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RESEARCH ARTICLE

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Spatiotemporal reorganization of electrical activity in the human brain associated with a timing transition in rhythmic auditory-motor coordination

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Abstract We used a 61-channel electrode array to investigate the spatiotemporal dynamics of electroencephalographic (EEG) activity related to behavioral transitions in rhythmic sensorimotor coordination. Subjects were instructed to maintain a 1:1 relationship between repeated right index finger flexion and a series of periodically delivered tones (metronome) in a syncopated (anti-phase) fashion. Systematic increases in stimulus presentation rate are known to induce a spontaneous switch in behavior from syncopation to synchronization (in-phase coordination). We show that this transition is accompanied by a large-scale reorganization of cortical activity manifested in the spatial distributions of EEG power at the coordination frequency. Significant decreases in power were observed at electrode locations over left central and anterior parietal areas, most likely reflecting reduced activation of left primary sensorimotor cortex. A second condition in which subjects were instructed to synchronize with the metronome controlled for the effects of movement frequency, since synchronization is known to remain stable across a wide range of frequencies. Different, smaller spatial differences were observed between topographic patterns associated with synchronization at low versus high stimulus rates. Our results demonstrate qualitative changes in the spatial dynamics of human brain electrical activity associated with a transition in the timing of sensorimotor coordination and suggest that maintenance of a more difficult anti-phase timing relation is associated with greater activation of primary sensorimotor areas.

Key words Rhythmic coordination · Transition · Motor cortex · Spatial reorganization · Human

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Introduction

Rhythmic coordination is common to many activities we encounter in everyday life. For example, dancing, playing a musical instrument, typing, riding a bicycle, all require that the brain integrate incoming sensory information and outgoing motor commands in a regular, patterned fashion. Here we focus on a simplified form of rhythmic coordination, periodic finger flexion paced by an auditory metronome. It is well known from previous studies that the stability of certain coordinative states under these task conditions depends on the frequency of coordination (Kelso 1984; Kelso et al. 1990; Wimmers et al. 1992). When subjects are directed to maintain a 1:1 relationship between repeated finger flexion and a periodic external metronome in a synchronized fashion, they are able to do so across a wide range of continuously increasing metronome frequencies (approximately 0.7–4.0 Hz for an auditory metronome). However, under instructions to flex *in between* successive metronome beats (i.e., in an anti-phase or syncopated manner), subjects spontaneously shift to a synchronized mode of coordination when the metronome frequency increases beyond a critical point. If the metronome frequency is subsequently decreased back to its initial rate, subjects do not spontaneously switch back to an anti-phase relation (Kelso et al. 1990), suggesting that synchronization is an inherently more stable timing relation at all frequencies. This conclusion is supported by the work of Scholz and Kelso (1990; see also Kelso et al. 1988), which investigated the ability of subjects to intentionally switch between syncopated and synchronized modes of coordination at a single frequency. Their results showed significantly longer switching times when subjects had to go from in-phase to anti-phase coordination when compared with the reverse. Also consistent are recent results demonstrating that a greater degree of attention is required to maintain an anti-phase versus in-phase mode of rhythmic bimanual coordination (Temprado et al. 1999).

Previous studies by our group have used the syncopation-synchronization transition to investigate neural pro-

cesses [as reflected, e.g., in large-scale electrode or SQuID (Superconducting Quantum Interference Device) recordings] that underlie stability and change in rhythmic coordination. We have consistently observed a periodic component in human brain electrical and magnetic activity at the frequency of behavioral coordination (whether unimanual or bimanual) and have found that qualitative changes in the temporal evolution of that activity accompany the transition from syncopation to synchronization. These changes include a parallel transition in the phase of magnetoencephalographic (MEG; Fuchs et al. 1992; Kelso et al. 1991, 1992) and electroencephalographic (EEG; Wallenstein et al. 1995) signals with respect to the metronome. In addition, just prior to the switch in timing, phase measures at brain and behavioral levels show enhanced fluctuations and increased relaxation times (Fuchs et al. 1992; Kelso et al. 1991, 1992; Wallenstein et al. 1995). These are both key features of instability predicted by theories of self-organization, particularly synergetics (Haken 1983, 1987).

Here we examine the question of whether the switch to a synchronized timing relation also entails a spatial reorganization of brain activity. Related studies have reported changes in the involvement of active brain areas during performance of rhythmic movement tasks as a function of several task parameters. For example, faster movement rates are associated with increased activation in primary sensorimotor cortex (SM1; Jenkins et al. 1997; Rao et al. 1996; Sadato et al. 1996, 1997), higher-order motor areas, including premotor cortex (on the dorsolateral hemispheric surface) and the supplementary motor area (SMA, in the medial wall of the hemispheric fissure), as well as the cerebellum (Jenkins et al. 1997). The way in which the movement is paced is also of importance, with self-paced movements resulting in stronger SMA activation than externally paced movements (Halsband et al. 1993; Larsson et al. 1996; Rao et al. 1997). A third movement attribute of particular relevance is the complexity of the movement. Several areas are thought to play a greater role in producing more difficult movement patterns, including SMA, premotor cortex, posterior parietal cortex, the basal ganglia, and ipsilateral SM1 (Boecker et al. 1998; Catalan et al. 1998; Chen et al. 1997; Gerloff et al. 1997; Kitamura et al. 1993; Lang et al. 1990; Sadato et al. 1996; Shibasaki et al. 1993).

We now report evidence that the transition from one stable mode of rhythmic coordination to another involves qualitative changes in the spatial pattern of cortical activity. Employing a full-head EEG electrode array, we found that different rhythmic timing relationships in behavior (syncopation and synchronization) are associated with unique spatial distributions of neural activity. We further show the spatial differences to be localized to left central and centroparietal recording sites, which most likely reflect changes in activity of the underlying SM1. Finally, we demonstrate that the timing relationship between stimulus and response (anti-phase or in-phase), rather than the rate of coordination, is the key contributing factor that determines the spatiotemporal pattern of electrical activity in this type of rhythmic coordination task.

