Phase transitions in spatiotemporal patterns of brain activity and behavior

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Abstract

Spatial patterns of brain electrical activity from 61 electrodes were recorded during a sensorimotor coordination task. Subjects were required to syncopate finger movement with a series of auditory stimuli whose rate of presentation was systematically increased as a control parameter. Spontaneous transitions from syncopated to synchronized behavior were accompanied by transitions in electroencephalographic (EEG) signals as calculated from relative phase measures. The transition was most prominent at left central and antero-central scalp sites. Fluctuations in relative phase in both the behavior and brain activity increased systematically before the transition, indicating the presence of dynamic pattern forming instabilities on both levels of observation.

In open, nonequilibrium systems a phase transition is a qualitative change in the system's behavior which takes place when a control parameter reaches a critical value [1]. Critical phenomena such as phase transitions have been shown to occur in a variety of physical systems including lasers [2], convection instabilities in hydrodynamics [3] and biological systems [4], as well as artificial neural networks [5,6]. Phase transitions are important phenomena in complex systems such as the central nervous system because their appearance can lead to specific theoretical predictions regarding state changes and also promote new lines of experimental investigation. This approach emphasizes the investigation of global properties of a system based on macroscopic quantities (commonly referred to as order parameters; see [1,2] for a review) and attempts to identify key pattern variables and their dynamical properties. Although features related to pattern formation such as the onset of phase and frequency locking have been observed in the mammalian brain [7,8,20], the existence of phase transitions[1] in brain function has only been considered recently [11–13]. Their presence points to a new kind of self-organizing mechanism for the cooperative action of neurons [10,11].

Following a previously developed paradigm [11,12,17], each subject's ($n = 6$) task was to syncopate peak flexion of the right (preferred) index finger with repetitive auditory stimuli (delivered binaurally at 1.1 KHz, 80 ms duration) that increased in their rate of presentation from 1 to 3 Hz in .25 Hz increments every 10 cycles (SYNCOPATE condition). A series of 10 cycles in which the presentation rate remained constant is referred to as a plateau and the

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[1] The term "phase transition" is incidental to the order parameter identified in the present experiment, "relative phase".

entire series from 1 to 3 Hz (90 cycles) is referred to as a run. Flexion of the right index finger was recorded as a continuous measure of pressure changes resulting from depressions of a small air cushion situated directly beneath the tip of the subject's finger. In an additional control (SYNCHRONIZE) condition, subjects were required to begin each experimental run by synchronizing peak flexion with the auditory stimuli. Both conditions consisted of 60 runs. The experiment was divided into two equal sessions run on separate days.

It is known from previous studies [11,12,17] that when subjects are asked to maintain a 1:1 syncopation pattern with the stimuli, a spontaneous change to the more stable, synchronized mode of coordination occurs at a critical movement frequency. Recent brain recordings using a circular 37-SQUID (superconducting quantum interference device) array showed that the behavioral transition from syncopation to synchronization was accompanied by an approximately 180 degree change in the phase relations of the brain signals relative to the stimuli over parieto-temporal regions of the left hemisphere [11,12]. In the present study we expanded the spatial extent of our analysis, using a 61-channel EEG recording to map the topography of task-related changes in the brain state over both hemispheres. This allowed determination of whether changes in phase relation were relatively uniform over the head, or were confined to specific regions. Of interest, in particular, was whether these changes might be localized over brain regions commonly associated with motor behavior.

The montage of 61 locations from which brain signals were recorded (based on the 10/20 International System of Electrode Placement [18]) is illustrated in Fig. 1. Each scalp electrode was referenced to the left mastoid during data acquisition, and later off-line to a balanced system of linked electrodes from the left and right sides of the scalp. Interelectrode impedance was reduced to less than 10 KΩ. Signals were amplified (10^5) using Grass 12A5 amplifiers with high and low pass analogue filters set at 0.1 Hz and 30.0 Hz respectively, and sampled at a rate of 128 Hz (12 bit analog-to-digital conversion using 2 VAXlab ADQ32s). To monitor eye movements, the EOG was recorded by
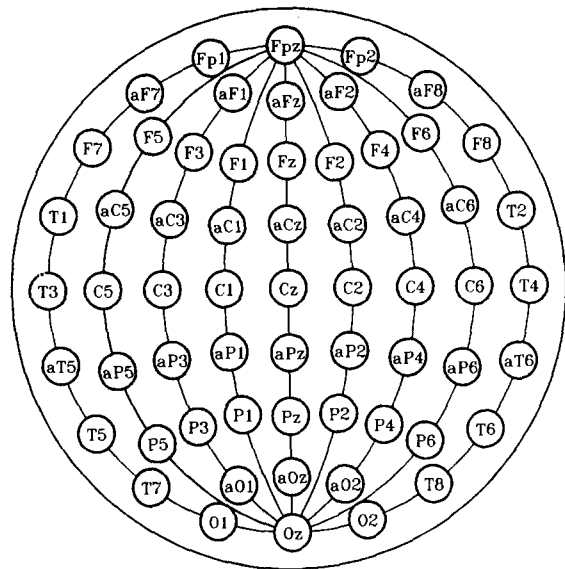

