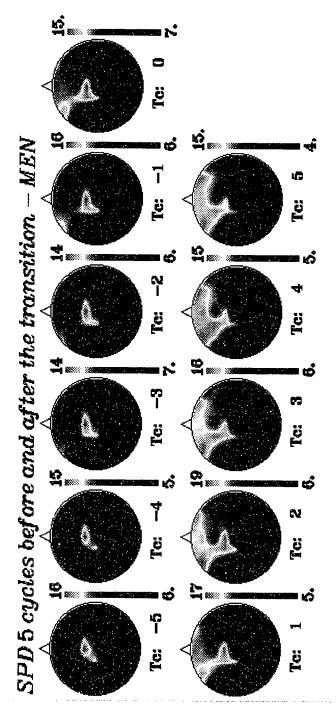


Figure 8 (b)

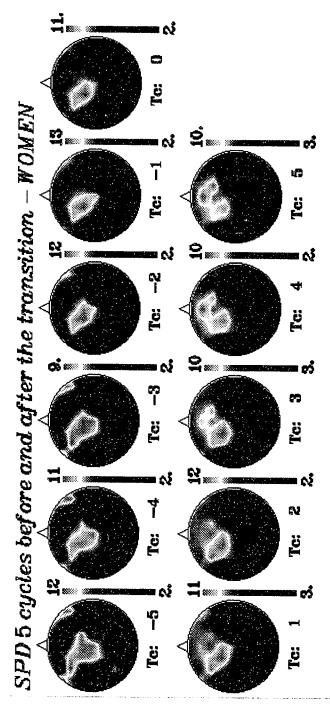


Figure 8 (c)

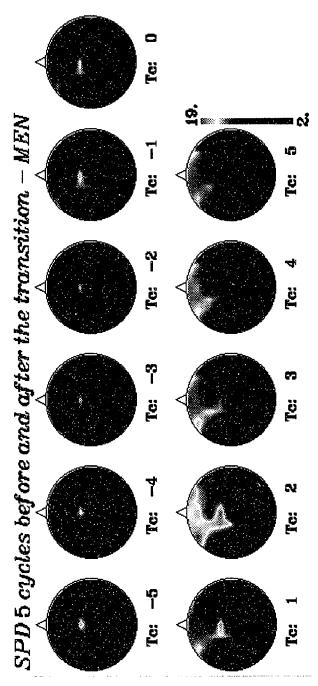
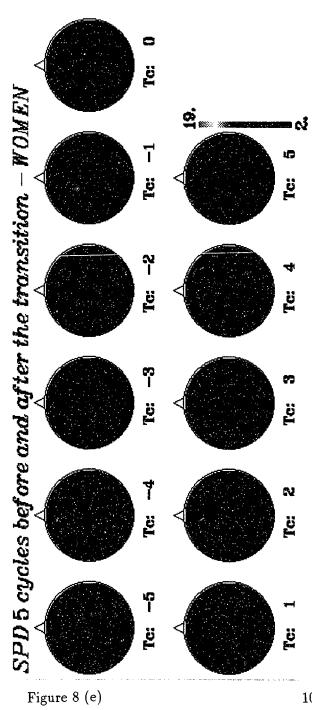


Figure 8 (d)

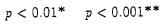


6.8. Fluctuations in spectral power density of the EEG before, during, and after the transition from reactive to anticipatory behavior

In order to determine how EEG spectral power density fluctuated before, during, and after the behavioral transition from reactive to anticipatory coordination, the standard deviation of this measure was computed over runs for transition-aligned cycles as for the mean outlined in the preceding section (also see Section 4.1.4 for further details) for five cycles immediately preceding and following the transition cycle. The analysis was restricted to five cycles on either side of the transition because previous work has indicated that the transition-aligned EEG averages become substantially smeared much beyond this limit (Wallenstein et al., 1995a). The topographical distributions of these values are displayed in Figure 9.

In order to quantify which groups of electrodes exhibited significant fluctuations in spectral power density as measured by the standard deviation of these values, a grand distribution (across subjects, cycles, and electrodes) was created from the data shown in Figures 9a and 9b. Each standard deviation in spectral power density was then converted to a standard Z-score (Section 4.1.4). Electrodes having a Z-score exceeding a threshold corresponding to p < .005 were considered to exhibit significant fluctuations in spectral power density. Using this criterion, men exhibited significant

Men:	Women:	
Fp1, 14.9**		
Fpz, 14.8**		
Fp2, 13.8*		
aF7, 15.1**		
aF1, 15.0**	aF1, 14.9**	
aFz, 14.4*	aFz, 15.0**	
aF2, 14.9**	aF2, 14.8**	
aF8, 12.7*		
F7, 15.0**		
F5, 12.4*		
F3, 11.9*		
F1, 12.5*	F1, 11.4*	
Fz, 12.6*	Fz, 12.1*	
	F2, 12.3*	
F4, 12.0*		
F6, 11.9*		
	i lada	



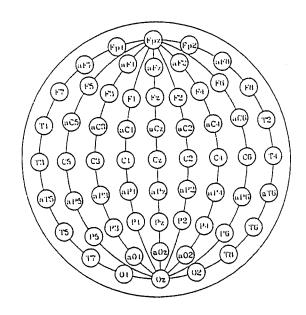
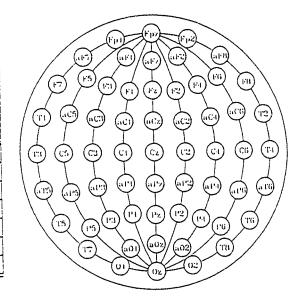


Table 3: F-values from posthoc analysis (Scheffé) testing for differences in EEG spectral power density due to behavioral mode (pre- and post-transition) revealed significant (p < .01; d.f. = 1, 8) differences in spectral power density at several left antero-central and frontal electrode locations for men and fronto-central electrode locations for women.

Pre-transition:	Post-transition:
	Fp1, 14.0*
	Fpz, 14.2*
	Fp2, 13.9*
	aF7, 14.4*
F1, 11.5*	
	aF8, 11.8*
	F7, 12.0*
F5, 13.6*	ļ
F3, 13.8*	
	F6, 11.4*
aC3, 13.2*	
aC5, 13.3*	



p < 0.01*

Table 4: F-values from posthoc analysis (Scheffé) testing for differences due to sex indicated significant (p < .01; d.f. = 1, 8) differences in spectral power density at several left antero-central electrode locations in the pre-transition patterns and several frontal locations in the post-transition patterns.

fluctuations in spectral power density at the frontal, left central, and left antero-central recording locations, aF7, F3, aC3, C3, and aP3 in the cycle immediately preceding the transition (Tc: -1) and at electrodes aC3 and C3 in cycle Tc: -2. Women exhibited significant fluctuations in spectral power density at the left antero-central electrode locations, aC1, aCz, C3, C1, and Cz, in the cycle immediately preceding the transition (Tc: -1) and at aC1 in cycle Tc: -2.

A three-way ANOVA comparing sex (2) by cycle (11) by electrode location (61) resulted in a significant three-way interaction, F(600, 5368) = 1.01, p < .05. In order to further investigate this interaction, posthoc analyses were performed by separating the data by sex. A two-way ANOVA comparing cycle (11) by electrode location (61) resulted in a significant two-way interaction for both men, F(600, 2684) = 1.25, p < .003 and women, F(600, 2684) = 1.19, p < .01. A test of simple effects (pair-wise comparisons of each successive cycle) revealed several electrodes in left antero-central and bilateral frontal locations (aF7, Fp2, aC3, C3 and aP3) for men and left antero-central and right frontal locations (F4, aC1, aCz, C3, C1 and Cz) for women which exhibited a significant increase in the standard deviation of spectral power density only in the cycle immediately preceding the transition cycle (Tc: -1). These results indicate that fluctuations in spectral power density increased just prior to a change in behavioral coordination.

This finding of "fluctuation enhancement" suggests that spectral power density is a relevant, task-specific collective variable (order parameter) in the brain (Kelso, 1995). It is interesting to note that although the physical instantiation of the observables is quite different when comparing the behavioral and brain signals, the dynamics governing the pattern change have similar stability properties.

Figure 9: The topographical maps of the standard deviation in spectral power density (across all subjects) for (a) men and (b) women aligned at the transition cycle (Tc: 0). Five cycles before and after the transition cycle are shown.

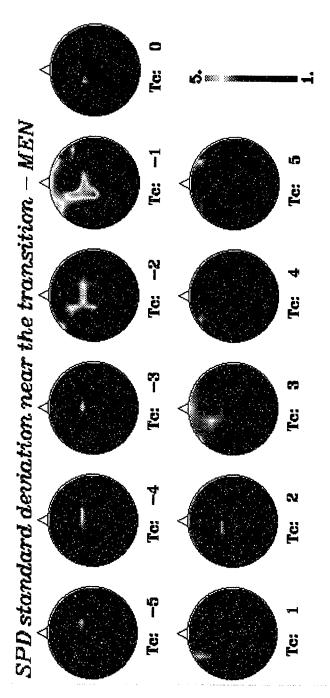


Figure 9 (a)

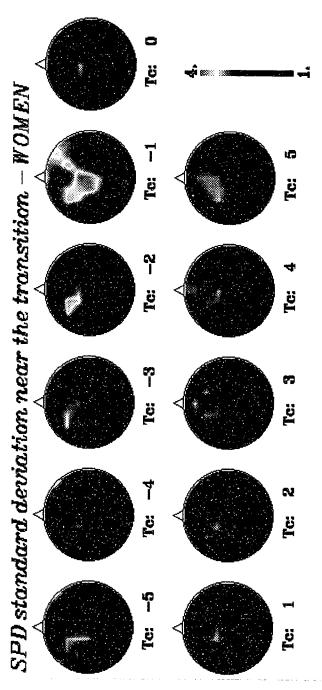


Figure 9 (b)

6.9. The synchronize control condition

The SYNCHRONIZE control condition was performed by subjects at a single frequency of 2.5 Hz for comparison with data from the REAC-TIVE condition at the same frequency (plateau 13). The data from this condition were treated as from the REACTIVE condition. The spectral power density was computed for each cycle of each run and sorted into reactive and anticipatory behaviors (see Figure 3) using the same criteria as outlined in Section 4.1.4. Topographical maps were then derived from the averaged power at the frequency matching the stimulus presentation rate. These maps are shown in Figure 6 for both men (Figure 6a) and women (Figure 6b). In order to determine if the REACTIVE and SYNCHRONIZE conditions differed, a series of statistical analyses were performed.

A four-way ANOVA comparing sex (2) by condition (2 - REACTIVE versus SYNCHRONIZE) by behavioral mode (2) by electrode location (61) resulted in a significant four-way interaction, F(60, 1952) = 1.36, p < .05. Several posthoc analyses were used to further investigate the interaction. A test of simple effects (Scheffé) due to behavioral mode (reactive versus anticipatory) revealed that significantly larger values of spectral power density appeared during reactive than anticipatory behavior within the SYNCHRONIZE condition at three frontal electrodes for women (Fp2, aF8 and aF2). No significant differences were found within the SYNCHRONIZE

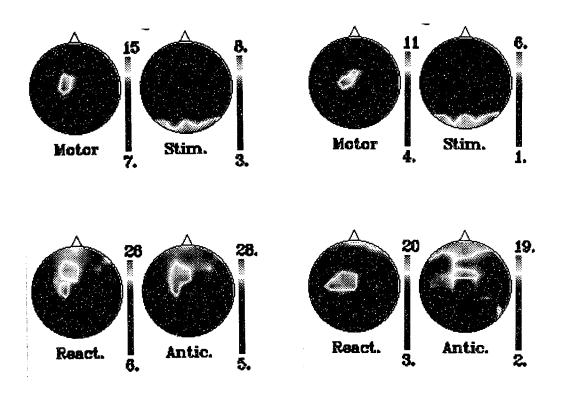


Figure 10: The topographical maps of spectral power density for the MOTOR-ONLY, STIMULUS-ONLY, and SYNCHRONIZE control conditions for (a) men and (b) women.