Materials and methods

Subjects

Six male subjects, aged 24–47 years, participated in all experimental conditions. All subjects were right-handed according to self-reported responses to the Edinburgh handedness inventory (Oldfield 1971). Informed consent was obtained from all subjects prior to the experiment and the study was approved by the institutional review board.

Task conditions

Four conditions were included in this experiment: two sensorimotor coordination conditions and two control conditions. In the coordination conditions, a series of auditory tones (1.1 kHz, 80 ms duration) were presented at a periodic rate, which increased from 1.0 to 3.0 Hz in increments of 0.25 Hz after every 10 tones. Each series of 10 cycles at a single rate is referred to as a *plateau*; nine plateaus constituted a run. Each subject performed 60 runs of each condition in two 30-run sessions. Instructions for the *syncopate* condition were to produce peak flexion halfway between consecutive tones, i.e., with a 180°, or anti-phase relationship. For the *synchronize* condition, subjects were told to coincide peak flexion with the tones (0° or in-phase). This condition provided a control for the effect of plateau frequency. In both coordination conditions, subjects were instructed to maintain a 1:1 stimulus-flexion ratio at all times, regardless of whether or not they could do so with the correct phase relation; that is, if they felt their motor pattern begin to change, they should not resist the change at the cost of abandoning the required flexion rate. In the *motor-only* control condition, subjects were instructed to flex their right index finger at a comfortable pace, with no stimuli being delivered. Finally, in the *auditory-only* control condition, subjects were instructed not to respond as they listened to a series of tones presented at a rate of 1.0 Hz.

Experimental procedure

All subjects were informed of the possible risks and benefits associated with their participation, as well as the nature of the experimental tasks. Subjects were seated in an armchair inside a sound-attenuating chamber (Industrial Acoustics Company). The auditory metronome was presented to subjects binaurally through plastic headphones. Each subject's right arm was abducted approximately 30° at the shoulder, with the forearm supported in a pronated position by an armrest. Movement of the right index finger was monitored via an air-cushion pressure sensor located beneath the fingertip. The air cushion was inflated such that subjects could not depress it all the way in order to ensure definition of peak flexion (i.e., maximal displacement). Since the tasks required timing of peak flexion with an external stimulus, it was not necessary to monitor EMG activity associated with contraction of the flexor muscles. Pilot work, however, revealed a consistent temporal delay (120±15 ms) between the onset of EMG activity in the flexor carpi radialis muscle of the subject's right arm and peak flexion measured with the same pressure device used in this experiment.

The onset of each run was cued with three rapid auditory tones. Subjects were instructed to maintain fixation on a marked point approximately 1 m in front of the eyes and to refrain from all body and facial movements. Short breaks were provided between runs and longer breaks after each block of five runs. To familiarize subjects with the experiment, the coordination tasks were demonstrated before recording began.

Data collection

EEG activity was recorded during task performance from 61 electrodes placed on the scalp according to an expanded 10/20 international system of electrode placement (Fig. 1). Electrode impedance was reduced to less than 10 kΩ. During recording, each electrode was referenced to a left mastoid electrode and then later, off-line, re-referenced to the mean of the left mastoid and electrode T8 (on the right side of the head) in order to minimize lateral bias. Signals were amplified (gain 10^5) using Grass 12A5 amplifiers (–6 dB at 0.1 and 30 Hz, 4.5 dB per octave falloff), and sampled at 128 Hz (12-bit A/D conversion using two Vaxlab ADQ32s). Eye movements were monitored by referencing the medial upper to lateral lower portions of the orbital rim. Auditory stimuli and finger pressure data were also digitized at a rate of 128 Hz as described above.

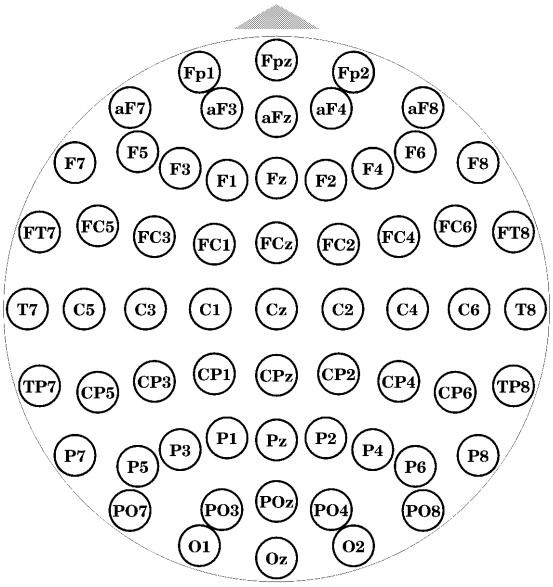


Fig. 1 Projected top view of electrode positions. The subject's nose would be in front of Fpz

