# Frequency and phase characteristics of slow cortical potentials preceding bimanual coordination

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## Abstract

The aim of the present study was to derive quantities which relate behavioral and neurophysiological levels of observation during a bimanual coordination task. We recorded the scalp electroencephalographic (EEG) signal preceding a sequence of 4 bimanual finger flexions of varying response rates in 12 subjects. A slow negative-going Bereitschaftspotential (BP) displayed larger mean amplitudes and earlier onset times for the faster required response rates. The amplitude of the BP was also larger for electrode locations contralateral to the side initiating the behavioral response. A Fourier transform showed two predominant frequencies (0.5 and 2.0 Hz) to be amplitude modulated as a function of the required response rate in addition to increased power on the contralateral side of the finger initiating the response. A measure of the phase relationship between the left ($C_3$) and right ($C_4$) hemispheres of the fronto-central cortex at each of these spectral frequencies was calculated as well as the variance in this measure and found to correspond closely to the variance in inter-response times derived from the subjects' movements. These findings indicate that changes in the stability and rate of a patterned movement are generally preceded by similar changes in the stability and amplitude of components observed on the neurophysiological level.

*Keywords:* Movement-related potentials; Bereitschaftspotential; Spectral analysis; Dynamics; Slow potentials; Sensorimotor integration

The tendency for the nervous system to exhibit preferred modes of timing and pattern formation has recently become a major theme in both theoretical and experimental neuroscience (e.g. Eckhorn et al. 1988; Kelso et al. 1992; Wallenstein et al. 1992, 1993). Interesting similarities have been shown to exist in terms of phase and frequency synchronization seen on the spinal (Cohen et al. 1988), cortical (Gray et al. 1989), and behavioral (e.g. Kelso 1981; Haken et al. 1985; Schöner and Kelso 1988) levels of observation.

On behavioral and neuromuscular levels, Kelso and his colleagues (e.g. Kelso 1984; Kelso and Schöner 1988) have shown that only a few phase and frequency relations between the hands seem stable enough to avoid spontaneously switching into some other pattern as an experimental parameter (e.g., frequency of movement) is systematically increased. These findings support the notion that certain behavioral patterns are reproduced more accurately and consistently than others.

On the cortical level, a small number of studies using human subjects have examined changes in motor-related potentials preceding rhythmical movements (Benecke et al. 1985; Lang et al. 1989, 1990). For example, Lang et al. (1989, 1990) have found that the Bereitschaftspotential (BP) which precedes the initiation of movement has a topographical distribution that depends on the "complexity" of the upcoming behavior. It was demonstrated that the BP is larger over the primary motor cortices during simple 1 : 1 bimanual movements where the left and right forefingers are in perfect synchrony, but that more complex ratios such as 2 : 3 additionally involve activation of the mesial fronto-central cortex which predominantly contains the supplementary motor area (Lang et al. 1989, 1990).

In the present study, the subjects were asked to reproduce a sequence of 4 bimanual finger flexions at a specific response rate which was cued by a pacing metronome. To date, only a limited number of studies have examined

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changes in movement-related potentials as a function of movement rate, with most being concerned only with unilateral behavior (e.g., Cooper et al. 1989). In general, the unilateral studies suggest that a high degree of correlation exists between movement velocity and amplitude of the cortical Bereitschaftspotential preceding the response. Considering this, our general hypothesis was that (1) there would be an increase in the BP preceding the sequence of movements which was larger over the site contralateral to the side *initiating* the movement, and (2) there would be an overall increase in the amplitude of the BP with faster response rates. The first hypothesis is based on the assumption that an ordering of behavioral responses (left or right initiated) is maintained at the cortical level, and that the first response in the sequence would contribute to an earlier and larger BP over the contralateral hemisphere. The second hypothesis stems from a recent study by Cooper et al. (1989) who found increases in the amplitude of the BP as a function of the velocity of movement in a unilateral visual tracking task. Since their results were for unilateral movements, it is an open question as to whether the BP is altered as a function of bimanual movement rate.

We further show that when these cortical signals are decomposed into their frequency and phase properties, a close correspondence is found between the stability characteristics of the EEG signals and the motor behavior they precede which depends on the timing necessary to accurately reproduce the required rate of movement. In particular, we show that the relative phase between different areas of the fronto-central cortex is a relevant observable for describing these cortical timing relationships and their stability.

## 1. Materials and methods

### Task

The general task of the subjects (n = 12) in this experiment was to reproduce a sequence of 4 bimanual finger flexions. Four specific variables were manipulated: (1) the required response rate (RATE) of the movement sequence was varied over a range from 0.5 to 5.0 Hz in 0.5 Hz increments; (2) the direction of rate change (DIR) in the required response was scaled in both the ascending and descending directions; (3) the side (left or right finger) initiating the response sequence (SIDE); and (4) the type of movement pattern (PATT), in which the subjects were asked to reproduce the sequence using two fingers (alternating index fingers) or three, where the only difference from the former was that the third response of the sequence was to be carried out with their middle finger.