Fig. 1. A projected top view of the electrode configuration. The subject's nose would appear just in front of Fpz.

referencing the medial upper to lateral lower portions of the orbital rim. Prior to statistical analysis, all signals were visually inspected for eye, head, orofacial, or body movement artifacts which were subsequently deleted from the records before averaging. In order to ensure that recordings from a given subject were from consistent locations during the experiment, all electrode positions as well as the inion, nasion and both preauriculars were recorded 3-dimensionally using a Polhemus 3-Space Isotrack system before and after each session.

An averaged (across 54 runs from the SYNCOPATE condition) behavioral signal from a representative subject is shown in Fig. 2a along with the averaged EEG signals recorded from three left and midline central electrode locations where the signals were strongest. In order to monitor changes in the spatial and temporal properties of the brain signals due to onset of the task, spectral power and coherence [2] estimates were computed. In Fig. 2b, the power spectra of the averaged signals obtained from electrode location aC1, recorded prior to and during the experimental task (SYNCOPATE condition), are shown. Before the task began, spectral power was distributed over

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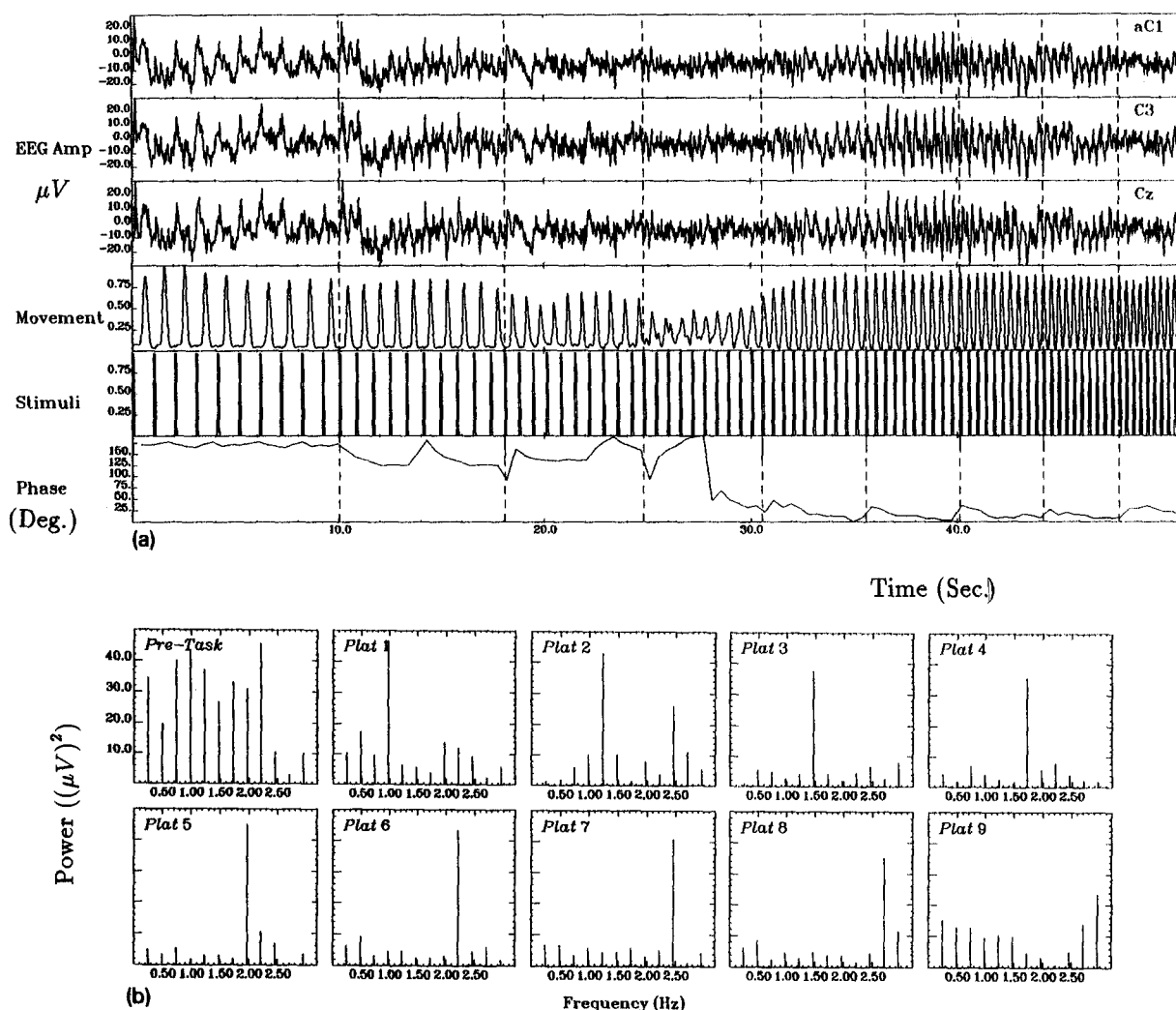[2] The frequency domain equivalent of a cross-correlation.