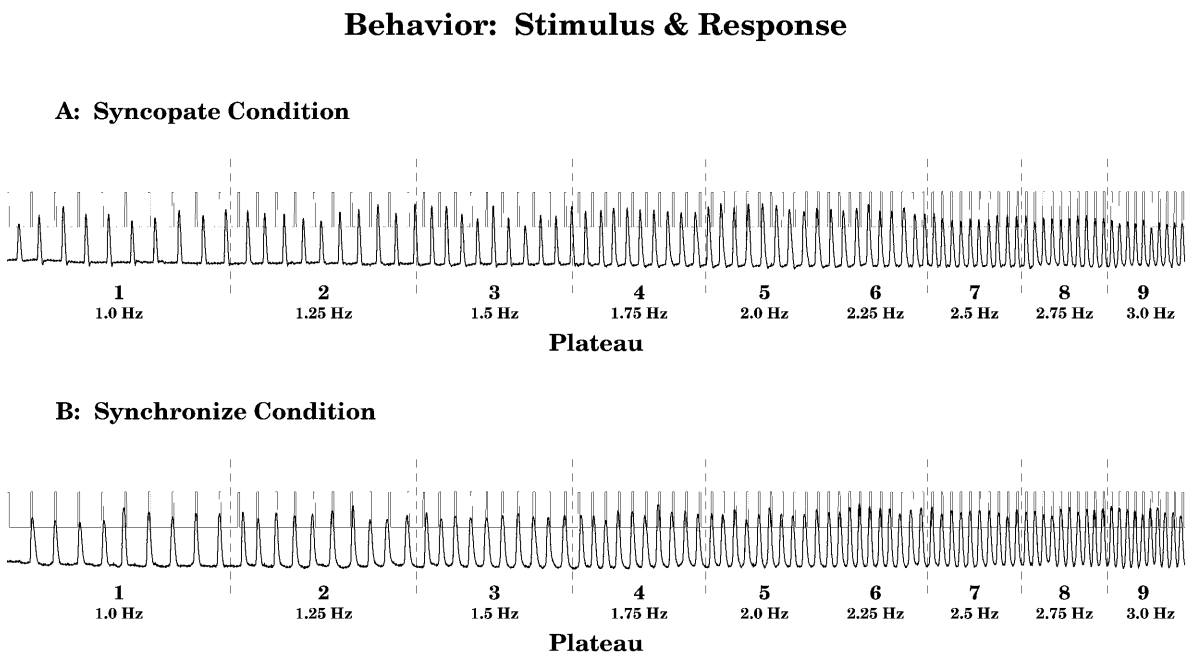
Behavioral analysis

The relative phase between peak flexion and stimulus onset was calculated for each cycle per run in the coordination conditions and then used as the basis for segregating cycles according to the type of coordination performed. Two modes of coordination were studied: syncopation and synchronization. Syncopation cycles were classified as those whose relative phase fell within a ±50° window centered on the mean relative phase value averaged across the subject's first three plateaus in the syncopate condition. Syncopation phase values ranged from 120° to 220° across subjects. For all subjects, synchronization cycles were defined as those within a ±50° window around 0° (with 0° representing exact coincidence of peak flexion with the stimulus). At least 5 consecutive cycles with consistent coordination were required to classify them as syncopated or synchronized. Where indicated, transition cycles refer to any cycle occurring in the transient region between stable episodes of syncopation and synchronization.

EEG analysis: averaging and topographic mapping

First, cycles for which the EEG was free from artifacts due to eye or other movements were selected and grouped into sets according to condition, coordination mode (syncopation or synchronization), plateau, and subject. Second, brain neuroelectric activity was averaged relative to stimulus onset for each set, which contained at least 50 artifact-free cycles. Third, the discrete Fourier transform was applied to the averaged waveshape to obtain power spectra. Because the duration of each averaged waveform equaled the metronome cycle period, the fundamental frequency in each spectrum was the required coordination frequency. Finally, power spectra were averaged across subjects (weighted according to the number of cycles) for combinations of condition, coordination mode, and plateau, having means from at least five of the six subjects. Grand-averaged power spectral values at the coordination frequency were

Fig. 2 Stimulus (*top trace*) and finger-pressure (*bottom trace*) channels from single runs for both coordination conditions. **A** Syncopate; **B** Synchronize. Note the loss of syncopated coordination beginning around plateau 5 in the syncopate condition, followed by a synchronized mode of coordination. There is no transition in the synchronize condition



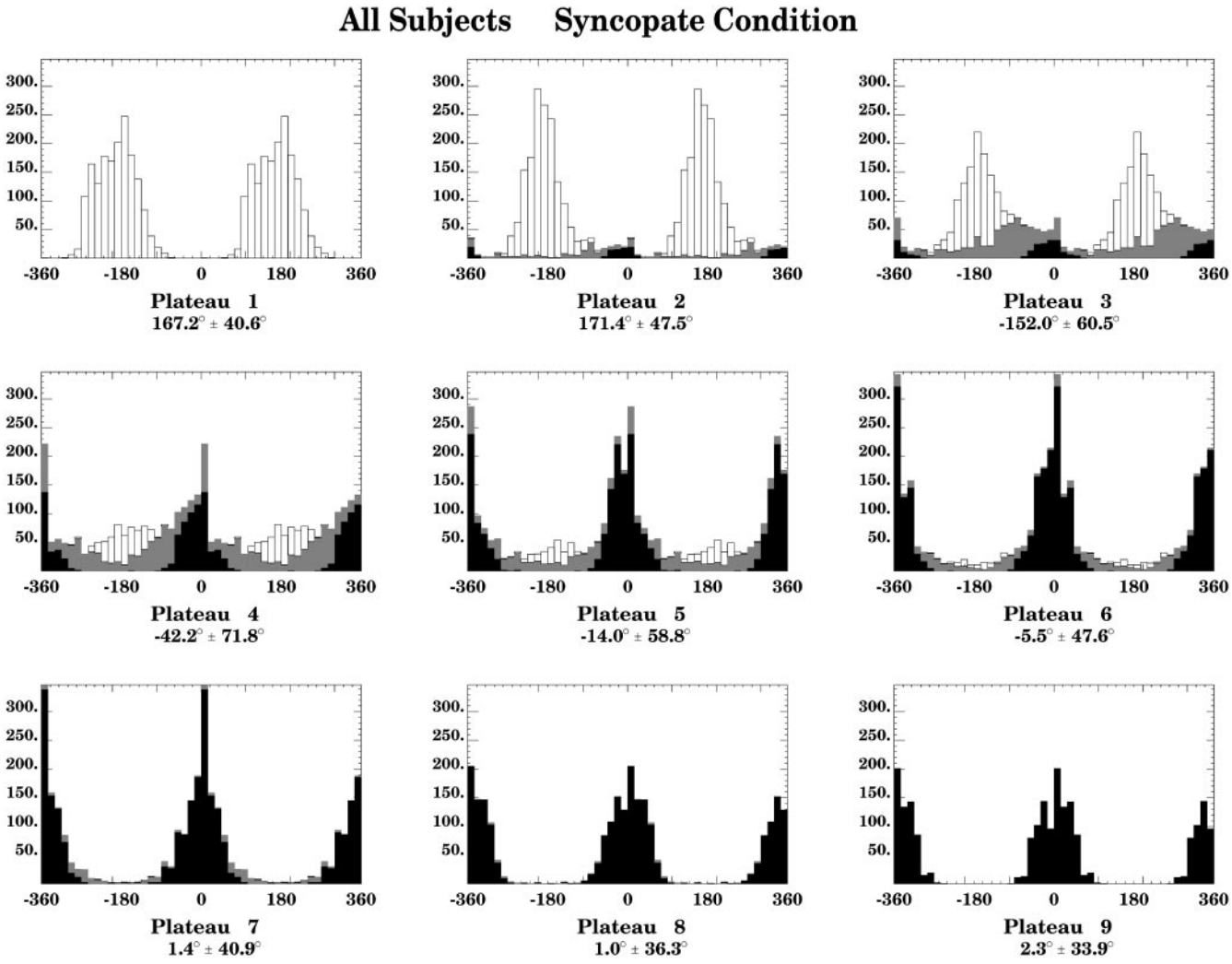


Fig. 3 Group relative phase distributions for the syncopate condition. *Bars* are shaded according to coordination mode: syncopation, *white*; transition, *gray*; synchronization, *black*. Note the onset of transitions as early as plateau 2 and as late as plateau 7