The subjects were seated in an electrically shielded, sound attenuating room with their arms abducted approximately 10° at the shoulder and their forearms lying supinated on both armrests of the chair. Two momentary push-buttons (with a travel distance of 15 mm) were mounted at the end of each armrest. The subjects were instructed to maintain their middle and index fingers on these buttons and fully displace them during the response sequence. The angular extent of movement at the proximal finger joint was approximately 20°.

Each trial began with a series of 4 auditory clicks which served as a metronome to pace the subjects at a given rate. After a delay (which varied from 1 to 4 sec depending on the rate), a warning stimulus (WS) was delivered, which was a tri-color light emitting diode positioned at eye level approximately 50 cm in front of the subjects. The warning signal gave the subjects information regarding the specific hand (right or left depending on the color of the LED for that trial) to be used in response to the forthcoming imperative signal (IS) which was an auditory tone. The foreperiod between the WS and the IS was a constant 2000 msec. Following the IS, the subjects were given 3500 msec to reproduce the required movement responses before the next trial began. Subjects were instructed to "anticipate" the IS and begin their response sequence as close as possible to tone onset without actually responding before it. Thus the subjects were to carry out the first response as fast as possible and adjust the remaining 3 responses to the required response rate.

For each run, the subjects began with either the slowest (0.5 Hz) or fastest (5.0 Hz) required response rate. They were given 3 trials at this rate before the rate was changed by 0.5 Hz. This resulted in runs of 30 trials each. Following a run, the direction of the required response was changed in the opposite direction. The same block of 60 trials was then repeated for the other type of movement pattern (2- or 3-finger). The side initiating the response was randomized within each run. All experimental sessions began with a run of 30 trials for a practice session.

In order to reduce the possibility of fatigue, the experiment was divided into two sessions of equal duration on separate days. Each session was carried out within a week of the other.

### Data acquisition

The first two response times were recorded from each of the response sequences by way of the momentary push-buttons being displaced by the movements.

The electroencephalogram (EEG) was recorded from 3 scalp locations, $C_z$ (vertex), $C_3$ (approximately 4 cm to the left of $C_z$), and $C_4$ (approximately 4 cm to the right of $C_z$), according to the 10/20 international system of electrode placement (Jasper 1958), all referenced to linked earlobes. In all cases, Grass E5S silver-silver chloride cup electrodes were used for recording. Electro-oculographic (EOG) activity was monitored from the right eye with two electrodes, one supraorbital and the other suborbital, each referenced to the other. For each subject, the electrode impedance for the EEG and EOG was less than 5 k$\Omega$.

The EEG and EOG signals were amplified by a Grass 79D polygraph with 7P511 amplifiers and filtered on-line

using a half-amplitude low frequency bandpass limit of 50 Hz (rise time constant of 3 msec) and half-amplitude high-pass limit at 0.01 Hz (fall time constant of 600 msec). An additional 50 Hz low-pass filter (fourth order) was placed in line to correct for biasing of the frequency data. The derived voltages were digitized at 170 Hz/channel for 3000 msec, beginning at the sync pulse (100 msec prior to the warning signal) which provided a baseline reference measure for the amplitude estimates of the EEG.

Data were averaged off-line after artifacts, such as eye movement or orofacial muscle response, were removed. In all conditions, a minimum of 45 trials was used for the averages.

### Measurements

In order to characterize the movement-related potentials and the motor behavior resulting from the experiment, the following measurements were performed in the time domain:

Means and variances were obtained for the first and second response times.

N-BP: mean negativity over the interval from 400 to 50 msec prior to the first response time of the movement sequence (BP, Bereitschaftspotential).

ON-BP: the onset time for the BP was calculated by using a procedure for estimating changes in mean square error with the signal and a linear fit through a series of overlapping time segments from it (Stagliano et al. 1991). The interval for this calculation was from 1500 to 100 msec prior to the first response time.

An additional analysis was performed in the frequency domain. A fast Fourier transform (FFT) was used to obtain power spectra for each of the single trials in the interval from 1250 to 100 msec prior to the first response time (a detrending procedure removed the linear component over this interval). The phase spectrum was also calculated at each of the spectral frequencies by taking the $\tan^{-1}$ (i/r) of the imaginary and real portions of the Fourier decompo-

sition. Means and variances were obtained for both the power and phase angles at those spectral frequencies corresponding to the required response rates (i.e., 0.5–5.0 Hz in 0.5 Hz increments).

For the N-BP and ON-BP values, a 5-factor repeated measures analysis of variance (ANOVA) using the 10 required response rates, by 2 directions of rate change by 2 movement patterns by 2 initiating sides by 3 electrode locations, was used to test for statistically significant effects.

Preliminary analysis was performed on the spectral data by using a series of univariate tests at each of the 10 spectral frequencies in question. Since no frequency modulation or significant effects for DIR were found, the data were classified for separate analysis by the 4 combinations of movement pattern (PATT) and the 2 electrode locations $C_3$ and $C_4$.

For the first and second response times, a 4-factor repeated measures ANOVA using the 10 required response rates, by 2 directions of rate change by 2 movement patterns by 2 initiating sides, was used for statistical comparison.