Fig. 2. (a) A representative subject's averaged signals. From top to bottom: the averaged EEG waveforms from electrode locations aC1, C3 and Cz, the subject's movement (maxima correspond to peak finger flexion), the stimulus markers, and the relative phase between the movement and stimulus (positive values refer to stimuli leading the movement). The dashed vertical lines represent plateau boundaries where the frequency of stimulus presentation increases. (b) Power spectra from a sample electrode, aC1, calculated from data recorded immediately preceding the sensorimotor task and from each plateau during the experiment. (c) The topographical distributions of spectral coherence between each electrode and the ensemble average at 1 Hz, before task onset (top) and during the first plateau (bottom) of the SYNCOPATE condition. The range of coherence in these topographical maps is from 0.09 (represented in white) to 0.81 (represented in black).

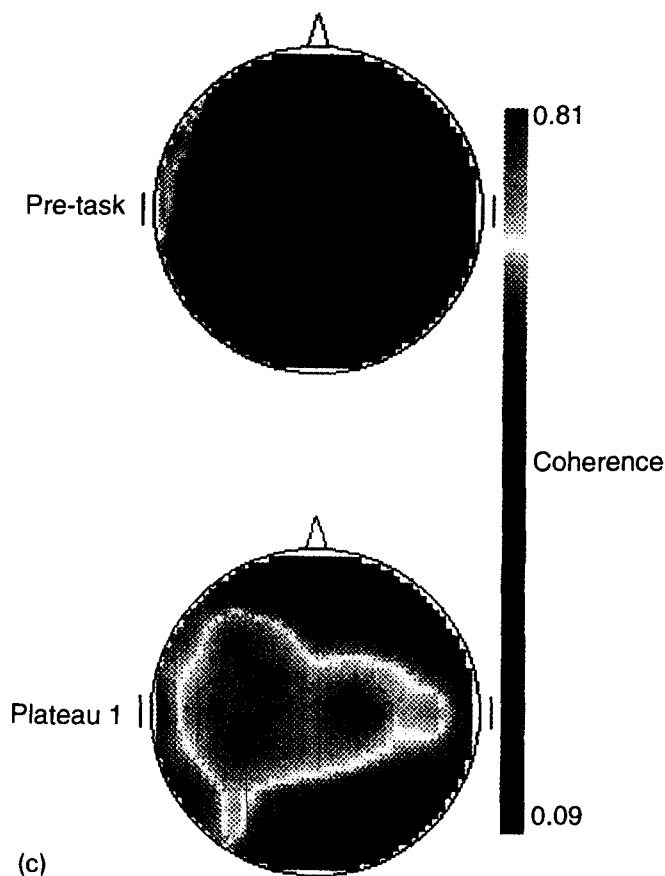Pre-task

0.81

Coherence

Plateau 1

0.09

(c)

Fig. 2 — continued.

multiple frequencies below 2.5 Hz. Following the task onset, however, the spectral power was concentrated at the frequency matching the stimulus presentation rate during each of the nine plateaus. This effect was consistently observed in all subjects and over broad regions of the scalp in both SYNCOPATE and SYNCHRONIZE conditions.

In order to determine the relative proportion of EEG activity at frequencies matching the stimulus presentation rate, a Fourier analysis of the averaged EEG signals from each electrode was performed. The spectral power at the stimulus rate accounted for an average 77% of the variation in the total power (across all possible frequencies) during each plateau in the SYNCOPATE condition and 76% in the SYNCHRONIZE condition. When the spectral power was calculated for each plateau, based on the first harmonic of the stimulus presentation rate, the two combined frequencies

accounted for an average of 88% in the SYNCOPATE condition and 87% in the SYNCHRONIZE condition, indicating that the predominant energy in the brain activity was concentrated at the stimulus presentation rate [see also 11,12]. These results suggest an increase in the temporal order of the EEG signals during the sensorimotor task compared to pre-task values.