mapped at standardized electrode locations on a three-dimensional model head. Map values for locations between electrodes were spline-interpolated.

Grand-averaged power spectra from the auditory-only and motor-only control conditions were computed relative to stimulus onset and peak flexion, respectively, in similar fashion. Due to the self-paced nature of the motor-only condition, each subject produced cycles having a characteristic inter-peak interval. The fundamental frequency component in the resulting power spectra thus corresponded to each subject's preferred flexion frequency.

Statistics

Topographic similarity between power maps was assessed with a Pearson correlation, using power values at each channel as observations. Power values were also subjected to two-way analysis of variance (ANOVA) to investigate statistical differences in the spatial distribution of power. These values were pooled across subjects and plateaus and weighted the same way as when calculating grand-averaged power. Post hoc pairwise channel comparisons for significant interactions were computed using the conservative Tukey's HSD procedure (Kirk 1968).

Results

Behavior

All subjects were able to maintain syncopated coordination in the early plateaus of the syncopate condition, and synchronized coordination throughout the entire run in the synchronize condition. Figure 2 shows the stimulus and finger-pressure time series (top and bottom rows, respectively) from representative runs in the syncopate and synchronize coordination conditions. In the run shown for the syncopate condition, a transition from syncopated to synchronized coordination occurred during plateaus 5 and 6 (Fig. 2A). Approximately 65% of all runs from this condition showed a transition to synchronization, although the plateaus in which the transitions occurred varied somewhat across runs and subjects. For example, one subject switched to synchronized coordination as early as plateau 2 (1.25 Hz), while another subject maintained syncopated coordination as late as plateau 7 (2.5 Hz) before switching. The majority (72%) of transition regions, though, included plateaus 4 or 5 (1.75–2.0 Hz). In the runs that did not exhibit a clear-cut transi-

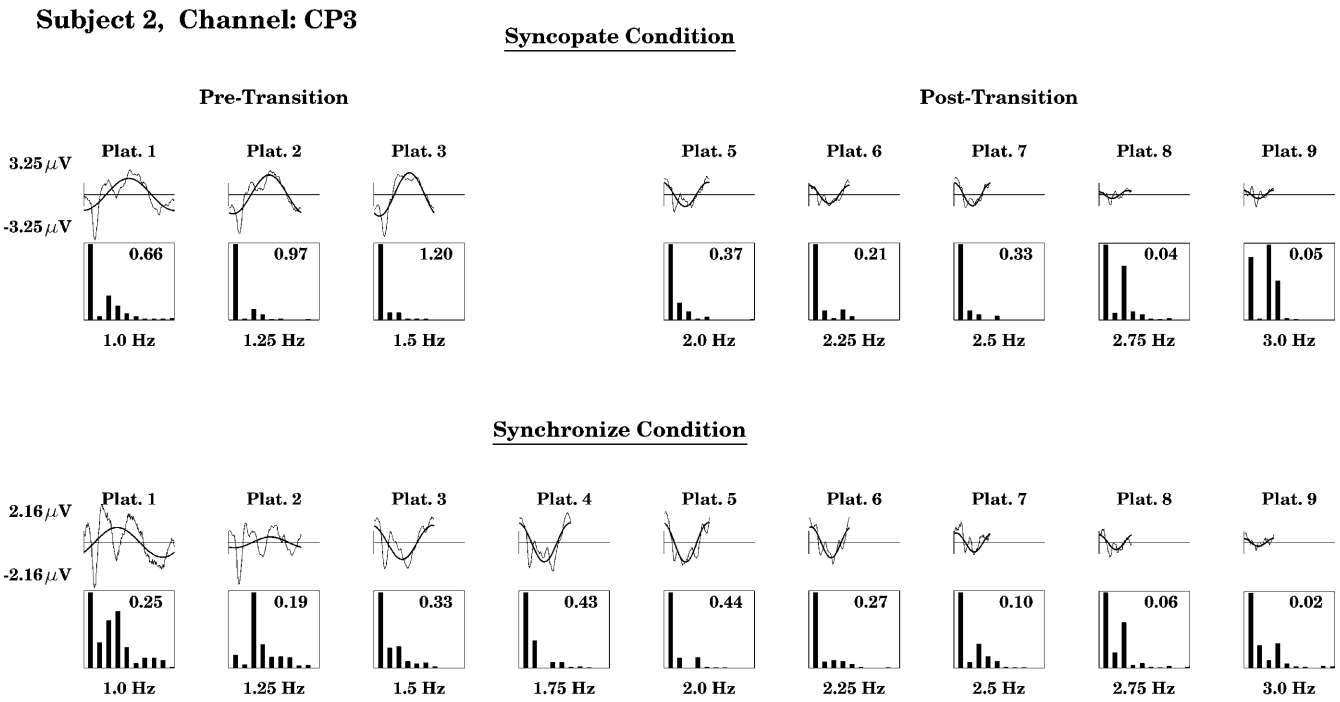


Fig. 4 Averaged brain activity and corresponding power spectra for one subject from electrode CP3 (which lies approximately over primary sensorimotor cortex in the left hemisphere) in both coordination conditions. Power is plotted for the first ten frequency components in the spectrum. (Higher frequencies showed negligible power). Due to the fact that each averaged waveshape is exactly 1 cycle period in duration, the fundamental frequency in each spectrum corresponds to the labeled coordination frequency. For both conditions, almost all channels showed a concentration of power at this frequency across plateaus. Means are scaled to ±3.25 μV and ±2.16 μV for the syncopate and synchronize conditions, respectively. Power spectra are individually scaled to illustrate the prominence of the coordination rhythm; values in the upper right hand corner indicate amplitudes of the largest frequency component in microvolts squared. Note the difference in power during syncopation versus synchronization at the same plateau frequencies (compare plateaus 1–3 across conditions)

tion, subjects either failed to syncopate from the beginning or were unable to settle into any stable pattern after losing syncopated coordination.