For each of the analyses, the outcomes of statistical calculations were declared significant if $P < 0.05$ using the conservative Huyhn-Feldt test for repeated measures ($\epsilon$ = adjustment to the degrees of freedom).

## 2. Results

### Motor sequences

The first response time did not differ significantly under any of the conditions. The second response time, however, was found to differ significantly as a function of rate only, $F$ (9, 81) = 142.11, $P < 0.01$, $\epsilon = 0.348$. Although the subjects in general were capable of following the required frequency, notice from Fig. 1a and 1b, which show the first and second response times plotted as a function of the
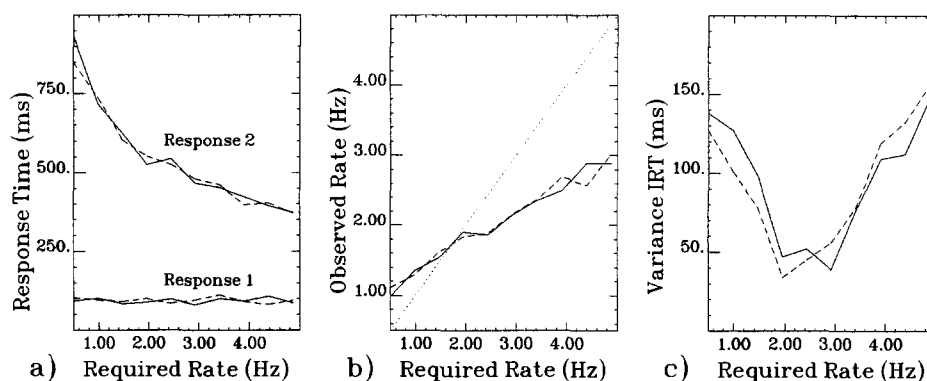


Fig. 1. a: the first and second response times for the left (broken) and right (solid) finger initiating the response as a function of the required response rate. b: the observed response rate for left (broken) and right (solid) finger initiating trials. The dotted line shows the function that would result from a perfect match between observed and required response rates. c: the variance in the inter-response time (IRT) interval plotted as a function of the required response rate and the initiating finger (left side initiated response has broken lines).

required response rates and the observed and required movement rates plotted against the required response rate (averaged across PATT and DIR), that the relationship between the requested and observed response intervals was not consistent. A $t$ test of simple effects (using the conservative Bonferroni method) indicated a significant difference between the required (expected) and observed intervals at the 0.5, 1.0, 3.5, 4.0, 4.5 and 5.0 Hz required response rates. Typically, the subjects had problems keeping pace with the higher required response rates as well as at the very lowest, which may in part be due to the fact that no feedback was given with regard to the accuracy of their performance. In fact the general tendency was to respond more slowly than the faster required response rates (i.e., 3.5–5.0 Hz) and faster than required at the lower rates (i.e., 0.5–1.5 Hz).

In Fig. 1c, the variance in the inter-response interval between the first and second response is plotted against the required response rate. Here, one sees a U-shaped (negative kurtosis) distribution showing a substantially increased variance at the very high and low ends of the required movement rates, suggesting greater consistency at the intermediate values which were also reproduced with greater accuracy, particularly at 2.0 Hz.

## Mean amplitude of the Bereitschaftspotential

In Fig. 2, the averaged wave forms are given by required response rate at each electrode location. A slow negative-going component, the Bereitschaftspotential (BP), can be seen to begin as early as 750 msec prior to the first response time (first response corresponds to 0 in the figure) for the faster response rates and typically persists until some 100 msec prior to the EMG onset, where the potential reached peak negativity. The mean amplitude of the BP (N-BP) was found to increase significantly when subjects were asked to respond at higher rates, $F$ (9, 81) = 5.23, $P < 0.02$, $\epsilon = 0.293$. There was also a significant 3-way interaction of electrode location with the side initiating the movement and the required response rate, $F$ (18, 162) = 5.19, $P < 0.01$, $\epsilon = 0.287$. This effect is illustrated in Fig. 3, where the dashed line corresponds to responses initiated with the left hand. A test of simple effects (Bonferroni) was used to unpack this interaction. A significant difference was found between the hands initiating the response at electrode location $C_3$ for all of the required response rates with the exception of 3.5 Hz. At the $C_4$ electrode location, a significant difference was found between all of the required response rates with the exception of 1.0 Hz, while no significant differences were
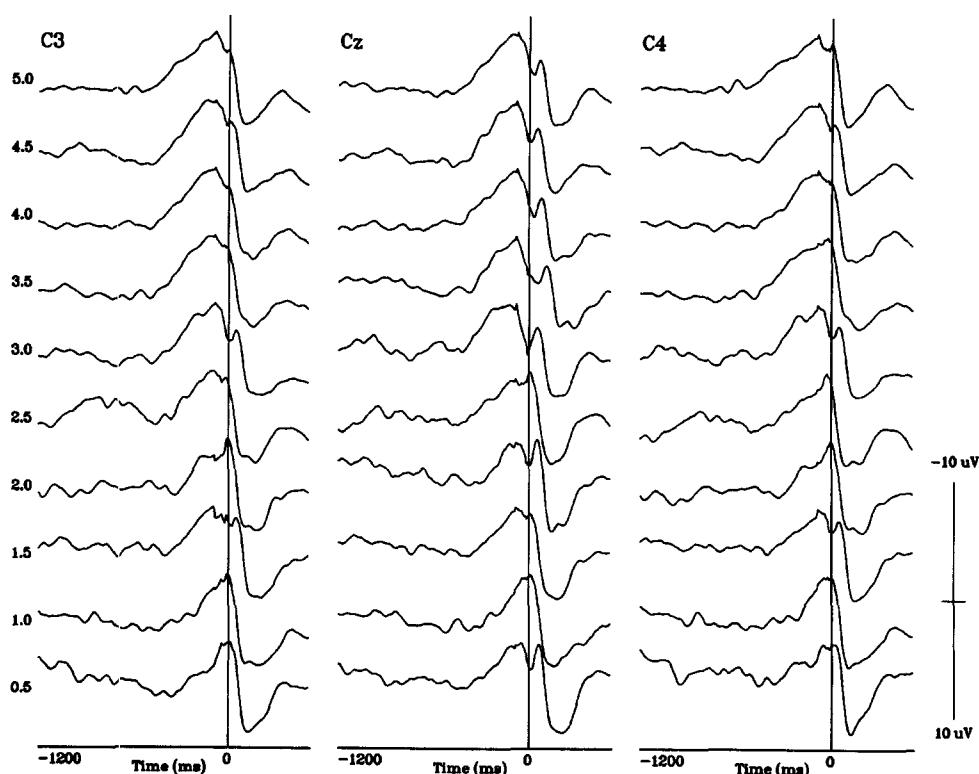