MEN:		
Reactive behavior:	MOTOR-ONLY	STIMULUS-ONLY
Plateau 8:	.63*	.10
Plateau 9:	.59*	.08
Plateau 10:	.64*	.09
Plateau 11:	.68*	.07
Plateau 12:	.72*	.11
Plateau 13:	.61*	.10
Anticipatory behavior:		
Plateau 3:	.32*	.08
Plateau 9:	.37*	.07
Plateau 10:	.31*	.12
Plateau 11:	.39*	.08
Plateau 12:	.37*	.06
Plateau 13:	.31*	.07

WOMEN:		
Reactive behavior:	MOTOR-ONLY	STIMULUS-ONLY
Plateau 3:	.67*	.10
Plateau 9:	.71*	.09
Plateau 10:	.74*	.08
Plateau 11:	.69*	.08
Plateau 12:	.75*	.10
Plateau 13:	.73*	.07
Anticipatory behavior:		<u> </u>
Plateau 3:	.30*	.04
Plateau 9:	.36*	.11
Plateau 10:	.28*	.09
Plateau 11:	.31*	.05
Plateau 12:	.17	.05
Plateau 13:	.21	.08

Table 5: Values of the grand average (across subjects) correlation (r^2) between the topographical maps shown in Figure 6 (plateaus 8 - 13) and those from the STIMULUS-ONLY and MOTOR-ONLY control conditions shown in Figure 10. Similarity was measured using Eq. (1) (Section 4.1.4). A perfect match would result in a similarity value of 1.0, while no similarity between two patterns would result in a value of 0.0.

condition for men. However, a main effect for condition was found for men, F(1,8) = 12.47, p < .01. Spectral power density was found to be larger for men during the SYNCHRONIZE condition than in the REACTIVE condition. This was true regardless of behavioral mode and electrode. No significant differences were found between the SYNCHRONIZE and REACTIVE conditions for women.

6.10. Similarity of spectral power density patterns from the REACTIVE condition to the STIMULUS-ONLY and MOTOR-ONLY control conditions

The spectral power density was calculated for both the STIMULUS-ONLY and MOTOR-ONLY control conditions (Section 4.1.4) in order to compare them with the patterns derived from the primary experimental condition (REACTIVE). Figure 10 shows topographical maps of the spectral power density calculated at the stimulus frequency (1.0 Hz) for the STIMULUS-ONLY control condition and the movement frequency for the self-paced MOTOR-ONLY control condition.

In order to quantify which groups of electrodes exhibited significant spectral power density, a grand distribution (across subjects, conditions, and electrodes) was created from the data shown in Figures 10a and 10b. Each spectral power density value was then converted to a standard Z-score (Section 4.1.4). Electrodes having a Z-score exceeding a threshold corre-

sponding to p < .005 were considered to exhibit significant spectral power density. Using this criterion, both men and women exhibited significant spectral power density at the electrode locations, aC1, aC3, C1, and C3, during the MOTOR-ONLY control condition and at electrode locations, T7, O1, Oz, aOz, and T8, during the STIMULUS-ONLY control condition. A series of statistical analyses were employed to answer two questions. First, are there differences between men and women in these two control conditions? Second, how similar are the spectral power density patterns from these two control conditions to the patterns observed during the REAC-TIVE condition?

A three-way ANOVA comparing sex (2) by control condition (2) by electrode (61) resulted in a significant main effect for sex, F(1,8) = 14.92, p < .01, indicating men exhibited larger spectral power density values than women in both conditions. A significant main effect was also found for condition, F(1,8) = 8.1, p < .03, indicating the spectral power density patterns were different during the STIMULUS- and MOTOR-ONLY control conditions.

In order to determine how similar the two patterns observed from the control conditions were to those seen in the REACTIVE condition (Figure 6), correlations between every possible pair were derived using equation 1 from Section 4.1.4. That is, for each subject, the STIMULUS-ONLY pat-

tern was correlated with the patterns obtained during reactive behavior from plateaus 8 through 13 and also with the patterns observed during anticipatory behavior from these plateaus. The same procedure was repeated with the pattern obtained from the MOTOR-ONLY control condition. This resulted in a data set consisting of 24 values per subject. Table 5 shows the grand average across subjects of these correlation (r^2) values.

A series of significance tests (p < .01) were performed on the correlation values (Section 4.1.4). First, a test of no correlation was performed using the standard Z-transformation. That is, did the r^2 values significantly depart from 0.0? The r^2 values which were found to significantly depart from 0.0 are indicated in Table 5 with an asterisk. Note that the MOTOR-ONLY control pattern, but not the STIMULUS-ONLY control pattern, was found to be significantly correlated with the REACTIVE condition patterns. Next, a test of a perfect correlation was performed investigating whether or not the correlations significantly departed from 1.0. Every correlation value listed in Table 5 was found to significantly depart from 1.0, indicating that the REACTIVE condition patterns could not be explained as resulting from either a simple motor or sensory event. Furthermore, since the STIMULUS-ONLY patterns were not significantly correlated with either behavioral mode pattern, the latter could also not be explained as resulting from a combination of simple motor and sensory events.

Finally, tests were performed within the MOTOR-ONLY correlation values. First, a comparison was made to test whether the correlations from the MOTOR-ONLY control condition from men were significantly different from women for both reactive and anticipatory behavior. That is, each correlation value from men was tested against the corresponding correlation value from women in the same behavioral mode. A consistent pattern of no significant differences was found between the sexes.

A similar series of comparisons was then performed to test whether correlations with the MOTOR-ONLY control condition differed significantly between behavioral modes (reactive versus anticipatory) within sex. Significant differences in the correlation values were found between reactive and anticipatory behaviors (with respect to correlations with the MOTOR-ONLY control condition) in every plateau (8-13) for women and all but the ninth for men. These results suggest that the motor-related component of the EEG contributed more to the spectral power density patterns obtained during reactive than anticipatory behavior in the REACTIVE condition. In general, the stimulus-related components did not contribute to the patterns from either type of behavior to a significant degree (Table 5).

7. Discussion

Are there quantities one can observe in the human brain which are related to the timing characteristics of on-going behavior? We have recorded whole-head EEGs during a sensorimotor task in which subjects are known to exhibit spontaneous transitions from one behavioral coordination mode to another (Engström et al., 1995). This approach stands in contrast to the more traditional experimental procedure of examining different classes of stable behavior in isolation. For instance, each behavioral mode, reactive and anticipatory coordination, might have been studied separately under stable conditions. In this scenario, an attempt may have been made to correlate the corresponding brain patterns with the accompanying behavior and make some inferences regarding how one pattern is related to the other. However, in such an approach, no information is attained about the dynamical evolution of one stable pattern to the other. No information about the instability is recorded, therefore one does not obtain an understanding of the neural mechanisms promoting the change in coordination.

A naive interpretation one might advance based on looking at the different behavioral modes in isolation is one in which the coordination patterns are thought of as being completely independent and can be combined in a linear way to form more complex behaviors. Indeed, this philosophy seems prevalent in the brain imaging literature and is exemplified in the "subtrac-

tive" methods used in PET and SPECT recording. This strategy rests on the assumption that one can subtract the brain pattern obtained during one condition (A) from the pattern obtained during a combined condition (A and B) and result in an image which is related solely to the remaining condition (B). By analogy, one should be able to fully characterize a task involving behavioral coordination with an external stimulus by superimposing the two patterns associated with the sensory and motor events in isolation. As has been demonstrated in the preceding sections, our results from the REACTIVE condition are not accounted for by either the STIMULUS-ONLY or MOTOR-ONLY pattern or by a combination of the two (see also Fuchs et al., 1992). Several features in the spatiotemporal scalp-recorded EEG, which we discuss below, were found to relate to changes in the relative timing between the stimulus and movement. Additionally, quantities were derived from both the behavioral and neural levels of observation which were found to share a common dynamic property known as fluctuation enhancement, a predicted feature often associated with pattern instabilities in physical systems (Haken, 1983; Kelso, 1995). We now discuss the novel conclusions of the study and their implications for understanding temporal integration in the human brain and behavior.

7.1. Brain activity patterns associated with reactive and anticipatory behavior

At relatively slow stimulus presentation rates (i.e. below .75 - 1.0 Hz), reactive behavior prevailed. During reactive behavior, the spectral power density calculated at the frequency matching the stimulus presentation rate exhibited maximal activity over central and antero-central locations. Typically, subjects exhibited a spontaneous transition from reactive to anticipative behavior as they reached faster stimulus presentation rates. This transition was accompanied by an additional spectral power density component with maxima situated over frontal brain locations.

In order to determine if the frontal activity was related to the change in sensorimotor coordination timing rather than the stimulus presentation rate, the data were sorted into reactive and anticipatory behavioral modes based on values of τ as shown in Figure 6 and outlined in Section 4.1.4. A series of statistical analyses confirmed that the increase in frontal activity was present in each plateau where anticipatory behavior was exhibited. This can be seen clearly in Figure 6 which shows that similar topographical patterns of spectral power density arise across plateaus within a given coordination mode (reactive or anticipatory) and that frontal activity patterns appear predominantly during anticipatory coordination (Table 1 and 2). Thus the following conclusions can be drawn: (1) during reactive behavior maximal

spectral power density resides at central and antero-central scalp locations believed to be situated over primary and premotor areas; and (2) during anticipatory behavior, an additional frontal component arises - different brain activity patterns arise for different modes of coordination timing.

These results support the concept of frontal involvement in temporal integration since the anticipatory state requires the temporal control of behavior not present in the reactive state (Fuster, 1989). Subjects were instructed to flex their right index finger as soon as possible following the presentation of the visual stimulus. At the slowest stimulus presentation rates, subjects were not able to anticipate the stimulus and consequently waited for its appearance and responded accordingly. Thus scalp activity believed to be over primary and premotor cortices dominated. At faster stimulus presentation rates (e.g. greater than approximately .75 - 1.0 Hz) subjects were able to anticipate the next stimulus and they automatically established a rhythm despite instructions to respond following its appearance. It seems the internalization of this timing information is related to an increase in anterior activity over frontal areas.

There is a growing body of experimental work in primates which supports the notion of frontal involvement in temporal control. Several groups have demonstrated that primates with frontal ablations, particularly those involving the dorsolateral convexity, fail to perform tasks involving time estimation (Mishkin, 1964; Pribram et al., 1977; Skeen and Masterton, 1982; Passingham, 1985). A number of studies have also investigated single-unit activity in relation to time estimation tasks such as the classic enforced delay paradigm (Kubota et al., 1974; Niki, 1974; Fuster, 1989). One group of cells has been found to fire in a sustained fashion during the interval between two events that must be bridged in time. These units maintain an increased firing rate even if the temporal interval between events is lengthened to one minute or longer and have been found to be more prevalent in the anterior portion of the frontal lobe than any other cerebral area (Fuster, 1973). Taken together, these observations have led some researchers to speculate that the anterior portion of the frontal lobe plays a direct role in sensorimotor integration tasks where a cross-temporal contingency must be internalized (Goldman-Rakic, 1987; Fuster, 1989).

7.2. Spontaneous transitions from reaction to anticipation: Fluctuation enhancement in behavior

In the main experimental condition (REACTIVE), subjects were asked to flex their right index finger following the appearance of a visual stimulus presented periodically. We emphasized to the subjects that they should try to provide one finger flexion for each stimulus (i.e. maintain a 1:1 behavioral relationship with the stimuli). Even though subjects were asked to show a movement following the stimulus, typically, as the stimulus presentation

rate increased, a critical frequency was reached at which time the subject began to produce anticipatory behavior (i.e. finger flexions which were time-locked to or preceded the stimulus). This transition from reactive to anticipatory behavior was quantified by calculating the time $\log(\tau)$ between the stimulus and finger flexion onset (Figures 3 and 4). The frequency at which subjects switched from one coordination mode to the other generally varied both within and between subjects. This reaction to anticipation transition in sensorimotor behavior replicates a recent behavioral study by Engström et al. (1995).

By aligning the data at the transition cycle and calculating the standard deviations in time lag for each cycle across runs, we were able to show that fluctuations in τ increased (on average) in the cycle immediately preceding the transition from reactive to anticipatory behavior. This result suggests that the relative timing in these behavioral modes is an important coordination variable and that the change from one pattern to the other is due to an instability. It is known from both experimental and theoretical work in the area of Synergetics (Section 2) that physical systems which undergo abrupt changes from one stable state to another often exhibit fluctuation enhancement just prior to the transition (see Haken, 1983 for a review). Dynamic instabilities in the brain, however, have only been observed recently (Kelso et al., 1991; 1992; Fuchs et al., 1992; Wallenstein et al., 1995a). Their ap-

pearance suggests that the switch from reactive to anticipatory coordination observed in the present experiment shares common dynamic features with a broad class of behavioral and physical phenomena previously characterized as displaying nonlinear phase transitions (Section 2).