The distribution of relative phase values from the syncopate condition is broken down by plateau in Fig. 3. Mean values were 174° (±37°) for syncopated coordination (shown in white), –75° (±74°) during the transition regime (shown in gray), and –4° (±32°) for the synchronized mode (shown in black). The greater variability in the transition mode reflects the presence of phase wrapping during the transition, that is, when the 1:1 stimulus/flexion relationship was lost.

For the synchronize condition, no transitions in coordination mode were observed (Fig. 2B). Approximately 4% of the runs in this condition were excluded due to unstable coordination, which typically occurred at higher plateau frequencies. The mean phase between peak flexion and tone onset for this condition was –8° (±32°). No noticeable differences were observed in the ability of subjects to maintain synchronization across plateaus. These results confirm the established result (Kelso et al. 1990) that, in this type of task, coordination for low stimulus rates is bistable (both syncopation and synchronization are possible), whereas only synchronized behavior is stable at higher movement frequencies.

EEG

Syncopate condition

Grand-averaged power spectra were computed in the syncopate condition for syncopated coordination on plateaus 1–3 (1.0–1.5 Hz) and for synchronized coordination on plateaus 5–9 (2.0–3.0 Hz). Figure 4 shows one subject's averaged EEG and corresponding power spectra for these plateaus from a left centroparietal electrode (CP3). The predominance of power at the coordination frequency, reflecting the prominent rhythmic component at this frequency in the brain activity, was observed in 86% and 91% of the channels averaged across pre-transition and post-transition plateaus, respectively. The dominance of the coordination frequency in the brain activity is further illustrated by comparing the overlap of this single component with the averaged waveshape (Fig. 4). Note that the time series of the coordination frequency component shifts in phase by approximately 180° when the behavior switches from syncopation to synchronization (compare left and right side of Fig. 4, top). The prominence of the coordination frequency in the brain activity as well as the parallel phase shifts on both neural and behavioral levels are consistent with previous results (Fuchs et al. 1992; Kelso et al. 1991, 1992; Wallenstein et al. 1995).

Topographic mapping of power at the coordination frequency was used to examine differences in involve-