Fig. 2. The averaged wave forms at the $C_3$, $C_4$, and $C_z$ electrode locations as a function of the required response rate. Zero refers to the first response time.
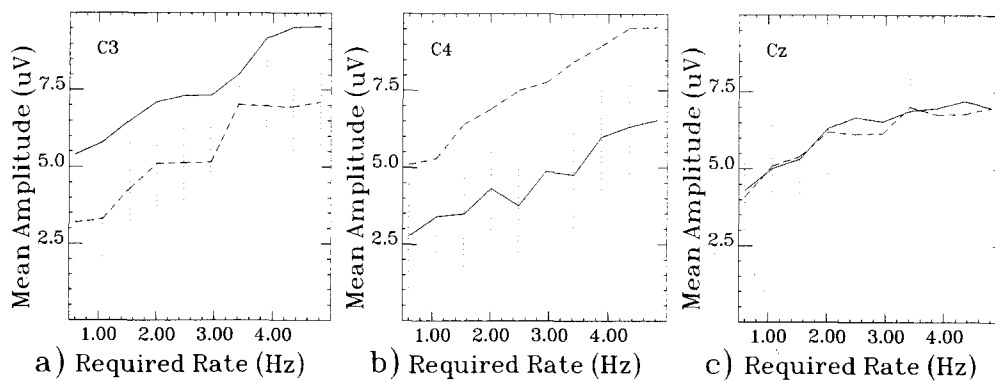
Fig. 3. The mean amplitude of the Bereitschaftspotential as a function of the required response rate and the side (left is broken) initiating the response at the (a) $C_3$, (b) $C_4$, and (c) $C_z$ electrode locations. Error bars refer to 2 times the mean squared error.

found at the $C_z$ location. The nature of the 3-factor interaction is shown in Fig. 3 by the general tendency for the amplitude of the BP to increase with faster required response rates and for the amplitude to be greater at the electrode location contralateral to the side of the initiating finger.

### Onset time for the Bereitschaftspotential

The relationship between the onset time of the BP and the required response rate is illustrated in Fig. 4. The onset time for the BP (ON-BP) was earlier (i.e., relative to the first response time) at faster response rates, $F$ (9, 81) = 5.71, $P < 0.02$, $\epsilon = 0.283$. There was also a significant effect for the type of movement pattern with the overall tendency toward earlier BP onset times for the 3-finger response sequence when compared to the 2-finger pattern, $F$ (1, 9) = 12.19, $P < 0.02$. A significant interaction was also found between the type of movement pattern and the required response rate, $F$ (9, 81) = 3.12, $P < 0.03$, $\epsilon = 0.485$. A test of simple effects (Bonferroni $t$ test) revealed significant differences in the BP onset times between the two movement patterns at each of the required response rates with the exception of 2.0, 4.5 and 5.0 Hz. In Fig. 4, this can be seen in terms of the difference between BP onset times when comparing the two movement patterns.

### Spectral analysis

The data were grouped by movement pattern (3-finger vs. 2-finger) and electrode location ($C_3$ and $C_4$) after preliminary analyses showed no significant effects for the direction of movement. Two frequencies (0.5 and 2.0 Hz) in the reduced spectra were found to show similar significant effects within this classification. For the 0.5 Hz mode, significant effects were found for both rate and the initiating hand at the two electrode locations, $C_3$ and $C_4$ (Fig. 5a and 5b), $F$ (9, 99) = 6.98, $P < 0.01$, $\epsilon = 0.412$ (RATE), $F$ (1, 11) = 8.93, $P < 0.01$ (SIDE) at $C_3$, and $F$ (9, 99) = 5.78, $P < 0.01$, $\epsilon = 0.716$ (RATE), $F$ (1, 11) = 7.96, $P < 0.01$ (SIDE) at $C_4$ respectively. That is, we find greater magnitude in the 0.5 Hz component with increasing rate

predominantly at the contralateral side of the hand initiating the movement.