7.3. Fluctuation enhancement in EEG spectral power density patterns immediately prior to reaction to anticipation transitions

The EEG spectral power density patterns changed abruptly at the transition from reactive to anticipatory movement coordination. Both men and women exhibited maximal spectral power density over left antero-central electrode locations prior to the transition. Men showed an additional maximal spectral power density component over a broad frontal region following the transition, while women showed a more confined region over fronto-central locations (Figure 8, Tables 3 and 4). These results are consistent with the idea that frontal brain regions are involved in the temporal control of movement where a rhythm must be sustained (Goldman-Rakic, 1987). In our experiment, the same digit was moved with qualitatively similar motions whether the subject produced reactive or anticipatory behavior. Thus the spectral power density pattern change exhibited at the transition seems related to the change in temporal coordination, rather than being directly associated with different muscular or kinematic demands per se.

Fluctuation enhancement was found in the sensorimotor coordination time lag values at the cycle just preceding the transition cycle (Figure 4). The EEG spectral values were aligned at the transition cycle in each run and the standard deviation was obtained (Section 4.1.4). A pair-wise analysis (by cycle, within electrode) of the spectral power indicated that the standard deviation increased for several electrode locations (Figure 9) during the two cycles immediately preceding the transition cycle. This result demonstrates fluctuation enhancement in the EEG just prior to the transition from reactive to anticipatory coordination timing and is consistent with recent experiments employing a similar sensorimotor task (Kelso et al., 1991; 1992 and Fuchs et al., 1992 demonstrated fluctuation enhancement in MEG signals; Wallenstein et al., 1995a in EEG signals during a sensorimotor phase transition). This finding in conjunction with those mentioned above suggests that reactive and anticipatory coordination are accompanied by qualitatively different brain activity patterns and the transition between these patterns is accompanied by fluctuation enhancement, similar to what was shown in the coordination movement data. Thus the manner in which EEG patterns change in this experiment from one to another resemble the classic order-order phase transition phenomena consistent with numerous physical systems which exhibit similar state changes (see Kelso, 1995 for a review). In the case of brain and behavior comparisons, of course, we had to identify the relevant quantities that constitute candidate 'state' variables.

7.4. EEG spectral density patterns appeared similar for men and women during reactive behavior but different during anticipatory behavior

As was shown in Figure 8, it is apparent that men and women exhibit different spectral power density patterns during anticipatory behavior. Men exhibit, on average, a broad, bilaterally distributed frontal component at the most anterior portion of the scalp, while women exhibit a more confined component over fronto-central locations (Tables 3 and 4). This finding is interesting given what is presently known about sex differences in brain function, particularly with regard to frontal regions.

Traditionally, it has been suggested that there is a certain degree of functional asymmetry in the frontal cortex, with the left and right sides being implicated in the control of internally and externally ordered events respectively (Milner and Petrides, 1984; Goldberg et al., 1994). Indeed, lateralized damage to left prefrontal areas has been shown to produce perseveration in delay tasks or extreme environmental dependencies, while right prefrontal damage can induce deficits in short term memory and motor planning (see Fuster, 1989 for a review). Asymmetries also exist in frontal brain morphology which depend on sex and handedness (Bear et al., 1986). Structurally, the right frontal area is typically wider and extends farther anteriorly than

the left and this asymmetry is more pronounced in men than women (Bear et al., 1986). However, the functional significance of this morphological asymmetry is unclear at present.

Many studies investigating functional asymmetry in the cerebral cortex have focused on language. For example, a recent study employing a phonological task in which subjects judged whether two nonsense words rhymed, demonstrated greater asymmetry of brain activation (as measured by magnetic resonance signal intensity) in males than females. Males exhibited brain activation patterns where the left inferior frontal gyrus region dominated. Females showed a broader region of activity in both left and right frontal regions (Shaywitz et al., 1995). This result differs from the patterns of brain activation shown in the present study which demonstrates a broader distribution of frontal spectral energy in men rather than women. We posit that the difference may be related to the paradigms used and that additional experiments which focus on the temporal aspects of language production and perception rather than static comparisons, may reveal findings more consistent with those shown above. However, the differences may also be due to the fact that Shaywitz et al. (1995) used a task involving phonological information. Thus, for the present experiment, the differences in brain activation patterns with respect to sex appear most consistent with past anatomical and morphological observations (Bear et al., 1986). Further experimentation will be needed to explore how timing in movement and language production are related neurophysiologically. Indeed, as this experiment has illustrated, certain behaviors reveal functional asymmetries between the sexes more than others. A clearer disparity between spectral power density patterns as a function of sex was found during anticipatory as compared to reactive behavior.

7.5. EEG spectral power density patterns associated with reactive and anticipatory behavior within the SYNCHRONIZE condition

Although subjects were instructed to synchronize peak finger flexion with the visual stimulus during the SYNCHRONIZE control condition, a distribution of time lag values resulted (Figure 3) so the data was grouped into reactive and anticipatory behavior using the same criteria that was employed in the REACTIVE condition.

The time lag distribution from the SYNCHRONIZE condition is similar in appearance to the highest frequency plateaus in the REACTIVE condition. This broad distribution during SYNCHRONIZE suggests many synchronization errors. These errors may come from two different sources. One factor that may have contributed to this variation is the stimulus modality. Evoked potential studies have shown that visual stimuli generally produce slower cortical responses (e.g. N100 component) and greater latency variation variation is the stimulus modality.

ability than auditory stimuli (Nunez, 1981). This may have translated into an increase in variability in the motor responses as compared to what would have been the case if auditory stimuli were used. However, a second possible explanation for the relatively broad time lag distributions is the fact that they are averaged across subjects. Indeed, the mean of the individual subject standard deviations of the time lag distributions is 161 milliseconds, while the standard deviation around the group mean is 183 milliseconds. This suggests that some of the variability in the group mean time lag distributions during SYNCHRONIZE and possibly during the later plateaus in the REACTIVE condition are due to individual differences.

The patterns of spectral power density associated with this condition resembled those during the REACTIVE condition at the same stimulus frequency (Figure 6). Statistical analysis showed that women exhibited larger spectral power density values during reactive behavior compared with anticipatory behavior within the SYNCHRONIZE condition at three frontal electrodes (Fp2, aF8 and aF2). By comparison, no significant differences were found for the men within the SYNCHRONIZE condition. When the SYNCHRONIZE condition was compared with the REACTIVE condition, men exhibited greater spectral power density at all electrodes in the former, while no significant differences were found for women. This pattern of sex differences suggests that a single condition grouped into separate be-

havioral classes is sufficient to highlight some differences between men and women. For instance, men exhibited significantly larger spectral power density at all electrodes during anticipatory behavior in the SYNCHRONIZE condition when compared to the REACTIVE condition. Contrasting this, women showed no significant differences between the two conditions during anticipatory behavior. This is an intriguing effect since the sensorimotor timing was similar across the two conditions (only the subject instructions differed), and one may have predicted that similar spectral power density patterns may arise as was the case with the women. However, men showed a broad enhancement of power at the frequency component matching the stimulus presentation rate during the SYNCHRONIZE condition. This suggests that similar behavior does not neccesarily correspond to similar brain activity patterns in a one-to-one manner. This disparity suggests that the context in which the behavior evolves is apparently a critical factor in determing the relative contribution of frontal and primary motor areas during anticipatory behavior.

7.6. Comparison of EEG spectral power density patterns from the MOTOR-ONLY and STIMULUS-ONLY control conditions with the REACTIVE condition

A comparison of the topographical patterns of spectral power density obtained during the primary experimental condition (REACTIVE) sepa-

rated by behavioral mode (Figure 6) was made with those obtained from the STIMULUS-ONLY and MOTOR-ONLY control conditions (Figure 10) using equation 1 (Section 4.1.4 and Table 5). The highest degree of similarity was found between the topographical patterns of spectral power density obtained during reactive behavior within the REACTIVE condition with the patterns obtained during the MOTOR-ONLY control condition. One may question why there should be any substantial differences in these patterns at all. A possible reason may be found in the subtle difference between the conditions. In the REACTIVE condition, there is a combined visual, sensorimotor task in which a degree of premotor activation might be expected in comparison with the self-paced movements which would tend to predominantly activate the primary motor cortices. A visual comparison of the topographical maps from Figures 6 and 10 suggest that significant spectral power density observed during reactive behavior in the REACTIVE condition extended further posteriorly and medially when compared with the MOTOR-ONLY control condition. This pattern of results is consistent with the notion of increased premotor, and possible supplementary motor area, activation during reactive behavior in the REACTIVE condition.

The spectral power density pattern obtained from the STIMULUS-ONLY condition consistently showed non-significant similarity values with patterns from the REACTIVE condition, suggesting that the contribution of the

LED flash to the overall pattern of spectral power density obtained in the experimental condition was small (Table 5). Neither reactive nor anticipatory behavior could be completely accounted for by the spectral power density patterns observed during the MOTOR-ONLY or STIMULUS-ONLY control conditions or by a combination of the two. Therefore, neither behavioral mode can be explained as resulting from a linear superposition of simple sensory- and motor-related events. These results are consistent with a recent experiment using a similar sensorimotor task with auditory stimuli (Wallenstein et al., 1995a; see also Fuchs et al., 1992).

7.7. Conclusions and implications for future research

To a large extent, the difference between reactive and anticipatory behavior is the control of timing. In the present experiment, the movement kinematics were virtually the same whether subjects were performing reactive or anticipatory coordination (Figure 2a), however, the brain activity patterns observed during these behaviors were significantly different. During reactive behavior, peak brain activity was situated over regions believed to be primary and premotor cortices, which shared some similarity with the MOTOR-ONLY control condition pattern (Table 5). Once the subject was able to internalize the rhythmic nature of the stimuli and anticipate their appearance, activity over frontal brain regions increased. Thus, it seems this additional frontal component is the manifestation of a neural control

process that adapts to the timing aspects of coordination rather than being related to any parametric properties of the movement itself.

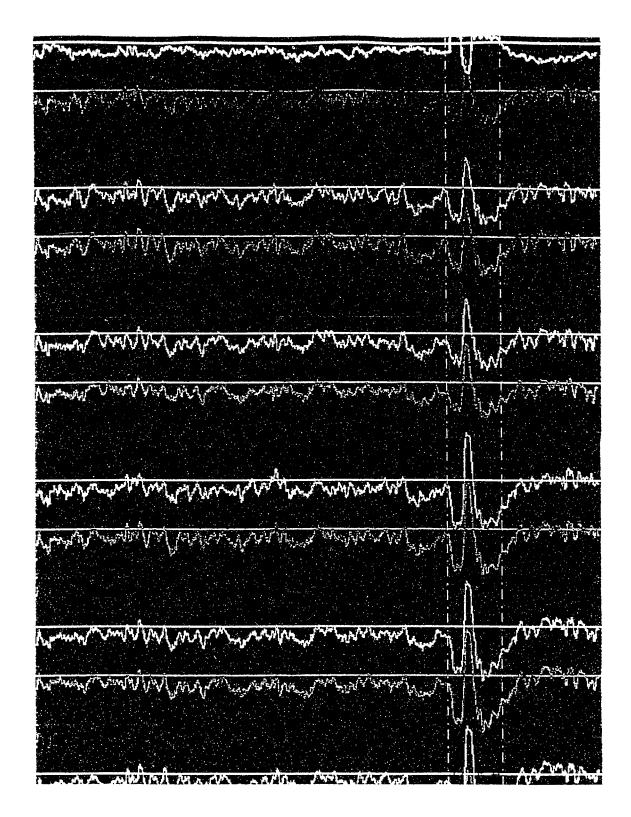
Of further interest is the observation that men and women showed similar brain activity patterns during reactive behavior, but different frontal spectral power density patterns during anticipatory coordination. Men exhibited a broad, bilateral component at the most anterior portion of the scalp, while women displayed a more topographically restricted component situated over fronto-central regions. This suggests that experiments should be designed which tend to emphasize frontal area involvement if sex differences in brain function are of interest. Indeed, the study of temporal integration in the nervous system, how the brain comes to internalize rhythms, will undoubtedly reveal insights into how humans carry out an assortment of cognitive tasks relying on this fundamental theme, such as language production and perception, sensorimotor integration, and perhaps learning and memory.