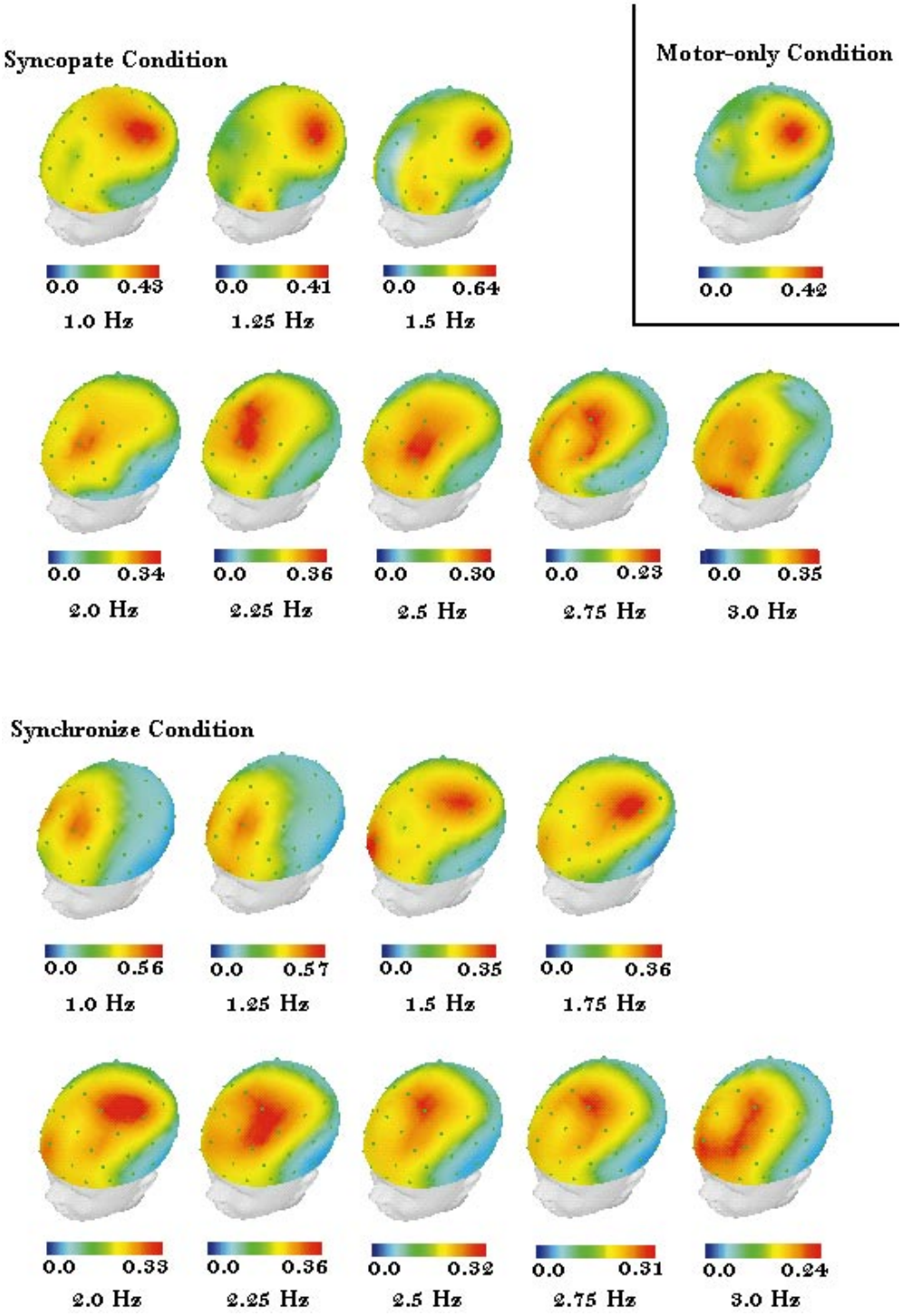


Fig. 5 Topographic patterns of grand-averaged EEG power at the coordination frequency for the syncopate condition (*top half*), synchronize condition (*bottom half*), and flexion frequency for the motor-only condition (*upper right corner*). Each plateau is independently scaled from zero to maximal power (in microvolts squared) at that frequency. Coordination frequencies associated with each plateau are shown beneath each topographic map. Syncopate condition: The three patterns in the *top row* (plateaus 1–3) are associated with syncopated coordination. Note the similar topography across the three different plateau frequencies (1.0–1.5 Hz) with maximal power at left centroparietal, central, and anterofrontal sites. Post-transition patterns for this condition (plateaus 5–9) show maximal power at more frontal sites. These patterns are also consistent across plateau frequencies, indicating a reorganization of cortical activity associated with the switch in coordination mode from syncopation to synchronization. Synchronize condition: Maximal power tends to be focused at left and midline frontal sites. Motor-only condition: power at the flexion frequency (mean 1.0 Hz) is focused at left central sites, consistent with activation of the underlying sensorimotor area during flexion of the right finger

ment of brain areas associated with syncopated versus synchronized coordination. During syncopated coordination, power was focused at left centroparietal, central, and frontal sites (Fig. 5, top row; Table 1, top left). High power in the left central region suggests activation of the underlying sensorimotor cortex (contralateral to the finger flexion). This suggestion is supported by significant correlation between patterns from plateaus 1–3 and the motor-only pattern (Fig. 5, top right; $r(59)=0.57$, 0.60, and 0.59, respectively; all $P<0.001$). After the transition to synchronized coordination, maximal power at the coordination frequency dropped in intensity and covered a broader left and midline frontal region (Fig. 5, second row; Table 1, top right). This shift in spatial distribution resulted in much weaker correlations with the motor-only control pattern (mean r-value=0.35).

Table 1 Electrode sites whose power at the required coordination frequency exceeded 75% of the maximum value for that plateau and coordination mode. Actual power values (in microvolts squared) are indicated in *parentheses* next to each electrode name. Electrodes are listed in order of decreasing amplitude

	1.0 Hz	1.25 Hz	1.5 Hz	1.75 Hz	2.0 Hz	2.25 Hz	2.5 Hz	2.75 Hz	3.0 Hz
Syncopate condition	C3(0.43) CP3(0.37) FC1(0.34) aF7(0.33)	C3(0.41) CP3(0.37) aF7(0.36) CP1(0.33)	C3(0.64) CP3(0.60) aF7(0.49)		F1(0.34) FC1(0.29) FCz(0.26) F3(0.26)	F1(0.36) FCz(0.36) FC1(0.34) F3(0.32) Fz(0.31) aFz(0.27)	F3(0.30) FC1(0.28) FC3(0.27) F1(0.27) aFz(0.25) C3(0.23) aF7(0.23) FCz(0.23) aF3(0.22)	FC1(0.23) F3(0.23) Fz(0.22) aFz(0.22) FPz(0.21) FC3(0.20) FCz(0.20) FP2(0.19) FP1(0.19)	FP1(0.35) F3(0.34) aF7(0.33) Fz(0.31) F1(0.30) FC1(0.30) aF3(0.30) aFz(0.30) FPz(0.28) FCz(0.27) F5(0.27)
Synchronize condition	F1(0.56) F2(0.50) FCz(0.45) aF4(0.42) FC1(0.42)	F1(0.57) aF4(0.52) FP1(0.50) aF3(0.46) F2(0.45) FPz(0.44)	FP2(0.35) aFz(0.33) C3(0.32) FPz(0.32) FC1(0.30) aF4(0.27) CP3(0.26) F2(0.26)	C3(0.36) FC3(0.32) FC1(0.32) aFz(0.30) F3(0.29) FPz(0.29) FP2(0.27)	C3(0.33) FC1(0.32) aFz(0.24) F3(0.30) FC3(0.29) FPz(0.28) FP2(0.28) FCz(0.27) Fz(0.25)	FC1(0.36) F3(0.36) FC3(0.35) FCz(0.34) aFz(0.33) F1(0.32) C3(0.30) Fz(0.29) F2(0.29) aF3(0.29)	FC1(0.32) F3(0.29) FCz(0.29) F1(0.26) aF3(0.25) FC3(0.24) aFz(0.24)	FC1(0.31) FCz(0.28) F3(0.28) FC3(0.26) Fz(0.25) aFz(0.25) aF3(0.23)	F3(0.24) FC1(0.24) aFz(0.23) aF3(0.22) FPz(0.22) FP2(0.20) FP1(0.20) F2(0.20) FCz(0.19) aF7(0.19) FC3(0.19)
Motor-only condition	C3(0.42) C1(0.37) FC3(0.32)								

Table 2 Electrode sites with significant differences in power at the coordination frequency. Listed are electrode sites having significant differences in power at the coordination frequency for the following cases: *Left* Syncopated (pre-transition, 1.0–1.5 Hz) versus synchronized (post-transition, 2.0–3.0 Hz) coordination in the syncopate condition; all sites shown had higher power values during syncopation (none of the 61 electrodes showed significant increases in power at the coordination frequency following the behavioral transition). *Middle* Low-frequency (1.0–1.5 Hz) versus high-frequency (2.0–3.0 Hz) synchronized coordination in the synchronize condition; power at the coordination frequency was significantly higher in the low than in the high-frequency plateaus at all sites listed. With one exception, the sites with significant differences in this comparison were in the right hemisphere, suggesting a stronger bilateral activation of frontal areas for synchronized coordination at low frequencies. *Right* Syncopated versus synchronized coordination at low frequencies (1.0–1.5 Hz from both coordination conditions); only two sites showed significant differences between coordination modes, both having larger power at the coordination frequency during syncopation. This implies that the drop in power at left central and centroparietal sites observed for post-transition plateaus in the syncopate condition was due to the change in timing relation from anti-phase to in-phase rather than an increase in coordination frequency