Under the 2.0 Hz mode (Fig. 5c and 5d) a similar set of results was obtained. That is, we find an increase in magnitude of the 2.0 Hz spectral component with faster required movement frequencies, which is predominant over the scalp electrode location contralateral to the side of finger initiating the movement. For this frequency mode, we found significant effects for both rate and the initiating hand at the two electrode locations, $F$ (9, 99) = 5.64, $P < 0.01$, $\epsilon = 0.562$ (RATE), $F$ (1, 11) = 7.38, $P < 0.01$ (SIDE) at $C_3$, and $F$ (9, 99) = 5.43, $P < 0.01$, $\epsilon = 0.794$ (RATE), $F$ (1, 11) = 6.98, $P < 0.01$ (SIDE) at $C_4$. No
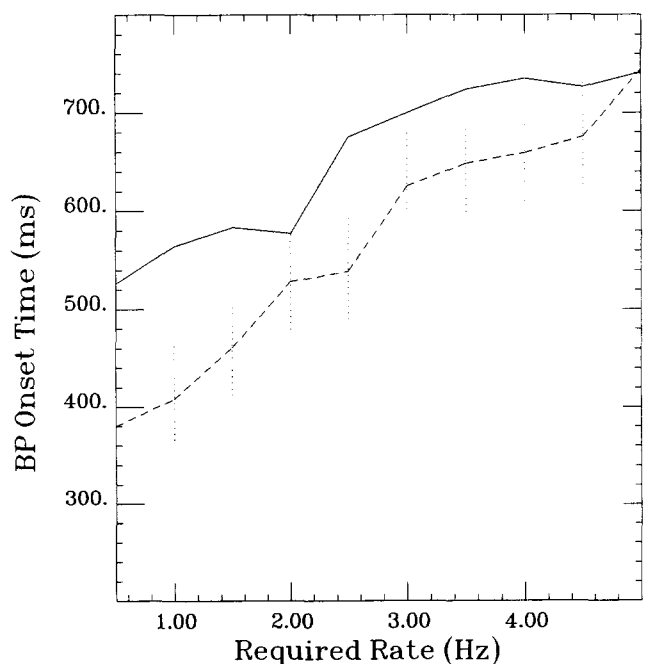


Fig. 4. The onset times for the Bereitschaftspotential as a function of the required response rate and type of movement pattern (large onset times indicate the BP began earlier). The solid line refers to the 3-finger response pattern, while the 2-finger pattern is represented by the broken line. Error bars refer to 2 times the standard error.

significant interaction effects were found at the $P < 0.05$ level for any of these conditions.

## Coherence

Since the phase values obtained from the fast Fourier transform are only valid for spectral frequencies of significant power, a measure of "shared power" between two signals is essential for reliable calculations of their relative phase angle at a specific frequency. Subsequently, a coherence analysis was performed in the frequency domain. To quantify this, the coherence magnitude at each spectral frequency was normalized by dividing this value by the summed coherence across the entire spectrum. When taken together, the 0.5 and 2.0 Hz spectral frequencies accounted for over 73% of the total coherence, indicating a substantially large portion of the shared power at these values of the spectrum.

## Relative phase

The phase angle at electrode locations $C_3$ and $C_4$ was calculated at both of the frequency modes showing high coherence, 0.5 and 2.0 Hz, and the difference between the angles (relative phase = $C_3 - C_4$) was then derived and averaged from these single-trial spectra. In the calculation of relative phase used here, positive values refer to elec-

trode location $C_3$ leading $C_4$. This value of relative phase indicates the degree of synchrony of two signals at a specific spectral frequency. Small values such as those near zero indicate the signals to be approximately in phase with each other.

The analysis of these data showed a significant side by required response rate interaction for both of the spectral modes, $F$ (18, 198) = 3.47, $P < 0.03$, $\epsilon = 0.584$ (0.5 Hz component), and $F$ (18, 198) = 3.29, $P < 0.03$, $\epsilon = 0.512$ (2.0 Hz component). In Fig. 6a and 6b, the averaged relative phase is plotted against the required movement rate for both the 0.5 and 2.0 Hz data. For both of these frequency components, there exists a distribution where the relative phase between electrode locations $C_3$ and $C_4$ becomes smaller over a restricted region of required response rates (e.g., 1.0 and 2.0 through 3.5 Hz), indicating a greater degree of synchrony between these cortical sites.