In order to examine changes in the spatial structure of the EEG signals before and during the task, spectral coherence was calculated between the EEG signal at each electrode and the spatial ensemble average (from all electrodes displaying spectral power equal to or greater than one half the maximum power value). The topographical distributions of spectral coherence estimations prior to task onset and during the first plateau are shown for the SYNCOPATE condition in Fig. 2c. Both distributions were calculated at 1.0 Hz, the frequency at which spectral power was concentrated during the first plateau. The averaged spectral coherence increased significantly ($p < .01$) from relatively low values before task onset (mean: .25 (standard deviation: +.12, −.14) prior to the SYNCOPATE condition and .27 (+.14, −.17) prior to the SYNCHRONIZE condition) to .65 (+.19, −.21) and .63 (+.16, −.19) during the first plateau of the SYNCOPATE and SYNCHRONIZE conditions, respectively [3]. Comparable levels of spectral coherence were observed in plateaus one through nine. Taken together, these results suggest that brain activity became more spatially ordered once the task was introduced.

During experimental runs, a measure of the relationship between motor behavior and auditory stimuli was estimated by computing the relative phase on a cycle-by-cycle basis. Notice from the bottom time series in Fig. 2a that in the beginning of the fourth frequency plateau (1.75 Hz) a qualitative change occurred in the phase relationship of approximately 180 degrees (auditory signal leading the response), corresponding to a change from syncopated to synchronized behavior. This transition from syncopation to synchronization was observed in all subjects. In con-

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[3] Statistics were computed after transformation of coherence values to Fisher Z values.
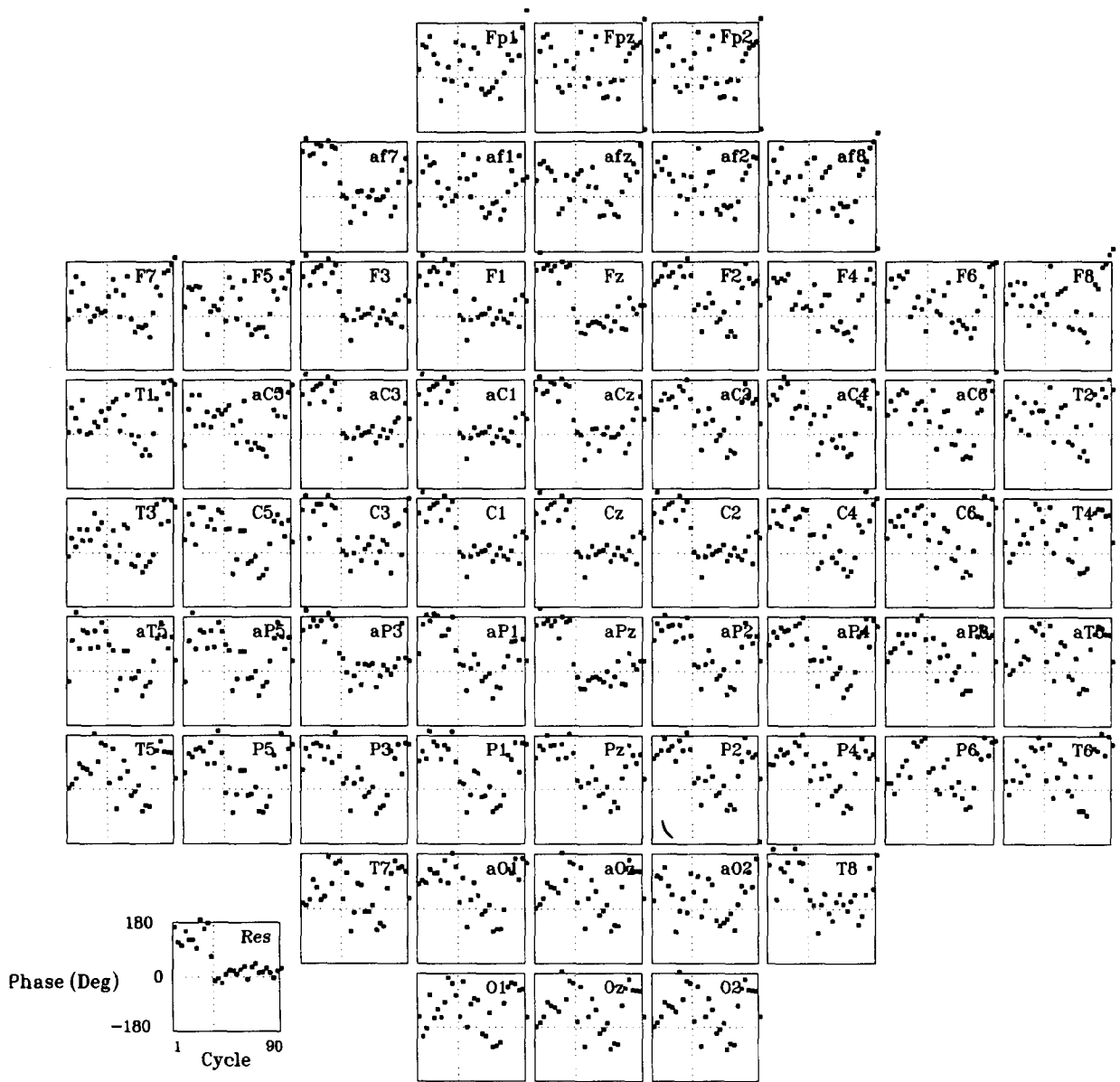
(a)