Pre- vs post-transition	Low vs high plateau frequency	Bistable plateau frequency
AF7**	AF4**	C3**
C5**	AF8**	CP3**
C3**	F1**	
CP5**	F2**	
CP3**	F4*	
CP1**	F6*	

**P<0.01; *P<0.05

Statistical evaluation of this difference in the spatial distribution of power by a two-way ANOVA, with coordination mode (syncopated or synchronized) and electrode location as factors, showed main effects of both coordination mode (F=120.11) and electrode site (F=10.01), as well as a significant interaction (F=1.91; all P<0.0001). Post hoc tests revealed that power at the coordination frequency decreased at the transition from syncopated to synchronized behavior at left centroparietal, central, and prefrontal sites (Table 2, left). No electrodes showed an increase in power after the transition. These results suggest a spatiotemporal reorganization of cortical activity coincident with the behavioral transition in timing from syncopated to synchronized coordination, but do not rule out the rate of coordination as a contributing factor.

Synchronize condition

The lack of a behavioral transition in the synchronize condition allowed us to differentiate effects due to the timing relationship from those due to increasing coordination frequency. Grand-averaged power spectra were calculated for all nine plateaus in the synchronize condition. As in the syncopate condition, the dominant power spectral component was at the frequency of coordination (at a mean of 92% of the channels across all nine plateaus; see Fig. 4, bottom row). The corresponding topographic patterns are shown in the middle and bottom rows of Fig. 5. To determine whether significant differences in power occurred with increasing rate of coordination, data were divided into two frequency classes: low (plateaus 1–3) and high (plateaus 5–9), and subjected to a two-way ANOVA (frequency class vs electrode location). Both main effects were again strongly significant (frequency, F=157.35; electrode site, F=19.26; P<0.0001), but the interaction between factors barely reached significance (F=1.33) at P<0.04. Furthermore, although post hoc statistical tests revealed a decline in power from low- to high-frequency plateaus at frontal and prefrontal sites (particularly in the right hemisphere), there were no significant differences at left centroparietal or central sites (Table 2, middle). Together, these results indicate that the decrease in power at left central and centroparietal sites observed in the syncopate condition was due to the change in coordination timing rather than in coordination frequency.

To further quantify the existence of frequency-independent topographic differences between states of syncopated and synchronized coordination, a final ANOVA was performed to compare the low-frequency plateaus (1–3) of each condition, at which coordinative bistability was observed.[1] This test confirmed that the topographic power patterns during syncopated coordination were significantly different (P<0.0001) from those in synchronized coordination (F=2.31). Post hoc tests showed that the difference was due to two electrode sites, left central and centroparietal (see Table 2, right), both of which exhibited higher power during syncopated coordination.

Control conditions

Unlike the coordination conditions, the strongest grand-averaged power spectral values in the auditory-only and motor-only control conditions were not, for most electrode sites, at the fundamental (rhythmic) frequency (i.e., the stimulus and flexion frequencies, respectively). Figure 6 shows why this was the case for the auditory-only condition. Shown on the left is the grand-averaged event-related potential from a frontocentral electrode (FCz). The characteristic N1-P2 evoked response to an auditory event can be clearly identified. The dashed line marks the return of the P2 component to zero at approximately a 330-ms latency. The N1-P2 complex was reflected in the spectral decomposition as can be seen by the largest concentration of power being at the second harmonic, 3 Hz (Fig. 6, right).[2] That is, 3 Hz corresponds to 1 cycle (N1-P2) in 330 ms.

For the motor-only control, however, signals recorded from left central electrodes did have a relatively large amount of power at the flexion frequency (see Fig. 5, top right; Table 1, bottom). As discussed above, these locations are consistent with activation of contralateral SM1, as expected for right-finger movements.

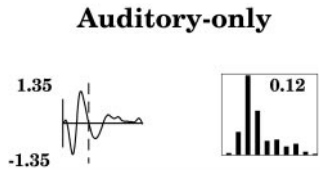


Fig. 6 A sample grand-averaged event-related potential (ERP) from the auditory-only control condition (recorded over FCz) is shown on the *left*. Since the metronome rate used for this condition was 1 Hz, the entire time series is 1 s (1 cycle) in length. The *dashed line* marks the end of the N1-P2 complex evoked by an auditory event and is 330 ms after stimulus onset. To the *right* is the corresponding DFT power spectrum. Note the maximum power value at the third frequency component in the spectrum, which is centered at 3 Hz (corresponding to the second harmonic of the fundamental cycle frequency, 1 Hz)

Discussion

This study demonstrates a spontaneous large-scale reorganization of neuroelectric activity associated with the transition between two modes of coordinative timing. The rhythmic nature of the coordination tasks was evident in the concentration of EEG power at the coordination (fundamental) frequency over large portions of the head. Concentration of power at the fundamental, or rhythmic, frequency was less prevalent for self-paced finger flexion and absent during passive listening to a auditory 1-Hz metronome. This suggests that the rhythmic EEG component during the coordination tasks is a dynamically emergent property of the integration of sensory and motor information and emphasizes the need for examining the timing of behavior with respect to the action-perception cycle rather than each component individually (Arbib 1985; Kelso et al. 1990; Pribram 1991; Warren and Kelso 1985).

[1] The topographic power spectral density patterns for plateaus 5 and higher in the synchronize condition were highly correlated with the corresponding post-transition syncopate patterns (mean r(59)=0.84) as expected, since both coordination mode and frequency were the same (compare Fig. 5, 2nd and bottom rows).

[2] Across all channels, the amplitudes of this component, although the largest in the spectrum, were still small relative to the maximal power values observed in the other three conditions, despite similar signal amplitudes for all conditions. This reflects a wider distribution of power across higher harmonics in the auditory-only control condition that was less prevalent during the coordination tasks.