Perhaps an even more interesting relationship exists, however, when examining the variance in the relative phase as shown in Fig. 6c and 6d. Both spectral frequencies show similar U-shaped distributions indicating greater stability in the phase (stability is defined as being inversely proportional to the variance) over the middle range of required response rates (2.0 through 3.5 Hz) with smaller values of relative phase approaching zero.
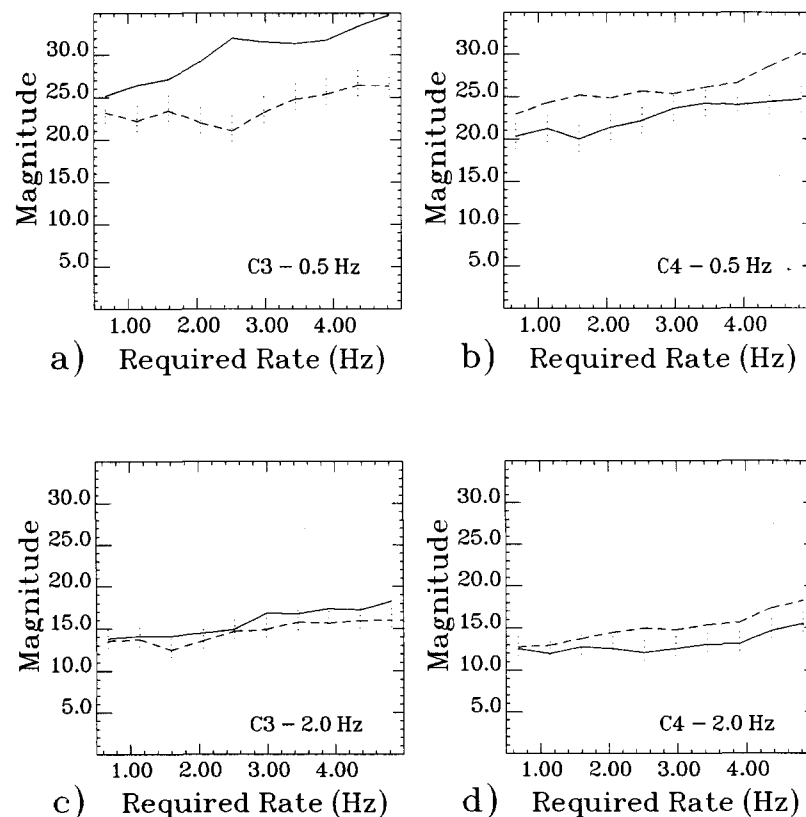


Fig. 5. The magnitudes of two spectral components presented by initiating hand (left is broken) and the required response rate at electrode locations (a) $C_3$ – 0.5 Hz mode, (b) $C_4$ – 0.5 Hz mode, (c) $C_3$ – 2.0 Hz mode, and (d) $C_4$ – 2.0 Hz mode. Error bars refer to 2 times the standard error.
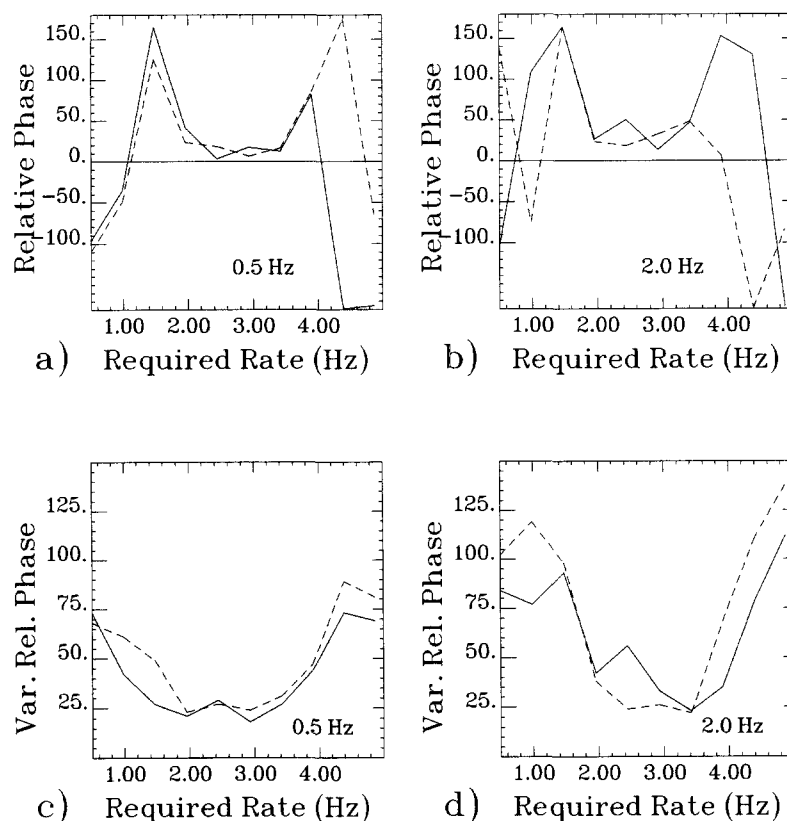
Fig. 6. a and b: the averaged relative phase (degrees) between electrode locations $C_3$ and $C_4$ as a function of required response rate and initiating hand (left is broken) derived at the 0.5 and 2.0 Hz spectral frequency modes. Positive values refer to electrode location $C_3$ leading $C_4$. c and d: the variance in relative phase plotted in a similar manner for the 0.5 and 2.0 Hz spectral frequency modes. Error bars refer to 2 times the standard error.