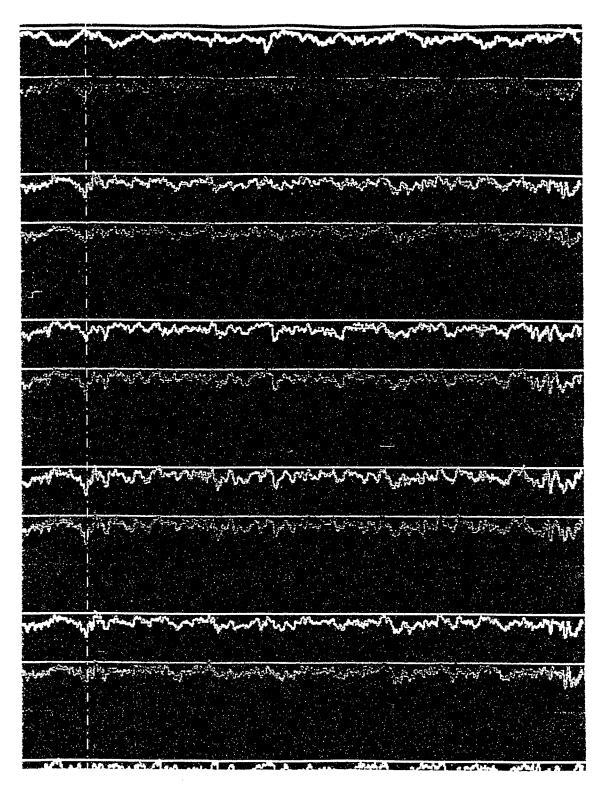
The paradigm employed here was ideally suited toward the study of timing in the central nervous system because it revealed how changes in coordination timing were related to the differential involvement of sensory, motor and frontal brain areas. Furthermore, it shed light on the underlying dynamics supporting the observed movement and brain activity patterns and their mechanisms of stabilization and change. It was shown that a

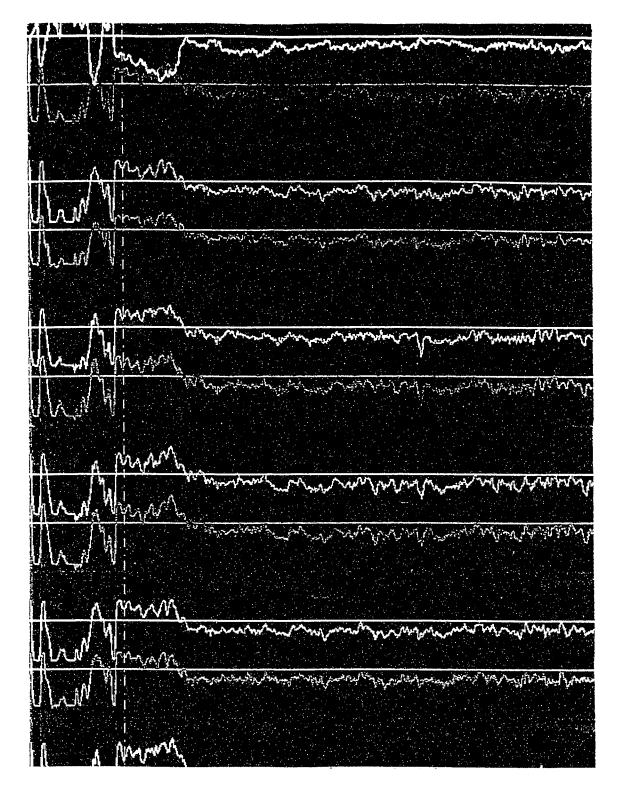
transition in sensorimotor timing was associated with a spatial (structural) and temporal transition in underlying brain activity. Just as the relative timing was found to be an important variable in characterizing the behavioral dynamics during sensorimotor coordination, investigation of the brain activity patterns accompanying this task revealed that spectral power density could be used as an order parameter on the neural level of observation. The spatial distribution of spectral power density changed abruptly at the transition from reactive to anticipatory behavior and also exhibited fluctuation enhancement preceding the switch between patterns. This dynamical effect was observable by utilizing a paradigm which focuses on studying instabilities in patterns rather than concentrating only on stable behaviors in isolation from each other (Kelso, 1995). Such experimentation brings the study of behavior and brain function a little closer.

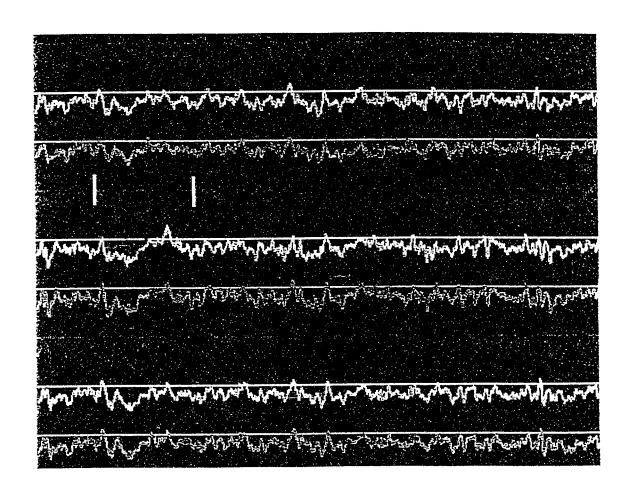
8. Appendix 1 - Artifact rejection

All EEG records were visually inspected for eye, head, orofacial, and body movement artifacts and deleted from the records before additional analysis. Below are some examples of the types of artifacts encountered during the procedure. These include a sample eye blink, a slower eye movement, a body movement artifact, and a single bad channel.





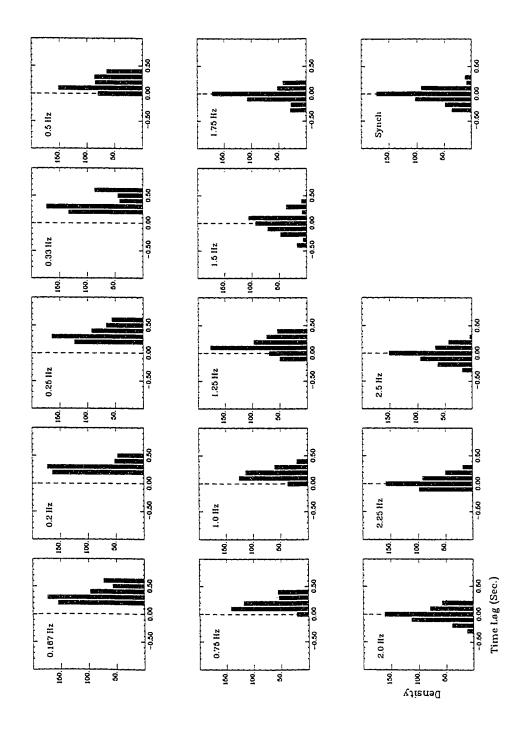


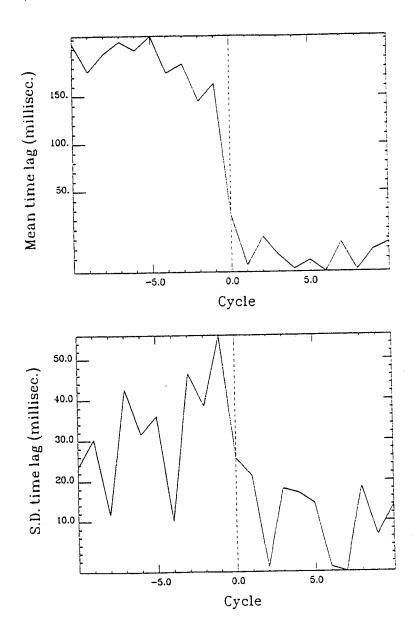


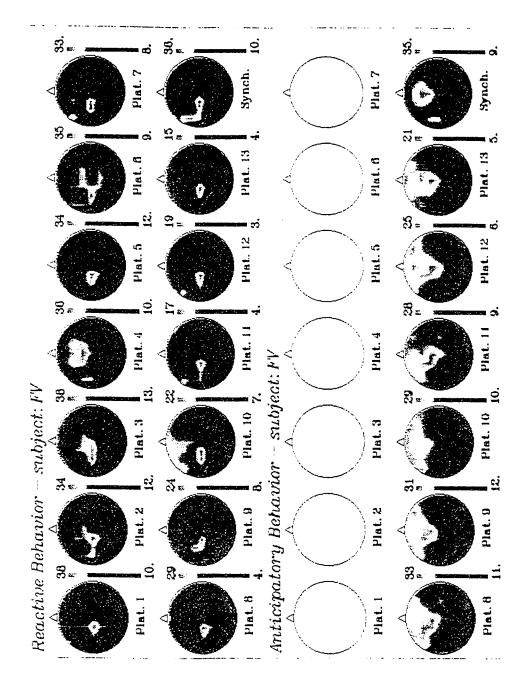
9. Appendix 2 - Individual subject data

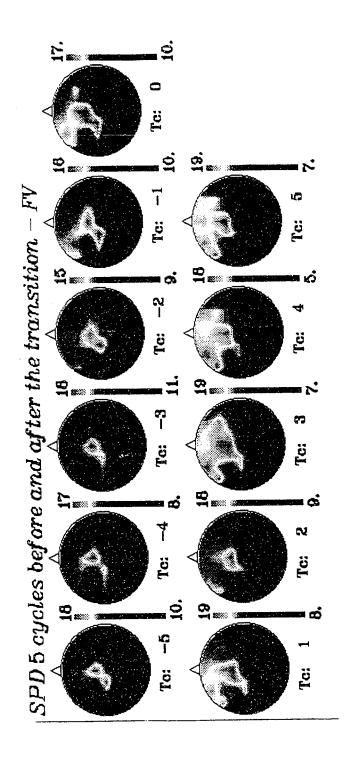
The following are averages obtained for each subject. Included are behavioral time lag distributions, behavior time lag values and standard deviations aligned at the transition, DFT by plateau and time lag, DFT relative to the transition, DFTs on all control conditions.

9.1. Subject - FV

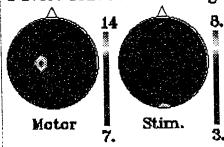




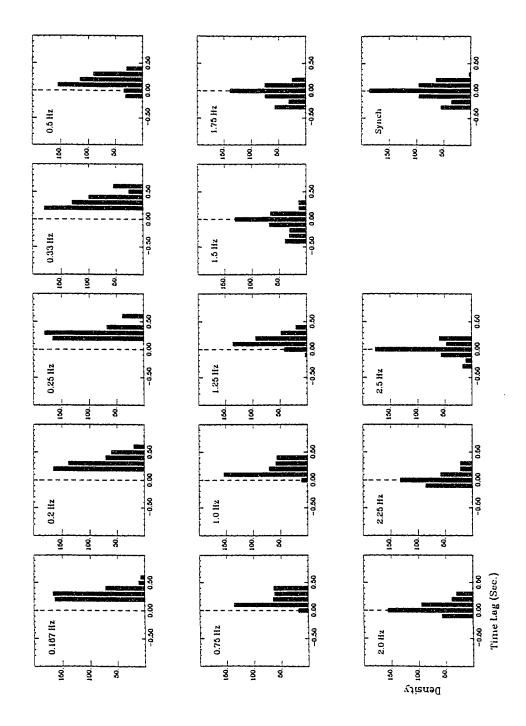


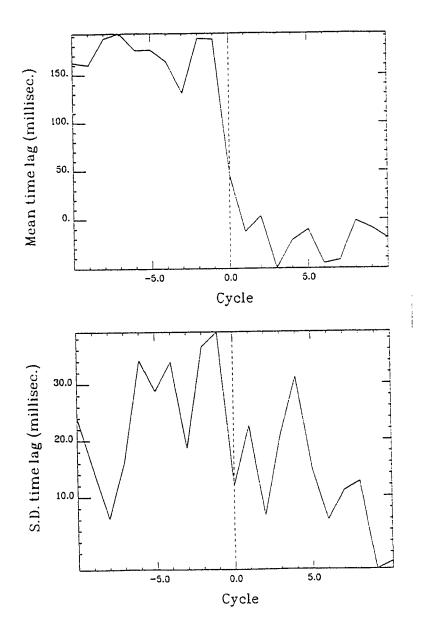


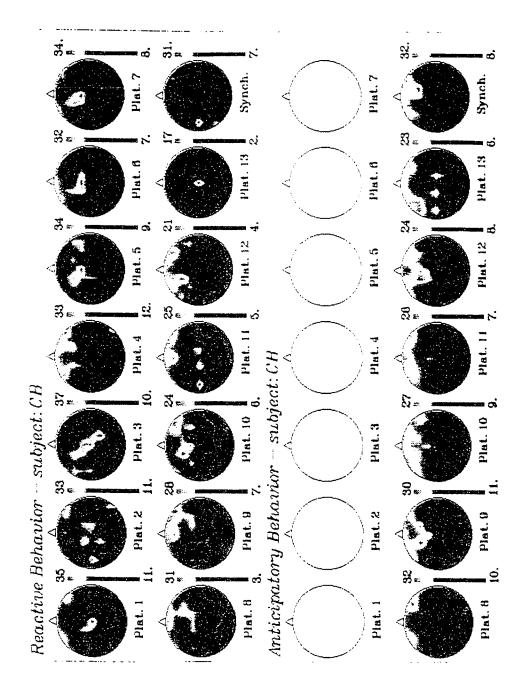
Controls: Motor only and stimulus only - FV