Fig. 3. (a) The mean relative phase between each EEG signal and the auditory stimuli from a representative subject (computed over two cycles). The dashed vertical line in each box represents the point in time where the transition took place in the behavioral response (shown in the lower-left corner). All plots are on the same scale. Note the dramatic change in the phase relationships spatially. At the same moment as the transition in the sensorimotor behavior, one can see a similar relationship in the EEG, particularly at left frontal and left antero-central locations. (b) When subjects began the run in the synchronized coordination mode, no transition was observed behaviorally or in the EEG.
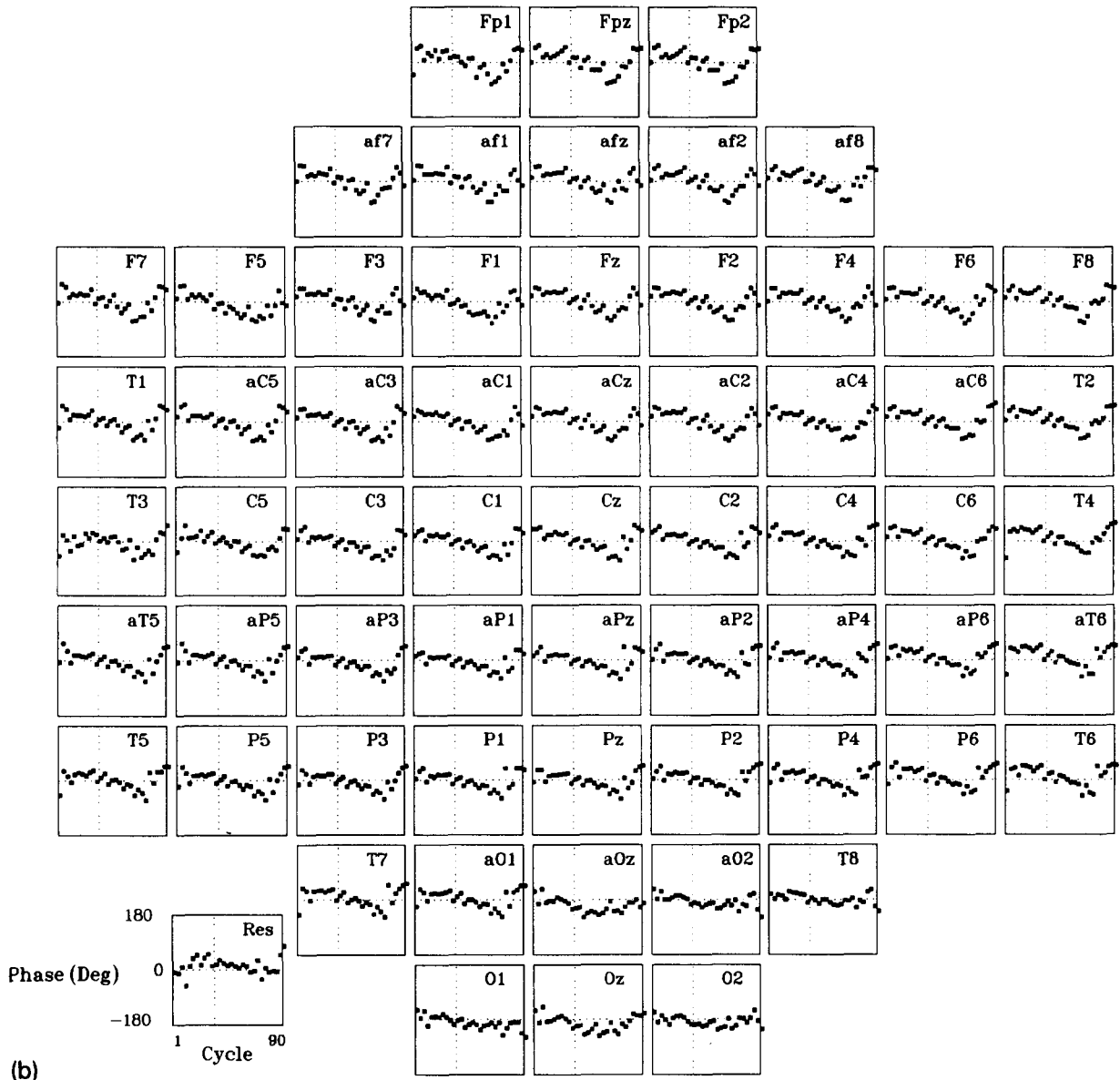
Phase (Deg)

180

0

-180

1   Cycle   90

(b)

Fig. 3 — continued.

trast, no such transitions were observed when subjects started in synchronization.