On comparison of these distributions with the inter-response times shown earlier in Fig. 1b, one can clearly see a striking similarity in their structure in terms of the quadratic quality. A chi-square test showed that both distributions of the variance in relative phase when compared with the variance in inter-response times are consistent with a single distribution, $\chi^2 < 0.3$, $df = 11$, $P > 0.95$ in all cases.

For the 0.5 Hz mode there appears to be a preferred phase relationship specifically at the 2.0–3.5 Hz response rates, as can be seen from the stability of the observables (i.e., variance in relative phase decreases). The relationship is less clear for the 2.0 Hz mode, however, as the distribution for the variance in the relative phase shows increased kurtosis (relative to 0.5 Hz from an averaged $-1.65$ to $-0.89$), while the standard deviation decreases from 101.2 to 72.5. Thus a phase preference is more difficult to see at this frequency mode.

## 3. Discussion

The study of timing in motor control has a long and rich history of looking for mechanisms (Church 1984). Various central time-keeping models have been advanced as a basis

for the production of temporal intervals (e.g., Vorberg and Hambuch 1984). This line of research has now progressed to the point where neurophysiological correlates of the phenomenon are being sought. For instance, Treisman (1984) postulated and subsequently rejected the idea that the cerebral alpha rhythm (8–12 Hz) may serve as an index for a central time base or perhaps be paced by it (Treisman 1984). Although the present study is not focused toward producing evidence for a *timer*, it is concerned with issues in *timing* on both the neurophysiological and behavioral levels of observation. The data suggest that certain observables at both the behavioral and neural levels (phase relations, spectral modes) share common temporal features, particularly with respect to their stability.

### The BP amplitude increases as a function of rate

Our principal finding for the BP amplitude showed it was enhanced at faster required movement rates, a result that was further accentuated at the site contralateral to the initial finger response. Even though our motor response had different characteristics than that of Cooper et al. (finger flexion rather than a tracking task), we found a similar effect on the mean amplitude of the BP with respect to the rate of the impending movement. However,

to our knowledge this is the first evidence of an increase in BP which is dependent on the rate of movement for a sequence of *bimanual* finger flexions. Moreover, recall from the behavioral data that the second response time (but not the first) changed significantly as a function of the required response rate. Thus it would seem that the amplitude changes in the BP are perhaps more related to the interval between the first and second responses than the first response itself.

### The BP begins earlier for the 3-finger motor sequence

The principal result from the analysis of BP onset times is that in general the BP begins earlier (prior to the first response time) for the faster required response rates (Fig. 4). This is not what one might have predicted considering past research. For example, Becker et al. (1976) found the BP to begin at approximately 800 and 1300 msec prior to fast and slow movements respectively. The authors suggested that in this case, the distinction could be made between "rapid ballistic" and "slower smooth" movements.

The apparent disparity in our results when compared with those of Becker et al. may be due to the language being used to describe the results in addition to the paradigm itself. One reason for their earlier BP onset times when compared to our results may stem from the fact that they employed a self-initiated response, while we used a signal-based paradigm (i.e., subjects were instructed to anticipate the imperative signal and initiate the response sequence immediately thereafter). The possibility that changes in the nature of the movement (i.e., including self-paced versus externally paced responses) produce changes in the structure of the BP has been suggested before (e.g. Deecke et al. 1985). Furthermore, our response was also different from Becker et al. in that we required a rhythmic sequence of movements while they only asked their subjects to produce a single response (Becker et al. 1976).

Still another problem in this area arises from the relationship between BP and contingent negative variation (CNV). CNV is a slow cortical event-related potential which is somewhat similar in appearance to the BP. It has typically been described as having an early and late component, with the early portion being more related to attentional aspects of a task and the later being related to motor preparation (Gaillard 1980). Rohrbaugh et al. (1977) have found the distributions of the BP and late portion of the CNV during a reaction time task to be similar. Thus it is possible that the two slow waves may have similar origins neurally, however, this still remains a mystery at the moment.

Given the nature of the paradigm we used in this study, it is likely that what we are calling BP may also have CNV contributions as well. However, the effects for the BP amplitude involving contralateral enhancement in addition to the method of back-averaging to the response are more consistent with a motor potential interpretation than CNV.

### Two spectral frequencies show an amplitude modulation as a function of the required response rate

A somewhat surprising finding of the present study was that the spectral data appeared to be amplitude modulated rather than frequency modulated as a function of differences in the required response rate. From earlier work on "assimilated rhythms" there is evidence to expect frequency modulation of the EEG with respect to a driving stimulus (John 1967). That is, following the removal of a rhythmic stimulus, there appear to be dominant frequency shifts in the EEG which correspond to that of the previous stimulus. Such effects are related to stimulus characteristics that persist in the EEG after a period of entrainment to the signal. In the present experiment, a possible reason for the lack of frequency modulation is that the pacing metronome was not on long enough for a sustained rhythm to develop in the EEG. No consistent frequency shifts could be found among the frequency bands that reliably corresponded to changes in the required response rate.