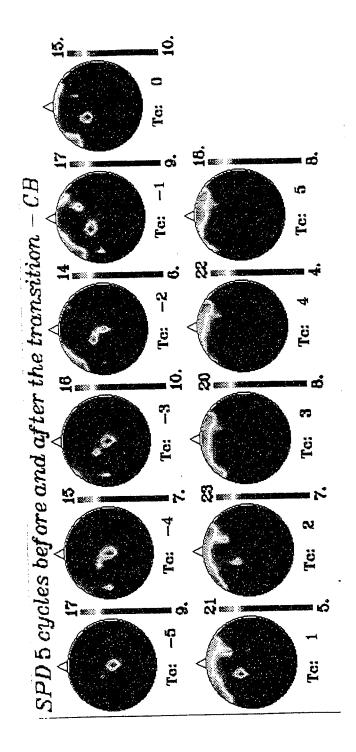


9.2. Subject - CB

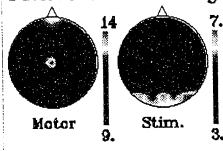




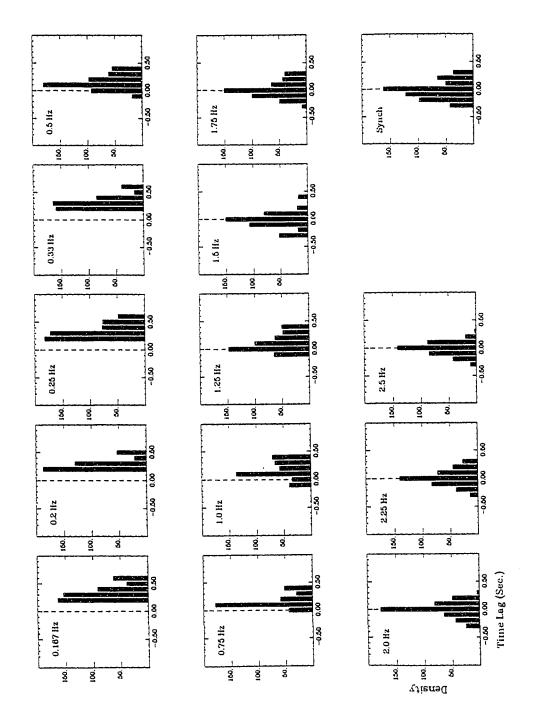


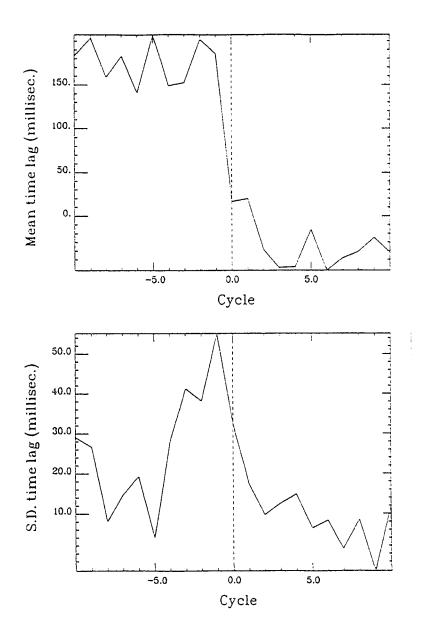


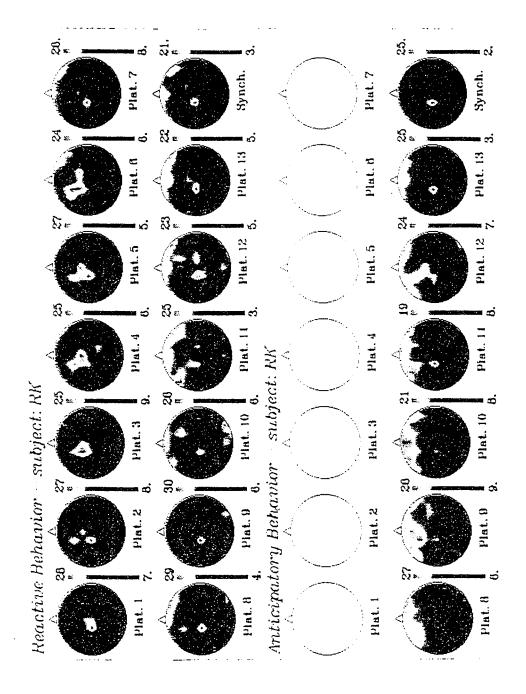
Controls: Motor only and stimulus only $-\overline{CB}$

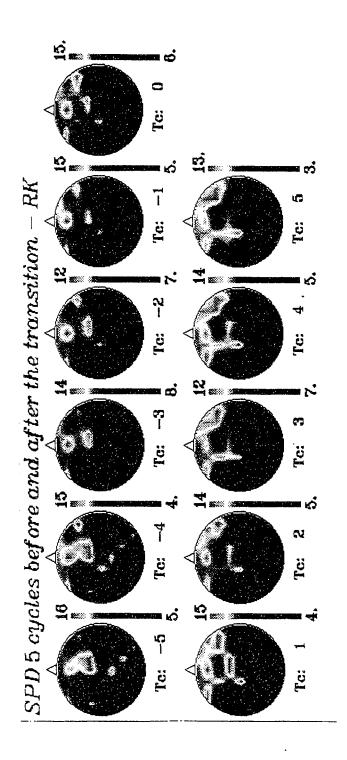


9.3. Subject - RK

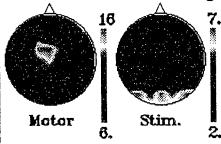




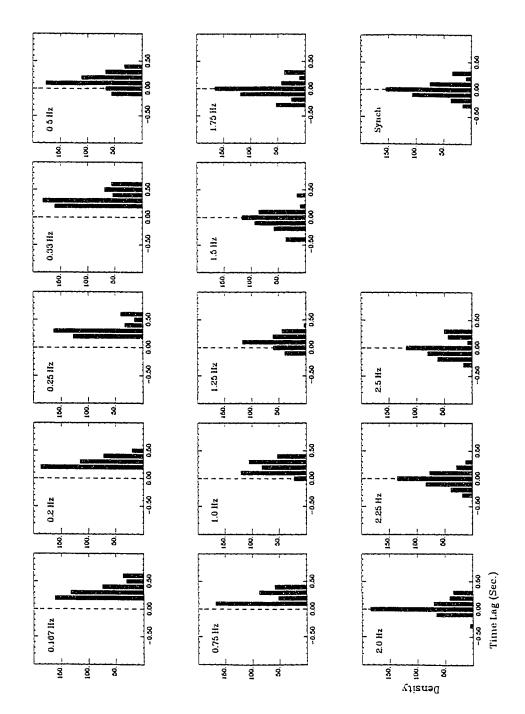


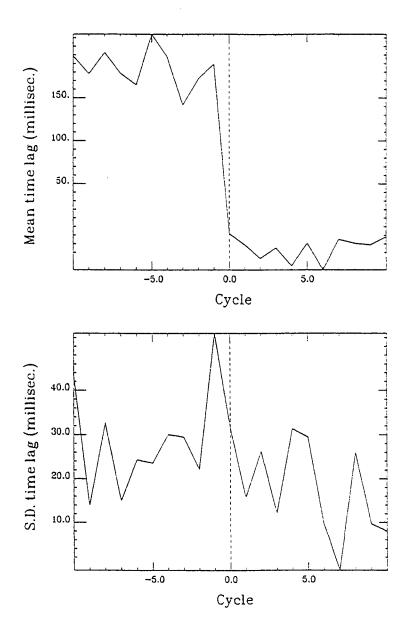


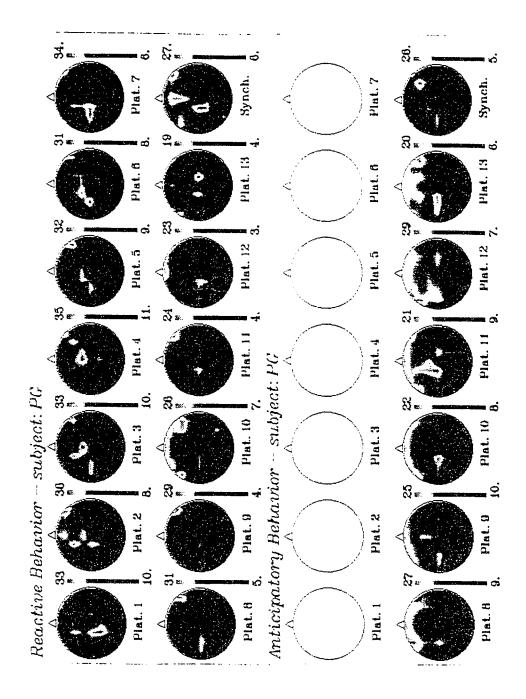
Controls: Motor only and stimulus only - RK