The cycle at which the transition occurred tended to vary from subject to subject as well as from run to run within a given subject's data (grand mean (sd) across subjects in cycles = 38 (21); i.e. plateau 4, cycle 8). Since in each plateau the power at the frequency matching the stimulus presentation rate represented a substantial portion of the overall power, the phase

angle of the brain data was calculated at frequencies matching the stimulus presentation rates. For purposes of establishing a consistent convention in this calculation, the relative phase between the negative peak in the EEG and the stimulus was used. In Figs. 3a and 3b, we show from a representative subject the relative phase between the averaged EEG signals at each site and the auditory stimuli (calculated over two cycles) computed in the SYNCOPATE and SYNCHRONIZE

SYNCOPATE condition   SYNCHRONIZE condition
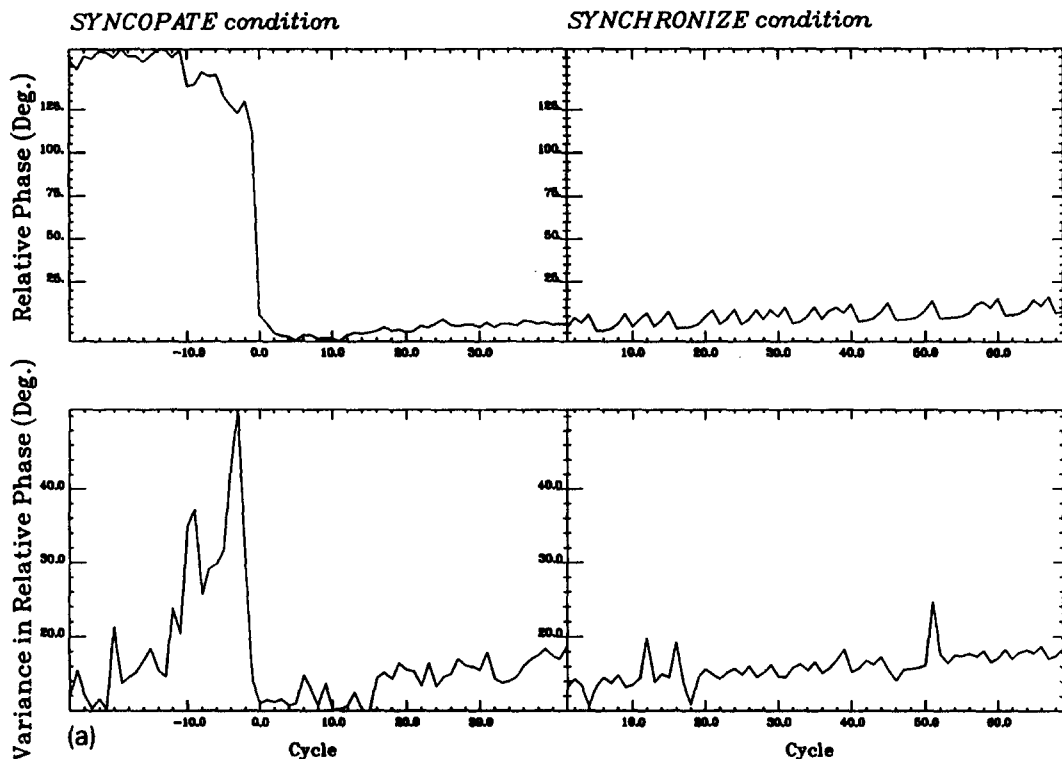

Fig. 4. (a) The back-averaged mean and variance of the relative phase between the response and stimuli from a representative subject. Notice in the syncopate condition (left) the marked increase in variance as the transition point is approached, demonstrating *fluctuation enhancement*. Also shown is the relative phase observed during the SYNCHRONIZE condition (right). Because there were no transitions in the SYNCHRONIZE condition, these data were averaged from the beginning of each run. To be consistent with the back-averaged data (SYNCOPATE condition), the same range in cycles is shown for both conditions. (b) The back-averaged relative phase between a representative EEG signal (electrode aC1) and the stimuli along with the variance in this estimate. Similar to the behavioral data shown above, the variance increased substantially as the transition point was approached, indicating an increase in fluctuations in the relative phase and a loss of stability. As shown in (a), the relative phase from the SYNCHRONIZE condition is shown over the same range as SYNCOPATE.

conditions, respectively. The relative phase between the behavioral response and the stimuli is shown in the lower left-hand corner of each figure. On comparison, a clear difference can be found in the SYNCOPATE condition at several central and left anterocentral recording locations (e.g. F3, F1, Fz, aC3, aC1, aCz, C3, C1, and Cz) which show an abrupt change of approximately 165 degrees in the relative phase at the transition from syncopated (175 degrees) to synchronized (10 degrees) behavior. In contrast, the relative phase remains consistently closer to 10 degrees during the entire run in the SYNCHRONIZE condition, although there is a tendency for upward phase drift toward the end of the run. This suggests the possibility of desynchronization at higher stimulus presentation

rates [17].