In general, we found an increased magnitude in both the 0.5 and 2.0 Hz frequency components that corresponded to increases in the required response rate. Furthermore, the magnitude of both frequency components was found to be larger at the electrode location contralateral to the side of the movement initiation hand.

Based on the properties of the FFT, we may think of the spectral frequency components resulting from this expansion as linear harmonic oscillators. One interpretation of the increase in magnitude at 0.5 and 2.0 Hz with increases in the required response rate is that these two oscillatory components increase their amplitude when faster response rates are required. The effect for 0.5 Hz component is somewhat predictable considering the structure of the BP. Despite removing the linear component of the signal prior to calculating the FFT, a quadratic component was still present in some of the trials, such that when considering the length of our spectral decomposition period (approximately 1150 msec), an increase in BP amplitude with faster required response rates might be reflected in the magnitude of the 0.5 Hz frequency component.

The 2.0 Hz component is a bit more difficult to interpret. From our perspective the 2.0 Hz component is an oscillatory mode that may be seen as a signature on the neurophysiological level which corresponds with the timing properties of the forthcoming response sequence, yet may not be specific to them [1].

Recall that the behavioral data strongly suggest a preferred movement frequency at the 2.0 Hz response rate. It has been shown before that the presence of a periodic stimulus can produce a similar rhythm in the EEG, and that this may persist in the EEG even after the removal of the stimulus (John 1967). However, to our knowledge it

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[1] It is interesting to note that Wang and McCormick (1992) have recently identified a subset of pyramidal cells in layer V of the cortex which fire autonomously in the 2.0 Hz range.

has not been previously shown that the presence of a dominant frequency in the EEG is related to the timing of the behavioral pattern it precedes. Consequently, one possibility is that the 2.0 Hz component may in some way be related to the increased accuracy of the movement times at the 2.0 Hz required response rate. This raises questions with regard to learning and the effect of practicing other time intervals on the frequency components in the EEG.

*The relative phase between $C_3$ and $C_4$ shows stability characteristics similar to the impending motor sequence*

Perhaps the most interesting effect in relation to the present work is the finding that the relative phase between electrode locations $C_3$ and $C_4$ at the 0.5 and 2.0 Hz spectral components is related to the stability of the behavior it precedes. As mentioned earlier, stability may be defined operationally as being inversely proportional to the variance in inter-response times. Thus from a visual examination of these distributions (Fig. 1c) when compared to both of the distributions of variance in the relative phase (Fig. 6c and d), a striking correspondence becomes apparent, namely, both distributions show greatest stability (minimum variance) for the required response rates of 2.0–3.0 Hz.

The above observations suggest the existence of specific properties (such as the relative phase between different parts of the brain) on the neurophysiological level which may be used to characterize some aspects of the movement itself. Of importance is the observation of a tendency toward increased synchrony between different spatial regions of the brain over a limited region of required response rates and that at these rates there is greater stability in this measure of synchrony which consistently precedes the more stable movement patterns observed on the behavioral level.

An increasing number of papers can be found addressing this issue. Some work has been done which has found phase reversals between cell groups in the basal ganglia (caudate nucleus) and the ventral posterolateral (VPL) nucleus of the thalamus preceding movement (Tsuda 1984). Other groups have found temporal coherence between cell assemblies in the medial thalamic region and premotor cortex in a CNV paradigm (Haider et al. 1979), however, no frequency analysis was performed on the data. From these experiments as well as the human EEG and MEG research presently being conducted in this area, a picture has emerged clarifying the need for more sophisticated analysis other than simply looking for temporal correlations (for a review see Birbaumer et al. 1990). Phase and frequency locking have also been found on the single cell level as well as between different columns in the striate cortex (e.g. Gray et al. 1989).

Perhaps still more ubiquitous, however, is the tendency for biological systems to be nearly phase-locked. In the finger adduction-abduction experiments by Kelso (1981, 1984), there is a *tendency* for homologous muscles to be

in-phase rather than pure phase-locking. Kelso has argued that by staying near but not *in* mode locked states, the organism retains enough flexibility needed to change from state to state in a rapid manner yet still maintains stability while in a specific state. This perspective has recently been advocated as a general theme for the functioning of complex systems with many degrees of freedom (Kelso et al. 1991).

More recently, several groups have found coherent oscillations in the 25–35 Hz range in the local field potentials of the primary motor cortex of monkeys preceding unilateral hand movements (Gaál et al. 1992; Murphy et al. 1992). The observed tendency in our own experiment toward a reduction in the variance in relative phase is suggestive of cooperativity among different parts of the brain. That is, one would expect a form of "information exchange" or "coupling" to have taken place for such a reduction to have occurred. These changes in the stability of the relative phase and the robustness of the 2.0 Hz spectral component indicate a high degree of coherence between the left and right areas of the fronto-central cortex prior to those movement sequences carried out with the greatest accuracy and stability, namely those performed at approximately 2.0 Hz. Thus it seems that frequency and phase stability properties (such as the appearance of frequency and/or phase coherence) may play an important role in the neural information processing which precedes movement.

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