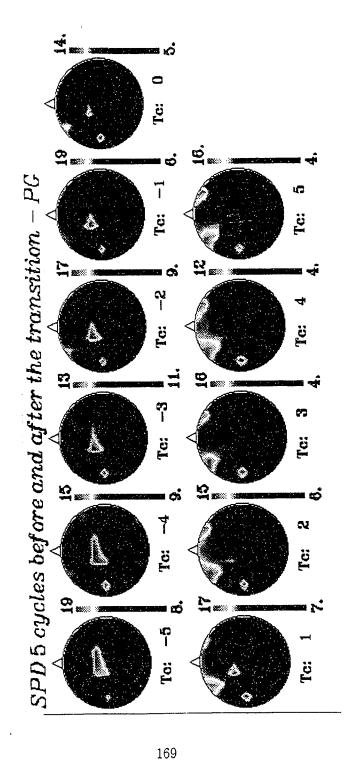


9.4. Subject - PG





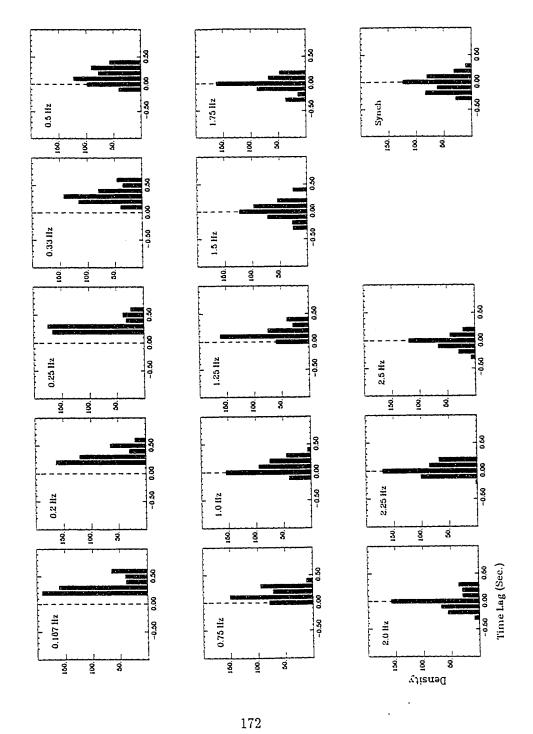


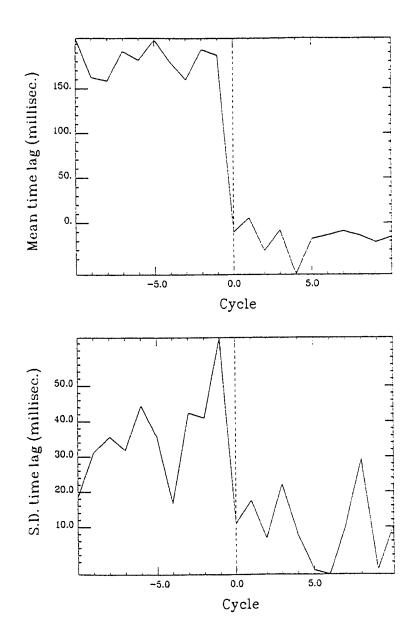


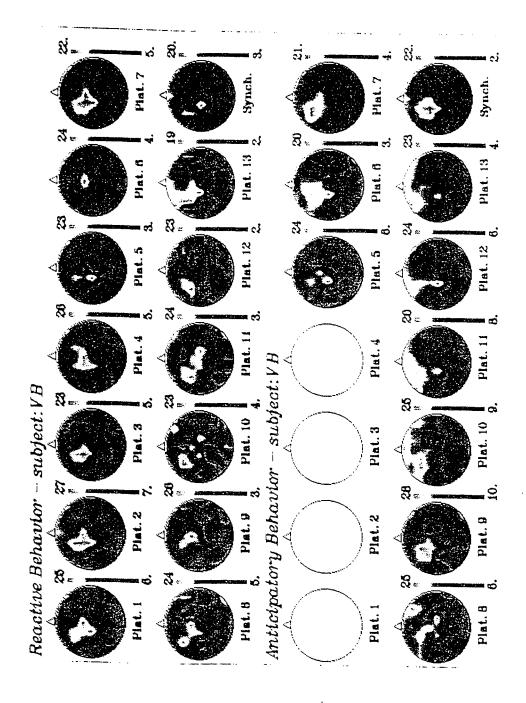
Controls: Motor only and stimulus only - PG

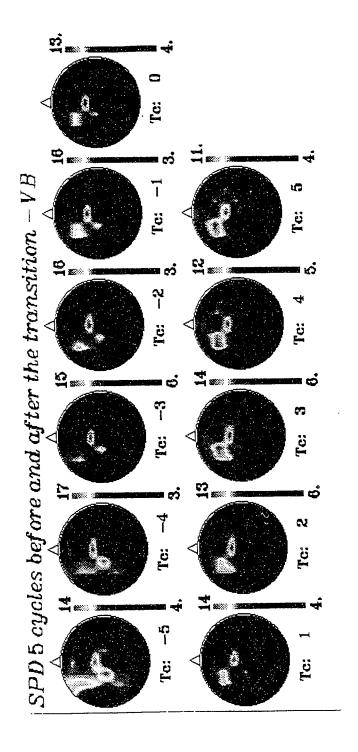
| Stim. 4.

9.5. Subject - VB

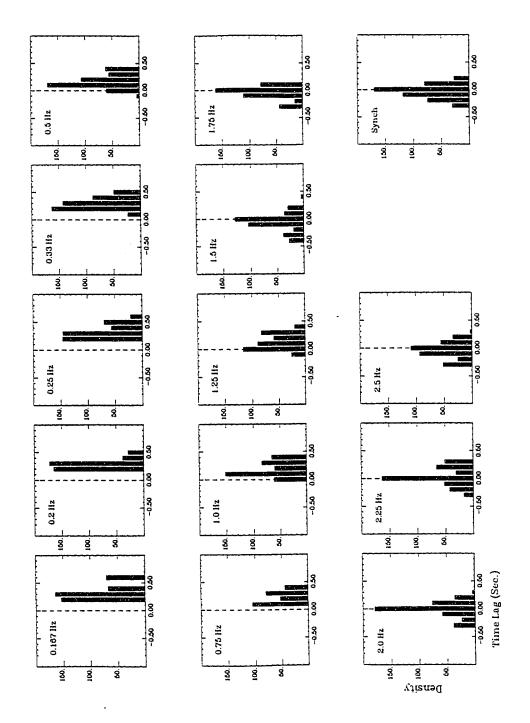


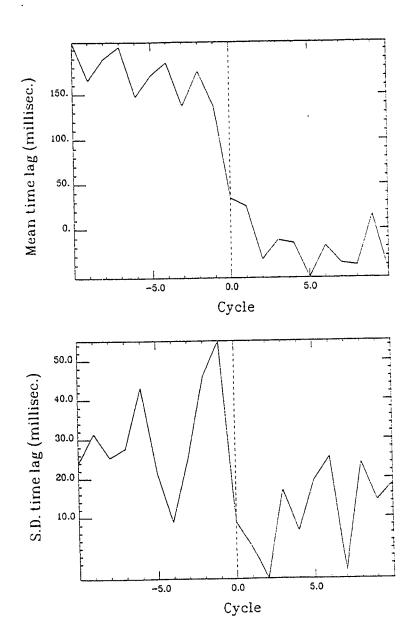


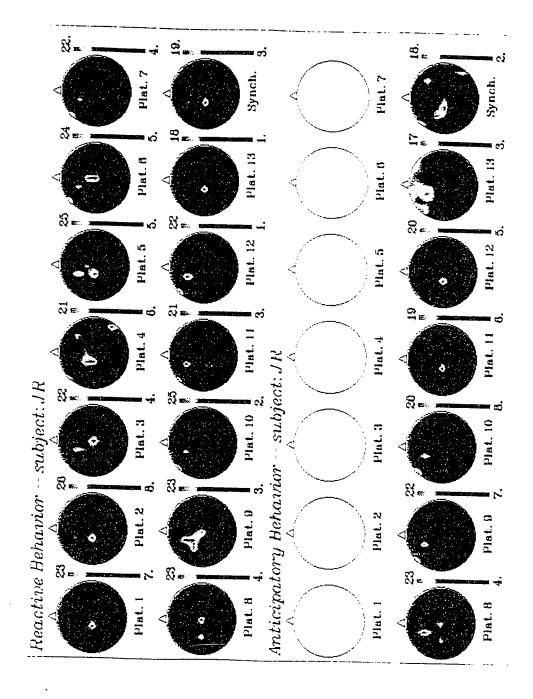


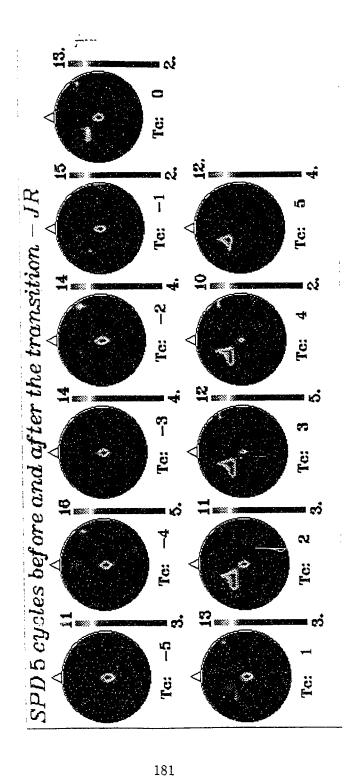


9.6. Subject - JR









Controls: Motor only and stimulus only - JR

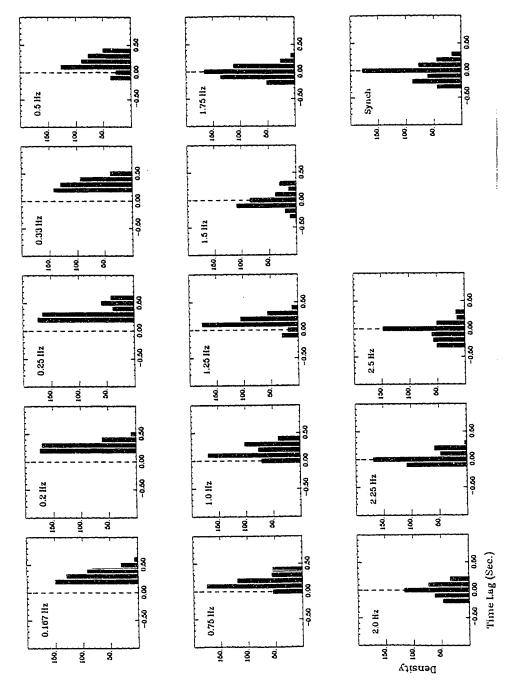
A

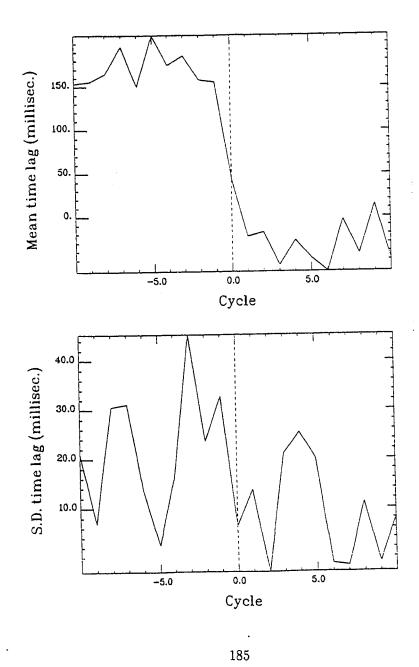
Motor

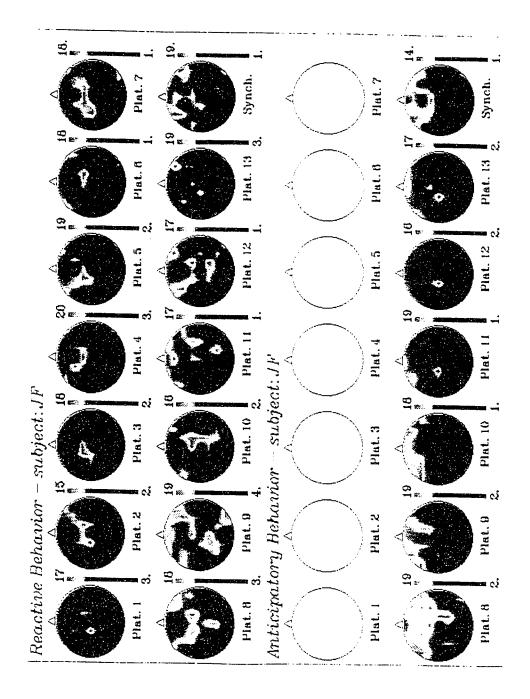
Stim.

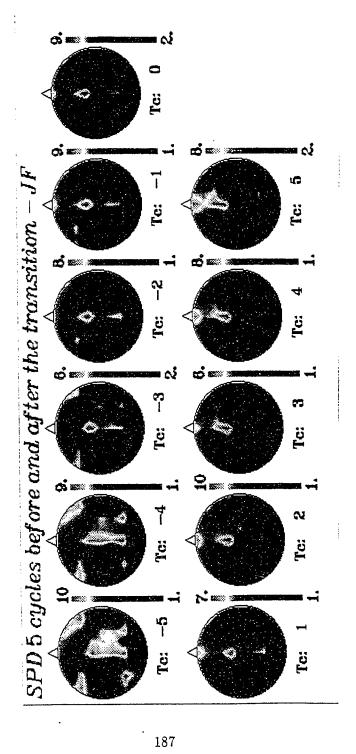
2.