Dynamic instabilities are the chief mechanism underlying pattern formation and change in nonequilibrium systems [1,2,10]. To look for evidence of a loss in stability, the variance in the relative phase was computed in both the behavioral and EEG data from the SYNCOPATE and SYNCHRONIZE conditions. Because a given subject exhibited transitions in behavioral coordination at different cycles for each run, the cycle-by-cycle relative phase values for each run were aligned at the transition point (SYNCOPATE condition) and back-averaged. In Figs. 4a and 4b, we show the back-averaged relative phase and variance for the behavioral data and a representative EEG signal (aC1), respectively. Notice that as the transition cy-
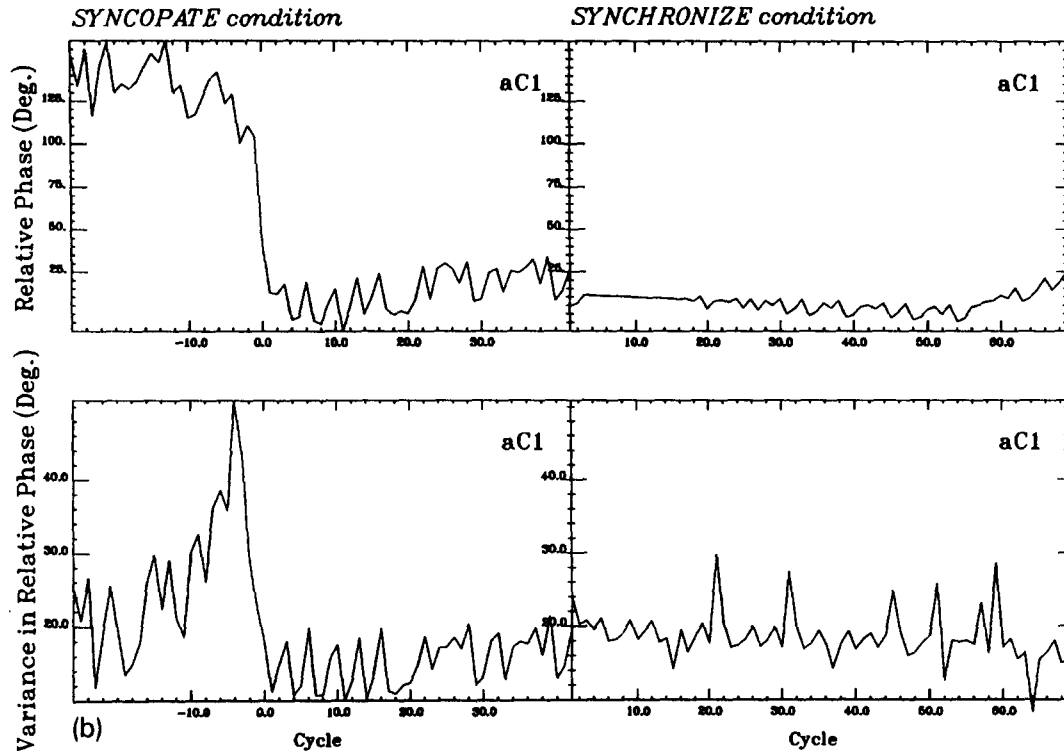
SYNCOPATE condition   SYNCHRONIZE condition

Fig. 4 — continued.

cle was approached, the variance in the relative phase increased markedly in both the behavior and EEG, signalling the onset of change in coordination from syncopation to synchronization. Once the behavior became synchronized with the stimuli, the variance returned to those values typical of synchronization (right side boxes). Notice that no such growth in fluctuations occurred throughout comparable cycles of the synchronize condition. These results indicate that as one gets closer to the critical point, the syncopated behavior becomes more susceptible to destabilizing forces before losing stability and switching to synchronization. Moreover, both the behavioral and EEG signals exhibit fluctuation enhancement beginning several cycles before the transition, thus revealing a change in the phase relations on both levels of observation.