Our main finding is a strong reduction in power at the coordination frequency at left central and centroparietal recording sites when behavior undergoes a transition from syncopation to a more stable synchronized mode of coordination. Since there were no observable shifts in power to other frequencies, this finding suggests a decrease in activity of SM1 contralateral to the performing hand. This conclusion may appear to contradict previous reports showing increased activity of primary motor areas with faster rates of repetitive movement (Jenkins et al. 1997; Rao et al. 1996; Sadato et al. 1997). However, the coordination task used in this experiment additionally involves a change in the inherent stability of the timing relation as well as the rate of flexion. Subjects report experiencing increasing difficulty in maintaining syncopated coordination as the plateau frequency increases and continue to satisfy task requirements (i.e., preserving the 1:1 stimulus to flexion ratio) by switching to flexion on the beat. The instability presumably arises because of centrally based constraints, e.g., an inability to prevent the auditory stimuli from entraining the central motor signals at higher coordination frequencies. Were it due to inherent biomechanical limitations, one would not expect subjects to be able to synchronize at higher rates either.

Empirical support for the hypothesis that syncopation involves a higher degree of central "effort" has been provided by several behavioral studies. For example, Scholz and Kelso (1990) demonstrated that, although subjects could intentionally switch from an in-phase to an anti-phase timing relation if expressly asked to do so, it took them longer than doing the reverse at the same metronome rate. Furthermore, in a recent dual-task study by Temprado et al. (1999), subjects showed significantly slower reaction times during maintenance of an anti-phase pattern of bimanual coordination when compared with an in-phase timing relation. This suggests that a greater degree of attention is required to maintain an anti-phase mode of rhythmic coordination, consistent with the hypothesis (Kelso 1994, 1995) that syncopation is less automatic, requiring more conscious control.

One possible explanation, then, for the decline in power of post-transition activity of the left SM1 is that the power reflects the degree of conscious control exerted in producing the motor output. The greater effort required to move at higher rates (previously associated with increases in SM1 activation; see above) may thus be masked by an even greater reduction in effort resulting from the switch in timing. This explanation is in agreement with the observation that, even at the same low plateau rates, two left central electrode sites showed significantly lower power when subjects performed a synchronized mode of coordination. The decline in amplitude may reflect a transfer of movement control from cortical to subcortical structures. Both the cerebellum and basal ganglia have been shown to be important for timing behavior (Ivry and Keele 1989; Rao et al. 1997).

An alternative explanation for the spatiotemporal reorganization is a "superposition" of auditory and motor event-related activity during synchronization that is not present during anti-phase behavior. Given that the EEG reflects extracellular current flows that are subject to volume conduction in the cerebral spinal fluid, it is possible that currents generated in distinct sources cancel each other before reaching electrodes at the scalp. While we cannot eliminate the possibility of such an interference effect, we do know from previous work (Fuchs et al. 1992) that, for the case of MEG, superimposing an auditory-evoked field with a motor-evoked field (with either an anti-phase or in-phase relation) fails to account for the spatiotemporal patterns that accompany auditory-motor coordination. This finding has limited usefulness, however, when one accounts for the effects of rate on brain activity known to exist for both auditory stimulation (Binder et al. 1994; Hari et al. 1982) and movement tasks (see Introduction). The latter consideration raises concerns about using evoked field patterns (associated with very transient events) to interpret rhythmic (steady-state) activity. Clearly, an experiment with ramped frequency controls is warranted. In addition, the auditory-evoked field described by Fuchs et al. (1992) was incomplete, since sensor coverage was limited to the centrolateral region of the left hemisphere.

A second finding in this report is the widespread left and mesial frontocentral and anterior frontal distribution of EEG power during both modes of coordination. This topography probably reflects activity in several cortical areas, possibly including left premotor cortex, SMA, and prefrontal areas, that contribute to the temporal organization of behavior. Preserving any rhythmic coordinative timing relationship in a stable fashion entails the ability to internalize the external rhythm so that one can anticipate the arrival of each metronome beat and plan one's movement to coincide with a particular phase of the rhythmic cycle. Lesion studies suggest that the timing and motor-control mechanisms that support rhythmic movements involve the cerebellum (Ivry and Keele 1989) and basal ganglia (Harrington and Haaland 1998) subcortically, as well as frontal cortical areas to which they connect, including premotor cortex, SMA, and prefrontal cortex (Halsband et al. 1993; Truelle et al. 1995). Additional support for premotor cortex, SMA, and prefrontal cortex involvement in rhythmic motor tasks comes from electrophysiological scalp recordings (Bressler et al. 1996; Gerloff et al. 1998; Lang et al. 1990) and functional magnetic resonance imaging (fMRI) imaging (Rao et al. 1997). In most of these studies, effects were significantly more pronounced during internally paced movement (e.g., reproduction of rhythms from memory) or when the rhythm was complex rather than simply repetitive (as in the Lang et al. 1990 study), thus indicating that the magnitude of premotor cortex and SMA activity relates directly to the degree to which a movement pattern must be preplanned. The present results do not differentiate between syncopated and synchronized movement patterns with respect to lateral frontal and frontocentral electrode sites, suggesting that the instability in syncopated timing is due to changes in

activation on a different level of the motor control system (perhaps in subcortical timing mechanisms). Further investigations with better spatial resolution (e.g., fMRI) will help to address this issue.

In conclusion, stable performance of anti-phase and in-phase rhythmic coordinative patterns appears to require cortical involvement of a number of central and frontal brain areas. The areas involved and the degree to which they participate depend on the specific timing relationship required between motor and perceptual processes, and may relate to the amount of central control necessary for maintenance of the coordinative pattern. An important feature of the task employed in this study was the spontaneity with which the coordination behavior and the EEG activity reorganized. This reorganization was a necessary consequence of the task requirement that the subject continue to successfully maintain an externally imposed rhythm under the cognitive load imposed by increasing frequency. To our knowledge, few studies have shown such spontaneous large-scale reorganization induced in real time by parametric task control. We suggest that the exploitation of such instabilities in behavior is a powerful way to more deeply understand the underlying neurodynamical mechanisms that contribute to flexibility in coordination behavior.

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