9.7. Subject - JF

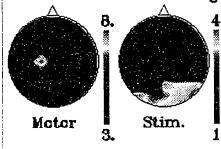




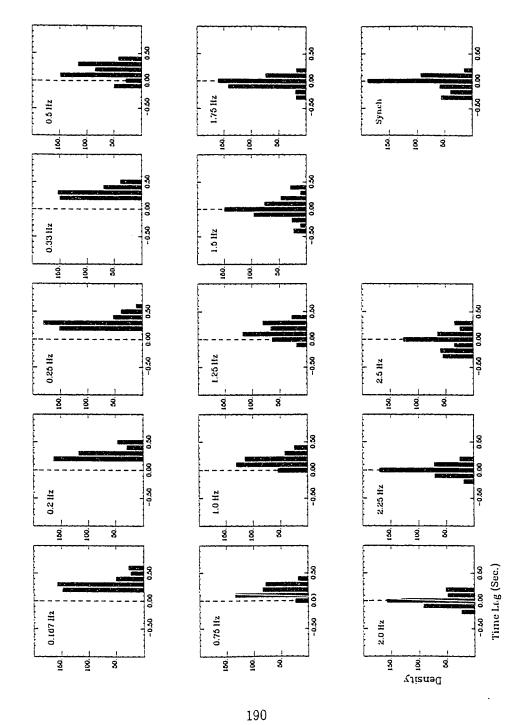


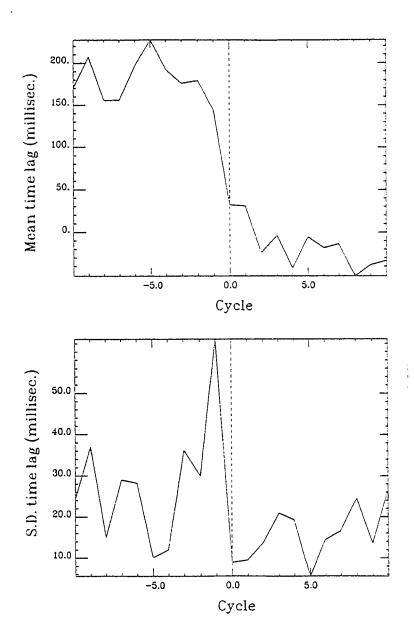


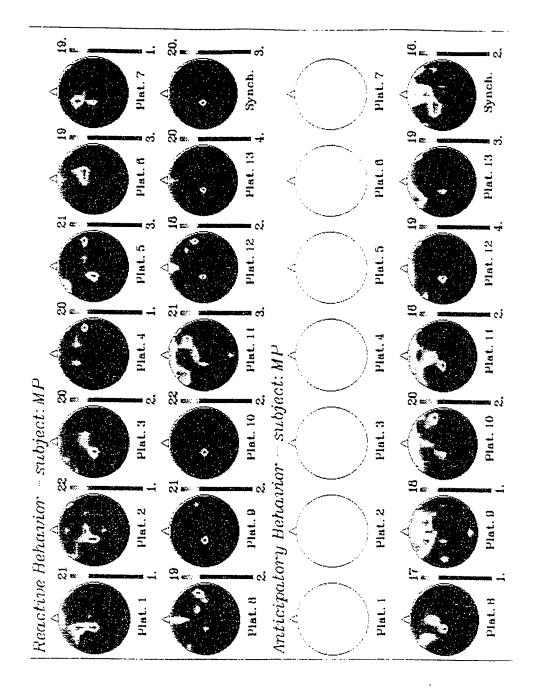
 $\overline{\it Controls: Motor only and stimulus only - \it JF}$

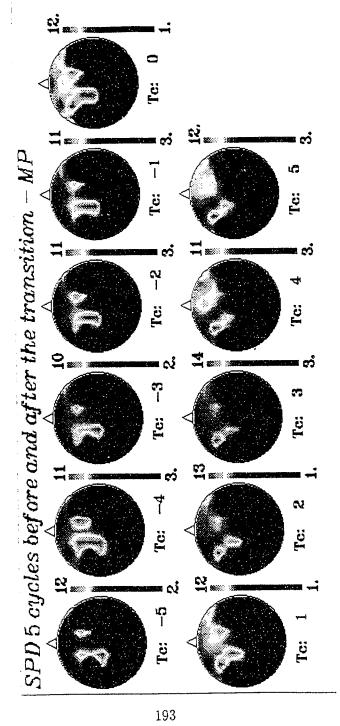


9.8. Subject - MP



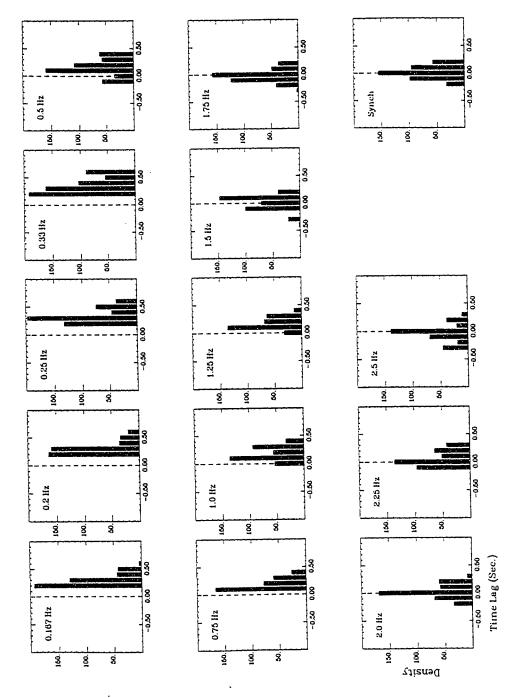


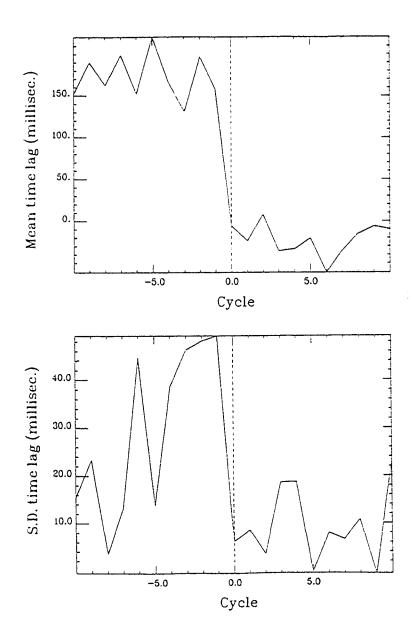


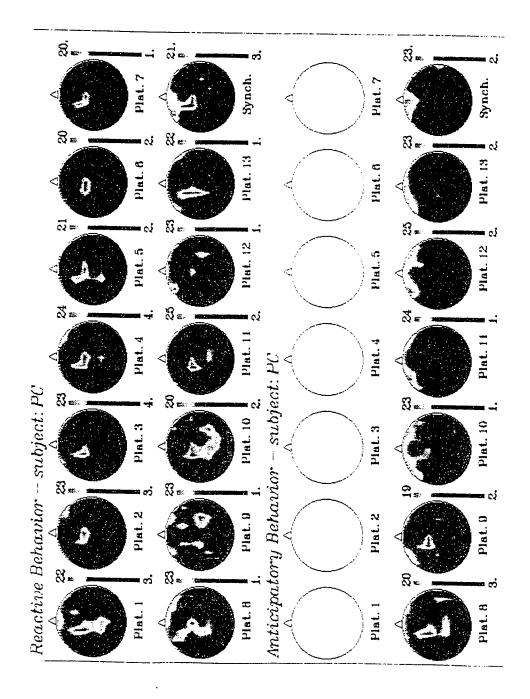


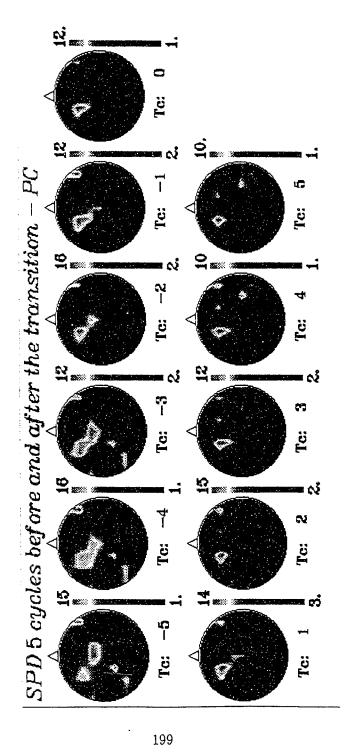
Controls: Motor only and stimulus only - MP Stim. 2.

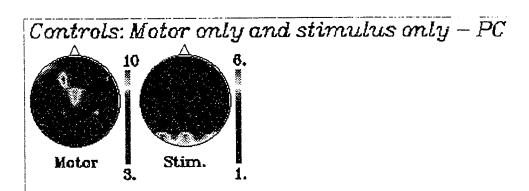
9.9. Subject - PC



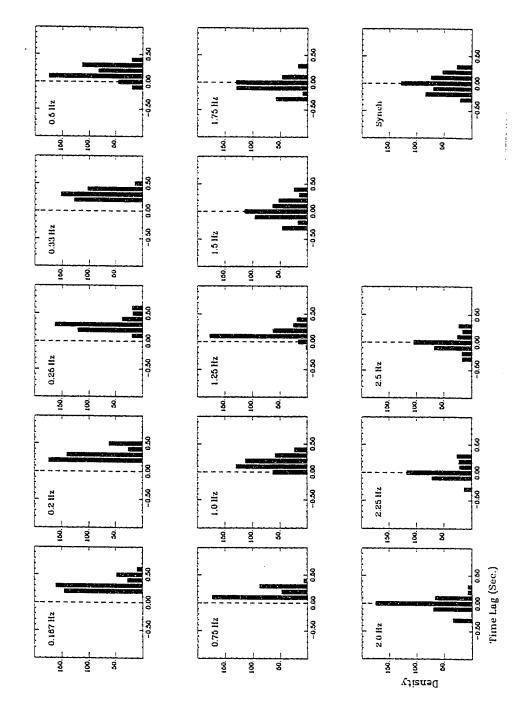


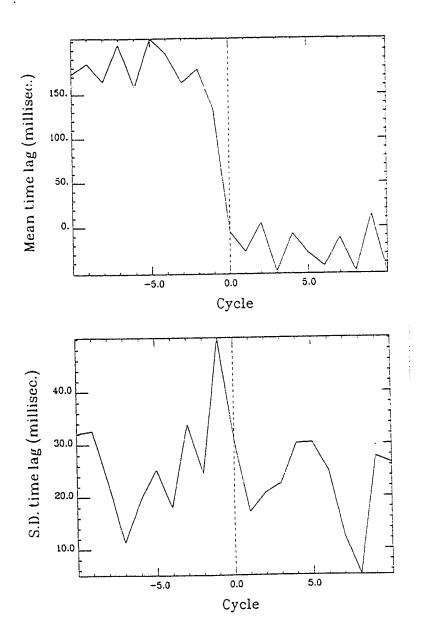


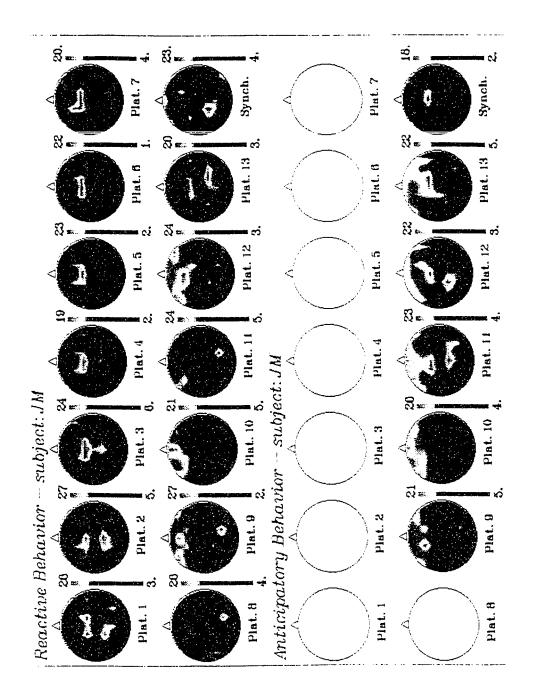


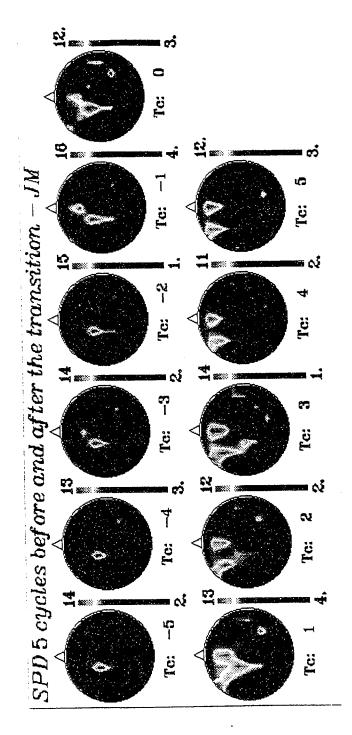


9.10. Subject - JM









Controls: Motor only and stimulus only - JM

Only only - JM

Notor 5. Stim. 2.