Observation of phase transition phenomena and accompanying fluctuation enhancement in brain signals and behavior is nontrivial because it suggests a common dynamical mechanism for pattern change on different levels of observation. It is also notable that these effects were most prominent at central and left

antero-central locations, lying over areas thought to be involved in movement of right-sided body parts. A theoretical model that predicted both the transition and fluctuation enhancement witnessed in earlier hand movement experiments [14] has recently been extended to account for phase transitions in the brain [19]. An important analytical result of this work is the finding that the dynamics governing the transition in both behavioral and brain activity involve a common, nonlinear coupling mechanism. It is hypothesized that such nonlinear coupling may represent a fundamental property inherent in systems that exhibit multistability and transitions [19]. Thus, generic (pattern) features such as multistability, instability, transitions, and so forth, may arise on several levels of description relatively independent of the specific nature of the interacting components.

The manner in which spatiotemporal brain activity patterns form and change is still a question of considerable debate. Although it is well known that dynamic instabilities play a key role in pattern formation processes in physical systems [1,2,10], so far only a

handful of experiments have examined the possibility that phase transitions are a prominent mechanism for pattern formation and change in biology in general, and the central nervous system in particular [10–13]. In this paper we have shown: (1) that during a sensorimotor coordination task, brain signals become more ordered both spatially and temporally when compared to activity recorded prior to task onset; (2) both behavioral and brain signals exhibit abrupt transitions of approximately 180 degrees in their phase relations; and (3) both the behavioral and brain signals display an increase in the variance of the relative phase (fluctuation enhancement) several cycles before the transition, indicating loss of stability on both levels of observation prior to switching. These results imply that multiple levels of observation may share common dynamic properties that are observable given the appropriate experimental design [9,10]. As far as brain function is concerned, studies employing the "nonlinear paradigm" have hardly begun. Such a realization is a challenge to neuroscience in its attempt to understand how neural patterns form, destabilize, and regain coherence according to environmental, cognitive and biophysical demands.

References

[1] H. Haken, Synergetics. An Introduction (Springer, Berlin, 1983).

[2] H. Haken, Information and Self-Organization (Springer, Berlin, 1988).

[3] P. Manneville, Dissipative Structures and Weak Turbulence (Academic Press, New York, 1990).

[4] J.A.S. Kelso, J.P. Scholz and G. Schöner, Phys. Lett. A 118 (1986) 279–284;
J.A.S. Kelso, Bull. Psychnom. Soc. 18 (1981) 63; Amer. J. Phys. 15 (1984) R1000–1004;
J.A.S. Kelso and J.P. Scholz, in: Complex Systems: Operational Approaches in Neurobiology, Physical Systems and Computers, H. Haken, ed. (Springer, Berlin, 1985).

[5] J.A. Reggia and M. Edwards, Neural. Comp. 2 (1990) 423–435.

[6] J. Shrager, T. Hogg and B. Huberman, Science 235 (1987) 1092–1094.

[7] C.M. Gray, P. König, A.K. Engel and W. Singer, Nature 338 (1989) 334–336.

[8] A.K. Engel, P. König, A.K. Kreiter and W. Singer, Science 252 (1991) 1177–1179;
E. Basar and T.H. Bullock, Induced Rhythms in the Brain (Birkhauser, Boston, MA, 1992).

[9] T.M. McKenna, T.A. McMullen and M.F. Shlesinger, Neuroscience 60 (1994) 587–605.

[10] J.A.S. Kelso, Dynamic Patterns: The Self-organization of Brain and Behavior (MIT Press, Cambridge, MA), in press.

[11] J.A.S. Kelso, S.L. Bressler, S. Buchanan, G.C. DeGuzman, M. Ding, A. Fuchs and T. Holroyd, Phys. Lett. A 169 (1992) 134–144.

[12] A. Fuchs, J.A.S. Kelso and H. Haken, Int. J. Bif. Chaos 2 (1992) 917–939.

[13] G.V. Wallenstein, S.L. Bressler, A. Fuchs and J.A.S. Kelso, Soc. Neurosci. Abstr. 19 (1993) 555.

[14] H. Haken, J.A.S. Kelso and H. Bunz, Bio. Cyb. 51 (1985) 347–356.

[15] G. Schöner, H. Haken and J.A.S. Kelso, Bio. Cyb. 53 (1986) 247–257.

[16] J.P. Scholz, J.A.S. Kelso and G. Schöner, Phys. Lett. A 123 (1987) 390–394.

[17] J.A.S. Kelso, J.D. DelColle and G. Schöner, in: Attention and Performance XIII, M. Jeannerod, ed. (1990) pp. 139–169.

[18] H.H. Jasper, Elec. Clin. Neurophys. 10 (1958) 371–375.

[19] V.K. Jirsa, R. Friedrich, H. Haken and J.A.S. Kelso, Bio. Cyb. 71 (1994) 27–35.

[20] S.L. Bressler, R. Coppola and R. Nakamura, Nature 366 (1993) 153–156;
J.E. Cook, Trends Neurosci. 14 (1991) 397–400.