10. Appendix 3 - Analysis of variance (ANOVA) tables

The following are the full ANOVA tables from the primary analyses. The posthoc results are already reported in tabular form within the text.

Behavioral time lag: sex (2) by plateau (13) – Section 4.2.3

Analysis of variance (ANOVA)

SOURCE -	MEAN SQ	UARE	DF —	F —	TAIL	PROB.

sex error	.00273 .01605	1 8	0.17	.7028
plateau error	.04760 .00818	12 52	5.82	.0008
s-p error	.00674 .00527	12 104	1.28	.6129

Behavioral time lag standard deviation: sex (2) by cycle (21) – Section 4.2.4

SOURCE —	MEAN SQUARE	DF	F. —	TAIL PROB.
sex error	.00290 .00829	1 8	0.35	.4293
cycle error	.01629 .00529	20 84	3.08	.0092
s-c error	.00041 .00091	20 84	0.46	.1927

Spectral power density: sex (2) by mode (2) by plateau (6) by electrode (61) – Section 4.2.6

SOURCE —	MEAN SQUARE	DF —	F	TAIL PROB.
sex	.15371	1	10.00	0056
error	.01199	8	12.82	.0276
mode	.14614	1		
error	.00918	8	15.92	.0211
plateau	.01925	5		
error	.00721	24	2.67	.0418
electrode	.00988	60		
error	.00592	244	1.67	.0083
s-m	.02073	1		
error	.00496	16	4.18	.0595
s-p	.00772	5		
error	.00427	48	1.81	.0694
s-e	.00629	60		
error	.00391	488	1.61	.0098
m-p	.00345	5		
error	.00326	48	1.06	.1921
m-e	.00501	60		
error	.00290	488	1.73	.0058
n-A	.00199	300		
p-e error	.00217	1464	.92	.2109

s-m-p	.00177	5		
error	.00128	96	1.39	.2203
s-m-e	.00155	60		
error	.00113	976	1.38	.0064
m-p-e	.00115	300		
error	.00102	2928	1.21	.0103
s-m-p-e	.00089	300		
error	.00081	2928	1.11	.0319

Spectral power density at transition: sex (2) by trans (2) by electrode (61) – Section 4.2.7

SOURCE —	MEAN SQUARE —	DF	F —	TAIL PROB.
sex error	.07063 .01296	1 8	5.45	.0493
trans error	.11449 .00812	1 8	14.1	.0071
electrode error	.00956 .00698	60 244	1.37	.0306
s-t error	.02693 .00302	1 16	8.92	.0080
s-e error	.00350 .00245	60 488	1.43	.0329
t-e error	.00457 .00232	60 488	1.97	.0002
s-t-e error	.00182 .00119	60 976	1.53	.0082

Spectral power density at transition (fluctuations): sex (2) by cycle (11) by electrode (61) – Section 4.2.8

SOURCE —	MEAN SQUARE —	DF	F	TAIL PROB.
sex error	.06595 .01103	1 8	5.98	.0415
cycle error	.02936 .00749	10 44	3.92	.0003
electrode error	.00606 .00424	60 244	1.43	.0439
s-c error	.00258 .00413	10 88	1.99	.0319
s-e error	.00428 .00332	60 488	1.29	.0592
c-e error	.00231 .00212	600 2684	1.09	.0301
s-c-e error	.00121 .00120	600 5368	1.01	.0472

Spectral power density (SYNCHRONIZE and REACTIVE): sex (2) by condition (2) by mode (2) by electrode (61) – Section 4.2.9

SOURCE —	MEAN SQUARE	DF	F	TAIL PROB
sex error	.17243 .01931	1 8	8.93	.0291
condition error	.08096 .01142	1 8	7.09	.0413
mode error	.03959 .00902	1 8	4.39	.0602
electrode error	.01510 .00839	60 244	1.80	.0002
s-c error	.06611 .00733	1 16	9.02	.0008
s-m error	.05903 .00529	1 16	11.16	.0001
s-e error	.00572 .00392	60 488	1.46	.0401
c-m error	.00942 .00310	1 16	3.04	.1013
c-e error	.00460 .00229	60 488	2.01	.0016
m-e error	.00508 .00221	60 488	2.30	.0001

s-c-m	.00373	1		
error	.00091	32	4.10	.0429
s-c-e	.00086	60		
error	.00067	976	1.29	.0620
c-m-e	.00056	60		
error	.00039	976	1.45	.0081
s-c-m-e	.00017	60		
error	.00013	1952	1.36	.0019

Spectral power density (STIMULUS- and MOTOR-ONLY): sex (2) by condition (2) by electrode (61) – Section 4.2.10

SOURCE	MEAN SQUARE -	DF	F	TAIL PROB
sex error	.17620 .01181	1 8	14.92	.0091
condition error	.06633 .00819	1 8	8.10	.0210
electrode error	.00541 .00420	60 244	1.29	.0591
s-c error	.01266 .00309	1 16	4.01	.0504
s-e error	.00251 .00229	60 488	1.10	.2620
c-e error	.00641 .00201	60 488	3.19	.0001
s-c-e error	.00179 .00183	60 976	.98 .	3593

11. Appendix 4 - The number of cycles used in each topographical map

The following are the number of cycles that were used in each topographical map (plateaus 8 - 13) from Figures 6a and 6b.

	MEN:		WOMEN:	
	Reactive	Anticipatory	Reactive	Anticipatory
Plateau 8	1567	703	1604	622
Plateau 9	1114	1251	1171	1279
Plateau 10	1196	1317	1112	1314
Plateau 11	929	1321	991	1432
Plateau 12	1062	1238	1019	1238
Plateau 13	984	1221	1004	1201
SYNCH.	1220	1539	1314	1531

The following are the number of cycles that were used in each topographical map from Figures 8b and 8c.

	MEN:	WOMEN:
Tc: -5	161	153
Tc: -4	183	195
Tc: -3	192	176
Tc: -2	145	152
Tc: -1	139	162
Tc: 0	134	141
Tc: 1	172	149
Tc: 2	166	159
Tc: 3	128	147
Tc: 4	159	162
Tc: 5	172	169

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13. Curriculum Vitae

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Areas of Interest:

Theoretical/Computational Neuroscience - Analytical and numerical simulations of biologically realistic neurons, cellular circuits, and large-scale neuronal networks. Studies of slow thalamic and cortical rhythmicity and how it relates to sleep, generalized epilepsy, learning and memory, and metabolic processes. Experimental Neurophysiology - Studies of the electroencephalographic (EEG) rhythms accompanying sensorimotor integration tasks.

Education:

1. B.A. in Biological Psychology, Florida Atlantic University, Boca Raton, FL., 1984-88.

2. Ph.D. in Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, FL., 1992-95.

Professional Experience:

- Graduate research assistant and systems programmer, EEG Research Laboratory, Florida Atlantic University, 1988-1990
- 2. Graduate research assistant, Center for Complex Systems, 1990-present

Professional Services:

- 1. Reviewer for the journal Physica D.
- 2. Reviewer for the journal Psychophysiology.
- 3. Reviewer for the International Journal of Bifurcation and Chaos.
- 4. Reviewer for the Journal of Experimental Psychology.
- 5. Reviewer for the International Journal of Neuroscience.

Professional Skills:

- 1. Several years experience working with GENESIS and NEURON.
- 2. Extensive experience programming in C and FORTRAN.
- 3. Six years experience in developing data acquisition, display, and signal processing software.
- 4. Five years experience in running and designing EEG experiments.

Honors and Awards:

- 1. 1988-1989 Florida Atlantic University Graduate Fellowship.
- 1989-1995 National Institute of Health (NIH) Predoctoral Fellowship (TS MH19116).
- 3. 1995 Daniel C. Brown award for excellence in graduate studies.

Professional Societies:

- 1. Member, Society for Physiological Research (SPR)
- 2. Member, International Brain Research Organization (IBRO)
- 3. Student member, Society for Neuroscience

Invited Presentations:

- "Estimating Lyapunov Characteristic Exponents from Biological Time Series", Dynamical Measures of Complexity in the Brain, Institute for Supercomputing Research, Florida State University, 1991
- "Spatiotemporal Mode Dynamics of Nonequilibrium Phase Transitions in the Human Brain", Annual Florida Conference on Cognition, Action, and Perception, 1993
- 3. "Spatiotemporal Dynamics of the EEG", NASPSPA Workshop on Complex Systems, Clearwater, FL., 1994
- "Spatial Mode Dynamics of the Human EEG in Relation to a Sensorimotor Phase Transition", Nonlinear Dynamics in the Brain and Behavior, Boca Raton, FL., 1994

Contributed Presentations:

- "Lyapunov Characteristic Exponents and Variation in the First Derivative Quantify the Dynamical Complexity of Event-related Brain Potentials", Society for Physiological Research Meeting, Boston, 1990
- "Calculation of Lyapunov Characteristic Spectra from Biological Time Series", Society for Neuroscience Meeting, St. Louis, 1990
- "Slow Cortical Potentials and Behavior", Workshop on Dynamics in Complex Systems, Florida Atlantic University, 1992
- "Spatiotemporal Dynamics of Phase Transitions in the Human Brain", Society for Neuroscience Meeting, Washington, D.C., 1993
- "Spatial Mode Dynamics of a Thalamo-Cortical Network", SPIE Conference on Chaos in Biology and Medicine, San Diego, 1993
- "Spatial Mode Dynamics of the Human EEG in Relation to a Sensorimotor Phase Transition", Society for Neuroscience Meeting, Miami, 1994

Publications - Theoretical/Computational Neuroscience:

- Wallenstein, G.V. (1993a) Spatial mode dynamics of a thalamo-cortical network. SPIE Proceedings on Chaos in Biology and Medicine, W.L. Ditto (Ed.), 2036, 301-312.
- Wallenstein, G.V. (1993b) Spatial, temporal, and global mode entropy in a thalamo-cortical network. International Journal of Bifurcation and Chaos, 3, 1487-1501.

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- 4. Wallenstein, G.V. (1994b) A model of the electrophysiological properties of nucleus reticularis thalami neurons. *Biophysical Journal*, 66, 978-988.
- 5. Wallenstein, G.V. (1994c) Simulation of GABA_B-receptor-mediated K⁺ current in thalamocortical relay neurons: Tonic firing, bursting, and oscillations. *Biological Cybernetics*, 71, 271-280.
- 6. Wallenstein, G.V. (1995a) Adenosinic modulation of 7 14 Hz spindle rhythms in interconnected thalamic relay and nucleus reticularis neurons. *Neuroscience*, In press.

Publications - Theoretical/Experimental Neuroscience:

- Wallenstein, G.V. and Nash, A.J. (1992) Slow cortical potentials and their frequency and phase dynamics preceding bimanual finger movements. Psychophysiology, 29, 4A, S73.
- Wallenstein, G.V., Bressler, S.L., Fuchs, A. and Kelso, J.A.S. (1993)
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- 6. Wallenstein, G.V., Bressler, S.L., and Kelso, J.A.S. (Manuscript in preparation) Antero-Frontal Shift in Spatial EEG Activity Associated with Transitions in Coordination Timing.
- 7. Wallenstein, G.V. (1995c) Spatiotemporal Dynamics of the Human EEG Associated with Transitions in Coordination Timing, Doctoral Dissertation.

Publications - Time Series Analysis of Biological Data:

- Wallenstein, G.V. and Nash, A.J. (1990a) Lyapunov characteristic exponents and variation in the first derivative quantify the dynamical complexity of event-related brain potentials. *Psychophysiology*, 27, 4A, S73.
- 2. Wallenstein, G.V. and Nash, A.J. (1990b) First order Lyapunov characteristic exponents and the correlation dimension quantify the dynamical complexity of event-related brain potentials. Society for Neuroscience Abstracts, 16, 577.

3. Wallenstein, G.V. and Nash, A.J. (1992) Does the first order Lyapunov exponent quantify the dynamical complexity of event-related potentials: An algorithm using adaptive step-size control for varying propagation times., Measuring Chaos in the Human Brain, D.W. Duke and W.S. Pritchard (Eds.), World Scientific, Singapore, 232-256.

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